Materials Horizons: From Nature to Nanomaterials

A. N. ArunKumar
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Rekha R. Warrier
N. Nataraja Karaba *Editors*

Indian Sandalwood

A Compendium

Springer

Materials Horizons: From Nature to Nanomaterials

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Dedicated to

Dr. H. Y. Mohan Ram

Doyen of Indian botany and

science populariser

Foreword

The sandalwood tree as likely to prove, sweetest that can even conquer hate, love and perfumes the cruel axe that lays it low.

Rabindranath Tagore

In today's world of human suffering, everyone is turning to the search for calming the mind and body from the rich to the poor. We are all looking for self-identity, security and stability, and trust. In human body, the seventh or root chakra of the body is associated with these virtues. Sandalwood is associated with the seventh chakra. Modern paganism provides a high pedestal for sandalwood. It is also associated with healing and purification. *Brahma Vaivarta Purana* considers the importance of Indian sandalwood and narrates that *Brahma*, the Lord of the Universe, created it through meditative contemplation. Such is the greatness of sandalwood.

If there is one wood that is both prized and pious, it is sandalwood. Sandalwood is termed as the second most expensive wood in the world. India's dominance in cultivating and using the species has been phenomenal for several decades now. This fame and use of sandalwood have made the species 'vulnerable' under the IUCN threat categories with overexploitation of the species in India, where the southern part of India counts the largest distribution of the species. Today, sandalwood is one of the most regulated species in the world for both cultivation and harvesting. Strict protocols exist for sale and export of this species.

It is not uncommon for one to be intrigued by the importance of sandalwood. This tree species has found its intricate linkages from *Vedic* times to current dispensations on the use of this species. It is therefore natural that several felt the need to learn more about sandalwood. Though Dr. Arun Kumar (one of the editors of this compendium) penned an informative brief on the species in 2012, in the journal Current Science, comprehensive information about this species is still scattered and scanty.

The current volume on sandalwood is, therefore, a much-needed addition to a whole range of information and knowledge about this species. The 33 chapters in this compendium offer a wholistic bouquet of in-depth insights into a range of topics, ranging from the religious and cultural history of the species that is intertwined with a number of civilizations to the use of modern technology like artificial intelligence (AI) in cultivating the species. It is indeed a great coverage for such a magnificent species.

I am sure the chapters presented here provide the needed in-depth understanding for scientists and researchers and those interested to know more about this species, in general.

All the authors and editors of this volume need our appreciation and plaudits for providing us with such a comprehensive knowledge product.

Balakrishna Pisupati
Head of Biodiversity, Land and Governance Programme, United Nations Environment Programme (UNEP); Former Chairperson, National Biodiversity Authority
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Preface

Indian sandalwood, *Santalum album*, is a tropical tree of the Santalaceae family. Its heartwood and essential oil have been a part of the culture and tradition of many civilizations, finding use in rituals worldwide to traditional medicines and fragrances. Indian sandalwood has gained renewed interest in modern days as it gains popularity in cosmetics and medicine manufacturing. Heavily sourced from the wild, its natural resources are quickly depleting due to habitat loss and destructive harvesting techniques. A major source of economy for India, trade has been waning in the past few decades; parallelly, Australia has taken the lead. In recent years, sandalwood plantations have received increasing attention as a renewable source for various downstream industries.

This book is dedicated to bringing together up-to-date global information about sandalwood, hence the title *Indian Sandalwood—A Compendium*. Despite its centuries-old existence, the biology of sandalwood remains elusive. Domestication efforts provide promising developments; however, we need to carry research forward drawing conclusions from past efforts. Scientists have identified critical components that affect productivity resulting from the tree host interactions. Advances in biotechnology and genomics of sandalwood have shed light on its cell machinery process in synthesizing authentic compounds of the essential oil, many of which are responsible for the unique fragrance. New pharmaceutical properties have emerged, and new threats with advanced technologies to address them are being developed. All these are covered in the chapters, providing researchers and the public a sourcebook of current knowledge on sandalwood.

The authors of this book were chosen from a broad array of organizations globally, based on their expertise in the subject and to ensure the contributors are diverse. This book, which includes seven parts, provides essential knowledge on the history, biology, present status of distribution in different countries, propagation, improvement and domestication, utilization, prospects and conservation of the species.

The first part, History and Culture, has four chapters describing its past glory and its introduction outside its native land. A global sketch of Indian sandalwood from 3000 BCE to 2020, a description of its overexploitation and dwindling over time, the importance of the species in Indian culture and its presence in Australia complete the first part.

The second part, which recounts the status of distribution in Karnataka, Tamil Nadu, and Kerala provides insights into the efforts to restore its past status. The current status in Sri Lanka, Sandalwood ravaging in Indonesia and its neighbouring countries, where once Sandalwood was used as fuelwood too, due to its abundance, and efforts to restore the once Sandalwood-populated forests, the success of Sandalwood plantations as an industry in Australia are also dealt here.

The third part provides readers with gainful insights into taxonomy, new vistas in wood anatomy, sifting through seed biology, leading us to the colourful world of pollinators and the dependency of hosts.

The fourth part describes the practical aspects of its cultivation and introduces us to different pests and diseases and a broad picture of its cultivation prospects.

In the fifth part, which is more technical, the variability existing in sandalwood and efforts to improve and domesticate the species for the two commercial traits, heartwood and oil is presented. Application of advanced technologies is dealt through tissue culture, assessment of genetic diversity and 'Omics' which revealed the secrets of the fragrance of the oil.

The sixth part provides reads with a utilization perspective of the species: the chemistry, evidence on the anticancer effects, its role as a pharmaceutical agent, the significant role the species plays in traditional medicine—Ayurveda and finally the market trends.

The seventh and final part unveils scope for newer technologies in managing sandalwood resources effectively and efficiently—the use of GIS and RS in threat mapping and scope for deploying artificial intelligence to make sandalwood cultivation easier.

Perspectives on varied topics have made this book a state-of-the-art reference material. Given its economic importance, such knowledge would be conducive in exploring and protecting the species. Readers may wish to focus on specific chapters rather than reading this book in its entirety. Bearing this in mind, we have retained some overlaps between chapters, rather than relying on merely cross-referencing between sections.

This book was conceived for a varied readership. It includes foresters of various countries, researchers within and beyond forestry, and academia in various disciplines and plantation growers. In regions extensively growing sandalwood plantations, the growers may like to learn how and why of its cultivation. Hence, it is planned to supplement this compendium with a handbook shortly.

This book is designed to nurture information exchange and to inspire sandalwood scientists. I hope this publication would serve as a basis for future research with *Santalum* genera across the globe.

Bengaluru, India	A. N. Arunkumar
Dehradun, India	Geeta Joshi
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Bengaluru, India	N. Nataraja Karaba
January 2021	

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About the Editors

Dr. A. N. Arunkumar heads the Silviculture and Forest Management Division at the Institute of Wood Science and Technology, Bengaluru, India. His doctoral thesis was on evaluating the Indian Sandalwood accessions for the heartwood and oil content. Dr. Arunkumar has over two decades' experience in Indian Sandalwood and has carried out several projects that entailed extensive surveys on sandalwood in the Indian states of Karnataka, Tamil Nadu, and Kerala and other sandalwood growing states. He has been involved in establishing clonal, seedling seed orchards, and progeny trials of sandalwood. He has delivered several lectures on tree improvement in sandalwood at various forums and has been providing scientific inputs in promoting sandalwood cultivation. Presently, Dr. Arunkumar is a member of Sandalwood Development Committee constituted by the National Institution for Transforming India (NITI Aayog), a premier policy think-tank of the Government of India.

Dr. Geeta Joshi is the Assistant Director General (Media and Extension) at the Indian Council of Forestry Research and Education, Dehra Dun, India. She has more than two decades experience on *Santalum album* on aspects related to seed collection, handling, germination, storage, standardization of protocol for mass production of quality planting material, and hardening of micropropagated plants in nursery. Dr. Joshi was associated in conducting trainings for farmers, State Forest Departments, plantation companies, and NGOs on sandalwood seed handling, nursery, and plantation technology. She had been involved in production of quality planting material of sandalwood for end users. Dr. Joshi has also worked on seed-related aspects of threatened and endangered tree species of Western Ghats, propagation and cultivation of bamboo, morphological and genetic diversity of *Melia dubia,* a fast-growing tree species. She has worked as principal investigator in 12 research projects and as co-principal investigator in 10 research projects. She has to her credit 45 research papers published in national and international journals of repute.

Dr. Rekha R. Warrier is Scientist-F at Plant Biotechnology and Cytogenetics Division, Institute of Forest Genetics and Tree Breeding, Coimbatore, India. She has put in 20 years in the field of forest biotechnology and is currently serving as Head of the group in Plant Tissue Culture. She has been working on different aspects of medicinal plants and their productivity, specifically, in the field of metabolite production. Some of her major activities include tissue culture facility for commercial production of plants and *in vitro* production of secondary metabolites through transformation, genetic improvement of medicinal trees, and participation in extension and training programs for foresters, research staff, students, and farmers. Dr. Warrier has been principal investigator in 20 research projects and co-principal investigator in 12 research projects. She has to her credit 70 research papers and 15 books/chapters. Currently, Dr. Warrier is the Assistant National Country Coordinator of the APFORGEN and Liaison to the Central Secretariat of the International Society of Tropical Foresters.

Dr. N. Nataraja Karaba is a Professor at the Department of Crop University of Agricultural Sciences, Bangalore (UASB). He has worked as a Scientist in Rubber Research Institute of India, Kerala, Government of India, and Institute of Wood Science and Technology, (ICFRE) Bangalore. He was a DST-BOYSCAST Postdoctoral Fellow at the Department of Molecular, Cellular, and Developmental Biology, Yale University, USA. He was Visiting Scientist at Plant Research International, Wageningen University (Netherlands), University of Groningen (Netherlands), and has active research collaboration with the University of Saskatchewan, Canada, and Friedrich Schiller University Jena, Germany. He is a recipient of the Sir CV Raman Young Scientists Award from the Government of Karnataka, and the Best Teacher Awards from the Indian National Science Academy. He serves as an Expert Member on the advisory panels of the Department of Science and Technology, Government of India, and Government of Karnataka. He is Associate Chief Editor of the journal Plant Physiology Reports (Springer). Dr. Nataraja's major research interest is to understand the molecular basis of plant responses to drought and other abiotic stresses. He has generated useful information on specific traits contributing to drought tolerance in the mulberry tree. Recently, as a continuation of his major focus on abiotic stress, he initiated research to explore endophytes for modulating crop responses to abiotic stresses. He has published more than 85 papers in peer-reviewed journals, 10 articles in books, and co-edited one book. He has over 20 years of teaching experience and offers courses for UG and PG students.

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Part I
History and Culture

Chapter 1
Indian Sandalwood's Heartwood of History: A Global Sketch from 3000 BCE to 2020

Christopher Cottrell

1 Introduction

For the global environmental historian, writing about the single sandalwood species *Santalum album* Linnaeus also called Indian Sandalwood and the white Sandalwood is an enormous task. Nonetheless, this chapter seeks to attempt such an initial global historical sketch of this sacred yet now threatened tree.

The immediate challenge pertains to the indigenous ecological ranges of the *S. album*. It stretches from southern India to the Kepulauan Nusa Tenggara (Lesser Sundas) islands of Flores, Sumba, Timor and the Alor archipelago in the Java Sea in Indonesia and Timor-Leste [3]. Different species range across the Pacific from Western Australia (*Santalum spicatum*) to Fiji (*Santalum yasi*) to Hawai'i (*Santalum freycinetianum*), to the Juan Fernández Islands (*Santalum fernandezianum*) off the coast of Chile. Nevertheless, Indian Sandalwood's mysterious indigenous distribution in just the Lesser Sundas and southern India needs further research. How best to compose a balanced global picture with independent regional overviews of these sandalwood histories while including the complexities of its usage over some 5000 years [1]? Of describing the southern part of the South Asia subcontinent and small islands of Kepulauan Nusa Tenggara who have separate yet convergent histories? How did they ultimately play a role in making a globalized sandalwood market with common interests in conserving these trees?

Answering these questions involves plying the histories of early human medicine and pharmacopoeias, the antiquity of Hinduism, two millennia of Buddhism across Asia, and concurrent millennia of sandalwood usage in terms of traditions and trade from the Middle East to Central Asia to Japan to Southeast Asia. It also entails probing over 400 years of European colonialism and imperialism to comprehend how Sandalwood contributed to linking Asia, the Indian and Pacific Oceans. More than seven decades of post-colonialism in South Asia, Indonesia and

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Timor-Leste coupled with a globalized appetite for a finite supply of Sandalwood today must also be measured.

Archival language sources about the environmental history present another challenge. It requires reading texts in languages ranging from Acehnese to Arabic, the Dravidian family to Dutch, Japanese to Javanese, Mambai to Manchurian to Mandarin to Mongolian, Portuguese to, Papuan, Sanskrit to Sogdian, and Tetum to Tibetan, among others. Primarily with English translations of extant texts, it is an attempt to mine this swirling array of languages, historical data and scientific literature into a humble, if ambitious, composite of *S. album*. In summary, this chapter blends a rich heartwood of history that Indian Sandalwood embodies in its perfumed past to shed insight to preserve it for a fragrant future. This work can hopefully hone the awareness of historians, policymakers, researchers, scientists and the general public about the history of *S. album* so they can reflect upon and pursue paths to protect all sandalwood species.

2 Essence and Roots of Sandalwood Medicine

Perhaps one way to start knowing the story of *S. album* is, to begin with some of the world's earliest medical texts. The *S. album* and the other related *Santalum* species across Australia and the Pacific Ocean appear in their localized medical traditions; from warding off malaria with *S. album* smoke in Timor to treating pulmonary bronchitis with *S. austrocaledonicum* in New Caledonia. Additionally, 'it is used in the treatment of common colds, bronchitis, fever, dysentery, piles, scabies and infection of the urinary tract, inflammation of the mouth and pharynx, liver and gall-bladder complaints and as an expectorant, stimulant, carminative, digestive and as a muscle relaxant' [1]. Sandalwood oil is also effective against methicillin-resistant *Staphylococcus aureus* (MRSA) and antimycotic resistance to Candida species. Its α- and β-santalol oil elements have shown, 'antibacterial activity against Helicobacter pylori, a Gram-negative bacterium which is strongly linked to the development of duodenal, gastric and stomach ulcers. Sandalwood oil exhibited virulence against isolates of drug-resistant herpes simplex virus type. The oil also showed anti-carcinogenic activity. Sandalwood oil elevates pulse rate, skin conductance level and systolic blood pressure and brings about higher ratings of attentiveness' [1].

In the acclaimed ancient Ayurvedic medical text, the Charaka Samhita, Indian sandalwood, known as 'candana' or 'chandana' in Sanskrit [चन्दन] is listed among 129 mono-herbal drugs with 403 proscribed recipes [20]. It is referred to as 'Shweta Candana' (white sandalwood) to distinguish it from red sandalwood (Pterocarpus santalinus), which is obviously not a *Santalum* species. The word candana in Sanskrit is likely of Dravidian origin. Candana is, 'possibly related to a term cāntu meaning 'daub, rub into a paste; sandalwood paste,' suggesting that this material came from, or passed through, a Dravidian-speaking area prior to being introduced into Sanskrit' [14].

Generally speaking, candana in early Indian medicine was used for 'rasayana' or rejuvenation, and for 'pittaja shotha' or inflammations. The rasayana for oral intake was made from a 'swarasa' or herbal juice mixed with milk and likely blended with sandalwood paste. The pittaja shotha treatment was only made of sandalwood paste and applied externally. Either mixed with juice or paste, it could be used with other ingredients for all manner of treatments from eye salves to enemas alleviating stomach or intestinal ailments. Indian sandalwood was also used in a heady admixture of bark, flowers, fruits, grasses, herbs, roots, and leaves that formed a healing and refreshing incense meant to be inhaled daily.

One formula for healing smoke included Abyssinian pea (*Pisum sativum* L.), Aloeswood (*Aquilaria malaccensis* Lam.), Beautyberry flowers (*Callicarpa macrophylla* Vahl.), Black Cardamon (*Amomum subulatum* Roxb), Black stone flower (*Parmotrema perlatum* Huds.) M. Choisy), Blue lotus (*Nymphaea nouchali* Burm.f.), Cinnamon (*Cinnamomum verum* J. Presl), Coco-grass (*Cyperus rotundus* L.), and 'Queen of Spices' Cardamom (*Ellataria cardamomum* (L.) Maton). It also utilized 'good bark' from the Banyan tree (*Ficus benghalensis* L.), sacred Boddhi tree (*Ficus religiosa* L.), herbal Guggulu tree (*Commiphora mukul* Hook. Ex Stocks), small evergreen Iodhra (*Symplocos racemosa* Roxb.), and the plaksha fig tree (*Ficus virens* Aiton). If further included Hribera fragrant root (*Plectranthus vettiveroides* Jacob), Indian Bay leaf (*Cinnamomum tamala* Buch.-Ham.), Indian frankincense (*Boswellia serrata* Roxb.ex Colebr.), Lemon grass (*Cymbopogon schoenanthus* (L.) Spreng), Longleaf Indian pine (*Pinus roxburghii* Sarg.), Red Kamala tree (*Mallotus philippensis* Lam.), Saffron (*Crocus sativus* L.), Spikenard (*Nardostachys jatam*ansi (D.Don.) DC), Tiger's footprint vine (*Ipomoea pes-tigridis* L.), Vetiver bunch grass (*Chrysopogon zizanioides* (L.) Roberty), White dammar (*Vateria indica* L.) and Wild Himalayan cherry (*Prunus cerasoides* Buch.-Ham ex D.Don).

Along with candana, 'All these are macerated, made as paste and applied on a hollow reed of *sara* plant, to the thickness of *yava*, on the reed of the size of the thumb and of eight *angula* (approximate 16 cm) in length. After the paste dries, the physician should remove the reed of *sara* plant, smear the wick with *ghee* and introduce it into the nozzle of the smoking apparatus, and light its front tip with fire and ask the person to inhale its smoke. This is *prayogiki dhuma* daily inhalation for the healthy person, and it bestows comfort. (Cha.Su.5/20–24)' [2].

During the Vedic age from 1500 to 600 BCE, highly specialized doctors carried out India's medical traditions mixing medicine with magic and mantras. In fact, 'The Vedic priest would spiritualize the medicine through hymns and sacrifice. Some foods were used as vehicles for certain medicines. In addition to oral medicines, inhalation, fumigation, and topical application of ointments were also done. Certain plants were used as amulets. The medicines were administered at specified places and times' [23]. From roughly 600 BCE, these doctors called vaidyas, or persons of profound knowledge, expanded Ayurvedic networks at early medical symposia and conferences—and with it prescriptions involving Indian sandalwood. Accordingly, 'Ancient texts place a lot of emphasis on the vaidya's knowledge of drugs. While prescribing a drug, a vaidya was supposed to keep in mind both its therapeutic and adverse effects. The vaidyas collected the herbs and other ingredients at auspicious times, spiritualized them with the recitation of mantras, and used them to prepare his own drugs' [23].

More tellingly, 'Vaidyas resorted to spiritual therapy for diseases whose cause were unknown. These were explained in terms of a patient's actions in his previous births. The cure involved appeasement of gods through prayers and offerings, recitation of mantras, and wearing of amulets and gems. Similarly, psychic therapy was applied to diseases of the mind. The vaidya prescribed various methods at his discretion, to keep the mind away from harmful thoughts' [23]. Sandalwood's gradual evolution from medicine into early Vedic religious hymns and into Hinduism makes strong sense in this light. It seems perfectly logical that this would happen as sandalwood became a standardized medical ingredient across the subcontinent with the vaidyas' work—particularly as a refreshing holy smoke. Indeed, from 600 BCE to 150 CE (when final dates of the Charaka Samhita's more finalized drafts were finally laid down by a Kashmiri physician named Charaka at the court of Kanishka), sandalwood prescriptions must have been spread to most urban and many rural places by the vaidyas across the subcontinent. As such, 'There were individual practitioners, vaidyas attached to hospitals, and vaidyas employed by the state. There is also mention of itinerant vaidyas, who moved around looking for patients and of vaidyas visiting the patient's house for treatment. Physicians in state service had to attend to the royal family, courtiers, and palace retinue. The highest position among these state physicians was occupied by the king's personal vaidya known as the Raja-Vaidya' [23].

In the Ayurvedic prescriptive and surgical manual the Sushruta Samhita, the Raja-Vaidya could prescribe sensual medicine baths to the King and 'rich men.' In one poignant passage, white sandalwood is graphically described as a way to treat 'Daha' or a 'burning sensation' associated with drinking too much alcohol. The proscription notes, "Remedies for Daha:—Now I shall describe the cooling measures which should be employed for alleviating the burning sensation (Daha) in the case of a wealthy patient. The body of such a patient under the circumstances should be smeared at the outset with Chandana white sandalwood pastes made cooler by the contact of cold beams of the moon, pearl-necklaces and the water produced from melted ice. He should be laid down in a bed of full-blown lotus flowers sparkling with dew drops or of lotus-leaves sprinkled with a spray of translucent water, and youthful damsels decked with necklace and bangles of lotus-stems cooler even than cold water, should be asked to touch him. He should try to alleviate the burning feeling by strolling on the banks of a tank in a garden in the soft, cool and sweet breeze bearing on its wings the soft perfume of Kalhara (red) lotus and water-moss dancing in the adjoining tank. 'Water cooled and charged with Us'ira, Vdlaka and (white) sandal paste should be sprinkled over his body, or he should be made to sport in a cleansed tank filled with freshly collected water embalmed with full-blown red and blue lotus-flowers and scents (e.g. sandal pastes) after being smeared with sandal paste and with the hairs of his body standing on their roots with the magnetic touch of beloved female hands' [4].

As candana became more closely associated with elite life, it evolved into a luxury trade item beyond local medicine and spiritual usages. This perhaps helps explain why it starts appearing as a luxury good that made its way to the Eastern Mediterranean and Nile River in Egypt. The Bible's King Solomon (c. 961–922 BCE), famed for his 700 wives and 300 concubines, constructed his temple with bannisters made of 'almug trees.' These trees are believed by some to be sandalwood or aloeswood (*Aquilaria malaccensis* Lam.) [24]. In fact, it was Queen Sheba of Egypt who visited King Solomon to press him about the source of fine goods such as almug wood coming from the mythic location 'Ophir', thought to be somewhere along the Arabian Sea coast of India. Regardless of what Queen Sheba might have learned of Ophir and sandalwood, in Egypt, sandalwood was used to embalm the elites in their mummification rites [1]. Later in Ptolemaic Egypt, white sandalwood boxes were decorated with inscriptions of grandeur. One such box fashioned between the third and first century BCE carries hieroglyphics which read, 'Beloved of the King of Upper and Lower Egypt, Ptolemy, may he live forever, beloved of Ptah', and 'beloved of Sokar-Osiris, the great god and of the brother sister gods (Theoi Adelphoi)' [7].

The most logical location for this sandalwood to have come from would have been the accessible forests near the Malabar coast—notably the Western Ghats of Karnataka, Deccan Plateau and down to Kerala. The probable location is likely from its heartland: 'Karnataka is critically acclaimed as land of sandalwood (*Gandhada Nadu*), while the region in and around 'Mysuru' is eulogized as a sandalwood shrine (*Gandhada Gudi*)' [1]. Headed east from the Deccan towards the Bay of Bengal, the *S. album* also grew in today's states of Andhra Pradesh and Tamil Nadu. Its indigenous distribution was mainly across the Deccan Plateau in dry deciduous forests. *S. album* grows up to 20 m and can attain a girth of up to 1.5 m. Moreover, 'it flowers and fruits twice a year during March–April and September–October. Trees start flowering from 3 years of age. Seed production generally is good in one of the seasons. Certain trees flower only once a year, and some do not flower regularly' [19]

By contrast, *S. album* in Timor and the Lesser Sundas grows as a smaller tree or shrub at a maximum height of 12 m with a width of 10 to 30 cm that flowers twice a year, 'at the beginning of dry season in May to September, and at the beginning of rainy season in November to March, with 4–5 months flowering period' in the 'semi-arid and tropical region throughout south-eastern and middle parts of Indonesia' [22] and in Timor-Leste.

Whatever be the height, width or flowering season, the qualities of its gradations were becoming ever more scrutinized and sought after in India. *S. album* from Timor and the Lesser Sundas would soon enter this world as an Indianized cultural, economic and political-religious ecumenical system formed in peninsular and island Southeast Asia.

3 Sacred and State Sandalwood

This political-religious regime emerged in India with treatises such as the Arthaśāstra. For example, in the first passages of the Arthaśāstra doctrine on statecraft formed sometime between 1 BCE and 1 CE, aloeswood, sandalwood and other aromatic woods are said to be essential to have in royal treasuries [14]. Indeed, the Arthaśāstra lists several grades of sandalwood: ‘Sātana sandalwood is red and smells of earth. Goāirsaka (Ox-head sandalwood) is dark copper (color) and smells of fish. Haricandana (Green sandalwood) is the color of a parrot feather and smells of mango, as is Tarnasa (sandalwood). Grāmeruka (sandalwood) is red, red–black and smells of goat urine. Daivasabheya (sandalwood) is red and smells of Parma leaves, as does Japaka (sandalwood)….’ [14]. While not all of these grades specifically pertain to *the Santalum album* and refer to other aromatic woods, they illuminate the importance of sandalwood to kingdoms across the subcontinent—making trade links of sandalwood from southern India to northern India essential for states and religious purposes. The two went hand in hand, especially with Sanskrit epics such as the Mahābhārata and the Ramāyana, and in other holy literature. In these works, candana is frequently mentioned as an adornment [14]. In the Mahābhārata, King Yudhishthira smears his body with yellow sandalwood as a paste with water in a rejuvenating morning bath. His brother Bhima took his ‘terrible club’ and had it ‘smeared with paste of candana and aloeswood like a desired, beautiful woman’ [14]. In the Ramāyana, it is used along with aloeswood, resins, pine (sarala) and padmaka wood, or as the actual tree itself, in King Dasaratha’s funeral pyre—a rite that would arise in sacred contexts for millennia in India and even with the funeral pyre of Mohandas K. Gandhi. The Ramāyana mentions the Thamirabarani river, which flows from the Western Ghats across Tamil Nadu and down to the Gulf of Mannar. It says that, ‘river islands covered with forests of sandalwood goes down the sea as a beloved maid to her lover’ [13]. This remarkable geographic reference depicts an image of sandalwood forest sources and points of transport from the Coromandel coast to the Gulf of Mannar to Sri Lanka, and for the Bay of Bengal—and by extension, its linkage with the budding Indianized culture to emerge from it in neighbouring Southeast Asia where sandalwood in the Lesser Sundas would soon join it.

Across the Vedic age’s vast expanse, the *S. album* was intimately intertwined with Indian life with many essential woods. Overall the, ‘Vedic and Indus valley period witnessed utilization of sandalwood in the form of fine woodworking artefacts or carving deities, ritual bathing of Hindu deities, temple construction material and for ceremonial causes. Its importance in Indian culture is referred in Vedic literature, Puranas (ancient Hindu texts eulogizing various deities), Subhashitas (collection of eloquent sayings written by ancient Sanskrit poets), mythology (stories on supernatural beings and events) and in the ancient scriptures (sacred writings). The Sanskrit manuscripts that are more than 4000 years old cite sandalwood oil as the oldest known perfumery material’ [13].

At the apogee of this Vedic world, a young Brahmin inculcated and privy to this sacred and state literature and traditions would come to walk away from it all. In so doing, he altered the course of the future of sandalwood as a critical element of Asian regional integration, and later the first stages of globalization in the Indian and Pacific Oceans more than a millennia later.

4 Buddha's Far Flung Forests

When Siddhartha Gautama (c. 563–483 BCE) left his earthly compound's confines for India's forests to wander and meditate, his most special tree of enlightenment was the sacred Boddhi tree (*Ficus religiosa* L.). However, Indian sandalwood was ever present in the Buddha's wanderings and would continue to be for his followers with nuanced traditions that would come to erect sandalwood Buddhas across China and Japan and see the minting of sandalwood flower faced coins across Java and Sumatra.

Indian sandalwood makes appearances in the Dhamma Pada, Anguttara Nikaya (The teachings of Buddha) and Vinaya Pitaka (300–400 BCE), Milinda Panha (200 BCE) and Patanjali Mahabhasaya (100 BCE), among other sacred Buddhist texts [13]. For example, in the 'Milinda Panha (Buddhist doctrine), a Buddhist sage while referring to the path of righteousness mentions that, 'No flower's scent can waft against the wind, not sandalwood's, nor musk's, nor jasmine flowers. But the fragrance of the good goes against the wind in all directions the good man's name pervades'. While describing 'nibbana' in Milinda Panha, the sage also mentions that 'Like sandalwood, it is hard to get, its fragrance is incomparable and it is praised by good men' [13].

The reference about sandalwood's rarity in this refrain illuminates a potentially telling phenomenon: over indulgence of sandalwood resources. Incense consumed by Buddhist temples and even carvings of the Buddha from sandalwood, combined with Hindu, Jain and Ayurvedic consumption may have put the wood at a premium between the last century BCE and first century CE in southern India.

During the Maurya Empire (c. 320–187 BCE), sandalwood usage arguably accelerated, particularly under King Ashoka (c. 304–232 BCE) in 261 BCE when he butchered the Kingdom of Kalinga and latter propagated Buddhism for his guilt over their slaughter. Ashoka's Buddhist edicts on stone pillars across India and the monks he sent to Central Asia and Sri Lanka advanced the faith—and ostensibly more sandalwood trees for incense. This would be crucial for the developments of *S. album* in both India and the Lesser Sundas. Through Central Asia along the Silk Road to China and onward to Japan, the tradition of the Udayana image or statue of the 'Buddha Sakyamuni' or 'Sandalwood Buddha' would come to form a unique cultural and trade element that would have long lasting implications for Indian sandalwood from the subcontinent, and later Lesser Sundas and Oceania. During this same period, a newly emerging port world of the Indian Ocean from the coast of Coromandel to Sri Lanka to the Malay peninsula and beyond to Java seems to have cultivated a confluence for the two locations to converge in a regular commercial network [24]. While tin was an essential commodity flowing from Southeast Asia to India, the region was also a source of ‘aloeswood [agarswood], which is mentioned in the Arthaśāstra as coming ‘from beyond the sea’, white sandalwood, camphor and other aromatics, dye woods, tortoiseshell, pepper, cloves, and other spices, as well as Chinese goods, notably silk and cinnamon, also figured’ [24]. Essentially, ‘The growth in the export of aromatics from Southeast Asia during the early centuries of the Christian Era may be in part attributed to the introduction of Hinduism and Buddhism into the region, to the direct links forged thereby between Indian and Southeast Asian Hindu and Buddhist rulers and the increase in traffic that was thus fostered between ports on either side of the Bay of Bengal.’ [24].

The precise flows of Indian Sandalwood between southern India and the Lesser Sundas between the first century and middle of the fifth century are speculative. Some scholars suggest that the cloves received in Rome during the first century CE were also traded by Indians who procured sandalwood from Nusa Tenggara Timur through regional links [26]. It also seems that during this time, a local Timor word for sandalwood, haumeni, was also joined in the regional religious and trade lexicon emerging for the tree: cendana [15]. The latter is a localization of the Sanskrit word candana. The acceleration of Chinese coastal imports of cendana and other wood from the Lesser Sundas that began from the fourth century steadily increased after the mid-fifth century primarily in Indian and Southeast Asian ships. As such, ‘sandalwood from Southeast Asia made its way with Buddhist images made of ivory into China’s Nanhai [Southern area] according to Chinese records’ [24].

The Kingdom of Funan (514 to 539 CE), based in the Mekong Delta region, served as an export and re-export market for aromatic woods to the Southern Liang Dynasty of Emperor Wudi (502–549) for incense in Chinese Buddhist temples. Funan’s Mekong river port of OC Eo had goods exported to China, Indonesia, India, the Middle East and the Mediterranean—with aromatic woods such as aloeswood, white sandalwood, benzoin and camphor traded in exchange for Chinese ceramics, gold and silver bullion [24]. Sandalwood from southern India and the Lesser Sundas, particularly Timor, could have graced the influx of Arab and Persian ships that began sailing into Guangzhou from 671 CE. They could have either directly purchased sandalwood from the Malabar or Coromandel coasts or in regional markets in Southeast Asia that cropped up as trade accelerated between 600 and 1000 CE.[24]. In 749 CE, the Cham Kingdom sold both aloeswood and sandalwood to China. The Malaya peninsula city of Fuluoan was said to hold a market with sandalwood that also flowed to the Cham. ‘All this suggests that the Chinese had no clear idea of the origins of the different varieties [of wood] and that Khmer and Cham aloeswood, like Timorese sandalwood, was brought to these ports, probably by Indian traders and re-exported thence to China’ [24].

Nevertheless, the Timor islanders and those in neighbouring islands where it grew were getting attention for cendana. After all, cendana was about to be indelibly stamped into the identity of the regional economy and political sphere.

5 Sandalwood Flowered Coins of Borobudur

Sometime between the late eighth century and mid-ninth century, silver alloy coins bearing sandalwood flower prints were minted by the state of Mataram in Central Java. These were 'either a flat or scyphate (cup-shaped) flan, known as a 'sandalwood flower' coin from the pattern stamped on their reverse. These 'sandalwood flower' coins were made of gold, electrum, silver, or silver alloy, depending upon minting time and place [27]. The coins moved with Mataram's expansion into sister states on Java and Bali with hybrid polities that linked their ports and fertile interiors by the tenth century.' Java's, 'silver alloy 'sandalwood flower' coins became a prototype for gold, electrum and silver coins of the same imprint in Sumatra and Malay peninsula during the tenth and eleventh century' [27]. From the 9th to fourteenth century, these sandalwood coins were used in states from Mataram to the Majapahit for trade, taxation, and shrines or holy rites.

In terms of design, 'These 'sandalwood flower' coins all bear on their reverse sides a pattern resembling a four-petalled flower or four-bladed pinwheel set in a deep square incuse. Although there was a degree of variation in the form of this stamp on the reverse, it remained recognizably the same pattern from the early ninth into the fourteenth century. The pattern was also stamped on one surface of the silver ingots found in central Java….' [27]. Further, 'The obverse sides of the silver alloy coins found in central Java, dating to the ninth or early tenth century, bear the character 'ma' in the same early north Indian nagari script that was used for writing late eighth Buddhist inscriptions of central Java. This character appears to be an abbreviation of the word masa, a term borrowed from Sanskrit and applied to the most common Javanese coin weight unit, equivalent to 2.4–2.5 g' [27]. Technically speaking, 'The flans of the early coins may have been produced simply by dropping measured quantities of molten metal onto a flat surface into cold water; the still hot—and in some case globular—flans must then have been placed on a flat anvil into which the character ma was engraved square or reverse die which produced a deep incuse with a raised 'sandalwood flower' pattern' [27].

This design is found on most pure silver and silver alloy coins in Java for six hundred years. This powerful sandalwood flower design was found on small copper coins in late tenth- or eleventh-century West Java and on silver, gold and electrum coins found in Sumatra and Malay Peninsula suggesting stratified purchasing power for specific transactions from low to high buys, perhaps used by all classes. And likely including Sandalwood sales of both raw lumber and refined incense.

Sandalwood flowered coins are most closely associated with the largest Buddhist monument in Southeast Asia, the Borobudur temple in central Java. More specifically, 'It is these coins, with their distinctive 'sandalwood flower' pattern, which are illustrated in at least two of the relief panels that decorate the major Javanese Buddhist monument of Borobudur. This enormous multi-layered stupa was apparently constructed over a period of some decades, starting in the late eighth century. The panels in which the coins are found are those illustrating a number of Jataka tales on the lowest galleries above the encircling reinforced base. Since the places of relief-carving seems to have begun at the top of the monument, these panels would have been among the last to be carved…These panels may thus date to the early or middle decades of the ninth century. These relief panels thus provide a *terminus ad quem* for the minting of such coins' [27].

Panels on Borobudur illuminate a rich telling of Indian Buddhist tales with forest products in the mythology and what was inherent in the Javanese and regional landscape [16]. These suggest a deep integration of sandalwood sources from the Lesser Sundas and Timor and add insight into why the usage of silver coins increased during the reign of Balitung (898–911 CE) with more port taxing in the Brantas delta in East Java [27].

It allowed for more control of the mid-point from the Central Java interior and sea access to the Lesser Sundas for white sandalwood. Shortly after Balitung left power, in 916 CE the Srivijaya empire city of Kalah Malay seems to have been getting sandalwood from this region of Java with interisland trade [24]. Demand for it was booming in China and regional supply chain markets in Southeast Asia would transform with increased trade volume. In fact, in the year 960 CE, Chinese Emperor Taizhou had to regulate overseas trade, including taxable commodities from Southeast Asia such as aromatic woods [24].

From the late tenth century, 'sandalwood and massive amounts aromatics from Southeast Asia into Chinese coastal ports including 4,423 kati of sandalwood from Java in 992; [and] 10,753 kati of sandalwood from Sri Vijaya in 1156.' [24]. In terms of weight, the Malay measurement word *kati* represented 1.3 pounds or 604 g. Hence, the year 992 CE figure represents 5,749 pounds or 2608 kilos of sandalwood, and 13,978 pounds or 6340 kilos for 1156 CE. The increase of Southern Song Dynasty imports of whole sandalwood logs saw Chinese taking the trees from Southeast Asia to India aboard large ocean going Chinese vessels and imperial navy ships [24]. Whether this suggests sandalwood was becoming scarce in southern India or that Lesser Sundas sandalwood was of higher quality is an area that needs further research.

In 1226, sandalwood from Timor was being bought by Chinese merchants, 'from two key entrepôts, Sanfoqi (Sri Vijaya) and Fuluoan (a dependency of Sri Vijaya maybe at Kuala Berang 30 km north of the Terengganu River on East Coast of Malay Peninsula)' [24]. It may also have been sold around the Indian Ocean from Salahit on Sumatra between Aceh and Inderagiri and, 'which may have indeed been one of the ports from which imported Timorese sandalwood was shipped.' A century later, by 1360, Chinese and Mongol Yuan Dynasty demand had become so insatiable that Chinese coins called pisis began replacing local sandalwood coins across Java. Whether brought from abroad or minted locally, the pisis were used for purchases, debts and taxes, with some older sandalwood coins still used with Buddhist, Hindu, and their blended Shaivism religious contexts [27].

As the robust Indian Ocean and Southeast Asia markets emerged where both indigenous locations of *S album*, of candana and cendana, could be sourced and exchanged, demand increased in the north of Asia where several centuries of Buddhist sandalwood culture had established a fine appreciation for this sacred, tropical tree.

6 Chinese and Japanese Sandalwood Buddhas and Incense Recipes

After King Ashoka's 261 BCE edicts for Buddhism saw missionaries enter Central Asia and eventually onwards to China, the faith grew gradually over the centuries across the early Silk Roads. Olfactory sensibilities are factored into its spread based on health and symbolic reasons. Buddhism's most prominent arrival in China began in earnest in the year 68 CE during the Eastern Han Dynasty, unfolding its ideas and rituals over dozens of decades before taking firm hold at the close of the Han 150 years later towards 220 CE. In terms of cultural convergences, Buddhism brought an entirely new kind of scent culture, based upon aromatics from the Indian subcontinent and the olfactory theories developed over many centuries. The role played by scents in Buddhist thought is profound; the Sanskrit term gandha गन्ध which means 'aromatic', also means 'pertaining to the Buddha' [17]. Hence, sandalwood can be seen as an essential scent in this transformation along with cloves, cinnamon, frankincense and aloeswood.

For the Chinese, 'smoke and vapor were believed to be one of the most important ways to communicate with the gods, spirits, and deceased ancestors, and that many sacrificial rituals were structured around burning particular items to produce the desired aroma, it is impossible to develop a full picture of ancient Chinese scent culture without considering the religious connotations' [17].

Moreover, 'Some Buddhist ideas concerning the role of aroma—such as the concept that scent could be used to expel malign influences and that a sacred space should be marked by the uses of particular religiously prescribed aromas—were easily adapted into pre-existing traditional Chinese uses of aromatics. Others involved replacing or recasting earlier theories into new forms acceptable to those responsible for promulgating the faith. Thus, although many of the spices and perfumes that would come to be associated with Buddhist practice had first been imported into China in the Western Han dynasty or before, they were used originally without reference to their religious significance. At least at elite levels, there was some prior knowledge of these foreign aromatics, which may perhaps have played a role in the adoption of Buddhist olfactory culture in China' [17].

From India, Buddhist candana would find a sweet spot in Chinese olfactory and directional cosmology with the character 香, or xiang. As far back as 239 BCE, the character xiang 香 denoted sweetness and a cosmological centre of nature's cycles in China. In the Qin Dynasty classic work Lüshi Chunqiu 吕氏春秋 (Spring and Autumn Annals of Mr. Lü) and Han Dynasty work Huainanzi 淮南 子 (Book of the Master of Huainan), xiang香 plays a prominent role. 'In this discussion of the yearly cycle, spring is associated with a gamey smell (shan 羶), summer with a burnt or charred smell (jiao 焦), autumn with the smell of blood (xing 腥), and winter with rot (xiu 朽). With the addition of the sweet scent (xiang 香) associated with the centre, this gives a five-stage rotation. This appears to be the earliest cosmological cycle to be preserved in ancient Chinese literature' [17].

Linking the olfactory senses with compass points and the five phases cycle, xiang 香 has a sweet centrepiece: ‘Why is the North associated with the smell of rottenness? The North represents the phase Water; it is the place where the myriad creatures hide in the dark. Furthermore, water collects and becomes foul and stagnant; therefore its scent is rotten and corrupt. The East represents the phase Wood; the myriad creatures are newly emerged from the ground; therefore its scent is gamey. The South represents the phase Fire. Yang is at its zenith and it burns; therefore its scent is charred. The West represents the phase Metal; the myriad creatures have reached maturity and they begin to decline; therefore its smell is bloody. The Centre is Earth, and its main duty is nurturing; therefore its scent is sweet.’ The ‘Monthly Ordinances’ says: ‘East smells gamey, South smells charred, Center smells sweet, West smells of blood, and North smells rotten’ [17]. Grounded with the sweet earth at the centre, sandalwood with xiang 香 began making its way into essential incenses at the later Han court. For example, the incense is known as Han Jianninggong zhong xiang 漢建寧宮中香 (Han dynasty Jianning Palace Perfume) contained the following ingredients, not all of which can be identified: ‘Four jin of huangshixiang, two liang of baifuzi, five liang of clove bark, four liang of patchouli leaves, four liang of Thai basil, four liang of angelica, one liang of frankincense, four liang of sandalwood, four liang of shengjiexiang, five liang of spikenard, one jin of Hierochloe odorata, two liang of gharuwood [aloeswood], two liang of storax oil, and five liang of jujube’ [17]. By Chinese measurements, a jin constituted 500 g or 16 liangs. One liang represented 32 g—with four liang of sandalwood in this recipe constituting 64 g. Whether this was made into a paste or as wood chips is difficult to say, but sandalwood’s olfactory appeal in China would sharpen as the tradition of whole carved Sandalwood Buddhas began to take hold.

This may have been the time when the first part of candana was changed into either an ideograph or portmanteau with the character ‘tan’ 檀. As a meaningful word, it was juxtaposed with xiang香 as tanxiang 檀香, and with the character mu 木 for wood, tanxiangmu 檀香木. Both can be used for sandalwood in Chinese. The character mu 木 can also be replaced for other meanings, such as the character for the mountain: shan 山. Many centuries later, tanxiangshan 檀香山, or Sandalwood Mountain, became the original Chinese name for Hawai’i when sandalwood from there was shipped to compete with Indian sandalwood in Guangzhou in the early nineteenth century. The wandering Chinese Buddhist monk Xuanzang’s seventh century account of his 19-year (626–645 CE) odyssey across Central Asia and India to explore Buddhism brought to China the tale of the Sandalwood Buddha with Udayana Buddhism. It would be transmitted to Japan from China and Korea a century later, inspiring in these regions a desire for Santalum album in the tradition of Udayana Buddhism. Of the seven Buddhist sculptures Xuanzang brought back to China from India, four were made of sandalwood. In his 646 CE account of the *Great Tang Records in the Western Regions*, he remarks on the Maitreya Bodhisattva that a Buddha at Pima was commissioned to make a ‘King Udayana and a chair made by a Brahman with the four feet carved in the shape of Maheshvaradeva, Vasudeva, Narayanadeva and Buddhalokanatha as having been made out of sandalwood’ [5]. Indeed, the sandalwood image was the very Buddha incarnate himself in the eyes of the faithful. He also details the 'chandaneva tree', which is hard to distinguish from the sandalwood tree, growing in 'the Malaya mountains of southern India,' which is the Western Ghats in present day Kerala. More precisely, he notes that east of this is 'Mount Potalaka' where the Avalokitesvara, the Boddhisattva of all compassion of all Buddhas, resides. Probably located in Tamil Nadu, Mount Potalaka and the Kerala 'Malaya Mountains' were dense with Indian sandalwood trees. This region was also 'linked to the Eleven-Headed Kannon Sutra, which specifies to use sandalwood when making an image of Avalokitesvara' [5].

Xuanzang notes the sizes and types of four Sandalwood Buddha themes:

'1. A sandalwood sculpture copying the sculpture of Sakyamuni Buddha giving his first sermon at Sarnath in Varanasi. 3 shaku 5 sun (approximately 106.05 cm.) in height, including mandala and pedestal.

2. A sandalwood sculpture copying the image commissioned by King Udayana when he was longing to see Sakyamuni Buddha. 2 shaku 9 sun (approximately 87.87 cm.) in height, including mandala and pedestal.

3. A sandalwood sculpture copying the sculpture, which resembles Sakyamuni Buddha's shadow left in the cave at Nagarahara. 1 shaku 5 sun (approximately 45.45 cm.) in height, including mandala and pedestal.

4. A sandalwood sculpture copying the sculpture of Sakyamuni Buddha making his daily rounds at Vaishali. Height is unknown' [5].

This tradition of the Sandalwood Buddha would continue onward from the seventh century throughout Chinese history, facilitating two particular ones that had lasting impacts. One became, 'a palladium, a National Treasure that protects the state and the ruling dynasty, and travelled in China, transmitted or stolen from one dynasty to another. Eventually, the Sandalwood statue arrived in 1163 in Beijing where it remained until 1900' [6]. In fact, this particular Buddha would influence one of the largest Sandalwood Buddhas ever constructed during the middle of the eighteenth century, representing the high watermark of all Indian sandalwood exchanges between India, Nepal and China.

Within a century of Xuanzang's work, Chinese and Japanese monks began in earnest the tradition of Buddhist danzō (the Japanese word for sandalwood images) and dangan (the Japanese word for portable sandalwood shrines). This tradition would last from roughly the 8th through the fourteenth centuries in Japan at its high point. There is debate that the tradition arrived earlier than this in the late seventh century, but beginning in the Nara period (710–794), the danzō tradition honed in on the, 'Udayana Shaka legend.' This recounts, 'how King Udayana of Kausambi commissioned a portrait sculpture of the historical Buddha Sakyamuni, which was made out of ox-head sandalwood and five shaku in height, to keep him company during the historical Buddha's absence' [5]. The dangans were brought from China with small Buddhas carved in relief with mandalas as portable shrines. Furthermore, 'This legend illustrates the choice of sandalwood for the most sacred of images, a portrait sculpture of the historical Buddha Sakyamuni himself and thus reflects the special sanctity of sandalwood as a material for particularly sacred images. All four translations of the Eleven-Headed Kannon Sutra, two of which were known in

Japan by the 730 s, stipulate that when making an image of this deity, only the finest quality of sandalwood' [5].

To the Japanese, sandalwood was the most sacred because it was literally the sculpture of the 'historical Buddha himself.' The Japanese also believed in its medicinal healing power from the Gandha-vyuha Sutra which said, 'There is a sandalwood treasure known as white sandalwood, which, when applied to the body, allays all forms of fever and gives coolness to all asylum. In like manner the white sandalwood of the bodhicitta cools off the fever of the passions, speculations, greed, anger and folly and gives happiness to the asylum of supreme knowledge' [5]. In 761, two sandalwood logs (one at 66.4 cm. long and 13 cm in diameter and one at 60.3 cm long and 9 cm in diameter) arrived in Japan that were incised with Pahlavi inscription, Sogdian characters, and another ink inscription. Whether or not the characters and inscriptions suggest the name of the owner, the weight or price of the wood, or a blend of all three is debatable. Quite possibly, 'the two pieces of sandalwood were imported from tropical Asia, their original place of production, to China either by land across Central Asia or by sea, with Persian and Sogdian merchants, who were active in the transit trade at the time, acting as intermediaries. The two logs of sandalwood must then have been imported from China to Japan. The fact that sandalwood was imported to Japan from China is further substantiated by the fact that the Shinsarugakuki ca. 1058–1065 lists sandalwood among objects from China' [25]. The Shinsarugakuki, a fictional work also known as 'An Account of the New Monkey Music' or 'A Record of New Sarugaku,' was of course not the only eleventh-century Japanese book to mention sandalwood. One of the foremost works of Japanese literature, *The Tale of Genji* by Lady Murasaki Shikibu, was published in its final form in 1021 CE. One line says that in, "Her Cloistered Highness's personal chapel, Genji has sacred images (jibutsu, that she will always have with her and the object of her daily devotions) dedicated in summer, when the lotuses are in full bloom, to which he added banners (hata), flower-stand covers, a 'Lotus mandala hung at the back' as well as statues made of white sandalwood of 'Amida and his two attendant bodhisattvas'(Kannon and Seishi) [25]. *The Tale of Genji* also notes the high culture of incense contests known as Kōdō (香道), or the 'Way of Fragrance'. This tradition became as meticulous and precious as Japanese tea ceremonies. Sandalwood, called byakudan in Japanese (白檀), along with aloeswood and camphor, were the most important woods used in the Kōdō. The Japanese character byaku 白 means white and the character tan 檀 stands for sandalwood—borrowing from the Chinese character tan 檀 from the earlier combination of tanxiang 檀香 with distant echoes of candana or chandana चन्दन from Sanskrit.

In terms of the source of this precious byakudan白檀, 'Up until the fourteenth century, incense materials was imported from Middle East, India, Indonesia, and the Philippines via China, Korea and Ryukyu Islands to the port of Dazaifu in northwest Kyushu where they were forwarded by the assistant viceroy to the imperial palace and great houses of the capital' [9]. They were scarce and expensive only for elite families, namely the Royal Fujiwara clan, and certain priests at the great temples in Nara and Kyoto. Trickling into Japan with Buddhism from the

Kingdom of Paekche in Southwest Korea, since the mid-sixth century, byakudan 白檀 became an essential ingredient in the early ninth century when it was codified with the 'Six Scents' in the text the 'Golden Age of Incense' during the time of Emperor Nimmyō (833–50 CE). The Six Scents ingredients are: aloeswood, cloves, seashells, amber, sandalwood and musk [9].

An author of the 'Golden Age of Incense', a court official and poet name Minamoto Kintada (889–948 CE), is noted for one of his famous incense blends called Lotus Leaf. The recipe for Lotus Leaf included:

'Spikenard: one bu
Aloeswood: seven ryo, two bu
Seashells: two rye, two bu
Sandalwood: two shu
Mature lily petals or musk: two bu
Cloves: two ryo, two bu
Benzoin: one bu' [9]

One ryo was 49 g, and equalled 4 bu and 24 shu—so in this recipe roughly four grams of sandalwood. The Six Scents were further defined in the 1159–116 mid-twelfth-century incense manual called the 'Kunshu Ruisho' as: Plum Blossom (spring), Lotus Leaf (summer), Chamberlain (autumn wind), Chrysantheum, Fallen Leaves and Black (deepest winter). Chrysantheum and Fallen Leaves are not give a season but are transitional from autumn to winter [9].

The recipe for 'Plum Blossom' by Prince Kaya called for:

'Aloeswood: eight ryo, two bu
Seashells: three ryo, two bu
Spikenard: one bu
Sandalwood: two bu, three shu
Cloves: two ryo, two bu
Musk: one bu
Amber: one bu' [9]

Plum Blossom was favoured by Genji himself [9]. He even had the secret recipe, something only women were purportedly permitted to possess: 'The narrator of 'A Branch of Plum' expresses surprise that Genji had acquired the secret formulae for two scents dating from the time of Emperor Nimmyō' [9]. 'It says in the Gōkō Hihō: For 'Raven' [Black], mix together four ryō of aloes, two ryō of cloves, one bu of sandalwood, one ryō of oil of cloves (add an extra two bu if desired), and bu of musk, and one bu of amber.' Heady recipes for incense with sandalwood like this not only graced courtships, they were used to scent clothing and established one's status and even personality. As one of the core cannons of elite Japanese reading, the *Tale of Genji* romanticized the Kōdō for centuries and with it elements of byakudan 白檀. Like Buddhist danzō sandalwood statues and portable dangan sandalwood shrines, byakudan 白檀 in the Kōdō came from limited supply channels of *S. album* between the eighth and fourteenth centuries.

While *S. album* was largely the domain of elite life in Japan during this time, it was becoming popular across China for a variety of elites, temples and merchants.

Its global production and consumption in Southeast Asia and throughout the Indian Ocean system was simultaneously accelerating between the eighth and fourteenth centuries too. Yet there would soon be profound shifts in these paradigms.

7 Timor and the Pearl River

Leading up to the 1351 Red Turban Rebellions in China that would come to rock then overthrow the Mongol Yuan Dynasty in 1368, it seems China was buying from Timor more so than from India. While this topic needs more exploration, India had its own domestic supplies, but China was emerging as the leading importer of the wood—perhaps more so from Southeast Asian markets than directly from India. But this is difficult to say. 'The earliest extant Chinese description of Timor which is contained in the *Tao-i chin-lüeh* (around 1350), states, among other things: [Timor's] mountains do not grow any other trees but sandalwood which is most abundant. It is traded for silver, iron, cups [of porcelain], cloth from Western countries and coloured taffetas. There are altogether twelve localities which are called ports… Formerly [a certain] Wu Chai of Ch'üan [-chou] sent a junk there to trade with over hundred men on board. At the end [of their sojourn] eight or nine out of ten died, while most of the others were weak and emaciated. They [simply] followed the wind and sailed back home… What a terrible thing! Though the profits of trading in these lands were a thousand fold, what advantage is there' [18].

Despite Chinese demand increasing following the 1368 establishment of the Ming Dynasty, regional network conflicts in Southeast Asia saw supplies disrupted out of Timor directly until the early fifteenth century. Some historians think that, 'sandalwood was shipped to China by both Chinese and non-Chinese merchants on the main commercial routes running via the Celebes, the Moluccas and the Sulus, before 1400, and via Java and Malacca after 1400.' [11]. The 1405 to 1433 CE voyages of Zheng He established greater Chinese demand for both raw logs and refined products directly. One observer from Zheng He's ship noted of markets in Java: 'The land produces sapanwood, diamonds, white sandalwood incense, nutmegs, long pepper, cantharides, steel, turtles' carapaces, and tortoise-shell. I As to their strange birds: they have such varieties as white cockatoos large as hens, red and green parrots, five-coloured parrots and the mina, all of which can imitate human speech, also guineafowl, 'hang-upside-down birds', pigeons with five-coloured markings, peafowl, 'areca-palm birds', 'pearl birds', and green pigeons' [12]. A footnote adds that this, 'Sandalwood would have come from Timor.' [12]. Likely, Chinese merchants would have bought both incense and logs to sell them in regional markets such as Melaka in competition with Javanese merchants at this time. Of course, a key river region would come to facilitate sandalwood's primary market flow into China, eventually influencing developments in Japan, Oceania and Australia—the Pearl River.

A long established port city over two millennia on the South China Sea, Guangzhou had contracted somewhat under Ming Dynasty trade restrictions.

However, following the sack of Melaka in 1511, the Portuguese had gradually engaged southern China, getting a permanent settlement in Macau at the western mouth of the Pearl River in 1557 with trade up-river to Guangzhou. After the Dutch seized Melaka in 1641, the Portuguese made Macau a more permanent home to dominate the sandalwood trade as a main lifeline with Timor. With their control of the primary source of *S. album* in Solor and Timor that took shape over the course this same period, the Macau-Timor sandalwood trade would come to heavily influence the flow of sandalwood into coastal China, primarily the Pearl River. The Dutch, too, would come for sandalwood in the Lesser Sundas, gripping Solor in 1646 and establishing Kupang in western Timor in 1653, giving the Portuguese a run for their money. Although the Dutch did not dominate the sandalwood trade into China the same way the Portuguese were able too, they gained a competitive monopoly to ship it directly into Nagasaki, Japan. Chinese were never fully cut out of the trade either, purchasing and selling back in coastal China and into Japan. Overall, the new coastal markets of East Asia saw Macau and Guangzhou in the Pearl River Delta rise as key sandalwood markets for both raw and refined sandalwood coming from the Lesser Sundas, particularly Timor—double so after 1644 when the Qing Dynasty emerged with greater global ambitions and sandalwood demands.

Bigger historical questions about how the flow of Solor, Timor and Lesser Sundas sandalwood moved mainly to East Asia and how candana trees were impacted during this in South Asia needs to be asked—because it marked a key shift in the story of *S. album*. In the relatively well versed histories of Portuguese and Dutch colonial control of sandalwood sources in Southeast Asia and the supply chains to coastal markets in China and southern Japan between 1521 and 1722—the fall of Melaka to the Portuguese and the death of Qing Emperor Kangxi—references suggest boom and bust cycles of sandalwood supplies in the Lesser Sundas.

These market cycles of sandalwood would have subsequently impacted Indian sandalwood traders from the subcontinent. One source notes that Gujarati merchants were avid sandalwood traders in Malacca in 1510, purchasing as much as 5,000 piculs. Whereas one picul measured 133 pounds or 60 kilos, this would have been 665,000 pounds or 300,000 kilos [18]. This flow to India would become complicated—perhaps not totally cutting off the subcontinent with desirable and competitive Indian Sandalwood, but certainly impacting it.

Portuguese inroads also faced fierce local resistance to sandalwood sources for two centuries. According to Timorese oral tradition, the southern area of the island where precious stands of sandalwood grew were part of a, 'mythico-ritual kingdom of *Waiwiku Wehale*' that controlled the trade [15]. They had a special alliance with the Makassarese sandalwood traders who put limits on Portuguese attempts to seize it—until a punitive mission in 1642 saw the, 'settlement of the 'Great Lord', Nai Bot of We hale' [15] razed. Moreover, this, 'action succeeded in destroying the symbolic authority of Wehale and many leaders of vassal domains celebrated the victory and pledged allegiance to the Portuguese. It also ushered in a century's long struggle for control over the sandalwood trade involving a complex triangle of Portuguese and Dutch trading interests, as well as a myriad of indigenous Timorese domains which sought to benefit through political opportunism and strategic alliances' [15]. Indeed, 'for indigenous Timorese too, participation in sandalwood politics frequently lay at the heart of endemic struggles for power and wealth. The capacity to exert control over sandalwood production and trade from the interior of the island was a direct measure of political authority and standing among rival Timorese indigenous domains… Thus to a significant degree the fortunes of Timorese society are mirrored in the history of sandalwood politics' [15]. From the mid-seventeenth century to the mid-eighteenth century, both Dutch and English sources said that sandalwood was impacted on both Solor and Timor first on the coast, and increasingly so in the islands' interiors [15].

Demand for it would continue to climb in the eighteenth century as the number of people in China quadrupled from 100 to 400 million between 1700 and 1800. In fact, sandalwood imports increased exponentially under Chinese Emperors Kangxi and Qianlong. Especially Qianlong's life from 1711 to 1799 [8]. During this fateful century sources of *S. album* experienced disease and war as it faced severe depletions in both India and the Lesser Sundas.

8 Qianlong's Maitreya and Sultan Tipu's Law

They were two great leaders in Asia that influenced the high-water mark saga of *S. album* before modernity's saws cut loose on all the world's sandalwood: Chinese Emperor Qianlong (1711–1799) and Mysore Sultan Tipu (1750–1799).

Born at the Tibetan Lama Temple in Beijing, the Emperor Qianlong would come to erect one of the world's largest standing Sandalwood Buddhas—at 26 m in height and 1.5 m in width, the Maitreya Buddha of the Futureland. When the Manchu ruled Qing Dynasty came to power in 1644, they built a special temple, the Zhantansi, for the sacred Sandalwood Buddha that had served as a 'palladium' of power since arriving in China from India in 1163. As a matter of politics, 'From the Manchus' perspective, the emblematic icon contributed to establish the Qing as a legitimate dynasty able to rule a multiethnic Buddhist empire. Its specific link to the Yuan dynasty helped the Qing emperors to claim to be successors of the Chinggisid Mongols. Besides, the Manchu rulers also needed this statue to protect their state' [6]. Although it was probably made from red sandalwood (*Pterocarpus santalinus*), it was still tanxiangmu,檀香木 and sacred to the Mongols, with the legend of the Sandalwood Buddha also of holy significance to Tibet—regions the Qing sought delicate balances of power with. In 1695, the King of the Mongols, 'Zanabazar, the First Jebcündamba Qutuytu (1635–1723) and emperor Kangxi met and exchanged scarves in 1695 in front of the Sandalwood Jowo [statue carving].' Both Kangxi's son, the Yongzheng Emperor, and his grandson Emperor Qianlong, 'ordered many copies of the 'original' statue to be made,' and in, '1735, a copy of the Sandalwood Buddha was carved for the Xianliang temple 賢良寺 located in the eastern part of Beijing.' [6].

Moreover, 'at least two copies of the Sandalwood Buddha were preserved in Chengde, the summer retreat of the Qing emperors. An eighteenth century copy was enshrined in elaborate case that was kept at the summer palace. It is a gold-lacquered wood statue…Other copies were enshrined in the temples of the imperial gardens' [6]. They were not alone. The, 'colossal Maitreya statue of the Wanfuge 萬福閣 was also carved out of sandalwood, as well as numerous statues of the Qing dynasty' [6]. The massive Maitreya stands at 26 m in height (18 above ground, 8 below) and 1.5 m wide and is believed to be the largest existing white sandalwood specimen of its kind today. It may have been the last long-haul log of its kind coming overland from India via Nepal to Tibet to Beijing during the eighteenth century. It arrived amidst intrigue in the Himalayas and was a state-level trade.

The Kathmandu Valley with its critical access to Tibet was embroiled in fresh conflict in the 1740s. Tibet simultaneously simmered with power dynamics. In Beijing, Emperor Qianlong began renovations to Yonghegong Lama Temple in the 1740s. 'When news of the emperor's plan to transform Yongegong into a monastery reached the Seventh Dalai Lama Kelsang Gyatso (1708–1757), he sent the costly and impressive gift of the trunk of sandalwood to the emperor. It was purchased from the Gurkha king in Nepal and transported through Tibet, Sichuan province, up the Yangzi river and Grand Canal, arriving in Yonghegong in 1747' [10]. It was assembled and gilded gold in the Pavilion of Infinite Happiness (Wanfuge 萬福閣). Another area of Yonghegong, the Hall of Eternal Protection (Yongyoudian 永佑殿), also featured three smaller white sandalwood statues of 'Buddhas of Longevity' standing each at 2.35 m in height: the Medicine Master Buddha, (Yaoshifo 藥師殿), Amitàyus Buddha (Wuliangshoufo 無量壽佛), and Simhanada Buddha (Shihoufo 獅吼佛, T. rgyal-ba seng-gehi nga-ro) [10]. Their origin was also likely from India via Nepal to Tibet by the same route as Maitreya with natural and human-made waterways to Beijing.

The 'Gurkha king' who provided Indian sandalwood for Maitreya at this time was none other than Prithvi Narayan Shan (1723–1775), who founded the Kingdom of Nepal in 1768. More research is needed to know about where he purchased this specimen of white sandalwood. Whereas he visited both Varanasi and Orissa and had procured large caches of guns for his 1744 victory to take the Kathmandu Valley, it is probable he purchased it from this region. In 1737, a flurry of temple building commenced in Varanasi as the Mughals awarded the city 'The Kingdom of Benares' status. Sandalwood from southern India must have flowed up the Ganges. The Maitreya may also have been an exogenous specimen of *S.album* grown in northern India or Nepal. Regardless, it would have allowed Prithvi Narayan Shan to directly establish trade more clearly with Tibet and onto the capital in Beijing—helping cement his conquest over Nepal in the coming decades.

Further up the Himalayas, 'This gift was sent at a time of political crisis in Tibet. During his rule in Tibet, [the regent] Polhanas had made efforts to limit the political influence of the Seventh Dalai Lama, who had been installed in 1721 with the aid of the Kangxi emperor. After Polhanas death in 1747, his son Gyumey Namgyal (T. Gyur-med-rnam-rgyal) took power, but rebelled against the Qing. It was during this critical time that the Seventh Dalai Lama sent the trunk of the sandalwood to the emperor. After Gyumey Namgyal was assassinated by Qing ambans, or appointed imperial representatives, the Seventh Dalai Lama was given temporal authority in Tibet in 1751.This suggests that the Seventh Dalai Lama, responding to the crisis, demonstrated his loyalty to the Qing court in part through this lavish gift, and received the military support of the Qing Empire in return' [10].

As the living incarnation of the Buddha, the Maitreya sandalwood bodhisatva would have been received with awe by the faithful when renovations were completed and it towered above them glinting with gilded gold at 18 m in the year of 1750—the same year that one of the major heroes of Indian sandalwood was born, Mysore Sultan Tipu. Known as the 'Tipu the Tiger,' the Sultan of Mysore heroically defended with his father Sultan Hyder Ali what is today part of the states of Karnataka, Kerala and Tamil Nadu from British invasion in a series of territorial conflicts known as the Anglo-Mysore wars from 1767 to 1799. As a primary source for *S. album*, these wars might also be viewed, in part, as conflicts for sandalwood.

Accordingly, 'One way to understand these wars is as part of the global struggle between the British and the French, where Mysore was a French ally. However, late eighteenth-century British East India Company wars need also to be understood as trade wars. They were about economic conquest as much as any other kind of expansion, and sandalwood was one of Mysore's most prized commodities' [21]. In south India, the tradition of sandalwood and other resources defining borders was centuries old. Some environmental historians of India contend that, 'the political boundaries of the Vijayangara Empire in the thirteenth to sixteenth centuries were possibly shaped by availability of bio-resources such as sandalwood in the Deccan, which its rulers could trade for commodities such as firearms and horses' [21].

Sultan Hyder Ali (1720–1782) certainly did this by carefully administrating sandalwood, spices, ivory and gold within his realm. His son Sultan Tipu saw the immense potential of sandalwood too from Mysore's forests [21]. Tipu, like his father, would not buckle to the British over them either. Beginning in 1786, Tipu Sultan suspended sandalwood sales to the British, along with cardamom and pepper. Whereas the British Empire was nearly bankrupt from losing the American revolutionary war three years prior, this was a deep insult. Indeed, Lord Cornwallis, who had been routed by the yanks at Yorktown in 1781 and was later sent to command troops in India, saw this cut-off as a bleak situation for the East India Company—even to suggest downgrading Bombay's status from a presidency to factory in 1788 [21]. A year after the Third Anglo-Mysore war erupted, in 1791 Lord Cornwallis captured Sultan Tipu's stronghold of Bangalore, a major centre of the Indian sandalwood trade. Tipu immediately suspended sandalwood to enter the city's markets. He also put a moratorium on cutting and stored candana reserves in his private forts to deprive the British [21]. A year later when Tipu was forced into 'the disastrous treaty' of Seringapatam with the British, he declared sandalwood a 'royal tree' and asserted a protective monopoly over it [21]. However, there seems to have been widespread poaching in this power vacuum, while others conserved [21]. In 1799, following the defeat and death of Sultan Tipu in the Fourth Anglo-Mysore War, the British East India Company further relied on Wodeyar

Maharajas puppet rulers and gradually squeezed them for sandalwood and mining resources in the coming decades for the China trade. In fact, 'The Company, with an eye to the Chinese market, negotiated the annual harvest of sandal resources with the Mysore *durbar*, overexploiting the tree but only so far as the market would allow' [21].

With the death of Sultan Tipu and also Emperor Qianlong in 1799, both the sandalwood supply chains in South Asia and markets in China would come under greater British pressure over the coming century. In fact, in 1799 the China market was quite eager to get sandalwood. The Third and Fourth Mysore Wars had disrupted sandalwood supplies, and the spike disease was damaging *S. album* across southern India. The 1788–1792 Campaign of the Gorkha military incursion into Tibet had also caused havoc with overland Himalayan trade of sandalwood into Lhasa and beyond to Beijing. Timor supplies were running low too. In southern India, even though Sultan Tipu was gone, his historic measures to protect sandalwood seems to have been in force. Yet new sources of faraway sandalwood forests were opening up that would soon join *S. album* in Guangzhou to form the first globalized sandalwood market.

9 Oceans of Sandalwood Time

Long used for medicine across Oceania, other varieties of sandalwood that had radiated across the Pacific would soon be caught in a pattern of boom and bust exploitation between Indigenous Islanders and European traders. Starting in 1804 with news of 'Sandalwood Island', as Vanua Levu would be called in Fiji, British ships from Port Jackson, Australia to Calcutta, India came looking for sandalwood —*S. yasi*. American ships too flooded in from New England. In exchange for sandalwood, they mainly sold guns which created internecine conflicts [8]. This pattern defined nearly all Pacific exchanges, except Western Australia. Pacific sandalwood tended to be more yellow and was not as popular as *S. album* in Asian markets. Still, it sold well enough.

The Fiji trade lasted from 1808 to 1814, then other sandalwood rushes emerged across Oceania where depletions and oftentimes violent power struggles ensued: the Marquesas (1815–1817), Hawai 'i (1810 to 1830s), New Caledonia, Solomons, and Vanuatu (1840s to 1860s), and Western Australia (1860s to 1880s) [8]. In fact, Western Australia saw more booms after the 1880s well into the twentieth century.

The island of Sumba in Indonesia even opened up after World War I until sandalwood was exhausted in the 1920s leaving the island awash with tiny transport horses called 'sandalwood ponies.' Sandalwood from Polynesia, especially Hawai 'i, came aboard American ships, while Australian based ships under British flags carried most of the wood from Melanesia—nearly all sailing to Guangzhou where it as transported nationally or manufactured locally into furniture, decorations, Traditional Chinese Medicine, or incense.

Sandalwood from Western Australia was sold in British colonial Singapore and Shanghai, while Lesser Sundas wood went to Batavia for regional markets in Southeast Asia and Japan. Portuguese controlled *S. album* from Timor-Leste also continued to be sold to its main markets at Macau from the nineteenth into the twentieth century.

On the subcontinent, 'the British monopolised the sandal trade in southern India, used it to balance their accounts in China, and overexploited the species as far as the market would allow. This represents a significant departure from the pre-colonial period where local elites were happy to trade with outside powers, but with eyes thoroughly fixed on the domestic market' [21].

While other products propelled trade from Oceania to China between 1808 and the 1880s, sandalwood as a species writ large was the key link owing to previous centuries of exchanges of candana and cendana—of *S. album*'s earlier interregional environmental history. In fact, one can argue that the study of *S. album* is a telling way to read the finer grains of the first stages globalization in the Indian and Pacific Oceans in the nineteenth century. It adds weight to creating further comparative analysis of how the markets evolved and what this meant to *S. album* trees in the forests when they were placed under colonial forestry laws by the British in India and Dutch in the Lesser Sundas. It informs, too, post-colonial forest policies that incidentally saw massive exploitation and the species itself threatened—severely so in India where it was almost wiped out by 1974, as Rashkow has written. Conservation movements and scientific studies from the 1970s through the 1990s did little to stave off widespread illegal poaching and even sandalwood mafia gangs in India, Indonesia and Timor-Leste. Forestry projects and private businesses since the 1990s over the past 30-years have been able to innovate exogenous plantings of *S. album* across Southeast Asia, Vanuatu and Australia.

Today, *S. album* conservationists and scientists (like many contributing to this book) are continuing the arduous task of saving the trees as global consumption for this essential oil propels all species of sandalwood closer to extinction. Hindu, Jain, Buddhist institutions need to raise their voices to support sacred and sustained groves of Indian sandalwood and all sandalwood—with discussions possible via internet interfacing from afar afield as Karnataka forests to Tokyo temples. The same can be said for government Ayurvedic departments and hospitals, and ethical perfumeries, incense makers and essential oil companies. They, like the concerned public, can join in hymn and chorus with the authors of this book to save sandalwood.

Since humanity found uses for *S. album* and all sandalwood species as medicine, it has been special to whomever has felt its oil, smelled its smoke or touched its sensuous fibres as they inhaled its heady and healing essence. We are just really understanding how its true global environmental roots, its heartwood of history, has perfumed our past —as imperfect as bad parts of this history of exploitation may have smelled. Knowing this, we must now take specific steps to ensure it has a fragrant and everlasting future.

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Chapter 2
Indian Sandalwood: A History of Overexploitation and Endangerment

Ezra D. Rashkow

1 Scandalwood

From the 1950s to the early 1970s, on average 480,000 Indian sandalwood trees (*Santalum album* Linn.) were supplied annually to the sandalwood oil factories of Karnataka in southern India. Then, a sample survey of Karnataka's forests found that by 1974 there were only approximately 350,000 trees left standing in all seven of the state's major forest divisions, with only a tiny fraction of those trees being mature enough for harvest [39, 40]. India's sandalwood industry for decades had been hurtling towards the brink of collapse. Now, in the mid-1970s, at the same moment as the modern environmental movement's birth, there was a dawning awareness that this species was facing extinction. The price of Indian sandalwood, long considered one of the most precious woods in the world, began to skyrocket. Karnataka's sandalwood oil industry dramatically curtailed production. Furthermore, smugglers could now make more money by felling sandal trees than by poaching elephants for ivory. Occasionally referred to as 'scandalwood', herein lies the scandal in India's sandalwood history.

In terms of geography, though usually called 'Indian sandalwood', *Santalum album* might most properly be referred to as Karnataka or Mysore sandalwood. This is because, globally, 90% of the world's *S. album* traditionally came from India (with most of the remaining 10% or so coming from the island of Timor) [10]. And within India, around 70% of *S. album* historically came from the area that was the Kingdom of Mysore, which is now the southern state of Karnataka, with an additional 20% coming from neighbouring parts of Tamil Nadu [42]. Yet whereas the history of the sandalwood trade in Australia, China, Hawaii and the South Pacific has been analysed in great detail, Karnataka sandalwood's story has received considerably less

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attention from professional historians than even that of neighbouring Tamil Nadu [16, 20, 26, 43, 45, 50].

This essay uses sandalwood history to assess claims about the nature and impact of colonial and post-colonial forestry, arguing that at least when it came to Karanataka sandalwood, European traders and foresters did overexploit the species and also failed to conserve it. The real watershed moment for the species came not during the colonial period but rather in the independence era when industrialisation led to a major endangerment crisis for the tree. This can easily be seen in one simple data set. Since at least the 1880s, through to the mid-twentieth century, some 2,000 metric tonnes of *S. album* were regularly harvested in this region [39]. Then, from a peak of 2,800 metric tonnes of sandalwood produced in Karnataka in 1956–1957, the quantities dropped dramatically to approximately 171 tonnes in 1982–1983 [40] and then to an all-time low of roughly only 3 tonnes in 2016–2017 (Fig. 1) [5].

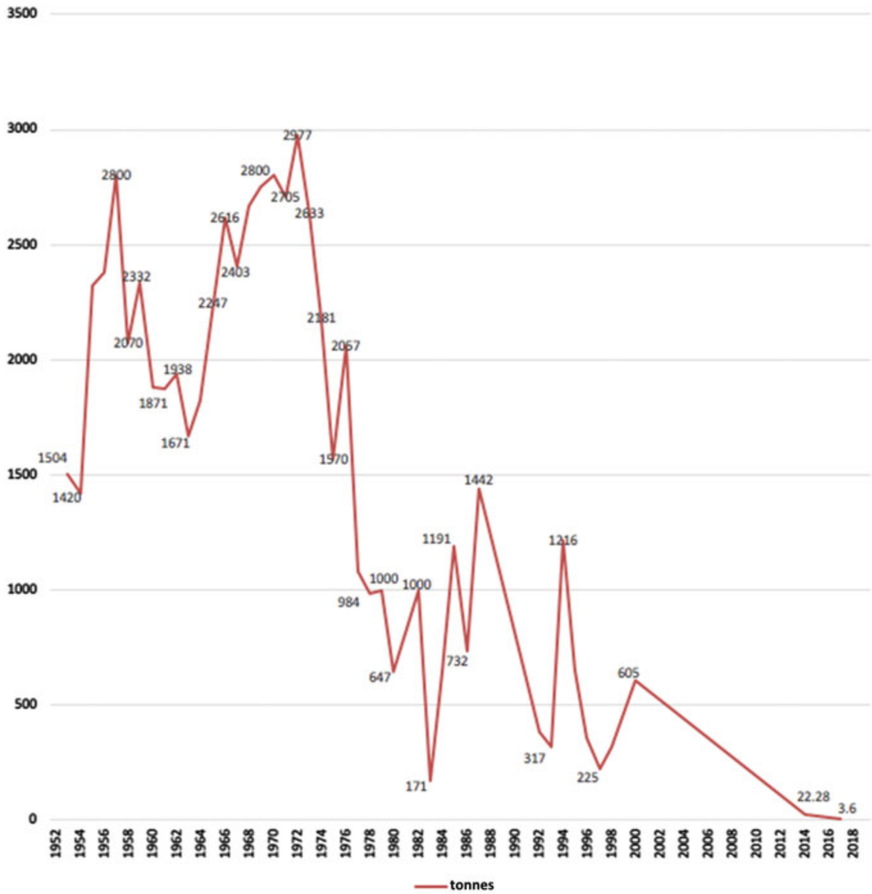

Fig. 1 Annual amount of sandalwood produced in Karnataka (metric tonnes)

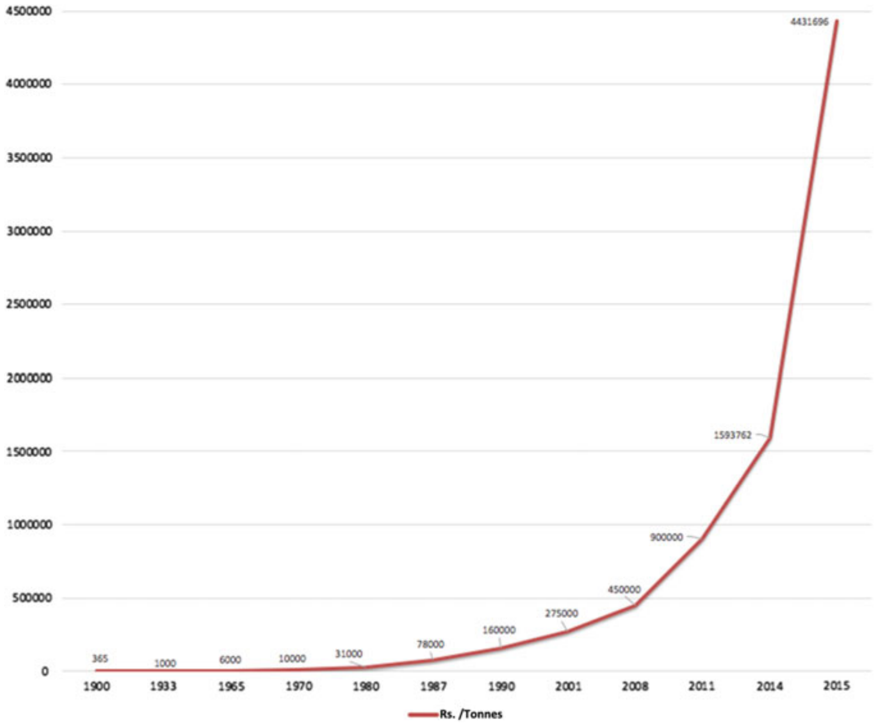

Fig. 2 Price of sandalwood in India (Rupees/Metric tonne)

Meanwhile, the price of sandalwood has shot up almost exponentially. At the start of the twentieth century, a tonne of sandalwood cost only Rs. 365; by 1970, it costed Rs. 10,000; in 2011, a tonne sold for Rs 900,000; the price of sandalwood has since peaked in 2018 at nearly Rs 5.2 million (Fig. 2).

The chapter argues that while both early nineteenth-century capitalist commodification and late nineteenth-century bureaucratic forestry department control were detrimental to the tree's population in southern India, it was not until massive overexploitation by the post-colonial state-run sandal oil industry in the 1950–1980s that the species came to the brink of extinction. Though sandalwood smugglers were often blamed for the tree's precarious status since the 1970s, in fact, illegal poaching only became a major problem because the state-industrial complex failed to manage this precious resource effectively. Moreover, smuggled quantities could never compare to those consumed by the state-owned sandalwood oil factories [6].

The research for this chapter makes use of numerous primary sources from the India Office Records in London, the National Archives of India in New Delhi and the Karnataka State Forest Department in Mysore and Bangalore. The first section of this chapter following this introduction examines the sandal story in the global context, adding some details to previously published histories from my own primary source investigations, explaining how regional narratives to date have often missed the broader picture. This global survey is offered primarily to contextualize the Indian side of the equation. The second section presents a detailed examination of primary sources from the colonial archive on the history of *S. album* in India, particularly in Mysore State. Indigenous resource management systems that suggest an awareness of this precious commodity's limited nature give way to intensive exploitation under the British East India Company after 1799. With an eye to the Chinese market, the Company negotiated the annual harvest of sandal resources with the Mysore durbar, overexploiting the tree but only so far as the market would allow. The third section deals largely with scientific forestry's failure in the late nineteenth century to conserve the sandalwood population effectively. Under the crown rule, the colonial state appropriated the vast majority of southern India's forest resources, yet could do little to control the tree's decline. Finally, the chapter concludes with independent India's twentieth-century history of endangerment of sandalwood. Using forest department records, materials from state gazetteers and scientific papers, this section argues that it was primarily industrial-scale state-run exploitation of sandal resources for the sandalwood oil industry from the 1950s onward that led to the tree's extremely precarious position in Karnataka by 1974.

2 Sandalwood 'Scandal' in Global Context

The scandal of how Indian sandalwood became endangered needs to be understood in the global context. Besides the fact that sandalwood was a key commodity in China trade and the emergence of colonial trading networks at the turn of the nineteenth century, sandalwood species fared dramatically different in different regions and under different resource regimes. By comparing and contrasting these various histories, we can more clearly understand how and why sandal at first survived better in India than it did elsewhere in the world during the colonial period and then eventually came to be just as overexploited by the time the modern industry took hold in the independence era. Comparing and contrasting regional variations also highlight the fact that a case study on a single highly valued species or commodity, in this case, sandalwood, can reveal in detail the functioning of various political and cultural ecologies and economies, the differences between power formations in various regions and historical epochs and the transitions and ruptures between them. As Michael Williams put it, deforestation stories do not happen in a vacuum: 'There is a need for each deforestation story to be firmly rooted in an intellectual and scholarly context that helps explain the society of the age in which it occurred' [52].

To date, most studies addressing the modern history of sandalwood have almost exclusively situated their narratives in the Pacific, with a focus on China trade, often ignoring India altogether, a problem often leading to faulty analysis and conclusions. For much of the modern era, the final destination for most of the world's sandalwood was, first and foremost, China. It is a well-known fact that prior to the Opium Wars, there was a net outflow of European gold and silver species to China. Less commonly understood is that before the trade in opium rose to crisis proportions in the 1840s, sandalwood was one of the few commodities that the Chinese were willing to purchase from European traders, in exchange for their gold and silver. Thus, we can correlate the fluctuating prices of sandalwood in China to booms and busts happening in the Pacific islands [16].

The history of the Pacific sandalwood trade contrasts markedly with the South Asian situation. India—rather than the Pacific islands or Australia—has been the largest supplier of sandalwood to the world market during the entire modern period, by far. Whereas the Pacific trade often involved island rulers newly introduced to the concept of world trade being pressured to plunder local resources and overharvest local species in order to maximize short-term profit, even Mysore's puppet rulers in the nineteenth century were more foresighted and conservation-minded than this. As opposed to these other regions, South Asia had long-established trade networks with sandalwood trade evidence that dates back to before the Common Era. It also had long-established resource management systems that benefited both *S. album* as a species and also the region's economy and ecology [12].

Thus, the colonial critique that only includes the Pacific overkill neglects that it is not until 1974 that supply of the most valuable species of sandalwood was depleted in the major sandalwood bearing region of India. Western Australia, too, entered the sandalwood trade from the 1840s and has stayed there until the present [21]. It might be hypothesized that the large size of sandal tracts in India and Australia allowed the tree to flourish while disappearing on the smaller Pacific islands much earlier. However, at least one case can be used to contradict this hypothesis: the island of Timor. The Timorese sandalwood trade has also survived, admittedly with large fluctuations, until the present. Part of the difference, then, lies in each region's history of governance and relationship to the market. Islands abruptly brought into the modern world system were quickly overexploited. In contrast, areas such as southern India and Timor, which had both been centres of world sandalwood trade since at least the eleventh century, managed to negotiate the pressures of the European trading companies and forest bureaucracies in the nineteenth century. In these situations, it was only with massive industrial exploitation in the mid-twentieth century (and wartime looting during East Timor's Indonesian occupation) that stocks of this precious wood dropped precariously low.

In contrast to regions such as southern India that had long been involved in world trade, much of the Pacific was introduced to the international market by sandalwood traders who moved from one island to the next harvesting the tree until there was no more left to harvest. India and Timor had been the sole suppliers of sandalwood to the world market until the late eighteenth century. While there had long been a world market for *S. album*, at the end of the eighteenth-century European, American and Australian merchants tried to control the sandalwood trade by selling newly discovered Pacific species of sandalwood to China. By the mid-nineteenth century, these sandalwood traders had systematically stripped most of the Pacific islands of this precious tree. Time and again sandalwood species were exploited until they went locally extinct, or nearly so, often with massive ecological damage, not to mention the political and cultural toll on the islands [48].

For all this, it is remarkable that only one species of sandalwood is considered extinct today, i.e. *Santalum fernandezianum* of the Juan Fernández Islands off the coast of Chile. Although this first-documented extinction of a species of sandalwood occurred only in the early twentieth century, with Carl Skottsberg the Swedish botanist and explorer reporting to have seen last live specimen of *S. fernandezianum* when he visited Juan Fernández Island in 1908, the extinction was the result of an extended history of colonial exploitation with naturalists and explorers reporting the species extinct as early as the 1870s. Europeans harvested *S. fernandezianum* at least since 1624 when L'Heremite 'reported that the precious sandal-wood was abundant', but it was not until the early nineteenth century that as elsewhere overexploitation led to endangerment and in this case extinction [46].

In Hawaii, also known as *Tahn Heung Sahn* or 'the Sandalwood Mountains' to the Chinese, the sandalwood trade collapsed by 1828, only decades after it began. The first shipwrecked Europeans to land on Fiji's second largest island, Vanua Levu, also called it Sandalwood Island. The sandalwood trade collapsed there within twenty years of its discovery and inauguration. In the Marquesas, the British and Americans decimated sandalwood in just three years, between 1814 and 1816 [49]. A similar story can be told in the case of *S. austrocaledonicum* of Vanuatu [51].

Though the broad outlines of the sandalwood story in the Pacific are familiar to many historians, the details are typically either glanced over in terms of sweeping ecological imperialism by post-colonial historians or glossed over in terms of an industry perspective seeking to revive supply of this valuable timber [20, 38]. For example, the most common narrative of sandalwood's modern history holds that European traders wiped out sandalwood groves across the Pacific islands in a remarkably short time span between the 1770s and collapse of the trade in the 1830s. However, instead of sheer rapacious felling causing local extinctions and the end of the sandal trade before the middle of the nineteenth century as in the Pacific, southern India's sandal stocks continued to provide the international market without interruption into the independence period. Thus, the question is why the tree survived better under some regimes than others, and the modern environmental history of southern India's sandalwood needs to be studied to solve this riddle.

3 Transition to Colonial Exploitation

The case of sandalwood vividly highlights the structural transformations in forest use that occurred with the British East India Company's coming to southern India. The standard reading of Indian forest history holds that in the precolonial period relatively autonomous villagers typically used forest resources as they pleased or as customary arrangements determined, that rulers made only limited interventions in the people's forest use and that there was greater ecological equilibrium than in subsequent eras [17]. Studying the history of sandalwood helps to modify this standard narrative at least slightly.

On the one hand, the limited evidence available on precolonial Mysore's forest villages does seem to back up this narrative about local autonomy and customary arrangements to some extent. One tradition which may have been an effective local precolonial conservation measure, for example, was to only harvest sandalwood once every dozen or so years [8]. Another indigenous institution that Buchanan describes was that of the *Gydda Cavila* or keeper of the forests, a position about which we have relatively little information and which seems to have disappeared by the early nineteenth century [8].

On the other hand, the rule that precolonial states stayed out of forests finds an exception in the case of sandalwood. State control over forest tracts was traditionally seen to have been a limited phenomenon before nineteenth-century colonialism. However, some recent scholars have argued that the Vijayanagara Empire's political boundaries in the thirteenth to sixteenth centuries were possibly shaped by the availability of bio-resources such as sandalwood in the Deccan, which its rulers could trade for commodities such as firearms and horses [18]. Further, establishing a state monopoly on sandalwood was not originally imposed by the British but by their precolonial predecessor in Mysore, Tipu Sultan.

Tipu Sultan and his father Hyder Ali before him certainly were shrewd administrators of the state's most valuable natural resources such as spices, ivory, gold and sandalwood. According to at least one biographer, Tipu Sultan established an ambitious commercial system and 'saw the immense potential source of wealth in Sandalwood' [14]. Starting in 1786, Tipu Sultan stopped trading pepper, sandalwood and cardamom with the British. As a result, trade prospects for the company were looking so bleak that by November 1788, Lord Cornwallis suggested abandoning Tellicherry on the Malabar Coast and reducing Bombay's status from a presidency to a factory. Bangalore had been a major centre of the sandalwood trade, but after 1791 when the British captured that city and turned it into a pressure point of resistance against the Kingdom of Mysore, Tipu Sultan would not allow any sandalwood from the region to enter the city's markets. 'He either did not allow it to be cut, or else stored up in his forts whatever was felled' [8]. The Anglo-Mysore wars were an attempt by the British to change all that. Nevertheless, it was only in 1792, the same year that Sultan was forced into a disastrous treaty with the British, and probably in direct response to European pressure, that he declared sandal a 'royal tree' and established a monopoly on its wood in his kingdom.

Although one cannot argue that it was sandalwood alone that led the British to battle local rulers in southern India (Hyder Ali and Tipu Sultan), establish a puppet monarchy when Sultan was defeated (the Wodeyar Dynasty) and thereby dominate Mysore for some 150 years, sandalwood certainly spurred colonial intervention. In particular, southern India represented a vast and untapped market to the British East India Company in the eighteenth century. Between 1766 and 1799, the British and the state of Mysore fought four wars known as the Anglo-Mysore Wars, which resulted in British control over most of the south and ultimately over the entirety of India. One way to understand these wars is as part of the global struggle between the British and the French, where Mysore was a French ally. However, late eighteenth-century British East India Company wars need also to be understood as trade wars. They were about economic conquest as much as any other kind of expansion, and sandalwood was one of Mysore's most prized commodities.

In 1799, at the Battle of Srirangapatna, Tipu Sultan was defeated. The Kingdom of Mysore became a princely state within British India and ceded surrounding areas (Coimbatore, North Kanara and South Kanara) to the British. Power of state was immediately handed to the friendly Wodeyar Maharajas on extremely unfavourable terms: the British 'enforced the payment of an annual sum equivalent to one-third of the new State's gross revenues, to be paid in cash by monthly instalments' [9]. However, the East India Company also immediately started paying the Wodeyars for the right to trade sandalwood [22]. At this point, the British did not take direct command of the region's sandalwood for themselves but as in the case of the Mysore's gold and silver mines progressively worked to expand their control [13]. In 1805, the government of Mysore asked for augmentation of the price paid for their sandalwood. The company responded that they would check if the China market would allow it. In fact, it would. In the previous three years, merchants were often turning 83% profits, even on consignments of inferior-quality wood. Also, the Chinese seemed willing to pay more and more [23]. Already at this early period, Indian sandalwood was acknowledged to be one of the world's most expensive woods. In contrast to evidence about some island chiefs in the Pacific, it seems that the government of Mysore, though friendly to British trading interests, was aware that it had an interest in keeping the cost of sandalwood high. The Wodeyars realized that sandalwood was dear and that underselling would not benefit them [22]. However, by 1812, company traders were getting impatient. They engaged in purchasing all the marketable wood produced in Mysore and grumbled that the Mysore government attempted to defraud the company by selling unmarketable wood. The steadily increasing selling price to the company led to dissatisfaction in the commercial department, which complained that sandalwood was one of the only 'productive sources of revenue of Mysore' [24].

There also seems to have been a relative free-for-all involving local elites cutting down sandalwood trees after the British victory at Seringapatam, which again indicates wider trends at the time. For example, in the hills and forests around Magadi, a town some twenty miles outside of Bangalore, a Brahmin who seemed to have been working only for his own private profit and was not under the authority of the *amildar* (district head) or any other local administrator 'procured about three thousand trees', bringing his own men as well as hiring local woodmen to cut them down and send them to market. Following this harvest, Buchanan reported, 'in less than ten years no more will be fit for cutting' [8]. At this time, numerous local overharvests probably occurred, yet the overall species population did not seem to be endangered. Sandalwood trees were supposed to be considered government property, but as one early British administrator reported, 'it would be ridiculous to suppose, that they will always be considered as such by the occupiers of estates, who undoubtedly commit frequent depredations upon them'. Mr Read, a collector in Kanara district, worried about this illicit felling and in 1807 suggested it would be beneficial to the Company to 'cut down immediately' all the eligible sandal trees in the region. To this suggestion, Francis Buchanan responded, 'Mr Read was probably not aware, that last year all the ripe sandal in Mysore had been cut, and a great danger has consequently been incurred of glutting the market; while some years hence it will probably be greatly enhanced in value' [8]. The British monopolized the sandal trade in southern India, used it to balance their accounts in China and overexploited the species as far as the market would allow. This represents a significant departure from the precolonial period where local elites were happy to trade with outside powers, but with eyes thoroughly fixed on the domestic market.

4 The Failure of 'Scientific' Forestry in India

This section documents the failures of colonial forest bureaucracy and so-called scientific forestry to conserve India's sandal stocks, arguing that, at least in the case of *S. album,* the for-profit mentality of the state far outweighed any movement towards conservation, a position that starkly contrasts with that of Gregory Barton and those who see the origins of environmentalism in empire forestry. By the mid-nineteenth century, British control over South Asia's natural resources was reaching its peak, and a sophisticated new imperial forest administration was being developed that sought to solidify state control of the sandalwood trade. In 1864, the extraction and disposal of sandalwood came under the jurisdiction of the forest department. By 1867, it was decided that collection from contractors was a failure. Colonial anxiety to maximize profits from sandalwood meant that a government agency was established to oversee the sandalwood trade and ensure that no precious wood be lost—to deterioration, destruction or smuggling—and so began the government sandalwood depot or *koti* system [28]. Forest administrators also focused on how to ensure continued profits from the sandal trade. From the 1860s the government briefly experimented with a survey tallying every sandal tree standing in Mysore, but these plans were abandoned by 1878 because of the impracticality of the task [34]. Instead, an intricate system of classification was developed to maximize profits. By 1898, an eighteen-tiered sandalwood classification system was instituted, up from a ten-tier system a decade earlier; it seems this led to much confusion and was eventually reduced back to twelve tiers as most traders simply could not tell the difference between all of the various grades of wood, and once the wood reached Bombay, merchants would end up simply mixing various classes [19].

One decision designed to maintain state monopoly was to crack down on landowners, making sure they did not privately gain from the trees on their lands. As the Chief Commissioner of Mysore would insist in 1871, 'fixing the responsibility for the due preservation of this class of trees on the only parties who could be so held responsible, viz., those on whose land the trees grow' would be the most effective way to guarantee compliance with state demand [32]. Such strictures gave no positive incentives to landowners to preserve the species, and so it was noted that 'Ryots are naturally much averse to having the sandal tree in their fields, as it is so strictly reserved wherever growing. Hundreds of seedlings are ploughed up yearly' [33]. Thus, state monopoly on sandalwood has repeatedly been argued to work against the interests of propagation and conservation [9]. Meanwhile, private

European companies also made significant inroads into Mysore territory at this time. By convincing the government to classify forests as 'wastelands' and arguing that Europeans would improve these tracts from their 'semi-savage state', starting in the 1860s, vast areas were taken from local inhabitants and converted into private plantations for the 'production of cardamom, pepper, coffee and Sandalwood' [2].

Attempts to cultivate sandalwood on both forest department and privately owned plantations proved to be a dismal failure. There were two major problems facing sandalwood supply in the period before the twentieth century besides overexploitation and European monopoly. First was the inability to cultivate. Before the first quarter of the twentieth century, European foresters could not figure out how to grow sandalwood trees effectively. The main reason for this is that sandalwood is what is now known as a semi-parasite or root parasite; besides the main taproot that absorbs nutrients from the earth, the sandal tree grows parasitical roots (or haustoria) that derive sustenance from neighbouring brush and trees. Already in the 1860s, the Public Works Department, which was then in charge of forests, informed the commissioner of Mysore: 'an increased production of the Sandalwood tree, either by cultivating or by aiding its natural growth and regeneration, would be most useful, and be productive of a large revenue', and 'asked whether the importance of the work would not warrant the introduction of a specifically trained and skilled Forest Officer either from Scotland or from the Continent of Europe' [29]. In 1865–1866, the government attempted to start a sandalwood plantation, but efforts failed miserably. A report from the plantation enumerated:

> One hundred and fifty germinated in the nursery at Kankanhullee; 60 were transplanted at Coongul, but notwithstanding the greatest care, 50 died, the remaining 10 are progressing favourably. Of the 90 left in the nursery, 10 are in good health; of the rest, a few died, but unfortunately, the greatest part was washed away by heavy rains [30].

By 1871, at least one scientist, John Scott, curator of the Royal Botanical Gardens in Calcutta, had discovered the secret of the sandal tree's root parasitism [44]. Yet Scott's paper 'did not receive the attention it deserved', remaining almost entirely unknown in forestry circles until the twentieth century. Dietrich Brandis often regaled as the father of Indian forestry reported being unaware of the paper when he worked at Kew Gardens in London on South Asian 'forest flora' in 1872–1873. Thus, it was not until 1902 that the issue started to receive attention in the scientific community, when C.A. Barber, a government botanist in Madras who was also apparently unaware of Scott's work, published a similar account in *Indian Forester* claiming to have proven sandal's root parasitism on his own. As Barber himself pointed out, 'no one seems to be at all sure whether the sandalwood is or is not a true parasite' [7].

Well into the early decades of the twentieth century, silviculture of sandal proved a complete failure. The problem was the typical monoculture approach of tree farming in which all other species were removed and so the tree could not survive. Some early pioneers dibbled sandal trees in hedgerows or found that they could make it grow by spreading the seeds broadcast, but these were both rather ineffective methods of cultivation. Colonial officials typically blamed 'natives' for being detrimental to sandalwood stocks and the general decline in the health of Mysore's forests in this period. As one administrator complained: ‘owing to the liberal spirit in which the jungles were thrown open to all ryots [farmers]… much damage was done to portions of the forests’ [29]. It was also observed that sandal trees mostly occurred in the vicinity of villages, rather than in the dense isolated jungles [15]. This fact suggests that these villagers possessed traditional environmental knowledge relating to sandal cultivation that the British plantation managers and foresters did not. Though this is a counterfactual observation, because no such study exists, perhaps if British silviculturists had studied village-level sandal cultivation, they could have solved their problem far sooner.

This inability to cultivate goes a long way towards explaining not only the ever-dwindling supply of sandalwood in India over the nineteenth century but also why sandalwood traders in the Pacific during this period would not take the time to invest in the regeneration of sandal stocks, a fact often overlooked or ignored by authors writing on the overexploitation of Pacific sandalwood. The long wait time until maturity of the tree must also be considered. Only sandal heartwood and roots develop the fragrance, and trees only begin developing fragrance in significant quantities after about thirty years [3]. Not only did traders, who were typically sailing through, not have the botanical know-how to replant the tree, but they almost certainly would not be there to see a return on their investments even if they did. On the other hand, the British Raj believed it would be in place to see the rewards of its silviculture experiments and so throughout the late nineteenth and early twentieth century pushed on with the overharvest of wild sandal trees.

The second major natural problem facing southern India’s sandal groves was spike disease, otherwise known as the sandal spike: the deadliest of sandal’s natural enemies. At the end of the nineteenth and the beginning of the twentieth century, spike disease was the number one killer of sandalwood trees, killing more trees annually than being harvested. This disease was first noted in Coorg (now part of Karnataka) in the 1880s. From Coorg, it spread into what is now called the Kodagu district of Karnataka, then to the rest of the state [40]. By the 1890s, spike had killed ‘an enormous number’ of affected trees. A June 1898 survey of Coorg plantations found 1640 dying sandal trees, 1990 dead and only 703 ‘fairly healthy’ [35].

Attempts in the earlier part of the twentieth century to halt the spread of the disease failed and actually contributed to the decline of the sandal population. In 1904, the government uprooted 700,000 of the diseased trees in an attempt to save the population at large [41]. By 1920, officials were getting so desperate to stop sandal spike that they offered an award of 10,000 rupees to anyone who could study and control the disease. One effort to eradicate it involved using arsenic salt to poison and kill all the spike-affected sandal trees. Then, a ring 100 yards in width was also cleared hoping that the disease would be stopped. Several hundred thousand trees were killed in this way. Predictably, this scheme did not succeed, and the spike jumped beyond the rings and attacked other trees [37]. Even today, the problem of spike disease has not been fully solved, and scientific investigation is ongoing. While antibiotic treatment has been proven effective in treating spiked trees, current antibiotic regimes cure the disease only temporarily. It is also nearly impossible to approach every wild sandal tree individually [25].

The problems facing sandalwood continued to compound in the twentieth century. The main problem facing the sustainable harvest and continued survival of sandalwood in India—worse than the forest department's emphasis on exploitation and control of the sandalwood market, worse than its failure to cultivate the species and protect it from its natural enemies— came from the advent of the sandalwood oil industry at the beginning of the twentieth century. During World War I, vast amounts of sandalwood were stockpiled in Mysore because perfumeries in France had stopped production, and it had become illegal to export to Germany [27]. In 1915, a Government Sandalwood Oil Factory was built in Mysore, opening in 1916. In 1917, it began distilling [36]. In 1918, the Government Soap Factory (the manufacturers of the ubiquitous Mysore Sandalwood Soap) was built. These two institutions, managed by the Karnataka State Government, were founded under Krishnaraja Wodeyer IV with the guidance of M. Visvesvaraya [4]. Traditionally burned in incenses and pressed into attars and oils, sandalwood had always been a consumable good, but with the coming of an industrial-scale sandal oil factory located in the heart of sandal country, sandalwood production now ramped up immensely. It was at this time that Mysore came to be known as 'the Sandalwood City'.

5 Industrial Sandalwood

Since the establishment of India's first Sandalwood Oil Factory (SOF), the oil obtained from heartwood has been used to manufacture everything from aromatherapies to shampoos, soaps, cosmetics and perfumes on an industrial scale. The production of sandal oil for government factories reached its climax in the mid-1950s. In the 1956–1957 season, sandalwood oil production was at an all-time high of 2,800 tonnes. Throughout the 1950s and 1960s, an average of 2,400 tonnes of sandalwood was being supplied to the SOF annually. According to Rajan, 'From the early 1960s, the Karnataka Forest Department found it rather difficult to supply about 2,400 to SOF annually… and started felling smaller trees' [40].

By 1974, when the Karnataka Forest Department completed its sample survey, it discovered only 4,360 sandal trees mature enough to cut (trees with more than 30 cm in diameter) left standing in all major forest tracts in the state [40]. When the forest department finally acknowledged what was happening, supply declined drastically, the price of sandal began to skyrocket, and the production levels plummeted. For many manufacturers, synthetic substitutes (which were coincidentally invented in the mid-1970s) became commonplace.

Thus, in 1977 Rajan wrote that [39], 'Till three or four years ago the manufacture of Sandalwood oil was steady… Now the state is unable to produce enough sandalwood to feed the two sandal oil factories'. He mentions that the sandal *koti* (depot) at Belgaum was closed in 1967, the Bangalore koti 1976, and worried that 'very soon two more koties will be closed down'. Rajan went on to say that, 'Very soon the supply position may further deteriorate to a disastrous limit forcing one of the sandal oil factories to be closed down'. Later on, Rajan [40] mentioned that both the Mysore and Shimoga Sandal Oil Factory closed in 1987 when they could no longer continue distilling enough wood, writing that 'Even before its closure, this factory and the one at Shimoga were producing 18% and 2% of their capacities, respectively of oil', and that 'It looks as though the Government sandal oil factories have no future' [40]. Unfortunately, however, B.K.C. Rajan, who was a renowned forester, passed away before I was able to contact him for comment on this information (Pers. Commu. Narayanmurthy, 2012). Subsequent communications with experts familiar with the Mysore Sandal Oil Factory operations failed to verify the 1987 closure that Rajan reported. Although there were frequent periods lasting several months at a stretch over the last few decades when production had to be suspended for a time, the factory never fully closed. One such suspension due to lack of wood occurred in 2015, for instance, but the factory continued the production again in 2016 to distil oil for its centenary celebrations (Pers. Commu. Arunkumar, 2020).

Meanwhile, throughout the 1970 and 1980s, sandalwood smuggling was on the rise. Of course, at least since the time that sandal had been declared a royal tree by Tipu Sultan, smuggling had been an issue. There is documentation of sandalwood theft occurring from government supplies at least as early as the mid-nineteenth century [31]. Hugh Cleghorn, in 1860, for instance, reported 'the existence of a large band of smugglers in an unfrequented path near the Carkur Pass, who were captured by the Mysore horse, to the number of seventy-eight, with the sandalwood tied on their backs'. And while Cleghorn optimistically believed that, 'this seizure effectually stopped a long-continued system of robbery on the Malabar frontier', centuries later this system of robbery has not abated [11]. In fact, Shyam Sunder who retired in 1989 as the Principal Chief Conservator of Forests in Karnataka, in his memoir published in 2020, responds to Cleghorn [11] writing, 'What a joke! Sandalwood smuggling continues to this day'. Sunder then goes on to discuss numerous encounters he had with sandalwood smugglers going back to the early 1960s, reporting that at that time smugglers could fetch 'Rs 2000 per tonne (and now more than a thousand times that)' and describing shootouts between police and smugglers taking place already in this period as well [47]. Similarly, Rajan [39] reported that 'large scale smuggling was rampant between 1958 and 1972' and that 'smugglers tolled the death knell to sandal in many areas'; he then, however, went on to suggest that smuggling actually decreased by the mid-1970s as 'due to the decrease in sandal wealth, the activities of smugglers are gradually diminishing' [39].

Writing in 1977, Rajan [39] could not have foreseen the astonishing rise to fame of a sandalwood smuggler: Koose Muniswamy Veerappan, often dubbed the Robin Hood of southern India. As sandalwood stocks disappeared in this period, the situation was further aggravated because smugglers could now make more money by poaching endangered sandal trees than by killing elephants. As smuggler-bandits amassed private fortunes from the wealth of public forests, such men came to be viewed as heroes by impoverished villagers who want to earn a living wage and by a public that finds solace in the actions of anyone who challenges the status quo. Veerappan, as he was known in the popular press, was by far the most notorious sandalwood smuggler in India. Becoming rich off this illegal trade, by 1997 the smuggler had a 4 million-rupee bounty on his head. For more than fifteen years, Veerappan made the newspaper virtually every day, becoming a constant source of headlines for the Indian press and an embarrassment for the government and police. Before 9/11 and the ensuing hunt for Osama bin Laden, the hunt for Veerappan was the most costly and largest manhunt in Asia. Veerappan was finally killed on 18 October 2004 in a police encounter, and now, other smugglers have risen to take his place. Thus, sandalwood smuggling remains a major problem today.

Part of the problem facing the survival of sandalwood throughout the twentieth century was that the government continued to maintain its monopoly on this royal tree after independence. This not only represented a clear continuity with the colonial past, but it also disincentivized growers and became a major liability for the species itself. Thus, especially in the post-1991 milieu of economic liberalization, there was a major push for privatization. Since the colonial era, conservation efforts focused on top-down government control of this resource. Chapter X of the Karnataka Forest Act of 1963 extended the rules, making sandal trees the government's exclusive property and making it illegal for landholders to fell trees on their own land. Advocates of privatization thus argued that such laws strongly discouraged growing sandalwood, as that private growers assumed all the responsibility and risk and gained none of the benefits. Already colonial administrators were aware of this issue, saying 'the people have now no common interest with us in the matter of sandal'. Since the colonial period, people found sandal a nuisance for this reason, and so rather than let it grow on their land, some would even feed it as fodder to their livestock [35].

Emerging from the long history of state monopoly, a large chorus of voices is now insisting that privatization is the solution for saving the *S. album* and southern India's sandalwood industry. It is not only landowners who are leaning in this direction. Even the environmentalist magazine *Down to Earth,* published by the Centre for Science and the Environment, has argued for privatization, going so far as to say that in the case of Veerappan 'A law creates an outlaw'. As one forest official put it, 'If the tree is allowed to come above ground the smuggler will vanish on his own'. In the words of one villager, 'If the sandalwood trees were mine, I would shoot anyone who tries to cut a tree that is so valuable'. Or as yet another villager put it, 'Everybody is on the run to make money, but when some villagers make a few rupees from their own forest, the sky falls on them. What kind of justice is this?' [1]. From 2002 to 2004, the government of Karnataka began making limited moves in the direction of privatization, but still, the state remains the only buyer for sandalwood trees, setting prices artificially low, thus maintaining a monopsony.

The choice, however, is not limited to state monopoly versus privatization. As Arun Agrawal has shown, while exclusionist policies against local communities have typically failed, and nation states worldwide have been forced to move away from them, new idioms of participation and democracy have often come to take their place [2]. Thus, there are policy options available besides privatization of sandalwood as a moneymaking resource for individual landowners. Social forestry and joint forest management, for example, might have the potential to ensure successful conservation and regeneration of the species as well as sustainable development for local communities (though it might also have the danger of spreading bureaucracy and corruption to the village level). In this model, ownership and control could go to village *panchayats* rather than private individuals.

There is a Sanskrit proverb that speaks to the history of the endangerment of *Santalum* species all over the world: 'In sandal trees there are serpents. In the waters with lotuses there are also alligators—there are no unobstructed pleasures'. Though scientists have actually tested the age-old adage that serpents live in sandal trees and found it to be a myth, metaphorically it is all too true. Sandalwood has become an endangered and obstructed pleasure. The long history of colonial overexploitation, failures of scientific forestry, bureaucratic mismanagement and industrial-scale devastation has reaped its toll on *Santalum* species the world over. Today's tough policy choices will determine the tree's future.

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Chapter 3
Sandalwood in Indian Culture

Krishnaraj Iyengar

1 Introduction

There is no fragrance in this world that does not emerge from a certain culture. Every scent that exists bears the mark of a particular part of the globe and preserves its ethos, climate, history, geography, topography and collective thought process.

While it is only later in its history that 'India' was deemed a nation determined by fixed political boundaries, the culture of this part of South Asia dates back several millennia. One of the oldest-known eras in its history is the Indus Valley Civilization which is considered the world's oldest cradle of creativity and innovation. It was then that 'perfumery', a modern term for the art and science of making fragrance or scent as a commodity or a product of utility was first discovered and invented.

2 India's Pioneering Contribution

Archaeologists are said to have excavated a unique distillation apparatus known today as 'Deg-Bhapka' from the remains of that great civilisation. This process was used to distil natural materials to derive fragrant oil. These oils were used as medicine, aphrodisiac and as many believe, perfume to scent the body and clothes. India, though being the world's largest treasure house of natural fragrant materials, namely flowers, woods, spices, roots and herbs, is particularly synonymous with Sandalwood, literally the scent of its soul. Although Indian distillers and perfumers lament about western perfumery's apathy towards acknowledging India's natural fragrant reserves and the fact that iconic perfumers of Europe themselves source mammoth amounts of raw material from here, her mind-boggling array of fragrant

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flowers, health-giving spices, herbs and many-old reserves of woods like ‘agar’ or ‘oud’ and ‘sandalwood’ are indisputably one-of-their kind.

As compared to Australian and African Sandalwood, India’s *Santalum album* with its formidable 95% santalol content is a key ingredient in world perfumery. Beyond the cheery effervescence of Mysuru or ‘Mysore’ and the happy bustle of the charming city lies the world’s greatest abode of Sandalwood. Dating back to the Vedic era, the wood and the oil derived from the ancient methods of distillation have been an integral part of liturgy traditions.

3 Sandalwood in Liturgy

Offered to the sacred fire during the age-old ‘Agnihotra’ or ‘Havan’ rituals, sandalwood, known in Sanskrit as ‘chandan’ is sacred for numerous reasons. Apart from its importance in spiritual rituals, the creamy, woody, rich, often musky, smoky and spicy accords of sandalwood oil are deeply healing, both psychologically as well as spiritually. When burnt over charcoal or offered to the sacred fire, the wood emits a soothing, calming, meditative aroma. The venerated Rishis and mystics of India have widely advocated the use of Sandalwood. It has been a way of life with them.

Although delving into the medical benefits of Sandalwood would call for an encyclopaedia in itself, classical Indian texts like Ayurveda which advocate a perfect balance of mind, body and spirit, acknowledge its incredible healing properties. The ‘Charak Samhita’ as well speaks about chandan as a decimator of foul odours, a reliever of burning sensations, infections, fatigue and psychological disorders along with several other ailments.

Chandan pastes are often used as face packs or as ingredients of skincare products considering their incredible skin-nourishing properties. This paste also bears a unique symbolism and is used as a ‘tilak’ on the centre of the forehead or between the eyebrows by Hindus and Jains.

In many regions of India like the south, chandan or ‘chandanam’ is an integral part of ‘pooja’ worship rituals and the paste and incense are offered to various deities. Those who can afford the oil and can avail of it consider themselves blessed by Almighty himself and include it in their spiritual routine.

The Zoroastrians, Iran’s original inhabitants share astounding theological and cultural similarities with ‘Sanatana Vaidic Dharma’ or ‘Hinduism’. When they fled the Arab invasion of their motherland and sought refuge on Indian shores, they adapted marvellously to Indian customs and way of life. One of them was Sandalwood which is a quintessential nuance of Zoroastrian religious liturgy. Pure Mysore sandalwood chips are offered to the ‘Atash’ or sacred fire in the ‘Atashgah’ or Fire Temple.

Zoroastrian shops situated close to fire temples selling religious items sell high-quality sandalwood sticks and chips to be offered to the scared fire. But not many can afford them as the price for each piece is over a Rs. 100–200. Hence, a lesser quality, affordable fragrant wood is offered instead as an alternative. ‘The generic term for fragrant woods we use is ‘sukhad’. ‘Su’ in Sanskrit is ‘pure’ or ‘good’, and ‘khad’ refers to wood’, explains senior Zoroastrian Mr. Rohinton Mehta, the proprietor of Minoi Meher, a Zoroastrian religious shop adjoining Mumbai’s towering Anjuman Na Atash Behram Fire Temple.

4 The Backbone of Indian Perfumery

Sandalwood is also the backbone of traditional Indian perfumery and India’s ancient fragrance heritage. There are two distinct varieties of Indian perfume oil distillate extracts. ‘Rooh’, Arabic for ‘soul’, or pure extract, and ‘Attar’, Arabic for ‘distillate’ which is pure extract over a sandalwood base. Both are oil concentrate varieties devoid of solvents like alcohol or water.

Experts differ when it comes to whether Sandalwood is chosen as a base on which petals of various flowers are distilled, or whether sandalwood oil is mixed with the floral distillates or ‘Rooh’. All the same, these classic Indian Attars contain judicious proportions of Mysore sandalwood, sought after for the richness of its aromas especially when aged.

One of India’s oldest-living traditional perfumeries is old Delhi’s Gulabsingh Johrimal, established in 1816. The seventh-generation torchbearer of this revered tradition is perfumer Mr. Mukul Gundhi. Speaking about Sandalwood in Indian perfumery, he explains that India’s stunning diversity of fragrant flowers, when distilled over a sandalwood base, give us the gift of the world’s most exotic natural perfumes. ‘While a lay person can be easily fooled by Indian fragrance vendors who sell synthetic compounds in the name of sandalwood for as cheap as Rs. 20, pure sandalwood is subtle, rich and provides a firm backbone to, and enhances the distillate extract of each flower, be it Gulab or rose, Jasmine, Kewda, Molshri, Gul Hina, Kadamba, Rajnigandha, Champa or Chameli to name just a few’ he explains.

He talks about how Sandalwood finds place in the classical Indian ‘Ashtagandha’ or selection of eight natural fragrant treasures. ‘The phrase ‘chandan-yugal’ or ‘sandalwood pair’, probably referring to white and red sandalwoods is mentioned in a poetic ‘Doha’ verse that speaks about these eight ingredients, which also include agar, saffron, camphor and musk’, he shares.

‘Attar Shamama’, one of India’s most sought after traditional fragrances, truly glorifies Sandalwood. Its inherent warmth makes it the world’s pioneering classical winter fragrance. ‘Several indigenous Indian herbs and spices are distilled through hydro distillation and the resultant extract is cooked with pure sandalwood oil in a special container called ‘Pateela’ for long periods of time. Sandalwood oil is a key ingredient in Shamama and the secret to its legendary richness. Shamama is also extensively employed in Arabian perfumery’ , explains Mr. Moosa Khan of Ali Brothers, one of India’s leading traditional fragrance distillers from Kannauj, Uttar Pradesh, known as India’s and the world’s oldest fragrance capital. The city upholds the authentic traditions and techniques of steam and hydro distillations to derive natural fragrance oils.

5 Sandalwood as an Incense Tradition

India also pioneered the art of incense making and Sandalwood along with agar or agarwood has played a pivotal role in the heritage. Although one might rightfully presume pure Sandalwood was once a form of Indian incense, today due to the exorbitant cost of pure Sandalwood and its unavailability, many synthetic alternatives have arisen in the incense market.

Artisans find the persistence of strict laws against the possession, sale or purchase of Sandalwood crippling. They explain that in India, while the possession of drugs is a bailable offence, Sandalwood is non-bailable. ‘Australian and African sandalwoods, despite possessing a lesser santalol content than the legendary Indian Sandalwood, are exported to India and supplied to agarbatti manufacturers to be included in their incenses. What a pity! Mysore’s Sandalwood is depleting despite being the sandal capital of the world. The reserves and the production are dwindling rapidly’, they lament.

The word ‘agarbatti’ or incense stick literally translates as ‘light of agar’ (agar-batti) considering that pure agarwood power was once the key ingredient of the most original form of agarbatti. But over decades, India has witnessed a growth in synthetic compounds and incense powders for the manufacture of agarbatti and dhoop incenses due to the unaffordability of pure agar. However, veterans like renowned agarwood distiller Mr. Tajul Islam Bakshi of Assam Aromas, a legend in the world of agarwood, have revived the original tradition of pure agarwood incense sticks that he manufactures from agarwood dust. ‘I have created these incense sticks without the inclusion of a single synthetic ingredient. The agarwood dust provides an untainted experience of the aroma of pure agarwood or oud and many of my clients purchase these incenses for meditation’, Mr. Bakshi says.

Sandalwood too has its passionate upholders who include a percentage of Sandalwood refuse to their incenses which also comprise of other materials to aid longevity, strength and to make the aromas palatable to those who remain unacclimatized with the authentic fragrance of Sandalwood. Though ‘pure sandalwood’ labels can be misleading and often disappointing, many of these incenses are masterfully crafted to successfully provide the user with the accords of original Sandalwood.

Incense manufactures throughout India dream of the day when restrictions with regard to the purchase and sale of Sandalwood will be finally eased and the ancient fragrant treasure will be made available to all Indians equally in its most original form and purest glory.

Chapter 4
A History of Indian Sandalwood in Australia

Grant Pronk

1 Introduction

The foundations on which the current Indian sandalwood (*Santalum album*) plantation industry in Australia has been built on are well established and deep-rooted. Sandalwood has been an important trading commodity for Australia since the early nineteenth century. The then vast quantities of tea imported from China and consumed by the British settlers were the precursor to Australia's involvement in the sandalwood industry. In 1823, it was recorded by a government official that tea from China was 'the constant accompaniment to the meals of the middle and lower classes of inhabitants' [5]. The settlers did not have a suitable locally produced commodity to trade with the Chinese in order to acquire tea, and the sandalwood sourced from the Pacific Islands became that commodity.

Sandalwood sourced from the Pacific Islands and traded through Australia into China was known as Sydney sandalwood. This valuable resource was gradually harvested from all the sandalwood yielding islands in the Pacific, including Fiji and Tonga (*Santalum yasi*), Vanuatu and New Caledonia (*Santalum austrocaledonicum*) and Hawaii (*Santalum paniculatum*). By the mid-1840s, the finite sandalwood resource on the Pacific Islands became virtually depleted and the quality decreased as younger trees were harvested. The discovery and eventual trading of Western Australian sandalwood (*Santalum spicatum*) around the same time all but finished the Australian sandalwood trading in the Pacific.

The British colony known as the Swan River Settlement (later named Perth) in Western Australia was founded in 1829. As experienced in the Sydney colony, the younger Western Australian colony also faced an enormous imbalance in trade.

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Fortunately, the discovery of vast tracts of Western Australian sandalwood nearby the settlement in 1843 led to four tons of sandalwood being exported to Bombay in 1844 on the colonial schooner Champion 'to test the market' (Perth Gazette 25.1.1845, Inquirer (editorial) 5.2.1845). This first shipment was eagerly accepted and attracted a very good price; in turn, it developed into a significant industry and international trade that still exists today.

Western Australian sandalwood being loaded at Fremantle Port Western Australia in the early 1900s. Courtesy of The State Library of Western Australia <010128PD>

The harvesting and trading of Western Australian sandalwood have existed for over 175 years. The harvesting, processing and marketing of the wild resource are managed by the forestry entity of the Western Australian Government. In recent years, the local demand for Western Australian sandalwood-derived products has developed in Australia, and the commodity, once exclusively exported, is now distributed between the domestic and export markets.

The global demand for sandalwood products began to significantly increase in the 1990s and 2000s, leading to the supply of raw wood from traditional sources around the world to diminish. Global prices steadily increased across all supply outlets leading to incidents of uncontrolled and unsustainable harvesting. The theft of significant garden sandalwood trees and natural resources across Asia and the Indian subcontinent increased. New legislation and harsher penalties were introduced in Western Australia to curb the increasing level of wild Western Australian sandalwood tree theft.

Wild growing Western Australian sandalwood (*Santalum spicatum*) near Kalgoorlie

Meanwhile, the understanding of the value and importance of a managed plantation-based sandalwood resource began to grow. In Western Australia, the first of the commercial Western Australian sandalwood plantations in the Wheatbelt region (east of Perth) started to appear. Both government and privately owned plantations began to become established in traditional agricultural farming land. In the tropical north of Western Australia, the Indian sandalwood (*Santalum album*) plantation research and trialling commenced by the Forest Department in Kununurra in the early 1980s began to attract considerable interest from the private forestry sector.

1.1 *Early Records of* Santalum album *in Northern Australia*

Santalum album occurs naturally in Australia and is found in monsoon vine thickets on coastal sand dunes and laterite in dry rainforest around the Northern Territory coastline. A dispersed and small population of Indian sandalwood trees currently exists across sections of the Northern Australian coastline; however, the majority of these populations has long gone.

A number of representative dried leaf, flower and fruit specimens collected from Northern Territory trees are housed in the Northern Territory Herbarium. The sample literature refers to an early specimen collected by Robert Brown, the botanist on Mathew Flinders' voyage of circumnavigation around Australia. It appears to be from Melville Bay near present-day Nhulunbuy in Eastern Arnhem Land and was collected in February 1803 (personal communications Cowie 2020).

Australia's closest neighbour is Papua New Guinea being 150 km from the mainland. Timor-Leste is less than 500 km away. Australia's close proximity to countries with natural sandalwood populations supports the likelihood of the species spread to Australia via migratory birds and by human visitors to the coastline.

Prior to the introduction of Indian sandalwood into Australia via seed procured from India in the 1980s, the first Indian sandalwood trees in Australia are believed to have been established by visiting Macassan fisherman fishing for trepang (sea cucumber) along the Northern Australian coastline as early as the 1700s. Physical evidence and historic accounts confirm the fisherman also traded goods with Australian Aboriginal people up until the early 1900s (per comms Cowie 2020).

1.2 Early **Santalum album** *Plantation Research in Kununurra, Western Australia*

The town site of Kununurra is located in northern Western Australia, approximately 2200 km north-east of Perth and 500 km west of Darwin, and is around 50 m above sea level. The climate is considered to be a local steppe climate. It has an average rainfall of around 720 mm, which mostly falls during the wet season (December to March). The average annual temperature in Kununurra is 29 °C.

Rainfall is captured in the nearby Ord River catchment and is stored in Lake Argyle and Lake Kununurra. This enormous volume of freshwater is then diverted via a series of open channels into an expansive irrigation system used for horticulture and cropping. Since their introduction in the 1990s, commercial Indian sandalwood plantations have quickly become the dominant land use in the irrigation area. Kununurra has Australia's oldest and largest population of commercial plantation Indian sandalwood trees.

The Forest Department of Western Australia had been very well acquainted with the global sandalwood industry since Western Australia's first export of *Santalum spicatum* to Bombay in 1845. Since 1845 to the present day, wild-grown sandalwood has been harvested, processed and exported from Western Australia almost consistently every year. The idea to grow Indian sandalwood in Australia soon eventually became a reality.

In 1980, the appeal of establishing Indian sandalwood trees in the Ord River Irrigation Area (Kununurra) materialized when government Forester Peter Richmond and members of the Australian Sandalwood Company visited India to become more familiar with the silvicultural intricacies needed to successfully germinate and grow the species. A small amount of seed was also provided by the Indian Forest Department for trialling in Australia. The seed imported into Western Australia was distributed for germination in various locations around the state of which only a small number of seedlings were successfully raised in Kununurra [2].

For over a decade, a small group of dedicated foresters, acting mostly through their own personal interest and in their own time, slowly realized the complexities associated with germinating and rearing Indian sandalwood seedlings in Kununurra. Some of the obstacles they encountered included seed availability, seed viability, seed treatments, host species selection, planting configurations, pests and soil diseases.

Later in the 1980s, the forestry component of the Department of Conservation and Land Management (CALM) increased its interest in the potential of Indian sandalwood in Western Australia and negotiated a long-term agreement with the Western Australian Department of Agriculture gaining access to irrigated land on a tropical agricultural research station (the Frank Wise Institute of Tropical Agriculture) to undertake nursery and field trials. The access to this land allowed the foresters to expand the Indian sandalwood research in Kununurra.

More seed became available from India from a variety of states including Andhra Pradesh, Karnataka, Kerala, Madhya Pradesh and Tamil Nadu. The subsequent increase in seedlings and the availability of suitable land allowed an increasing level of trialling. Over time, it became apparent to the foresters that the potential for commercial Indian sandalwood plantations on the irrigated plains around Kununurra was considerable.

In the early 1990s, the government directed profits gained from the ongoing Western Australian sandalwood industry to fund further research with a view to developing the potential Indian sandalwood industry in Western Australia. The funding supported a dedicated research scientist appointed to Kununurra to instigate and manage a series of trials aimed at improving nursery techniques, suitable host selection, site preparation, plantation design and weed control.

This research soon provided steady advances and successful conclusions that further increased the optimism surrounding commercial plantations. Research was expanded into other critical aspects including soil-type selection and moisture content, plantation bed design, irrigation schedules, planting timing, host combinations and soil pathogen treatment. Other tropical sandalwood species including *Santalum macgregorii* and *Santalum austrocaledonicum* were also trialled at the research station successfully.

Government managed research on Indian sandalwood trees in Kununurra Western Australia

Research-based inventory and harvesting conducted by the Forest Products Commission (FPC) in the mid-2000s to mid-2010s provided a further understanding of expected growth rates, heartwood and oil yields and oil qualities. Although the trials were primarily established for research purposes, the predicted average oil yield and quality indicated the trees had attained considerable commercial value.

In 2010, the FPC harvested and processed 32 Indian sandalwood plantation trees aged 16 years for a detailed heartwood analysis. Part of the analysis was used to develop growth models to predict the air-dry weight of heartwood in trees based on their stem diameter and age (Figs 1 & 2). The quality of the heartwood in the trees was generally good, with means of 5% oil, 44–50% α-santalol and 18–20% β-santalol. However, mean heartwood weights were only 6 kg heartwood tree^{-1} (air-dry weight, 12% moisture) in the 16-year-old trees, but dramatically increased to approximately 20 kg heartwood tree^{-1} in the 19–23-year-old trees.

The stem diameter–heartwood relationship developed in the study should be used only for *Santalum album* trees within a narrow age range, perhaps 15–17 y, due to heartwood formation being a function of age [3, 4]. It would be expected that trees older than those sampled in the study would generally have a greater proportional weight of heartwood in their stems. Separate stem diameter and heartwood equations will be needed for older trees [1].

The level of oil yield and quality variation between the trees grown in mostly the same conditions implied that the genetic difference between the seed originally sourced from India was significant. The direction of the FPC research moved towards seeking a greater understanding and exploiting favourable genotypes and developing plantation designs and silvicultural practices to maximize yield.

2 Commercialization of *Santalum album* in Western Australia

Western Australia's long history and experience in harvesting and supplying the world with its own native wild sandalwood species (*Santalum spicatum*) made for an accustomed development to diversify into the Indian sandalwood industry. At the time of establishing the first commercial Indian sandalwood plantation, Western Australia held a solid and enduring position in the world sandalwood market and was highly regarded for supplying a consistent supply of quality sandalwood products.

The Western Australian Government's pioneering success with the experimental *Santalum album* plantations in Kununurra was noted by domestic private forestry businesses. The opportunity to commercially grow high-value tree plantations that had a dwindling available natural supply and coupled with an increasing demand for products derived from it was an appealing prospect.

The prospects of commercially growing Indian sandalwood in the Kununurra area were supported by the availability of potentially thousands of hectares of developed irrigated agricultural land in the Ord River Irrigation Scheme (ORIS) in the East Kimberley region of northern Western Australia.

ORIS's broad sweeping plains consist of a variety of suitable soil types, a tropical monsoonal climate and an abundance of irrigated freshwater. The region already supported a range of established broad scale agricultural industries including cotton and sugar; therefore, the agricultural services required to support an emerging sandalwood plantation industry already existed.

Australia's first privately owned commercial Indian sandalwood plantation was established in the ORIS in 1999. The plantation comprised around 50 ha, and the design implemented many of the research outcomes accumulated by almost twenty years of government's forestry research. In 2000, the area of new privately owned plantations established reached 100 ha. By 2001, a second private plantation company commenced Indian sandalwood plantation operations in the ORIS. In 2009, ten years on from the establishment of the first 50 ha, 2620 ha of privately owned plantations had been established. Competition for suitable land intensified as investment into the industry continued to grow.

Substantial private investment into research and development to improve aspects of the plantation including silvicultural procedures, improved nursery practices and a firm understanding of the available genetic pool lead to rapid advances. Clonal propagation techniques to capture the most desirable traits of individual trees were deployed to improve the resource value at time of harvest.

15-year-old Indian sandalwood (Santalum album) in Kununurra Western Australia

While investment into genetic improvement, silvicultural and harvesting technology continued, the private plantation businesses also began investing into wood processing facilities and procedures to produce sandalwood oil from their harvested trees.

2014 saw the first commercial harvesting of privately grown Indian sandalwood in the ORIS, Australia. The harvested trees were locally processed into a preground material and then transported to the south of Western Australia for the oil extraction via steam distillation process.

The Australian plantation-based Indian sandalwood oil was immediately accepted into a wide range of products around the globe including cosmetics, perfumes, toiletries, pharmaceuticals, skin care products and traditional medicines. Unprocessed logs and other wood-based products (powders and chips) supplied the carving, religious ceremonies, religious artefacts and incense markets.

International interest has steadily grown, and global equity firms have consolidated their position in the Australian-grown Indian sandalwood plantations as shareholders. Operations expanded into the neighbouring Northern Territory and the state of Queensland.

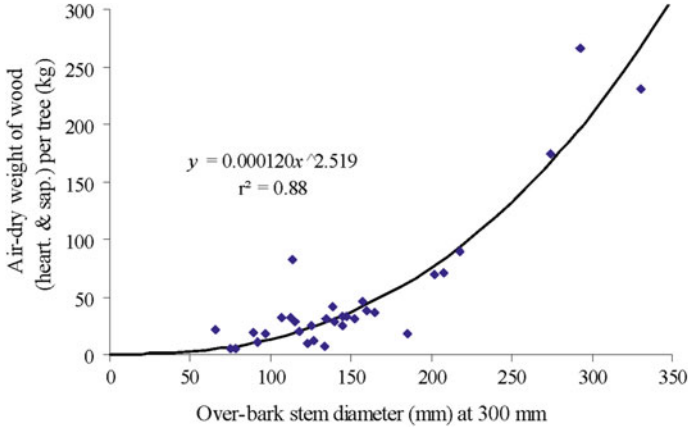

Fig. 1 Relationship between *S. album* overbark stem diameter (mm) at 300 mm above the ground and total commercial air-dry weight (12% moisture) of wood (heartwood and sapwood) per tree (kg), at age 16 years. A power function equation was used to relate the two parameters, where x = overbark stem diameter (mm) and y = total commercial air-dry weight of wood per tree (kg)

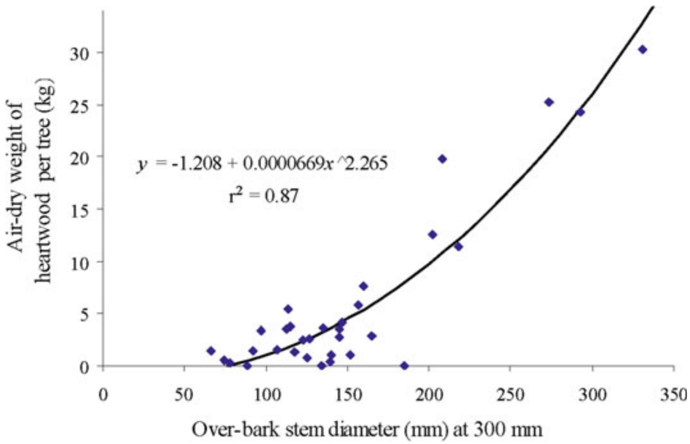

Fig. 2 Relationship between *S. album* overbark stem diameter (mm) at 300 mm above the ground and estimated air-dry weight (12% moisture) of heartwood per tree (kg), at 16 years. A nonlinear equation was used to relate the two parameters, where x = overbark stem diameter (mm) and y = estimated air-dry weight of heartwood per tree (kg)

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Part II
Status of Sandalwood Across the World

Chapter 5
Sandalwood in Karnataka—Past and Present Status

A. N. Arunkumar and Dipak Sarmah

1 Introduction

Sandalwood and Karnataka are inseparable entities. It is evident by the fact that Karnataka is also commonly referred to as *Gandada Naadu* in Kannada (roughly translated as land of sandalwood); *Gandada Gudi* (shrine of sandalwood) [1]. The traditional artisans of Karnataka, the *Gudigars,* are highly skilled and talented in carving exquisite handicraft articles with high global demand.

Tippu Sultan, the Mysore ruler (1782–1799) considering the value and revenue earning potential of sandalwood monopolized its ownership by declaring it a 'royal tree' and took over its trade [4]. Sandalwood continued to be state property during the subsequent rule of the Maharajas of Mysore. This practice continued at the time of formation of Karnataka State, and a provision making sandalwood tree exclusive property of government was incorporated in the Karnataka Forest Act, 1963. Alarmed at the dwindling population of sandalwood trees in forest areas and to encourage the cultivation of sandalwood in farmlands, Karnataka Government, in 2001, affected a course-correction by amending and revising the relevant provisions (Act 20 of 2001) of the Karnataka Forest Rules, 1969. The earlier stringent rules regarding ownership were relaxed, the legal ownership of trees growing on private land being vested with the landowners. Trade, however, continued to be under the supervision of the government.

Working Plans of Karnataka Forest Department were also referred.

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Sandalwood played a predominant role in the state's economy with the Sandalwood Department looking after the harvest and sale of sandalwood. There was an elaborate arrangement of collection and disposal of sandalwood through the revenue officers. Initiated by Tippu Sultan, sandalwood was collected through the *Amildars* of the taluks, who employed '*Managers'* to fell, prepare and collect the wood which was stored in local *Pattadis,* distributed all over the taluks. When sufficient wood was collected in the *Pattadis*, it was sent to the central stores where the wood was classified and sold. The forest department, established in 1864, took over the Sandalwood Department's activities which included the selection of trees for harvest and extraction also. Thus, the entire process was streamlined by the forest department. Only dead and diseased trees were extracted, considering the value of the root. The department then decided to change the harvesting procedure from cutting to uprooting of trees. Depending on various quality criteria such as heartwood, sapwood, soundness, length of the stem and root thickness, the sandalwood was grouped into 18 different classes for sale. Many forests having good stocking of sandalwood were notified as 'Sandal Reserves' with the same legal status as reserved/state forests. Major Nahor Hunter, the first Conservator of the Mysore Forest Department (1864), showed keen interest in sandalwood and brought to light the need for a host for the growth and development of sandalwood [5].

Sandalwood was a major revenue earner in the Mysore State. The annual average contribution to the exchequer during 1834–1861 was Rs. 1.5 lakh, the highest being Rs. 3 lakh. During 1878–80, sandalwood accounted for ~80% of the total revenue earned from forest produces. The per tonne cost of good and inferior wood of sandalwood for the year 1887–88 from Mysore and Coorg was Rs. 427, 52 and, 400, 32, respectively, and the amount realized by selling sandalwood was Rs. 0.421 million [2]. Considering the importance of sandalwood in the Mysore forest economy, while appreciating this extraordinary revenue, the Government of India cautioned that overdependence on sandalwood would divert the forest department's attention from other forestry works and delay the overall progress in forest conservancy in the state.

The department was also wary of sandalwood spike disease which resulted in mortality of many trees and started various initiatives to control it. Mr. M. Muthanna, an Indian Forest Service Officer, appointed in 1901 as Conservator of Forests and Ex-officio Secretary to the government encouraged sandalwood harvesting by providing a share to the private owners when sandalwood was harvested from their land. He instituted an award of Rs. 10,000/- for a remedy for the disease [7]. There is no information on any claims for the reward.

Before 1916, after dressing, sandalwood was sold by the forest department in public auction, and fairly good revenue was earned for the state. Soon after the First World War outbreak, auction sales proved unfavourable, and it was decided to set up an oil distillation factory at Bangalore, which commenced work in 1916. A larger factory was set up at Mysore during the next year (1917), and a third factory was set up at Shimoga in 1944 [6].

2 Sandalwood During the Pre-British Period

It has already been mentioned that sandalwood was an important commodity of the Mysore kingdom since 1700s. Lord Wellesley, a Governor General of British India, had instructed Dr. Francis Buchanan to prepare an elaborate report on the newly conquered territories of Mysore, Canara and Malabar. A Scottish physician by profession, Dr Buchanan made significant contributions as a geographer, surveyor, zoologist and botanist. His journal was published in three volumes, in 1807 as 'A Journey from Madras through the Countries of Mysore, Canara, and Malabar'. The publication reveals that sandalwood and teakwood were the most important commodities of the forest and were available aplenty. He also recorded the growth characteristics and ecology of the species. Sandalwood trees occurred in the woods towards *Chinapatam* (Channapatna), forests of *Savana-durga* in Magadi, forests of *Priya-pattana* (Periyapatna) bordering Coorg, *Serisi-soonda* (Sirsi-Sonda) areas of Canara, forests of Shimoga abutting Canara (Soraba-Shikaripura areas), *Manday Gudday* (Mandegadde) in between Thirthahalli and Shimoga, on the borders of a betel-nut garden in a place somewhere in between Hiriyur and Belur (Hassan), etc. He mentions: 'At two places in this hilly country the tree comes to great perfection; namely, at *Jalamangala*, between *Magadi* and *Chinapatam*; and at *Mutati Habigay*, near *Capala-durga*' revealing good quality sandalwood in Ramnagara district.

Buchanan had observed that trees with at least nine inches diameter at the root were matured enough to be felled as early as then. He also mentioned the prevalence of a payment system of gratuity to the landowner in recognition 'of his trouble in rearing it'. The smuggling of sandalwood trees was also prevalent then and noticed that the people in charge of extraction and disposal of sandalwood were not always honest, and there was leakage of state revenue.

3 Sandalwood During Erstwhile Presidencies

The British administration had given special attention to the extraction and management of sandalwood from the forest and non-forest areas that harboured the species. They had got working plans prepared for this purpose. For certain areas, working plans were prepared exclusively for sandalwood, and for certain areas, sandalwood working circles were incorporated into the working plans prepared for the general forest management. For the convenience of management, the sandalwood bearing areas were divided into several blocks, each block known as a 'felling series'. In each felling series, felling/extraction was carried out in a cycle of a fixed number of years known as 'felling cycle'. Normally, a felling cycle of five or ten years was adopted. The general prescription was harvesting of dead and dying trees along with spike infected trees. Artificial regeneration was attempted by dibbling sandalwood seeds under the bushes and in the sandalwood extracted pits. Seeds of host species such as *Cassia siamea* and *Cajanus cajan* were also sown alongside.

In Bombay Presidency, sandalwood was found in some proportion in all the four districts that are in the present Karnataka, namely North Canara, Dharwar, Belgaum and Bijapur. The working plans written exclusively for extraction and management of sandalwood were Mr. S. N. Kesarkodi's plan for the sandalwood forests of Dharwar, Bijapur and Haliyal and Mundgod ranges of North Canara (1932–43) and Mr. N. S. Kaikini's plan for sandalwood areas of Sirsi-Siddapur of North Canara (1944–1954). The sandalwood bearing forests of Belgaum district were covered by the working plan of Mr. D. B. Sothers (1928–1938). The sandalwood working circle of Sother's plan was extended by three years and was further revised by Mr. N. S. Kaikini (1941–1951).

In Madras Presidency, a working plan for the sandalwood bearing forests of MM Hills and Bailur of Kollegal forest division (then in Coimbatore forest division) was prepared in 1901 by Mr. P. M. Lushington. This plan had prescribed uprooting of mature sandalwood trees (above 32 inches girth at breast height) besides removal of dead and dying trees on a ten-year felling cycle. The working plans that were written for Kollegal forest division by Mr. J. Sadasiva Ayyar (1923), Mr. N. D. Sahani (1928), Mr. C. R. Ranganathan and Mr. M. H. Krishnaswamy under the direction of Mr. C. C. Wilson (1933) and Mr. V. S. Krishna Swamy (1941) had included a sandalwood working circle where similar prescriptions for sandalwood were given.

As regards the Bellary district in Madras Presidency, Dr. Dietrich Brandis, Inspector-General of Forests during his tour to Bellary forests in 1861, suggested that sandalwood should be reserved along with *Tectona grandis* and *Hardwickia binata*. The first working plan for the forests of the district was written by Mr. J. Sadasiva Ayyar (1928–38). It was the working plan for Anantapur forest division of which the forests of the present Bellary forest division were also a part. This working plan had a sandalwood working circle with four felling series of which one was in Bellary forests. The plan had prescribed tending (including climber cutting on trees) of the young crop and the extraction of dead sandalwood trees. Sadasiva Aiyyar's plan also had a sandalwood propagation working circle under which it was proposed to induce sandalwood artificially in selected plots, each of one-acre size, which would ultimately serve as centres for the natural spread of sandalwood to the rest of the reserved forests. It was prescribed that there should be ten such plots in each beat. Strict protection by fencing and tending from the third year onwards was prescribed. In the years 1925, 1926 and 1927 in Bellary district, dead sandalwood trees were uprooted and sold for Rs. 500, 529 and 1498, respectively.

Although the South Canara district of the Madras Presidency did not have extensive sandalwood bearing forests, attempts were made to manage whatever sandalwood was available and to propagate the species. A sandalwood working circle was included in the working plans by Mr. P. N. Davis (1931–1943) and Mr. B. S. Keshava Vittal (1943–1958).

In case of Coorg State, although sandalwood trees were very limited in the reserved forests, covering about 35 square miles, most of the trees were found in other government lands and private lands which together added up to about 500 square miles. During 1922–26, enumeration of sandalwood trees was carried out over 191,000 acres. Based on these enumerations, a mean annual increment (MAI) of 200 tonnes was estimated to be taken each year together with about 100 tonnes of spike killed wood. Only dead or diseased wood was extracted from the reserved forests, while green trees were also extracted from the *paisaris*. In 1929, a scheme was made for 29 square miles in reserved forest, and this was revised in 1933–34. In 1935–36, enumerations were started, and a proper working plan was compiled between 1936–37 and 1940–41 to cover 35 square miles of reserved forest, 318 square miles of unreserved government lands and 174 square miles in private lands, or a total of 527 square miles. The new working plan reduced the total annual yield to 147 tonnes (cleaned).

In the sandalwood bearing areas within Bombay or Madras presidencies, as also in Coorg State (C-State), extraction of sandalwood was carried out as per sanctioned working plans. In some of the areas, artificial regeneration through dibbling of seeds in bushes was also prescribed.

Sandalwood was sparsely distributed in some of the relatively better deciduous forests of Bidar, Raichur and Gulbarga districts which were then in the princely state of Hyderabad. Organized working of sandalwood was not prescribed in the earlier working plans for the forest areas of these districts due to the non-availability of sufficient material for harvest.

It is interesting to note that during the era of the presidencies and the princely states, naturally distributed sandalwood areas were managed primarily for extraction of mature trees and sale of sandalwood, and there was no serious concern for artificial regeneration as well as the establishment of plantations even though prescriptions were made in the plans. Even in areas where such prescriptions were followed, the results do not appear to have been encouraging; this was because the prescriptions were either not followed properly or adequate follow-up measures to nurture the incoming crop were not taken. As a result, no report about the splendid performance of the species is available on record. One reason for not giving adequate attention to the artificial regeneration of sandalwood was the abundance of mature trees in the forests. Another reason was perhaps that natural regeneration of sandalwood was quite satisfactory in any sandalwood bearing forest which had been protected well from fire and excessive grazing [6].

4 Sandalwood During Post-independence

The trend of management of sandalwood followed during the pre-independence period continued during the post-independence period also. Extraction of sandalwood was carried out as per prescriptions given in the working plans. The method of raising seedlings in the nursery had not yet been standardized, and whatever attempts were made did not meet with much success. In the Karnataka Forest Code, 1976, detailed guidelines regarding exploitation and disposal of sandalwood were provided covering various aspects such as enumeration, marking, harvest, conversion, transportation and subsequent auction. Even though dibbling of sandalwood seeds under bushes and sandalwood extracted pits was still in vogue, the propagation method to a certain extent was standardized, and attempts to plant nursery-raised poly-bagged seedlings were made. However, there were hardly any successful plantations of sandalwood established by the department.

5 Distribution of Sandalwood

Sandalwood was found to be extensively distributed in Karnataka. It is primarily a species of dry deciduous and scrub forests although it is found in moist deciduous and sometimes even in evergreen forests. It is a small to a medium-sized evergreen tree that grows up to about 8–10 m in height in very well-drained soil and full overhead light, although during its initial years of growth it has a preference for, or tolerance to, partial shade. These requirements are by and large satisfied in dry deciduous and scrub forests, and as a result, sandalwood trees are commonly met within these forests. Some of the forest types harbouring the species are dry teak bearing forest (5A/C1), southern dry mixed deciduous forest (5A/C3), dry deciduous scrub forest (5/DS1), secondary dry deciduous forest (5/2S1), laterite scrub forest (5/E7) and Southern thorn forest (6A/C1). However, sandalwood may not be typified exclusively to the above forest types. It is often found in the moist deciduous and evergreen zones, especially in disturbed or opened-up areas, along the edges of forests, and in hedges around gardens or agricultural lands. Such growth is mostly of secondary origin, the species having been introduced artificially or through birds which play a very important role in the wide-spread propagation of the species through their droppings. The presence of sandalwood in the private and *paisary* lands of Kodagu district and also in Sirsi-Siddapur areas of Uttara Kannada district is attributed to such methods of propagation. Well-grown sandalwood trees are also found in the coffee estates of the Chikkamagaluru district. The absence of the sandalwood tree in a closed evergreen or moist deciduous high forest is primarily due to the lack of sufficient light in the forest floor to trigger the growth of this fiercely light-demanding species.

The biggest enemies of a sandalwood tree in its initial stage of growth (seedling) are fire and browsing animals, which ironically are very common in dry deciduous and scrub forests. However, among the many seedlings that come to life in these forests, thanks mainly to cuckoos and other birds, the seedlings coming up in bushes or under the protection of thorny shrubs can overcome such hurdles and continue to survive and grow. At times, a small agave cluster is good enough to nurse a sandalwood seedling. This beautiful, evergreen tree with soothing green foliage (yellowish-green to greenish-yellow in drier areas) is strikingly conspicuous in the forest, especially so in the dreary-looking dry deciduous and scrub forests. Cattle-herdsmen often heavily lop the tree for its foliage, an excellent cattle-fodder.

Safe, so far	Smuggler in a hurry	Down but not out

Sandalwood puts on the remarkable growth in rich, deep and well-drained soil, but this does not necessarily assure commensurate formation and development of heartwood, for which the wood is in very high demand. Heartwood formation and the development are said to be better in relatively dry, sandy or stony, well-drained soils. However, it may be borne in mind that such small-sized, heartwood-bearing trees would have taken many years even to grow to that size in such difficult sites under harsh situations. Therefore, the rapidly growing trees on better sites need to be observed for more number of years to conclude their capability of producing heartwood. In the past, some of the sandalwood trees of larger girth were extracted from the forest areas of Shivamogga, Chikkamagaluru and Kodagu districts which are situated in areas harbouring better soil and receiving high rainfall, sustaining moist deciduous to semi-evergreen vegetation.

Distribution or presence of sandalwood abundantly or sparsely in Karnataka has been chronicled by referring to the earlier and present working plans of the forest divisions. A brief description of the distribution of sandalwood trees in different districts/divisions in the past and present is discussed. Generally, it is mentioned that in Karnataka, sandalwood was abundantly growing in various districts such as Bangalore, Belgaum, Chickmagalur, Kodagu, Kolar, Dharwad, Mysore, Shimoga and Tumkur [3, 9]. Efforts are made here to give a detailed account of its distribution by including all those areas in which the tree is found, either in abundance or sparsely.

In Ballari (earlier Bellary) district, sandalwood trees are found in relative abundance in the Swamimalai, Donimalai, Ramanmalai and North Eastern Blocks of the Sandur hill ranges. In these forest blocks, excellent regeneration is seen in certain patches (within the iron ore mining lease areas) that are retained as such and are free from fire and biotic interferences. Sandalwood is also found distributed sparsely in other forests of the district such as Joga, Bilikal, Bandri, Shivapura, Banavikal, Sunkadkal, Hyarada, Thimmlapur, Tonasigere, Shivapuram and Sogi. A complete enumeration was carried out during 1970–72 in the three taluks of Hospet, Kudligi and Sandur which had a sandalwood population (Fig. 1), and ~90% of the trees were in the girth class of 15–44 cm. Trees above 75 cm girth have been recorded only in

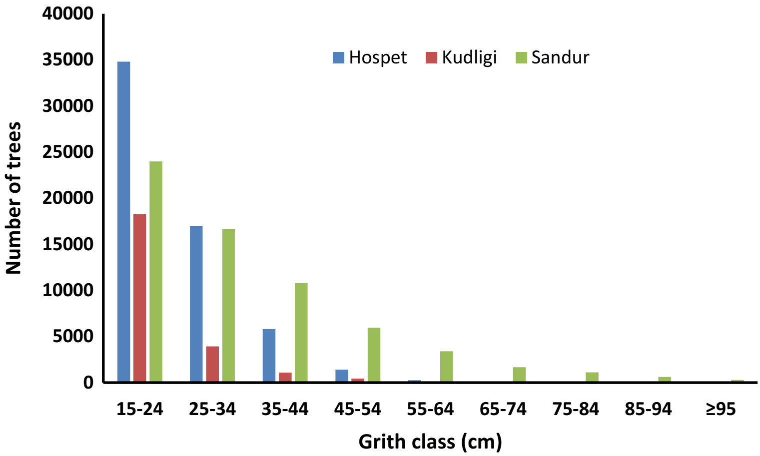

Fig. 1 Girth class (cm) distribution of sandalwood trees in three taluks of Ballari division as per the enumeration carried out in 1970–72

the Sandur area. At present, the population has considerably dwindled, and except in the Sandur forests, the district has a sparse population of sandalwood trees.

The forests of Belagavi (earlier Belgaum) district which adjoin Uttara Kannada and Dharwad districts are traditionally known to have an abundant sandalwood population. It is used to occur extensively in Khanapur, Nagaragali, Londa, Golihalli, Kakti, Gujnal and Nesargi ranges. The trees that were extracted were brought to sandalwood *Koti* at Dharwad. It was also found in Gokak areas, and profuse regeneration has been observed in Jalaga in the Khanapur range and Kadabagatti in Gokak Range. During the 1920s, a considerable population of sandalwood was observed in the Belgaum forest division (Fig. 2). Sandalwood trees of more than 40 cm in girth are now hard to find in the sandalwood belt of the Belagavi district.

The agro-climatic conditions in Bidar district are quite favourable for sandalwood regeneration, and its dry deciduous forests are ideal habitats for the species. Regeneration has been observed in several forests in the district such as Honnikere, Changler, Shahapur, Chitta, Chittaguppa, Bheemalkheda, Dhanura, Narayanpura, Benchincholli, Dhammsur, Shantabad, Kaudyal, Ghodepalli, Binkipalli, Kattali and Rampura. However, its occurrence is sparse except in localities such as Honnikeri which have been given rigid protection with chain-link mesh fencing resulting in a tremendous increase in its population.

Sandalwood is widely distributed all over the dry deciduous and scrub forests of Chamarajanagar district. In the past, the Kollegal forest division (present MM Hills wildlife division) which was under the Madras Presidency was well-known for its abundance of sandalwood. It may be recalled that the Malai Mahadeshwara Hills was also the safe hideout of Veerappan, the notorious sandalwood smuggler. As early as 1901, the sandalwood areas of MM Hills and Bylur were brought under a working plan prepared exclusively for the management of sandalwood. The Kollegal

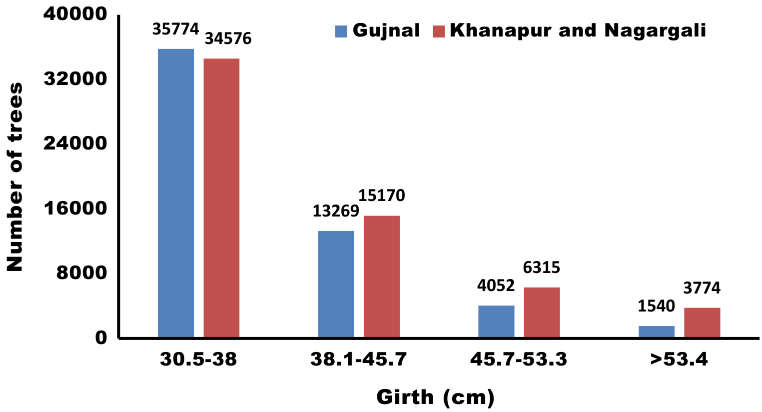

Fig. 2 Estimated number of sandalwood trees during early 1920 in Gujnal, Khanapur and Nagargali Ranges of Belgaum division

forest division continued to be an important area for sandalwood extraction. The forest areas of the entire Chamarajanagar district are now in the protected area (PA) network; as a result, the natural regeneration of sandalwood in the district has got excellent fillip, and it augurs well for the future of the species.

In Bengaluru Urban and Rural districts, sandalwood occurs in the relatively dry and well-drained localities in association with a wide range of dry deciduous and thorny species. Substantial forest areas of these districts have been planted with eucalyptus. However, the portions of the forests left with natural vegetation have scattered to a fairly good presence of sandalwood seedlings and saplings, although mature trees are rarely seen. Even though sandalwood has been found distributed in the Chickkaballapur district, large-sized trees are comparatively less. Regeneration has been found in Ittikaldurga state forest blocks (IDB) and Gedare state forest. The distribution of the species in the higher diameter classes is negligible, and trees are mostly less than 10 cm in diameter.

Chikkamagaluru (earlier Chickmagalur) district had several forests such as Tangli Sandalwood Reserve that was well-known for sandalwood trees. The dry deciduous and scrub forests of the district are ideal for the growth of sandalwood. Very good regeneration of sandalwood is visible in the deciduous and scrub forests of the district in parts of Chikkamagaluru, Tarikere and Kadur taluks. The coffee plantations of the district used to harbour well-grown sandalwood trees in their borders. The trees that were harvested in Chickmagalur forests were either transported to Tarikere Sandalwood *Koti* (Depot) which was started in 1905 or to sandalwood depot at Chickmagalur. Both these depots do not exist now, as the number of sandalwood trees has dwindled, especially after 1980–1990. In the Koppa forest division of Chikkamagaluru district, sandalwood was found to occur naturally over large areas in Koppa, Chikkagrahara, N.R Pura, Balehonnur and Sringeri ranges. However, most of these areas are now devoid of trees with a larger girth. Wherever the department has provided rigid protection, profuse regeneration has been observed; Mathavara forest and Tangli Sandal Reserve in Chikkamagaluru forest division and Karkeshwara plantation of Koppa forest division are examples of such areas.

In the Chitradurga district, sandalwood grows naturally in Hiriyur, Hosadurga and Holalkere taluks' forests. It occurs in a few pockets of Jogimatti, near Tanigehalli, Hirekandavadi and Kallavvanagathihalli villages in Nirthadi RF, near Lokadolalu, Guddadasanthenahalli, Madure and Mavinakatte villages and in Kudurekanive SF and Marikanive SF. Davanagere (a new district that was formed by conglomerating different areas from three districts Chitradurga, Ballari and Shivamogga) had a scattered natural population of sandalwood in most of the areas. Anagodukaval, Kudurekonda, Nirthady, Yeraganal, Uchangidurga, Sogi, Hyarda, Nirthadi, Kudrekonda, Thirtharameshwara, Madenahalli, Hamramgatta, Madenahalli and Chatnahalli are some of the prominent areas. Some of the forests of Kukkwada-Ubrani, Rangainagiri and Bhadrapura were known for having sandalwood trees of very large girth which are now uncommon. Harapanahalli range in Davanagere forest division in Bellari district had considerable population of sandalwood. Enumeration was carried out way back in 1970–72 for the Harapanahalli range. The survey indicated that there were 4799 trees (in the girth class of 15–24 cm); 424 (25–34 cm girth); 122 (35–44 cm); 58 (45–54 cm); 23 (55–64 cm girth); 16 (65–74 cm); 5 (75–84 cm); 2 (85–94 cm) and no trees above 95 cm girth. These areas can be a source of good sandalwood if protection is provided and regeneration is encouraged.

In Dharwar district, the forest areas of Kalaghatgi and Dharwar ranges adjoining Uttara Kannada district had considerable sandalwood populations in the past which have dwindled considerably now. Younger regeneration of the species is found here and there. In Haveri district, it is found scattered in the southern parts of the district especially in Hanagal, Hirekerur, Byadgi and Dundshi ranges. The forest areas are Mudur, Shirgod, Hanmankoppa, Makoppa, Varaha, Bellore, Bidarkatti, Katenally and Tadas. In the Gadag district, scattered growth of sandalwood saplings is found in the scrub forests of Kappat hills, especially in the valleys along nallas.

The dry deciduous forests of Hassan district have naturally growing sandalwood in varying proportions. The presence of sandalwood is conspicuous in the reserved forests of Belasinda, Desani, Gendekatte, Gobli, Kantenahalli, Karebore, Kolabore, Nakalgod, Ramadevarahalla, Seegegudda and Thirumaladevaragudda and Karjuvalli village forest.

Kodagu district (erstwhile Coorg State) and sandalwood have been closely associated with a long history under direct British administration (C-State). Sandalwood single-handedly used to contribute more than 10% revenue to Coorg. The main sandalwood areas of Kodagu were in the north and northeastern parts; sandalwood trees were abundantly found in Kushalanagar (Uddina Mani), Somavarapete and Shanivarasanthe ranges. Interestingly, many pioneering research outputs on sandalwood in the later part of the nineteenth century emerged from those who were associated with Coorg State. Presently, considerable regeneration has been observed in Kushalanagar (Uddina Mani) and Somavarapete (Athur section). Considering its history of being associated with sandalwood, the areas that were abundant with sandalwood can be protected, and measures to raise plantations can be seriously considered.

Kolar district also had a very good natural population of sandalwood. It was distributed in the forests of Kolar, Mulbagal, Srinivasapura, Bangarpet and Malur ranges. The trees were not of larger girth but had significantly higher heartwood and oil content. The reason may be attributed to the fact that the older trees had smaller girth, as they were growing in harsher conditions. Natural regeneration of sandalwood is good in different forests of the district such as Gokunte, Kashipura, Gajaladinne, Haralukunte, Chimtakunta, Hogalagere and Lalapur forests.

The forests of the Shivamogga (earlier Shimoga) district were once known for the abundance of sandalwood trees. Its dry deciduous forests are ideal habitat for the species. Even the moist deciduous forests used to support very good sandalwood growth. The forest divisions of Shimoga, Bhadravathi and Sagar were known for the sandalwood population. The state forests of Chandrakala and Gangavanasara of Sagar forest division, Kumsi state forest of Shivamogga forest division, Kukkwada-Ubrani state forest of Bhadravathi forest division, etc., were famous for sandalwood trees of appreciable girth. In the Sagar forest division, sandalwood was predominantly found in Shikaripura, Ambligola, Hosanagara, Soraba, Choradi and Anavatti ranges. In Bhadravathi, it was found in Bhadravathi, Chennagiri, Lakkavalli, Shanthisagar and Umblebylu ranges. In Shimogga Division, Madagadde, Thirthahalli, Arasalu and Shankar ranges had a large population of sandalwood. The abundance of sandalwood in these three divisions is depicted in the form of quantity harvested during the early part of the twentieth century (Fig. 3). However, the population has completely dwindled in all these ranges.

Sandalwood trees are found in almost all the dry deciduous and scrub forests of the Mysuru (earlier Mysore) district. In the past, the district was well-known for its abundance of sandalwood. Sandalwood extraction was a very important activity

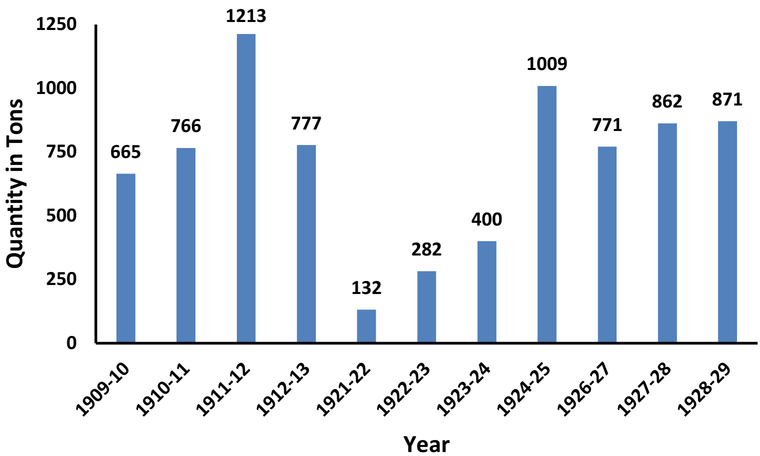

Fig. 3 Quantity of sandalwood collected from Shimoga, Sagar and Bhadravathi during various years from 1909–10 to 1928–29

even before the forest department was formed in 1864. Some of the natural populations that existed then include the Periyapatna range, Tirumakudlu Narsipura range, Chikkanahalli blocks (I and II), Chamundi state forest, Varakodu forest, etc. There were plenty of sandalwood trees in private lands also. Large quantities of sandalwood were extracted from the forest and non-forest areas of the district and were transported to Mysore Sandalwood *Koti* (Depot). The present crop of sandalwood in the district is very scattered and mainly consists of seedlings, saplings and younger trees. Mature trees are very rare. Considerable forest areas of the district are now in the wildlife reserves which is a boon in disguise for the sustained regeneration, conservation and propagation of the species. Mandya district, which was earlier a part of erstwhile Mysore district, had a good population spread across some of the forest areas such as Basavanabetta, Dhanagur, Shettihally, H.N. Kaval, Hulikere upper and lower blocks, Basavanakallu, Konankal, Narayanadurga and Mudibetta. Natural regeneration is also observed in Melapura, Hosaptana, BilibettalKaval and Hunjankere. Substantial extents of forests of Mandya district are also included in protected areas such as Cauvery and Melkote wildlife sanctuaries.

Sandalwood was previously found to be growing naturally almost in the entire Tumkur district. The Devarayanadurga forest area was extensively harvested for sandalwood during the last decade of the nineteenth century. Some of the other areas that harboured the good growth of sandalwood include Marashettyhalli, Kamalapur, Harenahalli, Korategere and Madhugiri. Due to overexploitation over some time, the population has considerably dwindled.

Ramanagara, a district formed in 2007, was part of Bangalore district and had a considerable population of sandalwood in its drier localities. Some of the forests in which sandalwood was found were Savanadurga, Chikkamannugudde, Hulthar, Handigundi, Gabadikaval and Chulur.

In the Uttara Kannada district, sandalwood was found in abundance in the eastern part of the district adjoining Dharwad, Haveri and Shivamogga districts. The dry deciduous forests of Haliyal and Yellapur divisions were well-known sandalwood growing areas of the Bombay Presidency, and sandalwood extracted from these areas was taken to Dharwad Sandal Depot. The moist deciduous/semi-evergreen stretch of forest in the eastern edge of the district comprising parts of Sirsi and Siddapur taluks (Sirsi-Sonda-Banavasi-Siddapur) adjoining Sagar division also had a fairly good population of sandalwood trees. Both these populations have now dwindled due to illicit felling but they can be ideal areas if protected from browsing and fire.

Sandalwood also grows in coastal areas but is found as a scattered population. It is reported in moist deciduous forests and in scrub jungles of Mandekolu, Medinadka of Sullia range, Bantaje and Kalnjimale of Puttur range, Veerakamba RF and Kodyamale RF of Bantwal range.

The resource survey organization of Karnataka Forest Department conducted an enumeration of sandalwood trees from 1962–63 to 1973–74. The trees above 10 cm diameter were considered for documenting the work. The survey was carried out in seven divisions, namely Bhadravathi, Chamarajnagar, Hassan, Hunsur, Kolar, Sagar and Shimogga which were supposed to harbour the sandalwood population. Interestingly, the Hunsur Division had ~50% of the total number of trees across the divisions having an average of 4.11 trees per hectare. This was followed by Shimoga which had 0.99 trees per hectare. Out of the total number of trees across different diameter classes—10–20; 21–30 and ≥31 cm, 91% (313,098 trees) of the trees were in the diameter class of 10–20 cm, and only 0.5% (4360 trees) were in the diameter class of 31 and above [9]

6 Present Status

With the increased demand for sandalwood and sandalwood oil by various end-users, reduced availability of mature sandalwood trees in the forest and non-forest areas, non-availability of sandalwood in the open market and very limited availability in the government depots (Sandal *kotis*), there was a steep rise in the price of sandalwood. This immediately resulted in extensive smuggling of trees in the forest, and the scattered mature trees became the prime target of illegal harvest. The smuggling cases increased in some of the major sandalwood growing areas such as Bangalore, Bhadravathi, Chickmagalur, Kodagu, Dharwad, Hassan, Mysore, Sagar and Shimoga. Even though strict rules and regulations existed, the sandalwood population dwindled, to such an extent that the department gradually resorted to the removal of stumps that were left over after illicit felling by smugglers due to lack of mature trees. There were some supplies from private lands or coffee estates but these also were shrinking. There was also another pertinent issue as far as the removal of stumps was concerned. The cost of the uprooting of old stumps was earlier very low. The rates for departmental extraction had not been revised for a long time. Besides, the rates prevalent were only for smaller stumps, and there were no rates for stumps of bigger size. This had resulted in the staff not evincing sufficient interest in the extraction and removal of sandalwood stumps from the forest. Stumps of bigger size had simply been left in the forest due to the prohibitive cost of extraction. With the revision of the schedule of rates (SR) for such activities in the early 1980s, there was a spurt in the extraction of sandalwood, and it sustained the depots for several years.

While increased smuggling activities had drastically reduced the availability of sandalwood in Karnataka's forests, which only a few decades ago were abundant with trees of all ages, other factors had also contributed to their depletion. They include uncontrolled grazing and browsing by domestic cattle especially goats, repeated fires, lopping for fodder, diseases and pests, etc. Besides, naturally growing sandalwood trees sometimes require intervention in the form of climber cutting and pollarding of overtopping branches of adjoining trees. These cultural operations were carried out on a very limited scale in identified sandalwood areas or plantations, but the vast forest areas harbouring sandalwood growth here and there were generally neglected.

Realizing the rapidly dwindling natural sandal population, the forest department decided that it would be necessary to enhance the population by artificial means. This paved the way for introducing the 'Sandal Estate Scheme' in Karnataka in the 1980s [8]. This scheme's primary objective was to artificially regenerate sandalwood in those areas where sandalwood grows well and to protect and develop the areas with substantial natural regeneration. The department created a few posts of Range Forest Officer exclusively for supervising the execution of the scheme. Nurseries were developed for raising sandalwood seedlings in poly-bags. Plantations were raised in some of the well-known and potential sandalwood growing areas. Dibbling of sandalwood seeds was also carried out especially in the bushes and hilly areas during the premonsoon season. Though there were some initial success and trees did come up well in some of the areas, the fact is that for the effective management of sandalwood trees/plantations, there should be sufficient funds on a long-term basis and not for a short period, say for three to four years. When such highly valued trees are being cultivated, protection is of paramount importance, and mere usage of barbed wire fence will not suffice. Therefore, without proper budget availability, the possibility of such schemes to deliver the desired results is rather thin. However, the aspirations of growing sandalwood continue in the department as is evident by the increase in the plantation area of sandalwood (Fig. 4).

Although the re-establishment of sandalwood has been an important goal of the forest department, attempts at developing pure sandalwood plantation from poly-bagged seedlings have given mixed results. The number of successful pure sandalwood plantations raised from nursery-raised seedlings is not many. Sandalwood has done reasonably well when introduced in mixed plantations in ideal, well-drained terrain with moderate rainfall. But the best result in the case of sandalwood so far has been from dibbling of seeds in its natural habitat. There are also numerous examples of sandalwood naturally regenerating into handsome and luxuriant patches across the state. The forest department made a renewed effort in reviving the concept of raising sandalwood trees in the form of an estate about two decades ago to protect the existing natural sandalwood stands and assist these in further propagation and growth. The result of this initiative has been quite encouraging. At present, the department under

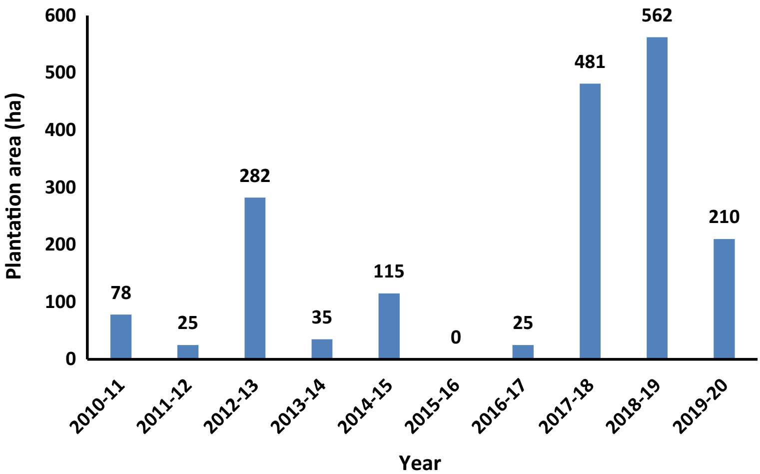

Fig. 4 Plantations raised by Karnataka Forest Department from 2010 to 2020

a new scheme titled '*Siri Chandana Vana*' has been focusing on such sandalwood areas and improving their status further by providing very secure barriers such as chain-link fence or stone/brick wall and also by planting and/or dibbling seeds wherever necessary. The plantations are provided rigid protection by engaging several watchers who keep watch throughout day and night. In some of the plantations, protection is further strengthened by engaging squads of native dogs.

The new concept of forming sandal estates has become popular throughout the sandal growing areas of the state. Some of the successful sandal estates so far developed in the state are Bellary circle (Gunda RF in Hospet range), Belagavi circle (Jalaga in Khanapur range and Kadabagatti in Gokak range), Bengaluru circle (Sulalappanadinne SF of Chickkaballapur range, 2011/2012 plantations of Bangarapet range and Turahalli plantation of Bangalore division), Canara circle (Oralgi of Katur range), Chamarajanagar circle (Chengadi in Kollegal division), Chikkamagaluru circle (Tangli Sandal Reserve in Kadur range and Karkeshwara plantation in Koppa range), Dharwad circle (Gungargatti plantations of Dharwad range and Kalikatti plantations of Dhunshi range), Hassan circle (Kamalapura SF of Kunigal range and Madhugiri SF of Koratagere range), Kalaburagi circle (Honnekeri plantations in Bidar range), Mysore circle (Elawala and Sandalwood oil factory compound in Mysore range and Mummadikaval of Periyapatna range) and Shivamogga circle (Yerekatte in Shikaripura range and Mavinakatte in Bhadrapura SF of Shanthisagar range). The list of areas given here is not exhaustive but indicative of the efforts made by the forest department in preserving and developing some of the sandalwood growing areas in the state. Similar potential areas have been identified by the department in various forest divisions.

Despite heavy extractions in the past, followed by rampant smuggling in the latter years, sandalwood has survived till today and is visible in most of our dry deciduous and scrub forests, in some places profusely and sparsely in others, although mature sandalwood trees are hard to come by. Through trials and errors, it is realized that assisting and protecting the natural regeneration of sandalwood is the best way of ensuring the long-term survival of the species. What emerges as very amazing is the resilience of the sandalwood species to survive. The sandalwood tree starts flowering quite early in its life, within four to five years. It flowers and fruits twice a year, i.e. in September/October and in March/April. The seeds of both the seasons perform alike. Birds are fond of the ripe fruits of sandalwood. Natural dispersal of seeds and spread of the species effectively takes place through birds, provided the area is free from recurrent fire and browsing animals. The seed that finds its way into a thorny bush has a better chance of growing into a tree because of the protection afforded by the thorns. While a sandalwood tree starts producing viable seeds within four to five years, the formation of heartwood takes place after 6 to 8 year (ref.). Thus, a sandalwood tree is quite safe from the axe (or saw) of a smuggler during its early age. This practically ensures that every healthy sandalwood tree will be able to flower and fruit at least for ten years (twenty times).

The benefit of natural regeneration of sandalwood is not restricted to forest areas only; any sylvan ecosystem, even a small garden with a tree or two, maybe good enough for a sandalwood seed to germinate and grow, provided there is adequate protection. Profuse regeneration of sandalwood is visible in and around Bengaluru city in extensive non-forest areas that have been protected by some form of barricading. Most of the defence establishments, public sector undertakings, educational institutions and other public/private institutions that have expansive lands covered with gardens, tree parks, woodlots, etc., have a sizeable population of sandalwood trees of all ages. The same is true for all the non-forest areas in Karnataka which have sandalwood bearing forest areas in the vicinity.

Karnataka Forest Department has taken various initiatives to popularize sandalwood; some of these have been successful, while some had partial success, and in a few cases, there were failures. However, the amendments in rules, as described earlier in the chapter, came as a big relief to the sandalwood growers especially concerning the procedure of extraction and further disposal of sandalwood. Earlier, persons having sandalwood trees in their lands had to go through a rigorous process of scrutiny and investigation in the eventuality of theft of, or damage to, the trees. This had instilled a sense of fear or apprehension in the public mind to own sandalwood trees. In the amended act and revised rules, the need of filing a declaration by the private owner with the forest department about the sandalwood trees standing on his land has been removed. The obligation on part of the owner to report all cases of damage or theft of sandalwood trees in his land to the nearest Forest or Police Officer has also been done away with. The grower/owner has been given the freedom to sell his sandalwood either to the state government or to any state government undertaking notified from time to time. The state government has already notified two undertakings, namely the Karnataka State Handicrafts Development Corporation Limited (KSHDC) and the Karnataka Soaps and Detergents Limited (KSDL) for this purpose. Provision has been made for extraction, stacking and transport of sandalwood by the owner himself, if he so desires, under the supervision of the forest department. It has been stipulated that the value of sandalwood shall be paid to the owner not later than three months from the date of receipt of the material in the depot. The rates at which the value of sandalwood has to be paid to the owner have to be fixed for each financial year based on average prices obtained for sandalwood in the public auction sales. The above initiatives of amending the provisions of the Forest Act and Rules and streamlining the procedure of extraction and disposal of sandalwood were intending to remove people's fear and apprehension of owning the tree and popularizing its planting in private lands. These initiatives appear to have born fruits as people are taking an increasing interest in planting sandalwood in their lands.

The forest department's unabated ambition to conserve and protect sandalwood trees throughout the state is continuing under the program '*Siri Chandana Vana'*. The '*Krishi Aranya Protsaha Yojane'*, a scheme of the department that has provision for the supply of good quality seedlings of various species and financial incentives to farmers and others to encourage them to grow trees in their lands, has also helped propagate sandalwood plantations in private lands. The dream of reviving back the glory of Karnataka to be *Srigandhada Gudi* is pursued in the right earnest.

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Chapter 6
Status of Sandalwood in Tamil Nadu

T. Sekar

1 Introduction

Southern India is known to be the home of Indian Sandalwood (*Santalum album* Linn.), and wood from the species yields the maximum per cent of scented oil by weight. It is the oldest known perfumery material of great commercial value and is perhaps the planet's most expensive superwood at present. There are references to Sandalwood in Indian mythology, folklore and ancient scriptures, which are at least 2300 years old. Fischer quoted some of the earlier writings '*Chandana',* the Sanskrit name ascribed to *S. album* Linn. and was known and used in India from the earliest historic times and is frequently mentioned in the ancient Sanskrit writings, some of which date before Christian era [1].

2 Distribution of Sandalwood Forests in Madras Presidency

Though the geographical distribution of the *Santalum* genus has been recorded globally, India is represented by monospecies, namely *S. album* [2]. It occurs as gregarious vegetation in the most suitable localities in the lower and mid-elevation dry deciduous forests and scrubs of peninsular India. It is possible to recognize the Sandalwood type within these dry forests as a distinct formation, which finds its optimum expression between 600 and 1200 m above mean sea level. Its' preponderance is for localities with an annual rainfall averaging between 880 and 1150 mm. Sandalwood forest occurs on red loamy or fine gravelly, well-drained soils on plateaus, hill slopes and undulating grounds. A slow-growing species, its annual increment, was recorded to be varying from 1.0 cm girth at breast height (GBH) in Javadhis to 0.63 cm in the Sanamavu RF of Hosur plateau [3, 4]. Depending upon the location

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factors, Sandalwood trees develop heartwood at 15–20 years [5]. They are known to attain commercial maturity after around 30 years, at which period heartwood is well developed at a depth of 5 cm below the surface. Significant variations in heartwood content are recorded between localities. For instance, in the Vellore division, Sandalwood trees in girth classes of 15–30 to 90–120 cm occurring in the plateau portion contained 15–93% more heartwood than outer slopes and plains [6].

In the erstwhile Madras Presidency, the Sandalwood was found in the Mysore Princely state and the Coorg, Coimbatore, Salem, Nilgiris (South East Wyanad), North Arcot, South Arcot, Cuddappah and Bellary districts. After reorganizing states on linguistic lines in 1956, Sandalwood-bearing forests spanned approximately 3045 km^2 in Madras state [5]. Distribution was confined predominantly to Javadhi, Shervaroy, Chitteri, Kolli, Pachamalai, Anamalai, Segur and Sathyamangalam hill areas. While in composite North Arcot, Salem, Nilgiris, Coimbatore districts, its occurrence was reported to be abundant, and the species was found to a small extent in Madurai, Tirunelveli, Tiruchi, Ramanathapuram, and South Arcot districts [7] (Fig. 1).

3 Early Management of Sandalwood

There is barely any recorded history on the management of Sandalwood in the first half of the nineteenth century in Madras Presidency. In Mysore Princely state, rights on the species, having been declared a 'Royal tree', were reserved entirely to the State. Extraction and disposal of Sandalwood came under its Forest Department in 1864 [8]. In the Presidency, Sathyamangalam, Talamalai and Bhavani in Coimbatore district happened to be the first regions where the working of Sandalwood commenced in 1864–65 with the help of overseers. All trees which had heartwood and showed signs of decay on the top were regularly cut [9]. Between 1870 and 1898, forests of Mysore and Coorg each yielded much larger Sandalwood than the other British districts, which was probably due to the protection given to Sandalwood as royal species in Mysore and Coorg [10].

4 Sandalwood Working in Tamil Nadu- Past and the Present

In the historical time frame, Sandalwood forests witnessed varying exploitation practices, and there was neither any uniform prescription nor systematic harvest of Sandalwood till 1896. The rough working schemes introduced in Coimbatore North division in 1896 continued till 1932 prescribed the extraction of the roots and stumps left from former fellings, dead trees, dying trees and trees over 82 cm girth at breast height [11]. Working plans, drawn in 1901 for specific sandal areas of Salem division, followed

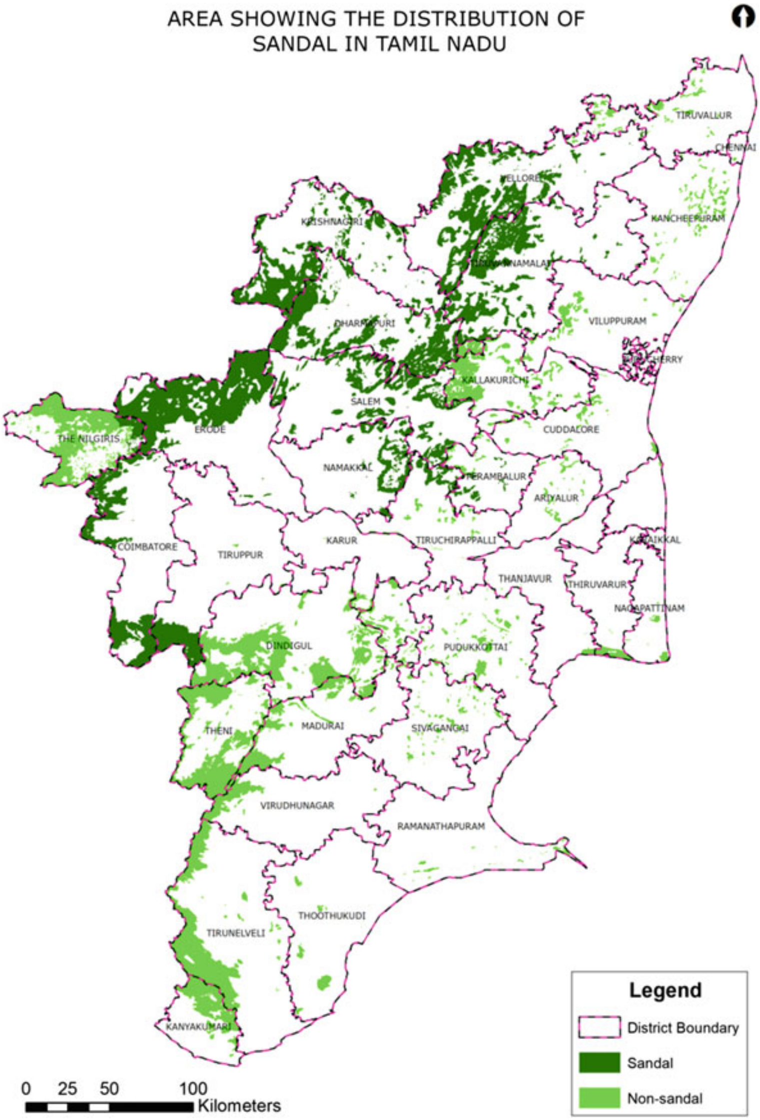

Fig. 1 Distribution of Sandalwood-bearing areas in Tamil Nadu

harvest of all trees of girth above 75 cm [4]. Elsewhere in Vellore East division, plan for specific reserves, written in 1907, adopted extraction of dead or dying trees and those with a minimum girth of 90 cm [3]. Felling girth seemed to have been fixed between 75 and 90 cm, probably based on optimal heartwood production and progressive tree reduction in higher girth classes in the reserves. All these schemes followed either a five- or six-year felling cycle. Because of irregular working, no attempt was made to fix the annual yield. The widespread onset of spike disease by the beginning of the twentieth century led to the harvest of living spiked trees, which upset the chronological order of the coupes resulting in irregular annual outturn. It is recorded that in the erstwhile Coorg state, about 350,000 trees were killed with an arsenic solution during the period 1903–1916 as a measure to control the spread of spike disease [12]. As the removal of spiked trees did not arrest the spread of disease, it was decided in the Conservator's conference held in 1927 that only dead Sandalwood trees should be extracted for the future. [3]. This can be construed to be a historical decision that charted the course of Sandalwood working in Tamil Nadu for the rest of the century.

In the comprehensive 10–15 year Working Plans for various Sandalwood divisions commencing with the early 1920s, regular Sandalwood working circles, felling series and annual coupes were constituted, with the felling cycle of either five or six years for Reserved Forests. However, a three-year felling cycle was adopted in respect of village series, comprising unreserved and *patta* lands possibly going over the area at a shorter interval to prevent theft and smuggling. With the continuous onslaught of spike disease on Sandalwood across the State, extraction was confined to dead trees and fallen or broken green trees alone in the annual coupes irrespective of age and size. Natural Selection cum Improvement felling system was adopted throughout, with no technical rotation age followed anytime. Yield regulation was by area. For the whole of the Presidency, Sandalwood trees were extracted over an extent of 225,318 acres (ca.900 km^2) during 1945–46 [13].

In all Working Plans of the post-independence period, the felling cycle in the Reserve series was uniformly reduced to three years, owing to raising spike mortality, the vulnerability of dead trees to fire damage and illicit removal. Dead trees along footpaths and places susceptible for theft were to be extracted irrespective of the coupe. For the same reasons, felling coupes in the Village series were ordered to be gone over every year. Extraction of Sandalwood was in the order of 141,838 trees during 1980–81 [14] and 64,615 trees during 1984–85 [15]. All through these periods, only departmental execution of felling was allowed. Marking, uprooting and extraction followed a set calendar of operations. It was done following the procedure laid down in the official publication 'Rules regarding selection, felling, cleaning, classification and disposal of Sandalwood and that of maintaining depot accounts and other registers', which is in currency. Removal of bark and rough cleaning was done in the forest depots within the divisions, as the case may be and then transported to the sale depots at Sathyamangalam, Salem or Tirupattur for final cleaning. Between 1980 and 2000, the annual outturn of final cleaned wood ranged between 968 and 2660 tonnes, the highest recorded during 1983–84 [16]. This system continued till the beginning of the new millennium, by which time harvestable growing stock in the Sandalwood forests and villages got almost wiped out. The dwindling natural stock of Sandalwood in forests is evident from the fact that heartwood sold in auctions dropped from 1000 to 2000 tonnes per annum between 1980 and 2000 [17] to less than 100 tonnes since 2006, barring 2010–11 and 2013–14, when 150 and 160 tonnes were sold. The department holds a stock of only 281.4 tonnes of final cleaned wood in its depots as of March 2016 adds credence to this situation [18].

5 Regeneration Practices and Their Results

5.1 Natural Regeneration

As Sandalwood harvest was confined to only dead, dying and fallen trees, mother trees abounded in the reserves under which natural regeneration was profuse. Birds are undoubtedly the prominent agents of dispersal, with bulbuls, barbets, koel serving as primary avian Sandalwood seed dispersers [19]. Campell Walker, the then Inspector General of Mysore, observed, '*The tree is naturally propagated by self-cast and bird-sown*' [10]. The highest germination and regeneration is noticed in the thickets of scrub and hedgerows, along with border trees and flood lines of narrow streams. As the seedlings are wary of direct exposure to sunlight, successful establishment of young Sandalwood crop is mostly recorded under the protective shade of bushes and scrub. As seedlings reach a certain height, Sandalwood becomes a light demander. The shrubs that protected the seedling from grazing and fire suppress and retard its further growth by smothering. Tamil Nadu State relied largely on the natural regeneration of Sandalwood for long. So long as conditions are favourable, Sandalwood propagates itself freely. The only protection needed is against smuggling and fire [20].

Vegetative propagation was also attempted to supplement natural regeneration. Though Sandalwood is a profuse coppicer, the shoots from stumps are considered useless, as they seldom progress to sapling or pole crop. Clearing undergrowth to a radius of 5 m around mature trees and digging of one m long interrupted trenches of 30 cm width and 30 cm depth was undertaken to induce regeneration through root suckers. Such areas were recommended protection by fencing for at least five years to develop into good trees [21]. This method was employed in the nucleus Sandalwood plots formed under the Sandal Estate scheme launched in 1989–90 in five prime Sandal divisions, namely Vellore, Tiruppathur, Dharmapuri, Salem and Tiruchirappalli. However, tampering and lax maintenance of fence protection resulted in grazing mortality of thrown out root suckers and failed efforts.

5.2 Artificial Regeneration

The earliest attempt in artificial regeneration in 1863 and 1865 with nursery-grown seedlings in pits and accompanying watering in the Badagalli sandal compartment was deemed a failure by Conservator Cleghorn in his report for 1865–66. Captain Morgan's plantations in 1874 at Bailur and Sigur were also declared a failure in 1875 by the Conservator Colonel Beddome [11]. Rickets noted in 1890 that artificial planting in the open, even on the most-rich soils, failed for want of shade for the seedlings in summer. Notings of Colonel Campell Walker's 'early promise and subsequent failure' and Pigot's 'good growth up to 10–12 years and subsequent decay' describe all Sandalwood plantations' fate eloquently during that period in Mysore, Coorg and other parts of the Presidency [10]. Planting operations were abandoned in favour of cheap methods of dibbling and bush sowing in situ.

Root parasitism of Sandalwood was not known until then. John Scott first established the phenomenon in 1871, though this vital finding came to be accepted after Barber gave a detailed description of haustoria in 1902 [11]. Since then, extensive field trials were laid with wide-ranging nurse-crops like *Cassia siamea*, *Casuarina, Albizzias, Acacias, Phoenix sylvestris,* bamboos, custard apple, lantana, *Scutia indica*—an armed evergreen shrub, pigeon pea, chilli, dhal, either as primary host in the nursery or secondary host in the field. Search for the most suitable host species pointed to Sandalwood's selective habit with its host and helped classify them into good, moderately good and bad hosts [5]. Results obtained in different localities narrowed down the list to *Casuarina*, Lantana and *S. indica.*

Tending and artificial propagation of Sandalwood was regularly prescribed in Working Plans after 1916. However, the performance of Sandalwood plantations raised in subsequent decades too was dismal. Consequently, it was decided that raising Sandalwood artificially on an extensive scale might have to be taken up after the experiments conducted under the Provincial Silviculturist's advice was known [13]. Many Working Plan Officers/Conservators considered artificial regeneration of Sandalwood unnecessary because of the disappointing results, as natural regeneration was abundant in all reserves. This is reflected in the first three Five-Year Plan achievements of the Tamil Nadu Forest Department, which were devoid of any Sandalwood cultivation schemes [22]. Instead, it was opined that '*if we must do anything for raising sandal, the best way to do is to dibble germinating seed or plant freshly germinated seedlings in bushes and other likely places*' [20]. The tasks of raking up soil and dibbling seeds were taken up as part of tending operations in most divisions with fair and optimistic outcomes [13].

5.3 Factors Impacting Sandalwood Management

Such factors are either natural or human-made. Infestation with climbers like *Pterolobium indicum, Ziziphus oenoplia, Acacia intsia, Asparagus racemosus, Sarcostemma brevistigma* is common, enveloping Sandalwood trees leading to branchiness and crookedness of stem, feeble crown development and poor growth. Large numbers of flower and leaf feeders, leaf miners, defoliator, twig and shoot borer are known to attack Sandalwood trees [11]. Though attempts to remove the plant pests by way of climber cutting and clearing are made in the field under cultural operations, nothing much was achieved in containing insect damage to the plants. Spike disease, initially thought of as a viral disease transmitted by insect vectors, came to occupy the centre stage in Sandalwood management since its discovery in 1899 by McCarthy, Deputy Conservator of Coorg [11]. The causal agent's current nomenclature for spike has been accepted as phytoplasma, a plant pathogenic bacterium [12]. Though its incidence was sporadic initially, the disease soon assumed epidemic proportion in Coorg, Salem North, Coimbatore North divisions by the first decade of the twentieth century

[4, 11]. In the Javadhis, the disease found expression much later, sometime around 1936–37 [3]. Despite such local variations, the Sandalwood future was found to be at stake, considering the virulent form and the tenacious proportion in which the disease spread to the length and breadth of Sandalwood forests. In the absence of any viable cure, spike disease came to govern the working of Sandalwood areas virtually all through the twentieth century, as seen in preceding paragraphs.

Many human-made causes operate as an effective check against the natural/artificial regeneration and the free spread of Sandalwood, among which grazing and fire stand out. Besides, intentional removal of seedlings predominates in cultivated fields. Grazing significantly affects the young seedlings and adversely impinges upon establishing Sandalwood in the reserves proximate to settlements. Kondas and Venkatesan observed that cattle damage to young regeneration is as serious as that of spike disease, noting that '*while the spike will not let the capital swell, grazing kills the very genesis of the capital'* [3].

Sandalwood is susceptible to damage by fire. Sandalwood-bearing dry deciduous forests are vulnerable to recurrent fires owing to a long spell of arid climate and availability of large quantities of dead burning material. Early foresters like Pigot, Maecarhenas recorded annual burning of large Sandalwood-bearing areas, destroying Sandalwood seedlings and injury to large plants or trees, with 90 per cent of the dead and just surviving stag headed trees in Coimbatore North district attributed to fire [10]. Likewise, large chunks of forests on the eastern outer slopes of the Javadhi hills were getting burnt annually, which killed regeneration and older trees of Sandalwood [3]. Observations in Hasanur plateau of Coimbatore North revealed that protection from grazing must be accompanied by effective fire prevention to safeguard naturally regenerated seedlings. Mortality in Sandalwood was also found attributable to drought at times. On the influence of drought, Colonel Campell Walker noted, '*The tree reproduces itself freely from seed, but the seedlings perish if exposed to hot sun or prolonged drought'* [10]. It is recorded that browsing, fire, invasion by Lantana and grass and openings created by biotic factors contributed to the extermination of Sandalwood in Yelagiris [6].

5.4 Smuggling of Sandalwood

Sandalwood was at least six times more valuable than teak bulk by bulk even at the end of the nineteenth century [8]. Easy accessibility of large-sized trees and higher possibility of concealment placed the species prone to theft. Operation of the Forest Hill Village System introduced in major sandal divisions in 1917 [17], which granted fire rewards and free grazing rights to tribal in place of successful protection of Sandalwood areas and maintenance of fire lines, worked satisfactorily till the 1980s. It was more of a symbolic, symbiotic relationship between the local community and the Forest Department. As the demand for Sandalwood grew, its price began to swell from the beginning of the decade. Villagers from the hills and plains uniformly fell to the temptation of quick earnings by illicit cutting and smuggling of both dead and green Sandalwood trees. It caused rapid decimation of Sandalwood wealth. The existence of rules governing Sandalwood's possession and transport by the individuals, namely Sandalwood Transit Rules, 1968 and Sandalwood Possession Rules, 1970, did very little to deter the woodcutters and smugglers.

Two major policy considerations during both the British Raj and independent India's forest administration contributed to smuggling. They are (1) Lack of technical rotation, with no rotation age fixed for Sandalwood. Sanitary cleaning of forests by harvesting only dead or dying trees left a large number of mature, green trees exposed to theft. (2) Absence of adequate incentive for the local tribal for supporting the improvement of growing stock and protection of existing Sandalwood wealth, particularly on village lands. This point needs elaboration.

Ownership of Sandalwood trees standing on *patta* lands assigned between 1907 and 1928 and after in different hills of the Presidency was vested entirely with the Government [21]. For this purpose, *patta* Sandalwood registers containing the survey number-wise enumeration of Sandalwood trees were maintained in the ranges. The tribals who were required to protect such trees were not entitled to any returns from the trees. Even in the pre-1907/1928 assigned lands where the landowners enjoyed certain ownership rights, the uncertainty and cumbersome method of determining the ownership of trees and delay in settling the compensation to the owner (to the tune of 47 1/2% of the value of the wood) served as major irritants [9]. The native tribals, primarily the Malayalees, felt that there had been hardly any incentive for them to protect the trees standing on *patta* lands. They began to use surreptitious methods to eliminate the existing trees while taking all possible steps against new recruitment. To offset this apathy, most Working Plan officers stressed the need for prompt settlement of compensation.

It is noteworthy to mention that the 1927 Indian Forest Act does not have any special provisions for Sandalwood. The absence of a uniform, comprehensive internal trade regulations on Sandalwood, applicable to different States regarding its possession, transport, value addition, etc., was also seen as a major hassle in addressing illegal Sandalwood removal from forests *patta* lands in Tamil Nadu. For instance, states like Uttar Pradesh, Pondicherry, which did not have any natural or human-made Sandalwood trees or very little growing stock like in Kerala, had a flourishing trade in wood form and operational oil distillation units. Thus, Sandalwood merchants and distillers were buyers of Sandalwood heart and sapwood in the State Forest department's auctions. Furthermore, to make the trade look perfectly legal, Sandalwood oil distillers most times boosted their average oil yield figures. In the process, they mixed illicit stock with legally sourced wood at ease.

The dynamics of Sandalwood protection around the late part of the last century were guided by the export policy guidelines on Sandalwood and its products. With the raw Sandalwood export ban in Indonesia in 1978–79, India stepped in to fill the export supply void. As exporting raw Sandalwood became more lucrative than making oil, merchants began to bid higher prices, which led to its widespread smuggling. The widening gap between production and demand and the unlicensed export of finished Sandalwood products under the EXIM policy led to a sharp increase in Sandalwood prices from 1992 in Karnataka and Tamil Nadu [23]. For the first time, in 1996,

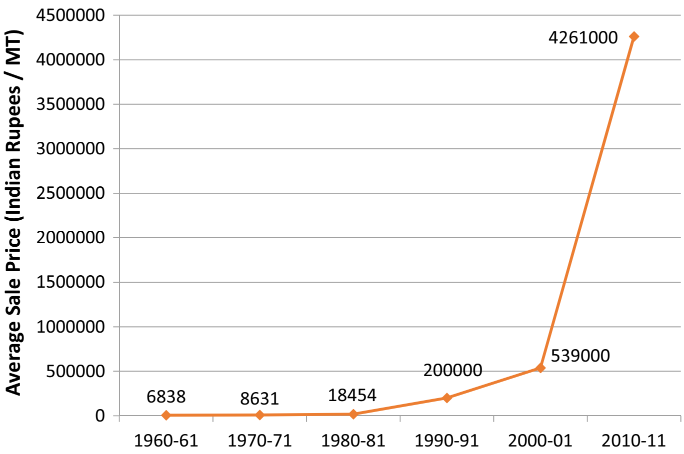

Fig. 2 Sandalwood sale price between 1960 and 2010

India imposed export quotas for regulating the export of Sandalwood and its oil. One could export the oil only if one bought the wood. This move constricted the supply and further jacked up the price of Indian Sandalwood and its oil (Fig. 2). The Government of India also brought into effect a ban on the export of Sandalwood in log forms and permitted the export of wood in the form of chips not exceeding 50 gm pieces. Present export policy for 2015–2020 bans export of Sandalwood in any form except listed items, of which finished handicraft or machine finished products are freely exportable. The chips, spent dust, dust, flakes and powder specified in the Schedule are permitted for restricted export under license by the Director General of Foreign Trade [24]

5.5 Administrative Responses and Their Outcomes

The period between 1985 and 2000 can be stated to be the most critical phase in Sandalwood management in Tamil Nadu. As both *patta* and forest Sandalwood stock witnessed uncontrollable but selective removal of mature trees—albeit clandestine and illegal—elite Sandalwood population declined uniformly in its distribution range. The State Government and Forest department responded with many legal, policy, administrative and scientific management interventions with mixed results.

Forest offenders were brought within the scope of Tamil Nadu Prevention of Dangerous Activities of bootleggers, drug offenders, goondas, immoral traffic offenders and slum-grabbers Act, shortly Goondas Act 1982 (Act No 14 of 1982) by way of an amendment Act No 1 of 1988 [17]. This Act provides for detention of a habitual forest offender for a maximum period of 12 months without trial by order of the District Collector cum District Magistrate upon receipt of proposal from the Forest Range Officer/Assistant Conservator of Forests, Forest Protection Squad, subject to provision of appeal with the State Advisory Committee and the Madras High Court. Hundreds of Sandalwood offenders were detained under this Act during the 1990s. However, the forest officers could only reach up to tree cutters and head loaders. Grass-root agents, middlemen procurers of illicit wood and the final users like the merchants and distillers in the long chain of invisible links in the illegal Sandalwood trade were still scot-free. Organized smuggling of Sandalwood continued to thrive without respite.

As the Sandalwood smuggling bore national and international ramifications, the Government established a Forest Vigilance Cell in 1983, later formed into Forest Cell CID with attendant officers and police to help in the investigation cracking the Sandalwood crimes involving interstate gangs [17]. But not to too much avail, the CID personnel at best supplemented the forest department's efforts at the local level.

Assistant Conservators were designated as authorized officers to pass an order of confiscation of vehicles seized during any forest offence, including Sandalwood offence by an amendment Act 44 of 1992, by which sections 49-A to 49-G were inserted in 1882 Tamil Nadu Forest Act. These subsections resulted in quick confiscation of vehicles during the Sandalwood offence commission, bringing some noticeable relief from the illegal movement of Sandalwood.

Field formations were intensified around the early 1980s by increasing the number of forest beats and check posts and by introducing many special units like rowing check posts, forest stations, etc. Several hundreds of Sandalwood protection and check post watchers came to be engaged on consolidated monthly wages. Frequent combing operations were organized, focusing on known intermediate storage points, critical foot-transit routes and bridle paths in the forests. Village-level informants under the Secret-Service Fund were set up. Sanctioning of rewards was extended to the staff for Sandalwood seizure made in the offenses in 1981 [14]. All these efforts improved the seizure rate of illegal wood and the vehicles engaged in its clandestine movement. In many prime sandal divisions, the number of Sandalwood offences peaked at over 500 per annum, annual seizure of roughly dressed heartwood from forest offenders ran to 100 tonnes and seizure of vehicles of all assortments went more than 100–150 in a year in each division (Fig. 3). Offence related to Sandalwood stock began to pile up in the department's godowns and depots, added to the final cleaned wood obtained from harvested trees. The department sold between 1000 and 2000 tonnes annually in auctions during 1980–2000 [17]. However, in the absence of a Sandalwood tree-friendly policy on the ground, local villagers continued to hack *patta* trees and later turned their heat on forest Sandalwood trees.

With an object of replenishing Sandalwood growing stock, nucleus plots were created in high-density Sandalwood-bearing areas within the Sandalwood estates during the 1990s. The chosen areas were provided with chain link or barbed wire fencing, fire lines cut along boundaries to prevent grazing and fire. Tending operations like climber cutting, clearing miscellaneous growth topping the leading shoots, bush sowing of seeds and artificial regeneration were undertaken. Villagers failed to cooperate, resulting in tampering with the fences and cattle grazing in nucleus plots.

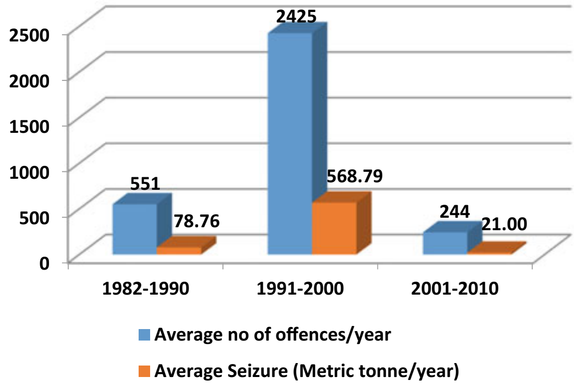

Fig. 3 Trends in sandalwood offences in Tamil Nadu

An increasing number of court cases relating to Sandalwood further debilitated the protection issue. The field staff got busy during the day with preparing seizure records, offence reports, remanding apprehended persons along with the seizures, etc., which took away considerable time. They were not able to undertake regular day patrol of forests and night raids along vulnerable routes. The Government established a Special Court at Tiruppathur and Salem in 1993 and 1994, respectively, for exclusively trying Sandalwood offences to achieve fast track hearing and disposal. Despite Sandalwood offences being non-bailable, the accused were granted bail. Though many cases ended in a conviction, the convicted gained relief through recourse to the Probationary Offenders (PO) Act. Soon they returned to their illegal acts of cutting and smuggling of Sandalwood trees with a vengeance.

Looking at the rampant manner in which *patta* Sandalwood trees were decimated, the Government during 2002 inserted a subsection 36-F into the Tamil Nadu Forest Act 1882 based on a Forest department proposal in 1998. Six years later, 'Tamil Nadu Sandalwood Trees on *Patta* Land Rules' (Act No 33 of 2008) [17] was notified. The rules conferred ownership rights on the tree to the owners of the land. The schedule for settlement of the value of wood harvested from *patta* fields by the Forest department was 20% of the net sale price within 30 days of extraction and the balance within 90 days is a positive note in the rules. However, the landowner's obligation to sell the Sandalwood trees only to the Government served as a block. Settlement of the *pattadar's* share of wood value invariably is delayed due to budget provision-linked disbursement. Only 80 ha of Sandalwood plantations have been raised on private lands in the State, accounting for barely 6.5% of the total extent of private plantations across states (1225 ha) [25].

The Government sanctioned a new Sandalwood plantation scheme at an outlay of Rs 100 crore for 2015–16 to 2024–25. Works include raising Sandalwood plantations over 15,000 ha in the traditional natural Sandalwood-bearing areas of Javadhi, Shervarayon, Kolli, Pachamalai and Chitteri hills incentive to tribal community in 300 project villages and research on improved seed pelletization. The programme is under implementation and its impact yet to be assessed [26] (Fig. 4).

Fig. 4 A young Sandalwood plantation

6 Future of Sandalwood in Tamil Nadu

Research on tree improvement considering the phenotypic and genotypic variations in the two desirable traits, namely heartwood content and oil yield, needs intensification. State Forest Research wing needs to focus and avail findings from other premier institutions of Government of India and the States.

Existing Sandalwood groves and regeneration sites in the reserves have to be surveyed, protection strengthened and preserved as seed production assets, and support and sustain future yields. Abundant natural regeneration is found in most traditional Sandalwood reserves. However, the pole crops' outer part is often chipped off by miscreants looking for heartwood formation. This jeopardizes the future growth and survival of trees. Strengthening protection by assigning reserve areas to Village Forest Committees and providing them adequate incentive could improve protection.

Having Sandalwood at one's farm or home garden is seen as a grave security threat. Farmers cultivating Sandalwood need to invest heavily in security that includes a natural fence of thorny acacias, a solar power fence, trenching all around, installing CCTV cameras and even armed guard once the trees become mature. The Forest department needs to take a proactive effort to promote *patta* Sandalwood plantations. This will include the supply of superior planting stock, appropriate package of cultivation practices, provision of fencing subsidy, extending tree insurance cover to *patta* Sandalwood, farmer-friendly procedures in buying their wood and prompt settlement of shares.

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Chapter 7
Marayoor Sandalwood Reserve—The Last Bastion of Indian Sandalwood

A. N. Arunkumar, Geeta Joshi, and Surendra Kumar

1 Introduction

Indian sandalwood (*Santalum album* L.) has been categorized as 'Vulnerable' by the International Union for Conservation Nature [2]. With retrogression in population size, especially in peninsular India where it is naturally found, it is exciting to note that 'Marayooor' in Kerala state has a substantial number of sandalwood trees even now.

Kerala and sandalwood have been strongly associated. Sandalwood cultivation was attempted near Quilon as early as 1858 in an area of 20 hectares; however, it was a failure [1]. Similar attempts were made at Aryankavu—again a failure. M. Rama Rao who succeeded T. F. Bourdillon as the Conservator of Forests in Travancore made attempts to introduce sandalwood in all the forest divisions under Travancore. As per the working plan of Marayoor Sandal Division (2010–2011 to 2019–2020), the present distribution of sandalwood in Kerala is those places in which attempts were made to grow the species. It is opined that the few successful trees that initially came up may also have helped in building a more significant population.

In Kerala, sandalwood trees are distributed across the length and breadth, from extreme North (Kasargod District) to South (Trivandrum District). Though trees are found in reserve forests and private lands, the population is maintained in the reserve forests. Trees of girth $\geq$ 30 cm at breast height are found distributed in

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Table 1 Names of the different sandalwood reserves and their notification year

Sl. No	Name of the reserve	Notification year
1	Sandalwood Reserve Marayoor-51	22 October 1901
2	Sandalwood Reserve Marayoor-52	14 August 1903
3	Sandalwood Reserve Marayoor-54	14 August 1903
4	Vannamthura Sandalwood Reserve Block I	14 April 1932
5	Vannamthura Sandalwood Reserve Block II	8 July 1932
6	Karayoor Sandalwood Reserve Block II	22 March 1933
7	Nachivayal Sandalwood Reserve I	23 July 1932
8	Nachivayal Sandalwood Reserve II	10 June 1932
9	Karayoor Sandalwood Reserve Block I	25 February 1933
10	Koodakkaadumala	30 September 1965 (proposed)
11	Thirthalar	13 June 1966 (proposed)

forests from Kasargod District in the North to Trivandrum District in the South. It is also found in Kollam District (Thenmala Division), Idukki District (Periyar Tiger Reserve, Marayoor Sandal Division, Chinnar Wildlife Sanctuary); Trichur District (Chalakkudy Division), Palakkad District (Nenmara Division, Parambikkulam Tiger Reserve and Mannarkkad Division); Waynad District (South Waynad Division, Waynad Wildlife Sanctuary); Kannur Districts (Kannur Division) and Kasargod District (Kasargod Division). Among these, the maximum number of trees (> 30 cm girth at breast height) is found in Marayoor Sandal Division (~60,000 trees) followed by Mannarkkad Division in Palakkad District (~29,000 trees). It is reported that this sandal reserve housed 1,86,594 trees above 30 cm in girth [9]. By the end of 2004, it had reduced to ~ 60,000 trees due to illicit felling, spike infestation, low seed setting resulting in lower regeneration along with browsing of germinated seedlings by domestic and wild animals [3].

Considering the abundance of trees growing in and around Marayoor, more than a century ago, under the Travancore Forest Act, the sandalwood forests were notified as 'sandal reserves'. Between the period 1900 and 1937, ten forest areas adjacent to the sandal reserves were also notified as reserves (Table 1).

2 Formation of Marayoor Sandalwood Reserve

Sandalwood oil distillations mostly privately owned were found in plenty in Kerala from the 1980s onwards. By 2000, more than 30 distillation units of various capacities were distributed from Kasargod to Palakkad Districts. These distillation units mostly depended on unauthorized raw material from the adjoining states, *i.e.* Karnataka and Tamil Nadu. However, with the gradually dwindled population in those states, sandalwood from private landholdings was illegally harvested/smuggled, and gradually, it extended to the government forests. This deleterious effect of smuggling had an impact on the sandalwood trees of Marayoor, and gradually, the issue became a serious concern. Realizing the adverse impact of these sandalwood oil distillation units, in 2004, the Kerala Forest Department took stringent measures on those distillation units operating without a valid licence and initiated confiscation proceedings. With the High Court of Kerala's intervention and its orders favouring the department, Kerala's forest minister had to resign to prove his innocence. Considering the extensive smuggling and illicit felling, the Government of Kerala realized that this area needs further care, support and protection. To augment this, on the 8 June 2005, new forest division named Marayoor Sandal Reserve (hereafter mentioned as Marayoor Sandalwood Reserve—MSR). This also paved the way for closing down all the sandalwood distillation factories. Therefore, the year 2005 can be considered a landmark year for the Kerala Forest Department and sandalwood trees.

The etymology of the word Marayoor is said to be as '*Mara'* means hidden and '*ur'* meaning land or village which when merged can be referred to as the land hidden in the mountains [7]. Apart from the huge population of sandalwood, this is the only known area in Kerala for rock shelter paintings and consists of the largest concentration of Dolmens—a megalithic structure typically formed from a large horizontal stone slab resting on two or more upright slabs [7].

The altitude of the Marayoor Sandalwood Division varies from 1000 to 2500 m above sea level. The land has all the aspects and is rugged, undulated owing to the numerous hills having both main and subsidiary ridges that take off in varied directions resulting in steep terrain. Geologically, the area is made up of gneissic metamorphic rocks. The soil is predominantly sandy loam and the pH varying from 6.5 to 8.2. The climate is comparatively drier as the area is located on the eastern side of the Western Ghats. The rainfall ranges from 1000 to 1500 mm. Even though the rainy season is from June to November, showers also intersperse during the summer. April and May are the hottest months, and the temperature varies from 20 to 36° C [4].

The MSR comprises two ranges, namely Marayoor and Kanthalloor. These two ranges have two stations each—Marayoor and Nachivayal, and Kanthalloor and Vannanthura, respectively. The reserve is situated between 77°5′–77°15′ East longitude and 10° 10′–10° 20′ North latitude falling within the Devikulam taluk of Idukki District. Marayoor division area entirely falls under the Anjanad tract, situated on the Eastern slopes of Western Ghats. The area is isolated by lofty peaks and ridges on three sides and two distinct valleys in the North and Northeast portion. This reserve's total area is spread across 6426 hectares, out of which 1438 hectares are designated as sandalwood reserve occupying 57.59% of the total reserve. Details of various reserves/blocks under the jurisdiction of Marayoor and Kanthaloor ranges are provided in Table 2. The maximum number of trees with $\geq$ 30 cm girth at breast height (19,446) was found in sandalwood reserve Nachivayal block No. I and the minimum (1829) in sandalwood reserve No.54 and its extension (Table 3). It has also been mentioned that ~ 370 trees are found in Pallanadu Vested Forest covering

Table 2 Details of total area (in hectares) of MSR

Range	Sandalwood reserve	Proposed reserve	Vested forest*	Ecologically fragile land**	Total
Marayoor	596.516	3541.00	7.550	18.030	4163.096
Kanthalloor	841.718	1185.00	0.000	236.28	2262.998
Total area	1438.234	4726.00	7.550	254.31	6426.094

*Vested forests mean any forest vested with the government under Sect. 3 of the Kerala Private Forests (Vesting and Assignment) Act, 1971 (26 of 1971); ** Ecologically fragile land is any forest land or any portion thereof held by any person and lying contiguous to or encircled by a reserved forest or a vested forest or any other forest land owned by the government and predominantly supporting natural vegetation

Table 3 Extent of area (in hectares) and number of sandalwood trees (≥ 30 cm girth at breast height) in different reserves/blocks in **a**) Marayoor and **b**) Kanthalloor range as per the enumeration in 2008

Sl. no	Name of reserve	Area (hectares)	Number of trees
(a) *Marayoor range*			
1	Sandalwood reserve No.51 and its extension	278.50	0
2	Sandalwood reserve No.52 and its extension	53.326	8339
3	Sandalwood reserve No.54 and its extension	18.078	1829
4	Sandalwood reserve Nachivayal block no. I	135.315	19,446
5	Sandalwood reserve Nachivayal extension—I, II & III	10.126	0
6	Sandalwood reserve Nachivayal block no. II	101.171	8511
Total		619.066	38,677
(b) *Kanthalloor range*			
1	Karayoor Sandalwood Reserve Block I	120.000	5119
2	Karayoor Sandalwood Reserve Block II	97.248	7742
3	Vannanthura Sandalwood Reserve Block I	114.566	2186
4	Vannanthura Sandalwood Reserve Block II	509.904	4690
Total		841.718	19,737

Source: Marayoor Division Working Plan, Kerala Forest Department

7.55 hectares. The density of trees per hectare was maximum (156 trees) in sandalwood reserve No.52 and its extension and the minimum (nine trees) in Vannanthura Sandalwood Reserve Block II (Figs. 1 and 2).

As per the working plan, enumeration of trees was carried out in all the Sandalwood Reserves of Marayoor Division after its formation. The number of trees in each girth class starting from 21 to 30 cm and > 120 cm found in the two Ranges is provided in Tables 4 and 5. Among the two ranges, Marayoor Range comprises ~ 68% of the tree population. Nachivayal I and II contribute ~ 50% of the trees. It

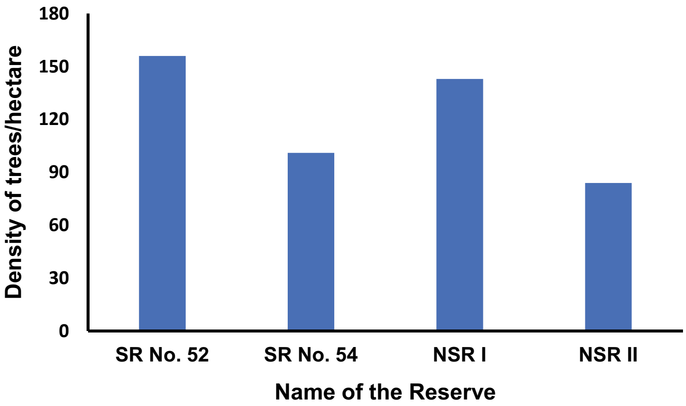

Fig. 1 Density of sandalwood trees/hectare in Marayoor range of Marayoor Sandalwood Reserve as per the enumeration in 2008 (SR—Sandalwood Reserve; NSR—Nachivayal Sandalwood Reserve)

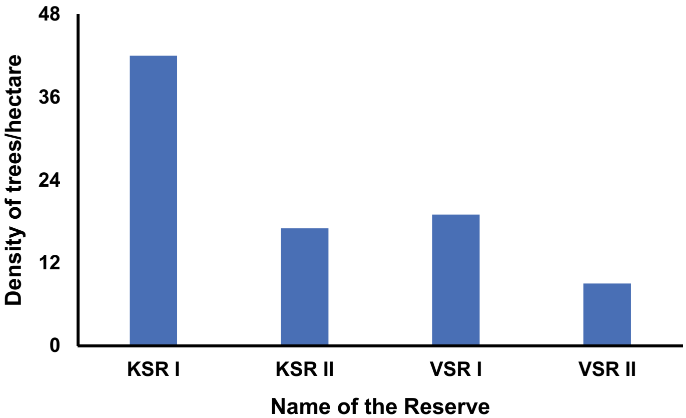

Fig. 2 Density of sandalwood trees/hectare in Kanthaloor range of MSR as per the enumeration in 2008 (KSR—Karayoor Sandalwood Reserve; VSR—Vannanthura Sandalwood Reserve)

is interesting to note that 46.54% of the trees fall under 41–70 cm girth class in the MSR as per the 2008 enumeration (Fig. 3).

Recent data on enumeration conducted during 2016 was obtained from the Kerala Forest Department and are provided in Tables 6 and 7. The total number of sandalwood trees has marginally reduced from 62,306 in 2008 to 59,016 in 2016. The percentage number of trees in the girth class 21–30 cm has increased from 9.89% in 2008 to 18.28% in 2016 suggesting that there is substantial recruitment of trees in the 21–30 girth class which is an encouraging factor (Fig. 4).

Sandalwood is primarily managed from a conservation perspective, and therefore, extensive protection is provided. Harvesting is carried out by removing only the

Table 4 Girth-wise number of trees in various reserves of Marayoor range of Sandalwood Reserve (as per 2008 enumeration)

Reserve	Girth class (cm)										
	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	101–110	111–120	> 120
Nachivayal-I	2102	8057	5477	3085	1482	718	345	170	76	51	31
Nachivalya-II	393	3740	2569	1642	909	442	214	115	42	27	14
SR-52	1545	3419	1853	877	412	150	63	20	0	0	0
SR-54	597	943	216	51	18	7	0	0	0	0	0
Pallanadu Vested Forest	26	220	161	68	41	20	9	4	1	0	2

Table 5 Girth-wise number of trees in various reserves of Kanthallor range of Sandalwood Reserve (as per 2008 enumeration)

Reserve	Girth class (cm)										
	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	101–110	111–120	> 120
Karayoor Sandal Reserve I	410	1445	1142	1067	575	307	118	65	25	18	10
Karayoor Sandal Reserve I	507	2707	1669	1234	1019	366	155	81	55	20	28
Vannathura-I	80	519	523	413	256	151	101	74	32	21	26
Vannathura-II	500	1399	1033	772	434	267	122	75	36	16	9

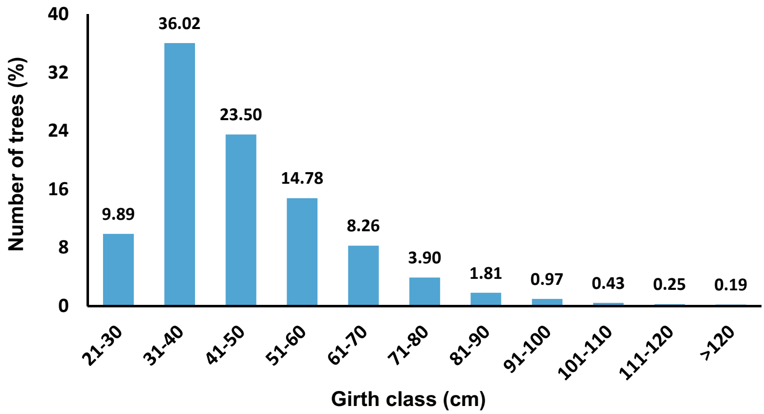

Fig. 3 Percentage distribution of sandalwood trees in MSR across various girth classes (as per 2008 enumeration)

dead/diseased and fallen trees. Though the felling of trees illegally has come down, however, the seized material and extraction of stumps of the trees illegally harvested are auctioned.

3 Impact on Tree Protection After the Formation of MSR

The formation of the new Marayoor Sandal Division in 2005 set a landmark in protecting the valuable trees. The number of staff involved in protecting sandalwood trees was enhanced. Under each forest station, protection blocks and protection units were established and each of them being headed by Section Forest Officers and Beat Forest Officers, respectively. Each protection block has 2–4 protection units depending on the size. Each protection unit has two to four protection watchers, and all the protection units are provided with walkie-talkies. Every night, patrolling is conducted by all the levels of officers of the division. Efforts have been made to erect a three-metre tall chain-linked fence all around the reserve boundaries to enhance protection. As extended support to the existing strong force, for the first time in the forest department, a dog squad was established in 2011. The dog squad brought fear in the smugglers' minds and helped in tackling a few cases.

As evident from Fig. 5, earlier there was substantial illegal felling of sandalwood trees in Kerala, and this increased once the availability of trees was drastically reduced in Karnataka and Tamil Nadu states. This was obvious from 2000 onwards. Between the years 2000 and 2005, the average number of offences and the number of trees felled were 251 and 1339, respectively. In 2004 alone, the number of offences and trees felled was 338 and 2660, respectively. The formation of this division was in 2005. During the next five years (2006–2010), the average number of offences and trees felled were drastically reduced to 55.8 and 551. During the last five years

Table 6 Girth-wise distribution of the number of trees in various reserves of Marayoor range (as per 2016 enumeration)

Reserve	Girth class (cm)										
	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	101–110	111–120	> 120
Nachivayal-I	2633	6042	5320	3173	1661	819	436	189	100	66	55
Nachivalya-II	1713	2959	2536	1623	928	477	254	131	56	28	21
SR-52	3038	2825	1154	480	236	101	33	12	4	0	0
SR-54	256	262	24	4	0	0	0	0	0	0	0
Pallanadu Vested Forest	41	93	118	52	49	13	12	3	3	0	2

Table 7 Girth-wise distribution of the number of trees in various reserves of Kanthalloor range (as per 2016 enumeration)

Reserve	Girth class (cm)										
	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	101–110	111–120	> 120
Karayoor Sandal Reserve I	1214	1781	1038	864	573	312	129	61	19	4	5
Karayoor Sandal Reserve I	879	2047	1425	933	582	330	141	64	28	22	10
Vannathura-I	325	412	376	247	165	107	68	37	26	16	21
Vannathura-II	692	1237	914	623	476	333	182	114	65	41	43

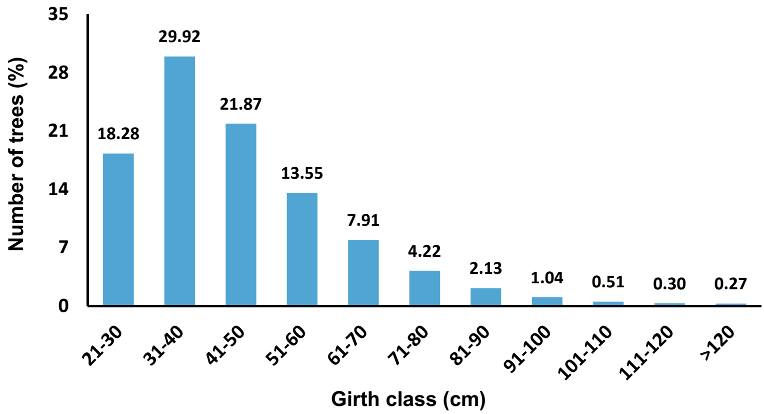

Fig. 4 Percentage distribution of sandalwood trees in MSR across various girth classes (as per 2016 enumeration)

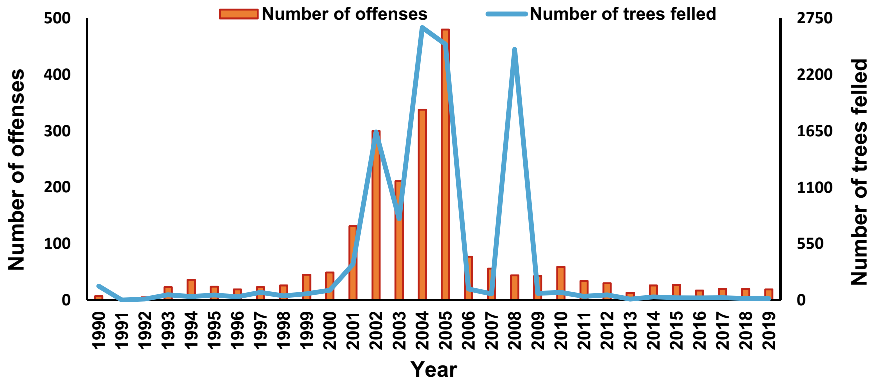

Fig. 5 Number of offences and trees felled in MSR between 1990 and 2019

(2015–2019), an average of mere 19.6 offences and 20.6 trees have been felled. The impact of protection provided in this reserve can be ascribed to the efficient and strict vigilance carried out by the forest department.

As per the working plan, the primary objectives of managing this reserve are to increase the growing stock of sandalwood trees, promote a participatory approach as a protection strategy and popularize the cultivation of sandalwood in private farms, enhancing the efficient marketing strategy of sandalwood.

Several scientific studies have been carried out in the Sandalwood Reserve by Kerala Forest Research Institute, Peechi. In one of the earliest studies carried out on aetiology, epidemiology, and possible methods of control of sandalwood spike disease, the disease was detected in this population at sandalwood reserves 51 and 54

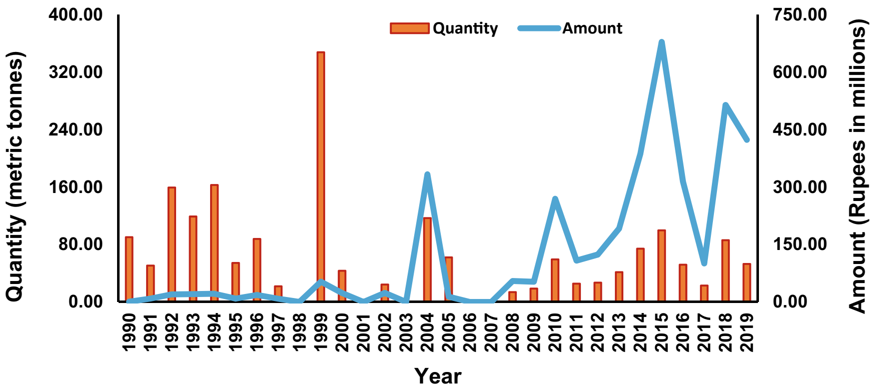

Fig. 6 Trends in sandalwood quantity sold and revenue earned in MSR for the period 1990–2019

and part of Chinnar Wildlife Sanctuary [5]. Marayoor sandalwood population, identified as one of the nine sandalwood provenances selected across India [6] revealed the highest genetic diversity among the eight provenances studied [8].

4 Sandalwood Production and Auction

Marayoor sandalwood depot is the only place in which sandalwood is auctioned. There has been a significant increase in the auction price. The cost per tonne in 1990 was 0.0066 million INR, which increased to ~ 0.54 million INR by 2000. The trend in the prices skyrocketed from 2008 onwards when it cost 3.97 million INR. The highest price at which it was auctioned in the past two decades was in 2019 when each tonne cost 7.99 million INR. The average decadal cost of the auction wood from 1990 to 1999, 2000 to 2009 and 2010 to 2019 was 0.15, 2.51 and 5.76 million INR, respectively (Fig. 6). Apart from auctioning, Marayoor has the only oil extraction unit owned by Kerala Government which is managed by Kerala Forest Development Corporation. The unit was set up in 2001 and is operational.

5 Way Forward

Apart from spike infestation, the trees in the area are damaged due to infestation by borers. A tree-to-tree survey has to be carried out to document the health status of individual trees. This would also help in controlling the source of spread. Though seed production is satisfactory, natural regeneration is a concern. Therefore, it is important to develop at least one hectare protected area as a seed stand in each reserve in this area. As this division has a vast and genetically divergent repository of trees, it is ideal

Fig. 7 A panoramic view of sandalwood trees in MSR

for initiating a tree improvement programme in sandalwood. Superior genotypes can be identified, utilized and conserved for posterity. It is also necessary to establish a germplasm bank of seedling origin that consists of seeds from superior genotypes which may be used as source material for further improvement. A state-of-the-art modern nursery has to be established to raise sandalwood seedlings, which can be used to augment artificial regeneration and provide seedlings for cultivation. Considering its value and protection rules, cultivation of sandalwood is not encouraged in farmlands. A private owner can neither harvest nor sell the sandalwood tree as green felling is prohibited both in government- and privately owned lands. It is hoped that the government would formulate certain measures that would encourage sandalwood cultivation in Kerala in the future.

The sandalwood population in Marayoor has stood the test of time despite all the threats and difficulties because of the Kerala Forest Department's tireless efforts in protecting the valuable trees (Figs. 7, 8 and 9). To the best of our knowledge, this is the only area in the world with the largest population of sandalwood that exists and should be conserved for posterity. Therefore, it is rightfully called the last bastion/frontier of the natural population of Indian sandalwood.

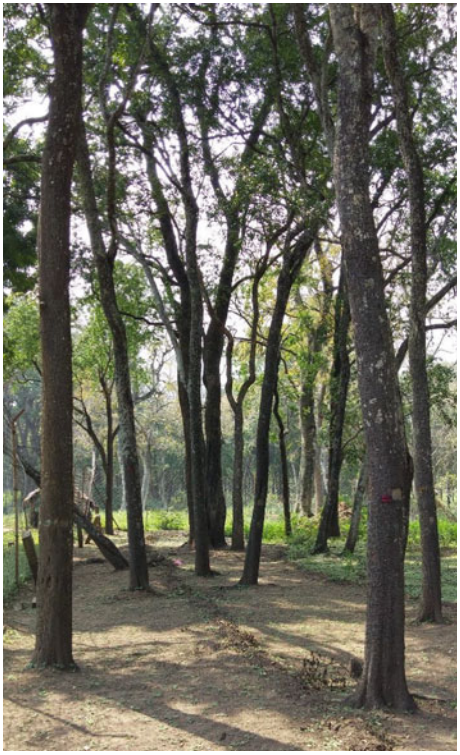

Fig. 8 A patch of large girth trees in MSR

Fig. 9 A large-sized tree in MSR

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Chapter 8
Santalum album: Current Status, Research and Future Perspectives in Sri Lanka

S. M. C. U. P. Subasinghe

1 History of Use of *Santalum album* in Sri Lanka

Santalum album is known as 'Sudu handun' (white sandalwood), and 'Sandanam' in local Sinhala and Tamil Languages [6], respectively, is mostly found in the home gardens of most of the areas other than mountains of colder climates in Sri Lanka. Although naturally found in India, Indonesia and several islands of the Indonesian archipelago, it is believed to be indigenous to India, with over 90% of the population recorded in Karnataka, Kerala and Tamil Nadu states [1, 5].

It was stated that *S. album* is not native to Sri Lanka [4] because it is not distributed in the natural forests of any climate region of the country. However, its value has been recorded in ancient poetry in Sri Lanka. Verse 51 of Loweda Sangarawa written by Ven. Thotagamuwe Sri Rahula (1408–1491) states that '*Feasting on delicious food that gratifies the palate, wearing sandalwood perfume that dazzles the senses and dressing extravagantly with jewellery are like performing a circus act*'. Verse 46 of Subhashithaya written by Algiyawenna Mukaweti (1521–1581) states that '*Great minds of boundless virtue and intelligence are not corrupted even in the face of endless struggle, just as the fragrance of sandalwood that pervades the air in all directions continues to spread its fragrance even when being wounded or cut*'.

S. album has been frequently used for Hindu religious and cultural activities, especially in cremations and wedding ceremonies. The antimicrobial properties of *S. album* were found mentioned on the roof of an ancient Hindu temple ruin in the Jaffna Peninsula, the most northern part of Sri Lanka where it was stated that '*Emulsion of sandalwood engulfs harmful organisms on skin*'. Its powder and oil have been extensively used for traditional medicine in the past in Sri Lanka by the practitioners mainly as an antiseptic and astringent and for the treatment of headache, common

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cold, stomachache, liver and gallbladder problems, haemorrhoids and urinary and genital disorders. The essential oil, emulsion or a paste is also used as a treatment for inflammatory and eruptive skin diseases. Its medicinal properties act against blemishes, pimples, suntan, wrinkles, skin ageing, dry skin and swelling while smoothing the skin. Moreover, sandalwood is used to treat scabies caused by a microscopic skin mite (*Sarcoptes scabiei*) (personal communication with traditional medical practitioners). The fragrance of *S. album* is used to treat mental disorders such as depression because it is believed to relax the mind while connecting the physical, emotional and spiritual self. Certain traditional medical practitioners stated that it helps to calm their minds during meditating practices (to bond with chakra) (personal communication with traditional medical practitioners).

2 Distribution of *Santalum album* in Sri Lanka

Though there are no records of *S. album* growing in natural forests, it can be seen growing in association with many different host species in homegardens and adjacent lands in all three major climatic zones, viz. dry, wet and intermediate in Sri Lanka (Fig. 1). Particularly its distribution is more common in the hilly areas of the intermediate zone, especially in the Badulla and Welimada regions of Uva Province, where there are distinct rainy and dry periods in a year. The annual rainfall of this area varies from 1000 to 1500 mm, while the average annual temperature ranges from 22.5 °C to 25.0 °C with warm day times and colder nights. It can also be seen in the other areas of rainfall and temperature varying from 1000 to 3000 mm and 22.5 °C to 32 °C, respectively. However, it is not recorded in the colder areas of the hilly regions where annual rainfall is higher than 2,500 mm, and the average temperature is less than 20 °C.

3 Growth and Population Dynamics

According to the Flora of Ceylon [4], *S. album* grows up to 4 m or slightly more with a straight trunk. However, Subasinghe [18] found much taller trees than that in Badulla, Hambantota and Kurunegala districts of Sri Lanka (Table 1) where *S. album* is frequently found in homegardens and adjacent vegetations. The trees found in Hambantota region are comparatively low in all tested parameters because those were the only ones left after a high level of poaching.

Due to the lack of long-term growth records of *S. album* trees, accurate estimation of growth rates is not possible. However, based on the information gathered from tree owners of various regions during the past 15 year period, it was estimated that the average annual diameter growth and height growth of *S. album* vary from 0.3 to 1.0 cm and 0.5 to 1.0 m, respectively.

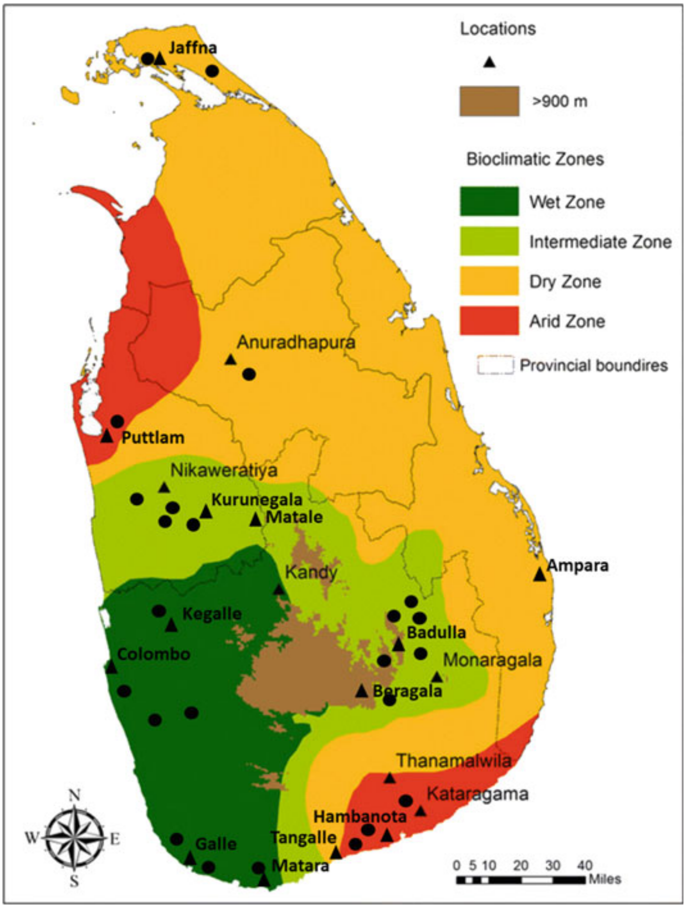

Fig. 1 Distribution of *S. album* in Sri Lanka. Black circles denote the *S. album* populated areas

Knowledge on *S. album* haustoria relationship with different host species is important in enhancing the growth, heartwood and oil contents [21]. Records of recently established *S. album* plantations in Sri Lanka confirm that the owners use leguminous trees, mainly *Sesbenia grandiflora* and *Gliricidia sepium* as the host species. In the homegardens, where the *S. album* spreads naturally, it can be associated with any potential tree. However, during a survey conducted in 2012–15 period, it was interesting to find out that *S. album* growing in the Badulla region is mainly associated with *Neolitsea cassia* of Family Lauraceae (44.2%; N = 50).

S. album population increase is very slow even in the areas where it grows naturally perhaps due to the very low germination rate of its seeds under natural conditions. Another reason could be the very low survival rate of seedlings under harsh environmental conditions in those areas.

Table 1 Variation of selected tree (±standard deviation) and climate characteristics of *S. album* in three regions of Sri Lanka

Characteristic	Badulla	Hambantota	Kurunegala
Mean diameter at breast height (cm) Mean height (m)	11.0 ± 2.6 8.6 ± 3.2	7.6 ± 1.5 4.5 ± 1.0	7.9 ± 1.9 5.5 ± 1.1
Mean heartwood% (at breast height) Mean oil% (at breast height)	28.5 ± 18.2 1.9 ± 1.3	32.8 ± 21.8 0.40 ± 0.30	43.4 ± 20.0 1.4 ± 1.0
No of dry months (year^{-1}) 75% expectancy of rainfall (mm year^{-1}) Agro-ecological region	5 1150 Intermediate-up (3)	6 890 Intermediate-low (3)	4 1100 Intermediate-low (1)

Climate variation Source: Somasekaran [17]

4 Legal Status of *S. album* in Sri Lanka

Due to slow population increase and high level of poaching, *S. album* was declared a protected species under the Fauna and Flora Protection Amendment Act No. 22 of 2009. Due to this act, permission should be obtained from the Department of Forest Conservation and the Divisional Secretariat for felling and transporting *S. album* within the country. Permission should be obtained from the Department of Wildlife Conservation for export purposes as well. However, this species is not listed as an important species in the Fauna and Flora Red List of Sri Lanka [14], even though the Global Red List updated in 2020 by the International Union of Conservation of Nature includes it in the 'Vulnerable' category at a global scale [2]. Furthermore, the Convention of International Trade of Endangered Species (CITES) does not recognize *S. album* as an important species in international trade.

The above restrictions were formulated in Sri Lanka mainly to control the poaching and illegal transport of *S. album* logs and export of oil. However, illegal trade still prevails in the country due to the high value of heartwood averaging USD 40.00 to 50.00 per kilogram. Due to this value, the poachers tend to cut any tree irrespective of its maturity and the amount of heartwood formed. Most of the time, they make a deep cut on the lower part of the stem, and if the aroma is not sensed, leave the tree which will later fall down due to wind. Even after the valuable parts of mature trees are taken away by the poachers, tree owners cannot sell the remaining parts due to the prevailing law. This is the main reason why villagers are not willing to plant and maintain *S. album* trees in their homegardens.

Table 2 Annual *S. album* seedling production in major nurseries in Sri Lanka (for the last 5 years)

Nursery location	Annual seedling production
Ampara	50,000
Badulla	25,000
Kurunegala	25,000

5 Trends in Plantations Establishment

Due to legal restrictions and lack of understanding of the growth dynamics, *S. album* plantations were not established in Sri Lanka until the last 10 years. Even to date, the *S. album* plantations have been established in Sri Lanka only by the private sector, and government involvement in those activities is not observed. In addition, there is a trend of growing *S. album* in Buddhist temple gardens, school gardens and homegardens in different areas of the country, which is reflected in the total seedling production in the major nurseries. Three main *S. album* nurseries managed in Sri Lanka produce about 100,000 seedlings (Table 2) per year (Jayasekara, pers. comm.). Out of that amount, about 50% is sold for plantation establishment, and the rest is sold for planting as individual seedlings or clusters in a small scale. However, the survival rates of the sold seedlings in the field are not available.

5.1 Constraints in Nursery and Plantation Establishment and Management

The value of *S. album* lies in the amount of heartwood formed inside the stem and roots and the oil content. Therefore, it is necessary to take the most appropriate steps at the right time in plantation management to increase the heartwood amount and oil content which are hindered due to some key issues described below.

6 Constraints in Nursery Management

6.1 Seed Supply

The supply of *S. album* seeds is highly restricted to a few areas of the country due to the lack of mother trees caused by intensive poaching. At present, Boralanda Region of Badulla District, Uva Province, supplies most of the seeds for the *S. album* nurseries. Though seeds are available in small quantities in the Kurunegala district of the north-western province, nursery managers still prefer seeds collected from the Uva Province due to the belief that the trees growing in that region produce better quality oil. Sometimes, even if suitable mother trees are available, most of the tree owners are not willing to engage with the seed collection processes due to the small seed size of *S. album,* lack of time and due to other commitments. However, this problem will be eased once the recently established plantations start producing seeds in large quantities.

6.2 Pests and Diseases

Although there were no large-scale damages to seedlings by pests, recently a mite attack became common and had to be controlled by applying suitable insecticides. Damping off caused by *Fusarium* and *Phytophthora* fungal species is the most common disease during the nursery period and is controlled by reducing the soil moisture levels of the seed beds and application of fungicides.

7 Plantation Establishment and Management

Ripe *S. album* seeds can normally be collected between January–February and July–September periods. The collected fruits are placed in water for three days until the pericarp is removed. Then, they are air-dried under sunlight for three days before storing in cotton bags in a dark, dry place. Before sowing in sand beds for germination, these seeds are soaked overnight in 0.1% gibberellic acid. Once the seedlings produce 2–3 sets of leaves, these are transplanted into polythene containers containing topsoil, sand and compost. Different nurseries in Sri Lanka use different proportions of the above mixture, and some do not use compost in order to reduce the pathogenic infestations. All nurseries use *Alternanthera* species as the seedling/container host. In a well-managed nursery, the seed germination rate varies from 40 to 60%, and the seedling survival is about 75–80% (personal communication with a nursery manager).

Private sector investors started establishing *S. album* plantations in Sri Lanka in 2008-09 with continuous expansion within a decade. Those plantations have been established in the wet zone (Kegalle Matale and Rathnapura districts), dry zone (Polonnaruwa district) and intermediate zone (Badulla and Kurunegala districts). Out of those plantations, about 1200 acres are maintained by four private sector companies, and the extents maintained by small-scale entities are not publicly available.

The majority of those plantations were established by keeping a 4 m distance between *S. album* plants. Two hosts are used, *Sesbania grandiflora* or *Gliricidia sepium,* at a 1.2 m distance away from each *S. album* plant on flat lands or lands with moderate slopes. The *S. album* planting distance may vary on high slopes depending on the contour pattern, but the distance to the host plant is kept at 1.2 m. When plantations are established in the dry and intermediate zones with shorter rotations, drip irrigation systems are kept in place for supplying water in the drier periods. Though there is a wider spacing, viz. 4 m between two *S. album* rows, intercropping is not usually practiced which could be due to the high amount of labour required to maintain such crops.

There are several problems faced by the large- and medium-scale *S. album* plantation managers which have become difficult to overcome due to various reasons, as illustrated in the following sections.

7.1 Poor Quality Lands

Due to the high cost of lands, the investors are reluctant to purchase or lease good quality lands to large extents for agricultural activities. Therefore, the lands available for reasonably affordable prices are poor in nutrient quality due to frequent use for agriculture or due to erosion in high slopes. Additionally, boulders are often present in these lands reducing the potentially available space for planting. Therefore, those lands do not support the optimal tree growth while requiring high maintenance cost. Even with all possible steps taken, the trees' growth enhancement to the optimal levels is not possible in such lands. Besides, heavy machinery use is not possible in lands with high slopes or frequent boulders.

7.2 Water Supply

Water supply is essential for the early stages of the commercial-scale plantations established in the dry and intermediate zones in Sri Lanka. *S. album* plantation managers supply 4–8 L of water per each *S. album* plant at daily or 2–4 day intervals depending on water sources' availability. Therefore, the availability of a water source to adequately supply required amounts is essential in plantation management, which is impossible if the plantations are located on hilly grounds. In that case, water should be transported from an outside source which is sometimes difficult due to poor access.

7.3 Wild Animals

Damages to *S. album* plantations by wild animals have become a major problem in Sri Lanka since they are located in remote areas. In the early stages, small mammals such as rabbits and barking deer eat the leaves, while porcupine and wild boar damage the root collar area of young plants. Rodents such as rats and squirrels damage the irrigation lines during dry periods to obtain water. Damage by wild elephants has also become an intense problem in the plantations established in the Kurunegala and Polonnaruwa districts, which cannot be eliminated with traditional methods such as electric fences because elephants can break those fences by pushing them to the ground or throwing logs. Once entering the plantations, they break or crush the trees and damage the irrigation lines and other properties. They also pose a threat to the workers, especially in the plantations maintained with small jungle patches to enhance the biodiversity.

7.4 Weeds

Heavy weeds can be observed in most of the *S. album* plantations located in Badulla, Matale and Polonnaruwa districts. The weed growth is aggravated due to the 4 m spacing between planting rows. The most common weeds are *Megathyrsus maximus*, *Glyceria maxima* and *Imperata cylindrica*, locally known as Guinea/gini grass, mana and iluk, respectively. Among them, control of *M. maximus*, a fast spreading alien invasive species seen in 16 administrative districts out of 25, is not possible using manual labour in hilly terrains due to its rapid growth and survival of the seeds under harsh conditions. Due to a lack of research findings, plantation managers are reluctant to use chemicals against those weeds as they fear that *the S. album* plant would absorb the same chemicals via haustoria formed with the roots of those weeds. In the plantations established on flat terrains, tractor weeding between planting rows is common. Manual labour is used in the rest of the areas where progress is slow and costly. However, manual weeding must be used along the planting lines and around the plants due to drip irrigation lines.

7.5 Disease/Pests

White root and brown root diseases caused by fungal species *Rigidoporus* and *Phellinus noxius* are the two fatal diseases of *S. album* in Sri Lanka. Field evidence has confirmed that those two diseases, especially white root, have become common in all climate regions in Sri Lanka. Early diagnosis of the symptoms is vital in controlling both diseases which will be difficult to control otherwise. Fusarium wilt caused by *Fusarium* species is also common in *S. album* plantation of Sri Lanka but is not fatal. Therefore, it is not considered as dangerous as the previous two diseases.

Red borer (*Zeuzera coffea*) is a destructive insect that lays eggs after making tiny holes in *S. album* stem allowing the larva to feed on the pith [20] which later causes breakage at that point. The infestation is frequent after rainy periods where the stem tissues are comparatively tender than in the dry periods. Since the holes made by *Z. coffea* in the stem are not detectable by the naked eye, it is difficult to control the damage.

7.6 Fire

The threat from fire is higher in the plantations that are bordered by paddy fields, as the farmers create intentional fire to control weeds to prepare those fields for cultivation during the forthcoming rain periods. The spread of fire to the nearby lands including the plantations is rapid due to the dry weather and prevailing wind. Therefore, when spread inside the plantations, fire control is a difficult task, especially if there is no adequate supply of water and machinery. Sometimes, even wide fire belts are not adequate for preventing the fire from entering the plantations under high winds.

7.7 Illegal Felling

As the sandalwood plantations in Sri Lanka are less than 10 years old, there is currently no potential threat of poaching those trees. However, this threat will be manifested in the future once the trees mature and start producing oil in the heartwood. This risk will be more intense in areas where the plantations are bordering government forests and scrub jungles and in remote areas where the poachers' movements cannot be detected from a distance. Due to this reason, plantation owners are even currently looking for potential prevention mechanisms varying from increasing security to advanced technological methods to protect their trees from illegal felling.

7.8 Lack of Labour

The common practice established by managers to maintain their plantations is to use the workforce of nearby farming communities. However, maintaining such a labour force consistently is difficult because these farmers need to engage with their own farming activities during the rainy seasons where the plantations also have intensive management activities varying from planting, fertilizing, weeding, etc. Bringing labour from distant areas while providing the worker accommodation is also not financially feasible for plantation managers. Therefore, the lack of labour hinders plantation management's efficiency in most of the areas in Sri Lanka.

7.9 Legal Issues

The present legal situation in Sri Lanka on exporting *S. album* products, including heartwood and oil, acts as barriers to the private sector entering the plantation establishment. The value of *S. album* heartwood was reported to be about USD 16,175.00 per MT, while the oil price was reported to be about USD 1,000.00 per kg by Jain [12]. The value could be much higher at present due to the high demand. Therefore, if Sri Lanka's Government lifts the current export ban on *S. album,* it could be significantly beneficial for gaining foreign income. This could also play a role in poverty alleviation by contributing to the increase in the workers' income living in rural areas. Since *S. album* is not a tree species native to Sri Lanka [4], current *S. album* plantation owners expect its export ban to be lifted at least once their trees become mature enough in the future. The country's current legal status also prevents many new private sector investors from entering into *S. album* plantation establishment.

8 New Trends Emerging Among Small-Scale Plantation Owners in Sri Lanka

A few smallholding *S. album* plantation owners in Sri Lanka expect to conduct nature/culture-based tourism activities on their premises till the trees are harvested. This interest mainly lies among the owners who maintain their plantations in hilly areas such as Bandarawela and Badulla with beautiful sceneries. They expect to construct eco-friendly solitary cottages inside the *S. album* plantations facing highly scenic landscapes allowing tourists to practice meditation and other cultural activities under sandalwood scent produced by burning heartwood of *S. album.* As they expect to keep their *S. album* trees for about 20–25 years on the ground before harvesting, this will be a profitable intermediate income generation method.

S. album plantations managed scientifically also allow the owners to manufacture certain products from the branch wood removed while pruning. Incense sticks and toothpicks have become more popular options among them in this regard. Though the amount of wood produced in branches removed in pruning is low, plantation owners believe that it will be sufficient to generate a reasonable income due to the rarity of those products in the market, especially in the hotel industry of Sri Lanka.

9 *Santalum album* Research Conducted in Sri Lanka

9.1 Microscale Oil Extraction

Obtaining a 0.5–1.0 cm diameter core sample is the best option for the non-destructive sampling of *S. album* stems for oil- and heartwood-related studies. However, the sample size is small due to the smaller size of the trees available in most areas. Collection of all the oil extracted during hydro-distillation including the oil remaining on the inner surfaces of glassware is essential for proper calculations with smaller sample sizes. Therefore, the normal hydro-distillation was further improved to effectively extract oil from 2 g of heartwood sample using Clevenger's apparatus with 10 ml collecting arm and a smaller round bottom flask. In this method, the collection arm should be filled with 5 ml water and 2 ml n-hexane before the distillation process. Distillation is carried out for 8 h in 50 ml of distilled water. Once the distillation is complete and cooled to room temperature, another 3 ml of n-hexane is used to wash and collect the remaining condensate in the condensers and collector arm. This organic layer is dried with anhydrous sodium sulphate and evaporated to dryness under reduced pressure in preweighed glassware [9].

9.2 Host Selection at Nursery Stage

Brand [3] found that the survival and growth of *S. spicatum* (Australian sandalwood) were differently affected by different *Acacia* species where both the highest survival and growth were recorded with *A. saligna,* while the lowest was recorded with *A. hemiteles.* They also stated that the highest nitrogen, phosphorus, potassium, calcium and magnesium levels in leaves of *S. spicatum* were found when grown under *A. saligna* and the lowest was recorded under *A. hemiteles.* Therefore, it is important to carefully select the most suitable host species matching climate and soil conditions. Gamage [8] conducted research to identify the most suitable host species for *S. album* seedling growth enhancement during the nursery phase using *Alternanthera* sp. (family: Amaranthaceae), *Cassia tora, Clitoria ternatea, Desmodium triflorum, Mimosa pudica* (Fabaceae) and *Tagetes erecta* (Asteraceae). Out of the selected host species, the tallest *S. album* seedlings were produced by *D. triflorum,* followed by *M. pudica, A.* and *C.ternatea,* respectively. The lowest growth was produced in the containers maintained without any host species. Leaf analysis of seedlings grown with all selected host species indicated the nitrogen levels varying from 3.4% to 4.0% while phosphorus varying from 0.21% to 0.33%. The results also revealed that the highest nitrogen and phosphorus contents were present in the *S. album* seedlings grown with *D. triflorum* and *M. pudica,* respectively.

9.3 Field Host Selection

To identify the most suitable field host species which can be used in *S. album* plantation establishment, Subasinghe [19] researched for a 3-year period in Amupitiya, Balangoda of Rathnapura district where the annual rainfall is about 1,500 mm, the average temperature is 25–30 °C and elevation of 590 m from the mean sea level. *Acacia auriculiformis* (Aa)*, Calliandra calothyrsus* (Cc)*, Gliricidia sepium* (Gs)*, Sesbania grandiflora* (Sg) of family Fabaceae*, Coffea arabica* (Ca) of family Rutaceae and *Grevillea robusta* (Gr) of family Proteaceae were tested in this research in all possible two-host combinations. Although the leaf nitrogen, phosphorus, potassium and magnesium contents of *S. album* plants were not significantly different due to different host combinations used, the height showed significant variations. The tallest *S. album* plants were produced by Cc × Cc host combination followed by Aa × Sg, Cc × Sg, CC × Gs and Aa × Cc. The results revealed that *C. calothyrsus* was in 4 out of the best 5 host combinations proving a successful host. Some sandalwood researchers believe that there are more financial benefits if grown with a commercial crop as a host. However, *C. arabica* used in this trial did not support the growth of *S. album*. Further, *C. arabica* does not grow well in lower elevations and drier climates, so the information of the suitable host species for different climate regions is still lacking in Sri Lanka. This could be the reason that *Pongamia pinnata*, *Casuarina equisetifolia* and *Azadirachta indica* were good hosts for *S. album* in the southern parts of India [15].

9.4 Oil Content Variation

Oil content analysis of three *S. album* trees of 20 cm average diameter and 12 m average height harvested from Welimada of Uva Province indicated that it reduced from 4.0% to 2.3% (Fig. 2) within the first 3 m above the ground level [7]. This indicates that there is a rapid loss of oil content (%w/w) along the stem. However, those trees' age was not identified due to a lack of planting records with tree owners [7].

A recent study conducted by Subasinghe [18] on oil content variation of *S. album* trees growing in different agro-ecological regions in Sri Lanka is given in Fig. 3 [18]. According to that study, the highest average oil content was recorded in the IU3 zone (2.05 ± 0.23) followed by IL1 (1.01 ± 0.31), WM1 (1.00 ± 0.15), WL4 (0.95 ± 0.56) and DL3 (0.6 ± 0.49), respectively. The lowest average oil contents were observed in WM3 (0.17 ± 0.02) and WL2 (0.10 ± 0.08). During the analysis

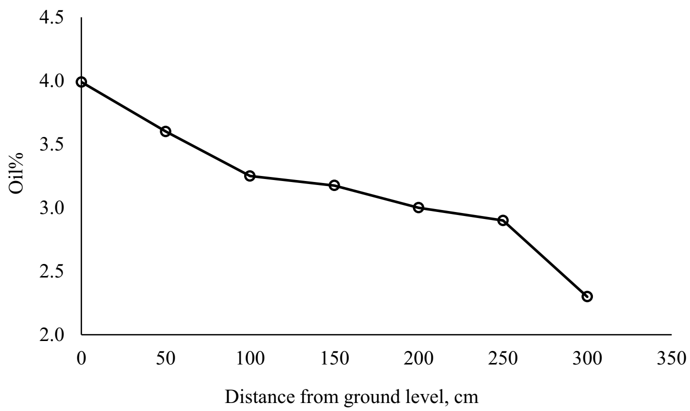

Fig. 2 Average oil content (% w/w) variation of harvested *S. album* trees

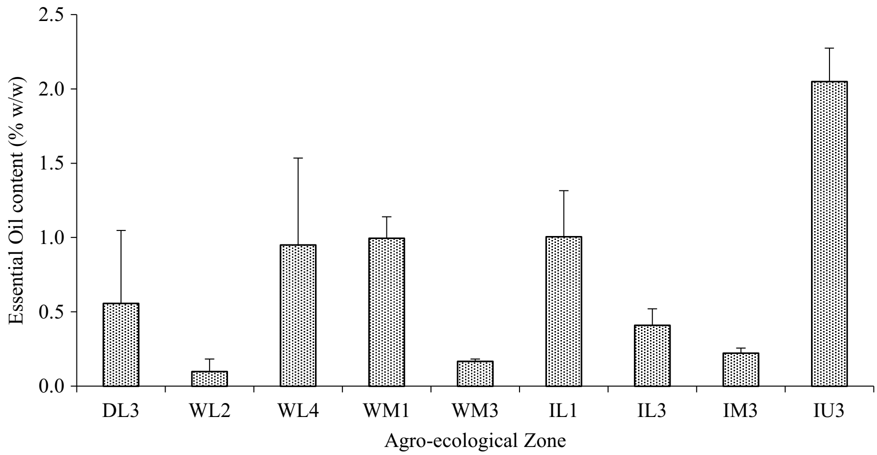

Fig. 3 Variation of *S. album* heartwood oil content in different agro-ecological regions. *Source:* Subasinghe [18] D = dry zone; W = wet zone; I = intermediate zone; L = low elevation; M = mid; elevation U = up elevation

of the above data, it was not possible to identify a correlation of oil content with the elevation or rainfall of the growing sites.

ISO standards of the cis-α-santalol and cis-β-santalol of *S. album* are above 41% and 16%, respectively [11]. The above samples' oil constituent analysis indicated that the average cis-α-santalol and cis-β-santalol levels of DL3, WL2, WL4, WM1 and WM3 regions are over the ISO standards [18]. It was also not possible to identify a significant correlation between oil content and the above two constituents.

9.5 Physical and Chemical Properties of Seed Oil

The demand for vegetable oil is also gradually increasing worldwide [13], as they are a healthier alternative than animal fats that contain more unsaturated fatty acids. The *Santalum* seed oil could be used as a substitute as they are a rich source of unsaturated fatty acids. Manufacturing of edible oils using *S. spicatum* (Australian sandalwood) has already been started [10]. Therefore, *S. album* seed oil extraction could be used as a secondary income source and an economic incentive for poverty alleviation. Fatty acids such as palmitic acid, palmitoleic acid, stearic acid, oleic acid, linoleic acid, linolenic acid, stearolic acid and ximenynic acid are remarkably present in the seed oil fatty acid profile of *S. spicatum.* According to the findings of *S. spicatum,* seed oil is a rich source of natural and highly stable acetylenic fatty acid and ximenynic acid. Thus, it is useful as an anti-inflammatory agent, to increase dermal microcirculation for varicose veins and cellulitis and reduce hair loss, fat deposition under the skin and skin oiliness [10].

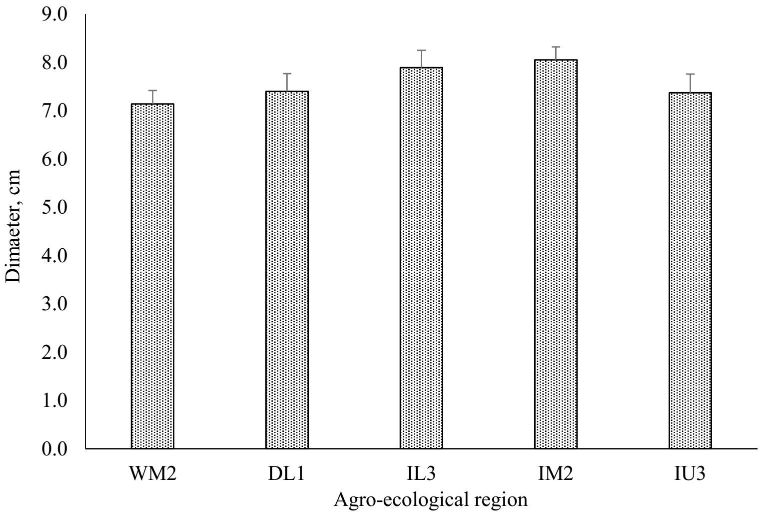

Fig. 4 Variation of plantation grown *S. album* seed diameter in different agro-ecological regions. W = wet zone; D = dry zone; I = intermediate zone; M = mid elevation; L = low elevation; U = up elevations

Piyarathne [16] conducted a preliminary study on seed oil variations of *S. album* in Sri Lanka. According to the results, the seeds obtained from plantations of 5–7 years of age from different geographical regions varied as illustrated in Fig. 4.

The authors also tested the *S. album* seed oil's physical parameters of the geographical regions mentioned in Fig. 4 (Table 4). They were not able to find significant variations of those parameters between tested geographical variations. The same study found that the ximenynic acid content is high in *S. album* and is similar to that of *S. spicatum.* However, the amounts of palmitic acid, stearic acid and especially oleic acid are comparatively less in *S. album* seed oil (Table 5). More research, however, is needed regarding seed oil extraction and properties in Sri Lanka to arrive at proper conclusions in this regard.

10 Conclusions and Future Perspectives

Although *S. album* is not native to Sri Lanka, it has been distributed in most areas other than in higher elevations of colder temperatures. Traditionally, it has been used for medicine, and its value has also been recorded in ancient literature. Currently, the number of mature tree populations is rapidly declining due to the high level of poaching, which occurred during 2000–2010. This has forced the government to take action against *S. album* tree harvesting and export of its products. Though commercial-scale plantation establishment of *S. album* was started about 10 years ago, the managers and owners face numerous constraints such as lack of seed supply,

Table 4 Tested parameters of *S. album* seed oil

Oil yield, %	Specific gravity	Acid value (mgKOHg^{-1})	Free fatty acid (mgKOHg^{-1})	Iodine value (g I2 100 g^{-1})	Peroxide value (mequiv O_2 kg^{-1})	Refractive index
74.0 ± 18.2	0.94 ± 0.05	7.29 ± 0.84	14.57 ± 1.67	88.02 ± 2.98	6.67 ± 1.97	1.02 ± 0.07

Table 5 Comparison of major fatty acid constituents of *S. album* and *S. spicatum*

Chemical constituent	*Santalum album*	*Santalum spicatum**
Palmitic acid	0.8–1.0	3.6
Stearic acid	0.4–1.5	1.8
Oleic acid	12.3–18.0	50.1
Ximenynic acid	45.0–87.0	35.1

**Source* Hettiarachchi [10]

poor quality in land available for plantation establishment, lack of adequate amount of water supply, wild animal threats, heavy weed growth, threats of pests and diseases, fire, illegal tree harvesting, lack of adequate amount of labour and current legal status on tree harvesting and product export.

Some *S. album*-related research has been conducted in the past, especially on nursery establishment and field planting, geographical variations on oil content and constituents, seed biology, seed oil, etc. However, more research on silviculture practices, increasing heartwood and oil contents, plantation health management and oil processing and product manufacturing is yet to be conducted.

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Chapter 9
Status of Sandalwood in Indonesia and Neighbouring Countries

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1 Introduction

Indian, Egyptian and Chinese texts mention sandalwood dating back to 5000 years. The species formed the link between Timor, Java, India and China. Considered a luxury and prestige item, it found its way into the culture of these countries. Many of the islands of Indonesia and neighbouring countries describe the lush presence of sandalwood in their forests. With large-scale extractions, the populations dwindled and trade declined steadily. Realizing the need for long-term management and ecological sustainability, many of the regions once famous for the species natural distribution have drawn up plans on their road to recovery.

2 Indonesia

Santalum album is an important species of Indonesia. It is reported to be endemic to some ecoregions of East Nusa Tenggara (Nusa Tenggara Timur, NTT), an island in Indonesia. It is distributed in East Nusa Tenggara (Nusa Tenggara Timur, NTT) provinces in the islands of Timor, Sumba, Alor, Solor, Pantar, Flores, Rote and other islands. Besides in NTT, sandalwood is also found at Gunung Kidul, Imogiri, Kulon Progo at the special province of Yogyakarta (DIY), Bondowoso (East Java) and the island of Sulawesi [2, 52]. Several references point to Timor, Sumba and the NTT area

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as the centre of the natural distribution of sandalwood in the world as the ecological conditions have proven to be very supportive for the growth of sandalwood [53].

Historical evidence shows that the sandalwood trade existed since the second century AD between Indonesia and India. China also started trade with Indonesia during the fifth century, trading various products, including sandalwood [54, 65]. One of the first mentions of the trade of sandalwood dates back to 1644 when a Dutch vessel, Luijpaert, was despatched to the Lesser Sundas to collect a debt of '*12,000 real of eight worth sandalwood (Equivalent to 2,40,000 USD)*' from Larantuka, East Nusa Tenggara, Indonesia [27]. Sandalwood trade with Indonesia continued during the Portuguese and Dutch colonization. Sandalwood extracted from Timor, Sumba, Flores, Solor, Alor and Wetar was shipped to Sulawesi and sold to various countries [18]. In 1436, Chinese traders transported sandalwood from 12 ports in Timor, making Solor a strategic transit as they had difficulty stocking sandalwood on Timor Island, which led to the emergence of multicultural Solor society as reflected in its ethnic, religious and linguistic diversity [37].

Information on sandalwood extraction in Indonesia between 1969 and 1997 was huge, with an average harvest of 606,000 kg annually. The prices ranged from Rp. 1000 (for sapwood) to Rp. 118,000 (for class A) per kg based on the quality of wood. It provided a substantial revenue to the country with an average of Rp. 4,071,000,000 annually during 1990 and 1998, which accounted for 50% of the country's revenue [2].

Realizing the rapidly diminishing resources of sandalwood, the government brought out regional regulations in 1953, 1958, 1966, 1986 and 1966, attempting a radical change in the policy and regulation of sandalwood harvest and trade. The last order of 1996 led to unrest among the communities; the protectors of the wood were provided only 15% share from the sale of sandalwood. Data on the existing stock of sandalwood in 1998 revealed that the sandalwood population remained intact in the districts of Kupang, South Central Timor (Timor Tengah Selatan, TTS), North Central Timor (Timor Tengah Utara, TTU) and Belu. Presently, the natural habitat of sandalwood is widely available sporadically grown in nine districts of Kupang, TTS, TTU, Belu, West Sumba, East Sumba, Manggarai, Alor and Solor [25].

Realizing the need for sandalwood protection involving communities, the government in 1997 issued a moratorium on felling sandalwood for five years. Despite this, there was a steady decline in the sandalwood population. Data provided by the Forest Department of TTU [16] showed that the natural population of sandalwood in TTU comprised only 33,678 trees—98.82% less compared to stocks in 1997 [7, 8, 56]. Trees that are less than 3 m in height were counted and the ones that were of more than 30 cm girth and a height of more than 3 m were marked and measured. Figure 1 summarizes the results of the sandalwood census conducted in Timor and surrounding islands. There has been a sharp decline in numbers over the past.

About 100,000 trees were harvested from 1969/1970 to 1986/1987, (9,510,444 kg of sandalwood). The number of trees felled dropped to 143,316 trees in the following decade (7,465,917 kg of sandalwood). Ten years later, between 2001 and 2007, sandalwood production amounted to a low of 2,178,697 kg, reflecting productivity decline in Indonesia's sandalwood population [10, 38]. Seran [53] implies that the

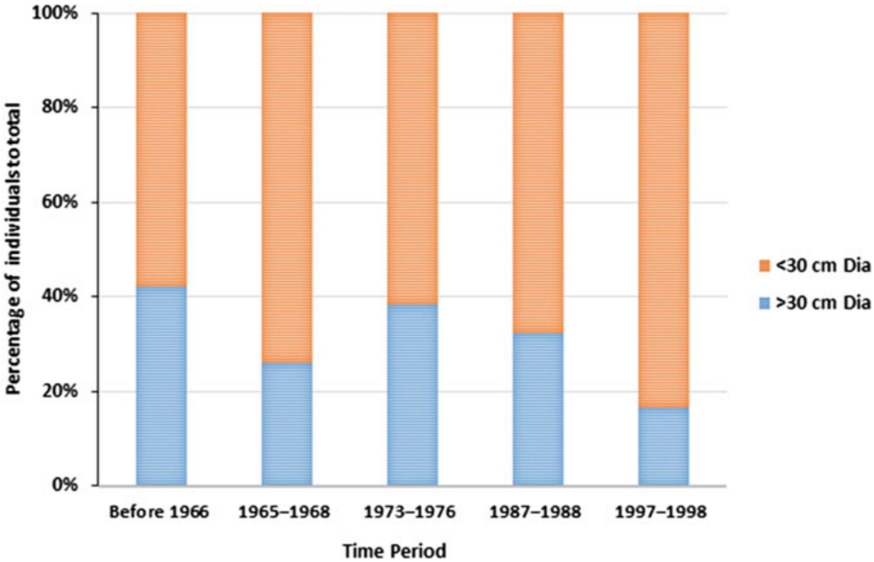

Fig. 1 Sandalwood census conducted in Timor and surrounding islands. Adapted from [22, 42]

significant factors that affected the decline in sandalwood population are the limited conservation efforts, slow reforestation efforts, poor community-friendly policies, ambiguities in laws related to ownership and trade of sandalwood, limited sources of sandalwood seeds, lack of institutional support to sandalwood farmers and limited funds to support sandalwood conservation [56, 57, 59]. An analysis of these factors prompted the Indonesian Government to develop a 'masterplan on sandalwood development and preservation in the NTT Province 2010–2030' to help NTT become a sandalwood province by 2030 [53].

One of the master plan implementations is by doing an inventory of the number of sandalwood populations that still exist today. Census by the Forestry and Estate Crop Service of TTS District show that a total of 1405 trees available, 1286 trees had a girth between 10 and 49 cm and an average age between 10 and 23 years, while those with a girth of 50–100 cm numbered only 119 [15]. Another study using sampling plots on private land in three districts in NTT (TTS, TTU and Belu) showed that TTS has the highest number of tree stages than two other districts (76 trees in TTS, 12 trees in Belu and six trees in TTU), in contrast to the seedlings stage, which was mostly found in TTU (1303), followed by Belu (428) and TTS (308) (Table 1) [24]. Both studies indicated the success of the NTT government programme to involve people in planting sandalwood on their private lands and the potential development of sandalwood in NTT in the future.

Recent studies have also shown similar results on community-owned gardens/lands and natural forests in the TTU and TTS districts [53]. The author compared the present status with the earlier records revealing that sandalwood trees' density ranges from 0 to 23 individuals ha-1, 80–322 poles ha-1 poles and 60–1289

Table 1 Structure of sandalwood distribution on community lands in three districts in NTT

	TTS	TTU	Belu
No. of villages studied	11	10	8
• Number of trees	76	6	12
• Number of poles	188	29	47
• Number of saplings	255	156	140
• Number of seedlings	308	1303	428
Competition index (IC)	0.18	0.07	0.10

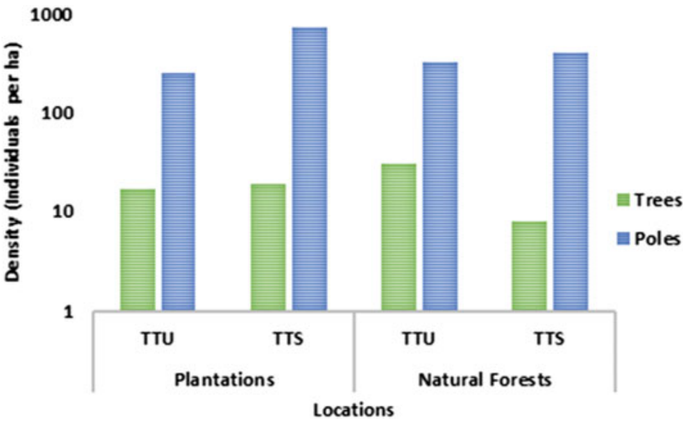

Fig. 2 Sandalwood populations and regeneration in plantations and forests of TTU and TTS

saplings ha-1. Natural regeneration is to the tune of 2000–27,813 seedlings ha-1 in Indonesia. Figures 2 and 3 show that the best sandalwood populations and regeneration are found in plantations (TTS), followed by forests of TTU. Although these results are slightly different from previous studies [24], all studies show a dominance of the growth stage of poles and seedlings compared to the tree stages.

TTU has a higher density (48 trees per ha) than TTS (27 individuals per hectare)—a situation considered deplorable, as these districts had 42,266 and 80,651 individuals/ha at the beginning of the century [7, 9]. The sandalwood trees could reach a height of 12–15 m and a diameter of 20–35 cm [50].

The Government of Indonesia has now initiated many programmes to support the conservation of the species through strengthening policy frameworks, providing incentives and participatory management through local institutions for sustainable sandalwood management. There is a notable increase in the seedling availability as compared to its density in 1987–1990. It defines the government's role in motivating the local communities to cultivate sandalwood outside forests and protect sandalwood stocks in the forest.

Figure 4 shows that the sandalwood population experienced a tremendous increase during the last decade, almost 200–500% compared to the sandalwood population

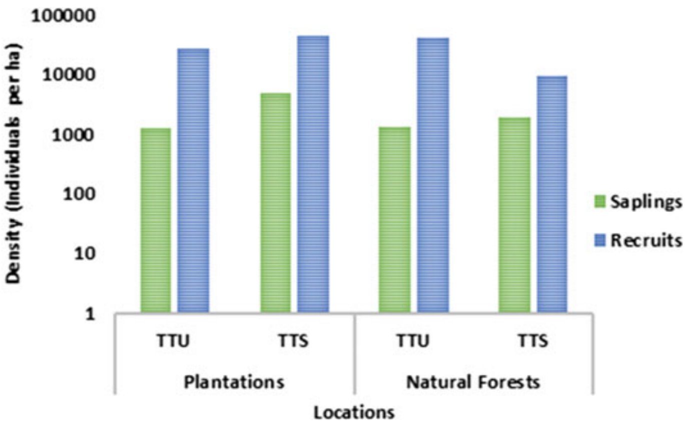

Fig. 3 The increase in recruits and saplings in plantations and forests of TTU and TTS

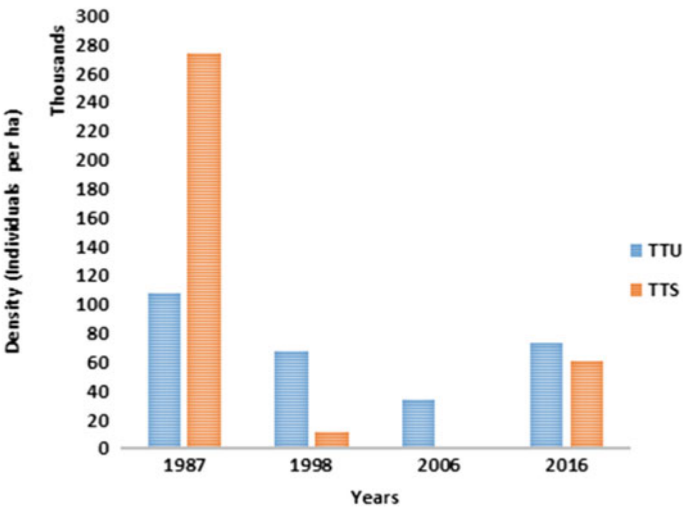

Fig. 4 Past and 2016 sandalwood population dynamics in the districts—TTU and TTS. TTU: Timor Tengah Utara, TTS: Timor Tengah Selatan

in 1998, but it is still very low compared to the sandalwood population in 1987. This increase is attributed to sandalwood cultivation by farmers in trees outside forests to ensure better prospects in the future. The efforts of the government in motivating the community to cultivate sandalwood are commendable.

Studies on land suitability of sandalwood development in Indonesia revealed that about 56.08% of NTT is suitable for the species. Suitability within each district of NTT revealed TTS, having an area of 278,818.77 ha (70.64%), to be the most suited, followed by TTU with an area of 163,554.16 ha (61.26%). Belu Regency with an area of 125,216.69 ha (51.32%) and Kupang covering 263,677.77 ha (44.73%) and Kupang City covering an area of 8994.48 ha (49.89%) of the total land area was also found fit for sandalwood cultivation [25, 55]. Secondary dryland forests were the most suited regions. These are regions where sandalwood had existed earlier and are presently devoid of it. The focused efforts of the country towards making NTT a sandalwood province are turning into a reality (Fig. 5).

The main distribution of sandalwood is in NTT, especially on the islands of Timor and Sumba. However, currently, its distribution has extended from Bondowoso District in East Java eastwards to Timor, Sulawesi and the Moluccas and as far as northern Australia [45]. Data from the herbarium of the Bogor Forest Research and Development Center showed that sandalwood specimens had been collected from Maluku (Moluccas Island) in 1924 and 1937; Manado (Palu) as part of Sulawesi Island in 1932 and 1938; Kediri in East Java in 1919 and 1937; and some regions in Sumba (1923), Pulau Timor (1923), Kupang (1925), Manggarai (1935) and Timor Tengah (1975) are a part of NTT.

Sandalwood on Java islands is believed to have existed more than 100 years ago. The herbarium specimens at the Indonesian Institute of Sciences (LIPI) recorded that the oldest sandalwood was collected in 1853 in the Makam Raja-raja Imogiri, and the other collections include Situbondo (1893), Madura (1894), Kediri (1922), Wonogiri (1922), Pasuruan (1922) and Malang (1930). All these regions are a part of the Gunung Sewu Global Geopark Network, an area consisting of three GeoAreas, namely Gunung Kidul (Yogyakarta), Wonogiri (Central Java) and Pacitan (East Java) [46].

Sandalwood in Java is likely to have originated from NTT. An example of sandalwood in Gunung Kidul was initially introduced as part of the critical soil rehabilitation programme in Gunung Kidul Yogyakarta in 1967 in the Wanagama Research Forest. In the beginning, more than 6800 seedlings were planted, out of which only 11 of them were able to survive. Four years after the first planting, many saplings were found under *Melaleuca cajuput, Acacia tomentosa* and *Acacia catechu*, indicating the ability of sandalwood to naturally regenerated outside its endemic area in NTT. Natural regeneration of sandalwood in Wanagama Research Forest in Gunung Kdul now has occurred extensively over a radius of more than 5 km [21].

Many landraces of sandalwood in Java have been formed because of planted and naturally regenerated stands [47]. Eight types of sandalwood landraces in Mount Sewu, which were having a clear history of the establishment, are naturally regenerated, reproduce sexually and represent each geographical zone identified [47] and shown in Table 2.

Provenance trials established in Wanagama as a tree improvement programme, which helped in the conservation of sandalwood, have also been developed in Petak 18 in 1993. The provenance trials developed using genetic material collected from three provenances, namely Bu'at (TTS, NTT), Netpala (TTS) and Tilomar (East Timor); and four landraces, namely the Bromo Mountains (East Java), Imogiri (Bantul, Yogyakarta), Wanagama I (Gunung Kidul, Yogyakarta) and Karangmojo (Gunung Kidul, Yogyakarta). Provenances Bu'at, Netpala and Tilomar and Wanagama landraces represent dry conditions (semi-arid), Bromo landraces for

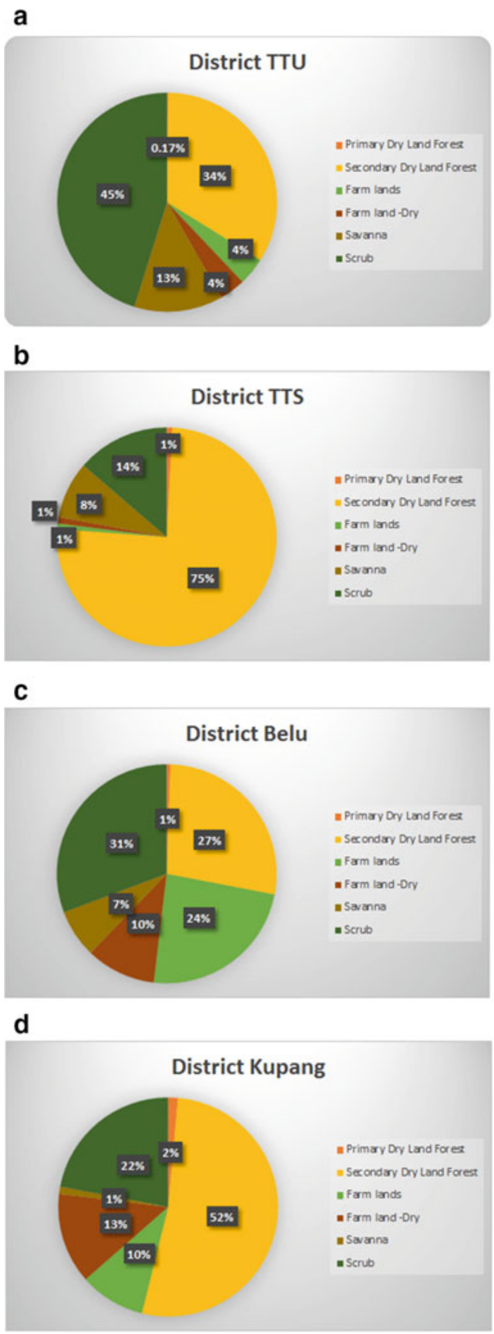

Fig. 5 Land suitability of sandalwood in different landuses in the districts—**a** TTU, **b** TTS, **c** Belu, **d** Kupang. TTU: Timor Tengah Utara, TTS: Timor Tengah Selatan

Table 2 Sandalwood landraces in Gunung Sewu regions

Regions	Landraces	Number of individu	
		Adult	Seedling
Lowland of Middle Zone	1. GSM1-Bleberan 2. GSM2-Mulo 3. GSM3-Wanagama	1834 41 276	364 12 78
Highland of Northern Zone	1. GSN1-Nglanggeran 2. GSN2-Sriten	1145 330	93 50
Lowland of Northern Zone	1. GSN3-Bejiharjo	496	124
Karst area of Southern Zone	1. GSS1-Petir 2. GSS2-Botodayakan	9190 151	2945 72

mountainous areas, while Imogiri and Karangmojo landraces suit lowland tropical areas [21].

Other approaches to conserve sandalwood in Gunung Kidul in Yogyakarta include two ex situ conservation plots in Watusipat (KHDTK) using 18 populations from NTT (Alor Island, Timor, Sumba, Rote, Flores and Pantar Island), Java Island (landraces of Karangmojo (Gunung Kidul) and Imogiri (Bantul). The plots established in 2002 and 2005 covered a total area of 3.5 ha [14]. After seven years of planting, the survival rate of the plot ranges from 30 (population of Pollen, South Mollo, TTS) to 95% (population of Waisika, Northeast Alor, Alor) for 2002 plot, and 27 (population of Bama, Flores Island) to 95.3% (population of Soebala, Rote Island) for 2005 plot. Sandalwood in the Watusipat plot was able to naturally regenerate, showing their potential as seed sources, natural laboratory for sandalwood studies, and a demo plot for sandalwood planting [14].

Sandalwood is not only found on the islands previously mentioned, but it can also be found on the island of Sumatra (Aceh), making Aceh the only region with sandalwood on Sumatra Island. The results of the genetic analysis indicated that sandalwood in Aceh appears to have been introduced from NTT. The habitat of sandalwood in Aceh and NTT are similar—dryland dominated by grasses and shrubs with an average temperature of 24–31 °C, low levels of organic C, N and P along with a neutral acidity level [39]. Sandalwood in Aceh is a potential seed source and has developed as the centre of sandalwood in Aceh. Sandalwood from Suka Makmur in Aceh has the highest genetic diversity [40].

Sandalwood, a non-timber forest product, has an important economic value in Aceh. Data showed that a total sandalwood utilization in Aceh province from 2003 to 2015 reached 357,124 tons or 29,760 tons per year [39]. However, the number is decreasing and mentioned in the Governor of Aceh Regulation Number 44 of 2017 [51]. It states that the production of sandalwood in Aceh in 2018 was planned at 14,000 kg. Sandalwood management is not carried out sustainably as indicated by the sandalwood trees' structure dominated by young trees, no cultivation activities and low harvesting efficiency with harvesting method using tree-length logging plus root [41]. Analysis vegetation of sandalwood in Pidies Besar District found a total of 227 stands, 225 stands dominated by seedling level (seedling, sapling and pole), and only two stands are mothers tree-level dbh ≥15 cm [39]. This is in line with the results of research on sandalwood in Aceh Besar and Pidie district that found 493 individuals of young trees (seedlings and saplings) with a volume of 1.02 m^3, while the mature trees (poles and trees) were only 51 individuals of 1.75 m^3 [41].

3 Timor-Leste

Timor-Leste is a natural habitat for sandalwood and the producer of high-quality, highly perfumed sandalwood. Two varieties of this species exist on the island: *S. album var. album*, characterized by small leaves and *S. album var. largifolium*, which has larger leaves [19, 49]. The smaller leaf variety is a better producer of wood and contains higher oil content [34]. Sandalwood is among the few valuable species that survive in a hostile environment, with low rainfall and low fertility soil [11, 35].

The island of Timor was visited by Chinese and Arab traders, who bartered sandalwood long before the Portuguese settled in Timor in the early sixteenth century [1, 6, 61]. Sandalwood trade intensified and remained active and profitable for many centuries. The Portuguese exploited the rich sandalwoods of the island. At the beginning of the nineteenth century, trade declined and, consequently, the colony's economic prosperity [6]. Realizing the reduced amount of adult trees and harvest of very young trees, the Governor of Timor Celestino da Silva, in 1901, issued an order prohibiting cutting and exporting sandalwood trees. This order remained in force up to 1910. Despite protective measures taken, sandalwood exports continued to grow at an accelerated rate (in 1913, sandalwood exports reached 907 tons) and stocks rapidly depleted.

In 1934, the cultivation of sandalwood was initiated. Nurseries were established for the renovation of existing forests and the formation of new forests. In the last quarter of Portuguese colonization (1950–1975) and during the period of part of Indonesia (1975–1999), there are few records on the export of sandalwood (Fig. 6), the total value exceeding 100 tons [48]. According to the few data available, the annual average export of sandalwood oil from Timor was around 30 tons in the late 1960s, decreasing significantly to an annual average of 7 tons in 1994 [64]. When Timor-Leste was part of Indonesia, there is a global estimate for logging and export of around 50 tonnes per year and an indication that this figure was only about 18 tonnes in 1989–1990 and reached 54 tonnes in 1991 [17]. After independence, in the years 2000–2003, there was total exploitation of about 200–300 legal tons, especially in border areas [6, 11].

Between March 2002 and November 2003, the police authority confiscated about 800 tonnes of sandalwood, mainly of low quality, whose destination was contraband to neighbouring West Timor, Indonesia [35]. Sandalwood census in Timor-Leste, carried out in 2003–2004, by the National Directorate of Forests and Water Resources [35], reveals a reduction in the natural occurrence of sandalwood in East Timor. The total number per hectare is only 128 and most standing trees had a diameter less

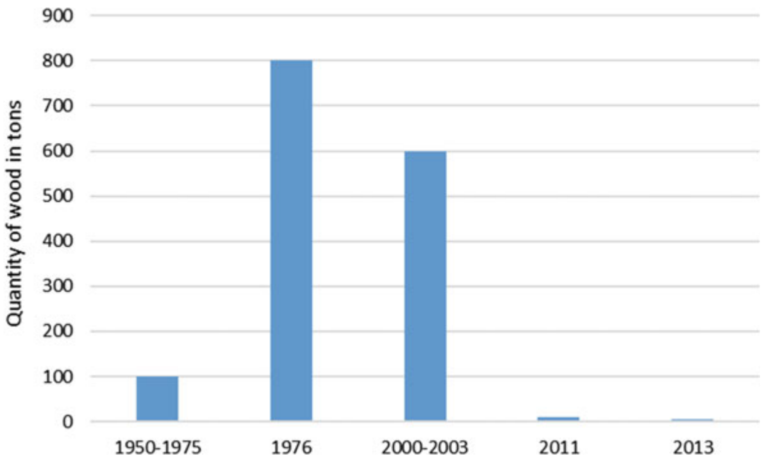

Fig. 6 Exploitation of sandalwood in Timor-Leste, between 1950 and 2013 [11, 35]

than 5 cm and that the percentage of trees with sufficient dimensions for commercial exploitation (diameter >30 cm) was less than 1% [35].

Currently, sandalwood produced in Timor has its origin, almost entirely, in natural regeneration, as the plantations that were established with great efforts at the beginning of the twentieth century did not have continuity and today, there are almost no plantations. There is a 53.95% decline between 1987/1988 and 1997/1998 [56] based on data from available inventories. On the one hand, the slow growth of sandalwood, the widespread perception that sandalwood only grows naturally, without being able to be cultivated and total ignorance about the methods of cultivation and propagation make farmers reluctant to plant the species.

A crucial step for the recovery of sandalwood in the country was a reforestation project, Support Program for Rural Development in Timor-Leste (PADRTL), within the scope of Portuguese agricultural cooperation with the Ministries of Agriculture, Forest and Fisheries and Education and Culture. This project aimed at planting 6500 trees of sandalwood in five schools in each of the country's 13 districts [20]. In 2003, the government carried out a programme to raise sandalwood plantations in 17 ha with a 70% survival [11] (Fig. 7).

Due to several decades of misuse, forest productivity in Timor-Leste is declining and sandalwood distribution is much lower than those needed for commercial exploitation. Timor-Leste is now facing soil degradation, a decrease in groundwater, threats to wildlife and decreases in food sources. However, forest degradation is reversible and sandalwood, given its value and potential, is viewed as a priority species in the forest protection policy. A strategic plan 2011–2030 has been drawn to address the country's agriculture, fisheries and forestry development.

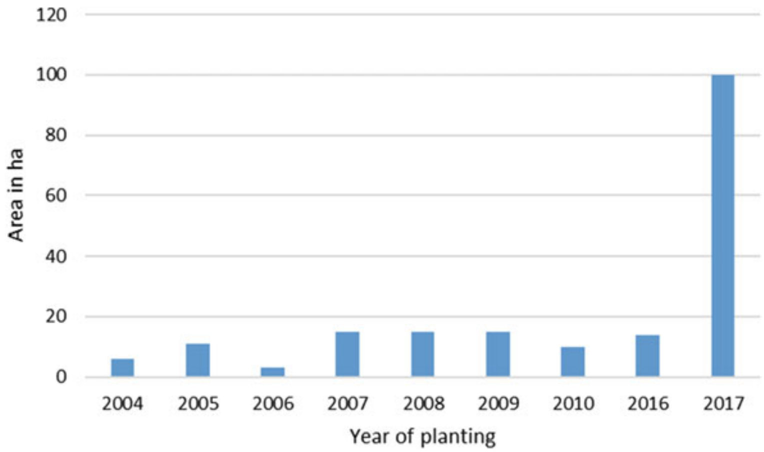

Fig. 7 Planting efforts in Timor-Leste from 2004 to 2017

4 Nepal

Santalum album was introduced to Nepal when it was first planted in the Royal Botanical Garden and Royal Palace Garden using a handful of seeds [23]. The species is reported to grow well in Gorkha and Pythun districts [36]. Natural regeneration is good in the introduced sites suggesting scope for cultivation of the species.

5 China

Indian sandalwood was first introduced in mainland China in 1962 into the South China Botanical Gardens [26]. After repeated efforts to identify appropriate sites for successful plantations through small scale trials, sandalwood is presently in China in the late eighties. Selections have been made to suit the subtropical environment and annually, over 60,000 seedlings are produced [44]. The first experimental plantation was established in 1989 in the Hainan Province with sources from Indonesia. Significant progress has been made over the years [60]. China being the largest importer of Indian sandalwood, most of the product caters to the growing domestic demand [63]. Today sandalwood plantations are available in Guangdong, Hainan, Yunnan, Fujian and Guangxi in south China [29–31, 33].

An interesting study was conducted to promote the heartwood formation in six-year-old young sandalwood trees. Filling the trunk with exogenous gas increased the area of the heartwood significantly. The effect on the use of gases is of the order: nitrogen > carbon dioxide > ethylene treatment = mechanical damage treatment; Sandalwood heartwood promoted by ethylene treatment had the highest essential oil content, with an average content of up to 17.11%, which exceeds the normal oil content range of sandalwood, and is also significantly higher than the essential oil content of other treatments. Heartwood formation begins from the tenth year. A 21-year-old sandalwood plantation in Jianfengling, Hainan, was studied for growth and sandalwood oil. The average heartwood to sapwood ratio was 38.01%, and the average essential oil content 5.52% [32].

For identifying better area for sandalwood cultivation, niche modelling studies were conducted [28] using data of environmental factors, including temperature, rainfall and altitude, collected from wild and cultivated geographic regions across the globe. Further, the performance of *S.album* in different cultivated regions was compared with the predicted map. Besides the traditionally accepted regions such as the hills of the western Hainan province and Leizhou Peninsula of Guangdong province, the southeast coast of Guangdong and Fujian Province has also been identified as highly suitable for cultivation [62].

6 Status in Melanesia

6.1 Fiji

Santalum album was first introduced into Fiji during the 1980s from Australia under the South Pacific Regional Initiative on Forest Genetic Resources (SPRIG) programme of the CSIRO [5]. In 2005, SPRIG introduced two more seed lots. The genetic base of the population is very narrow. The main seed source is a small SPA of about 100 trees established with seeds from the first plantation of the Island country in Drasa. The species is well adapted to the drier western part of islands, evident from the large numbers of natural regeneration invading adjacent trial plots. *S.album* is used as a rootstock to hybridize with *S. yasi* to produce F1 hybrids. Grafting enhanced the mass production of seeds at an early stage of one and a half years to two years [43]. A seed production area of *S. album* has been established in Vunimaqo in 0.14 ha with 150 trees and spacing of 3 m × 3 m. A study in 2007 to assess the performance of Indian Sandalwood in Fiji revealed that the trees have vigorous growth and a higher percentage of heartwood than sapwood. A 26-year-old sandalwood tree yielded 259 kg heartwood fetching FJ$7700. Export destinations are mostly Asian countries.

Putative hybridization is observed between *S yasi* and *S. album* in Fiji, with no apparent reproductive barrier or hybrid breakdown [4, 13]. This option is now exploited in clonal seed orchards, and the hybrids show improved vigour, wider environmental tolerances and are less dependent on forming host associations. Doran and Brophy [12] proposed that interspecific hybrids may provide the opportunity to improve the planted form of sandalwood, particularly given the high vigour of F1 hybrids between *S. album* and *S. yasi*.

6.2 Vanuatu

Vanuatu sandalwood (*Santalum austrocaledonicum*) is the native species in this Pacific Island Nation [58]. Considering India's superior oil quality, a small number of *S. album* seeds have been introduced from India. The Department of Forests, Vanuatu has established germplasm banks of the native sandalwood with one source of *S. album* in two locations, Bamaga and Lockhart River site in 2012. Clonal seed orchards were also established using 12-month-old *S. album* seedlings as rootstock S. *album* was cross-compatible with the native *S austrocaledonicum.* This crossing is promising as it opens up the potential for introgression of desirable traits into the native species [3] and enables a hybrid approach to sandalwood domestication in Vanuatu, which would be lucrative in the long run. However, the two impeding factors of Indian sandalwood—rotation age and late heartwood production—bring in uncertainties. These factors make the breeders reluctant to adopt the species for hybridization despite its superior oil. Heartwood development influences the commercial viability of plantations. So, an assessment of resultant progenies would reveal its feasibility [44].

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Chapter 10
The Current Status of Indian Sandalwood Plantations in Australia

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The Western Australian Government's commitment to growing and comprehending Indian sandalwood plantations in Australia lasted almost 40 years. The results of the various research studies provided a robust knowledge base for a range of aspects including seed germination and seedling health, plantation design and irrigation, pest management, host species selection, tree nutrition and silvicultural treatment. Harvested research trees provided an excellent insight into developing tree growth, heartwood and oil yield models. The knowledge gathered from the research provided the emerging commercial plantation industry with the confidence to invest in Indian sandalwood plantations in Australia. Variations to the initial government designs and silvicultural treatments continue to develop as foresters seek to develop more efficient growing systems and greater final yield outcomes.

The first privately owned commercial plantations of Indian sandalwood (*Santalum album)* were established in Australia in 1999. Over twenty years later, the planting of Indian sandalwood continues across the tropical northern half of Australia including the Western Australia, Northern Territory and Queensland. Land ideal for growing Indian sandalwood in Australia is not overly abundant; factors such as a suitable climate, water availability, topography, soil types, supporting services and competing agricultural land uses restrict the expansion of this plantation species throughout Australia.

Although the vast majority Indian sandalwood plantations in Australia have been established on suitable land in the tropical northern two thirds of the country, Indian sandalwood can be successfully grown below the 30° line of latitude in some areas not exposed to frost. These trees are usually limited to non-commercial garden-based trees requiring a high level of attention and protection from unfavourable climatic elements.

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Commercial Indian sandalwood plantation, Kununurra Western Australia

In 2020, it is estimated that there are around 15,000 hectares of established Indian sandalwood plantations under irrigation in Australia consisting of around 6.5 million sandalwood trees. The majority of the commercial investment into the industry plantation resource is located in the Ord Valley in northern Western Australia.

Typically, mature trees in Australian plantations are being harvested around the age of 15 years. It is at around this age that the quantity of oil yielding heartwood is at an amount that makes the operation commercially viable. A series of studies has shown that as Indian sandalwood trees mature the proportion of heartwood within the stem increases; therefore, harvesting plantations at 20 years of age or greater may become a more plausible proposition.

New plantations continue to be planted each year with older, mature plantations being harvested and the processed into a variety of products. The technologies and systems used to design, establish, maintain, harvest and process are sophisticated and of the highest standard. Prior to establishment, each plantation is individually assessed to ensure the greatest return is received at harvest. Meticulous planning is critical to the success of the plantation, of greatest importance is the soil. Soil testing involves the analysis of soil samples to determine their characteristics, such as texture, stability, plant nutrients, soil biology, fertility, acidity or alkalinity, or toxicities and contaminants.

Once the capacity of the land is known the plantation is designed for maximum growth. In most cases, plantations are established using genetically superior seedlings or clonal progeny and a selection of suitable hosts. A combination medium- and long-term host trees are incorporated into the design; greatest success has been had with local native leguminous species including *Sesbania formosa* and *Cathormion umbellatum.* Commonly used exotic long-term host species include *Dalbergia latifolia, Casuarina equisetifolia.* Proven pot hosts include *Alternanthera nana* and species from the Phyla genus.

The major commercial Indian sandalwood companies in Australia own and manage their own nurseries to produce both the sandalwood and host seedlings. A very high standard of nursery hygiene is required to prevent the introduction and spread of soil disease and pests. In the early stages of growth the seedlings are mostly grown under shade with daily overhead mist spray, as seedlings mature they are slowly exposure to a full sunlight environment in preparation for planting in the field.

Planting the sandalwood and hosts is usually performed at the same time into prepared moist and raised mounds. The configuration varies according to the environmental aspects and constraints. The availability of irrigated water is critical for Australian grown Indian sandalwood in northern Australia; water is delivered onto the plantation either through piped or flood irrigation systems.

A newly established Indian sandalwood plantation in Kununurra Western Australia

Within the initial one to three years, a high level of vigilance and management is required to control the negative effects associated with invasive weeds and vines, insects and grazing native animals, mostly wallabies (a small kangaroo-like marsupial). A series of precise programmes is required to ensure the health, and survival of young seedlings is not compromised.

Maintenance continues through the life of the plantation, watering, pruning, weed management and nutrition are the mainstay of the groundwork. The programmes are administered through a combination of modern technologies and manual labour. Young international travellers visiting Australia, known as ‘backpackers’, are commonly employed in rural areas to provide a reliable casual workforce for a variety of fieldwork including sandalwood plantation duties. The industry provides for around 300 direct full-time jobs.

During the plantation lifecycle, forest mensuration plays a critical role in providing for appropriate plantation management and to access the standing resource. Forest inventory and measurements provide information about the stocking of plantation, the size distribution of trees within stands, health status and the expected growth rate of trees and the overall stands. Australian forestry has embraced the technological advances to measure and monitor trees in sandalwood plantations. The use of drones, terrestrial and airborne laser-scanning, satellite imagery and other advanced remote sensing techniques is commonly used.

Harvesting Indian sandalwood plantations in Australia is a relatively new activity, and a range of systems and mechanisms exist and continue to be developed. The fundamental objective is to harvest the trees to produce the highest amount of commercial grade wood at the least expense. Most trees are extracted from the ground to retrieve the higher yielding amounts of heartwood associated with the base and root section of the tree. At 15 years, it is expected that only small amounts of heartwood are recovered from the upper portion of the tree. Low-yielding heartwood sections are considered commercial and gradually sold into the market.

Harvested trees are promptly debarked using large drum tumblers, the tumblers rotate the harvested material onto itself physically pounding the bark away from the stems. In some cases, high-pressure water is jetted onto the harvested wood to remove the bark. Sections of the tree are usually segregated and then processed according to customer requirements, products include large logs, logs, pregrind and powders.

Sandalwood oil sourced from Australian grown Indian sandalwood is produced by a number of growers and businesses in Australia. Steam distillation is the most common form of oil extraction. The Australian produced oil is used in a range of products including medicinal, cosmetic, skin care, aroma therapy and fragrances.

1 Future Prospects of *Santalum album* Plantations in Australia

The global appetite for Indian sandalwood products continues to grow as the traditional supply from the world’s wild resources is thought to be nearing exhaustion. A global supply based primarily on plantation resources has been accepted as a sustainable and environmentally favourable substitute for the traditional wild supply. This trend is likely to be maintained in Australia as greater interest and capital investment enters the forest and plantation industry sectors.

Australia's stable government, modern infrastructure and technology attract a range of sophisticated foreign investment. Sandalwood plantation companies operating in Australia are recognized as world leaders in the production and supply of ethical, sustainable and reliable Australian grown Indian sandalwood oil and products. The accomplishment of this status is internationally recognized through the attainment and maintenance of various ISO certifications.

Australia has quickly evolved from the new frontier of Indian sandalwood to the world's largest producer. Western Australia's long-standing history and involvement in the global sandalwood market, based on the local sandalwood species, has provided the platform for the Indian sandalwood plantation industry to flourish. The Australia-based industry is well positioned to continue to grow and has great capacity to adapt market forces and technological advances.

Part III
Biology of the Species

Chapter 11
The Botany of Sandalwood

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Sandalwood is known since ancient times for its fragrant heartwood and essential oil distilled from it. Perhaps it is one of the earliest fragrances used by mankind. The history of sandalwood goes back to the remote past, the beginnings of which are not clear but use of sandalwood and its oil in India has no comparable history elsewhere in the world. The Hindus have used sandalwood as incense for its sweet fragrance in religious and cultural ceremonies. In modern days, the oil is used for making incense and expensive perfumes and cosmetics. Several review accounts on various aspect of *Santalum album* L. have been published from time to time [2] and an excellent review on sandalwood basic biology, tissue culture, genetic transformation, etc. [21]. In this paper, we deal mainly with taxonomic botany of the sandalwood yielding species in general and *Santalum album* in particular, the only species of the genus known in India.

Botanically, sandalwood plants belong to the genus *Santalum*, a name considered to have been derived variously from the Sanskrit word *candana* or *Chandana* referring to sandalwood/incense wood, Persian word *Sandal*, signifying useful; Medieval Latin word *sandalum*; ancient Greek word *sántalon*, 'sandalwood', all referring to fragrant wood. *Santalum* belongs to the family Santalaceae, which consists of about 44 genera and 1100 species distributed mostly in the tropical and subtropical regions, but a few extending to temperate regions of the world [12]. In India, the family is represented by ten genera (*Dufrenoya, Ginalloa, Korthalsella, Phacellaria, Santalum, Scleropyrum, Pyrularia, Osyris Thesium,* and *Viscum*) 29 species in India including genera and species transferred from Viscaceae.

Linnaeus (1753) described the genus *Santalum* with a single species *Santalum album* based on *Santalum verum* Breyne, Prodr. Fasc. Rar. Pl. 1: t.5, f.1. 1680, from Timor (Plate 1a). No reference was made to other prelinnaean works such as Garcia de Orta (1563) [11] in which *santalum* is listed for the first time from India

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in a European publication along with discussion of its use and trade. Subsequently, Van Rheede (1678) while dealing with basically medicinal plants of Malabar on the South-West coast of India, not only described and illustrated sandalwood (Plate 1b) using its local names *Mall-katou-tsjambou, Catu-tsjambu, Tsjandana-maram, Sriganda* but also recorded its local uses. It was also described and illustrated as *Santalum album* [17].

Subsequently, Linnaeus (1771, 1774) described two other genera in the family, viz. *Sirium* and *Fusanus* each with a single species *Sirium myrtifolium* (based on a collection from India) and *Fusanus compressus*, respectively. *Sirium myrtifolium* was transferred to *Santalum* [16], and the monotypic *Sirium* is now considered congeneric with *Santalum* and its species as synonyms of *Santalum album.* Mitchell (1839) [10] described *Eucarya* with a single species *Eucarya murrayana* based on materials collected from Australia (New South Wales), which is also now treated as congeneric with *Santalum.* So far, 57 species (including three species of synonymized genera) with 35 varieties and seven forms of *Santalum* are discovered and described all of them from Pacific Islands and Australia. The species of Santalum grow in coastal plains to about 1250 m altitude. The valuable sandal wood of commerce is mostly produced by a few species, viz. *Santalum album*, *S. spicatum*, *S. yasi and S. autrocaledonicum.*

Although the taxonomy of the species of *Santalum* is difficult and confusing due to tremendous variations observed in most species occurring in Pacific Islands, it is not all that difficult to identify *Santalum album*, the only species found in India. A detailed taxonomic description of the genus and of the only species *Santalum album* with its synonyms, common/local names, illustration, flowering and fruiting phenophases, distribution and uses are provided. In addition, a complete global list of all recognized and accepted species of the genus *Santalum* with updated nomenclature, citations, synonymy, type specimens, geographical distribution, common/local names, literature pointers to description, illustrations/photographs and distribution maps are given.

Santalum L., Sp. Pl. 1:349.1753; Gen. Pl. ed.5: 165.1754; R. Br., Prodr. Fl. Nov. Holl.: 355.1810; Roxb., Fl. Ind. 1:462.1820; Miq., Fl. Ind. Bat 1,1:771856; A. DC., Prodr. 14:681. 1857; Benth. in Benth. & Hook. f., Gen. Pl. 3: 224.1883; Hook. f., Fl. Brit. India 5:231. 1886; T. Cooke, Fl. Bombay: 554. 1906; Gamble, Fl Madars 1925; Pigler in Engl. & Harms, Nat. Pflanzenfam. 16b:81. 1935; Backer in Backer & Bakuz., Fl. Java 2:78. 1965; Hewson & George, Fl. Australia 22:61.1984; Philcox in Dassan. & Clayton, Rev. Fl. Ceylon 13:201. 1999. Type: ***Santalum album*** L.

Sirium L., Syst. Veg. 14:160. 1784. Type: *Santalum myrtifolium* L.

Sandalum Rumph., Herb. Amboin 2:42, 47, t.11.1741. Type: *Santalum album* L. (as *Sandalum album*)

Fusanus L., Syst. Veg., ed.13. 765.1774; R. Br., Prodr. Fl. Nov. Holl.: 355.1810; A. DC., Prodr. 14: 684.1857; Benth. Fl. Austral 3:215. 1895; *Santalum* sect. *Fusanus* (L.) F. Muell, Trans. & Proc. Victorian Inst. Advancem. Sci.1:41. 1855. Type: *Fusanus compressus* L.

Eucarya T. Mitch., Three Exped. Australia 2: 100.1839. Type: *Eucarya murrayana* T. L. Mitch.

Hemiparasitic evergreen trees or shrubs. Leaves glabrous, subcoriaceous, opposite, rarely subopposte, entire. Flowers hermaphrodite, axillary or in terminal trichotomous paniculate cymes; bracts minute. perianth-tube campanulate or ovoid, adnate to the base of the ovary; perianth lobes 4 (rarely 5 or 6), valvate with a tuft of hairs from the base. Stamens 4 rarely 5 or 6, adnate to the base of the perianth lobes; filaments slender, short; anthers ovate, theca distinct, parallel. Disk of fleshy spathulate or tongue-shaped scales, alternating with stamens. Ovary at first superior during anthesis, ultimately becoming inferior; ovules 2–3, inserted below the summit of a long acuminate free central column; style elongate; stigma 2–3-lobed. Fruit a subglobose drupe, annulate on the top by the deciduous perianth; endocarp rugose. Seeds subglobose; albumen copious; embryo linear, terete, straight or nearly so, in the centre of the albumen; radicle longer than cotyledons.

Distribution: Presently, out of 99 names belonging to 57 species, 35 varieties and seven forma, only 20 species with 13 varieties are recognized and accepted (Annexure 1); nine species (and 13 varieties) are distributed in Pacific Islands (Austral Islands, Cook Islands, Hawaii Islands, Juan Fernandez Island, Marquesas Islands, New Caledonia, Pitcairn Islands, Society Islands, Tonga, Tubuai Islands and Vanuatu), seven in Australia (West Australia, Southern Australia, New South Wales, Northern Territory and Queensland), two in Papua New Guinea and one each in India (throughout drier parts) and Indonesia (Java: Bondowoso District eastwards to Timor, through Sulawesi and the Maluku Islands) and Japan (Bonin Islands). Of all the accepted species of *Santalum*, only *Santalum album* is disjunctly distributed in Australia, Indonesia, Timor and India. The rest of the species including their varieties are endemic to different groups of Pacific Islands, Australia, Papua New Guinea and Japan (Annexure 2, Map). *Santalum fernandezianum* F. Phil. endemic to Juan Fernandez Island (Chile) is reported extinct.

In India, *Santalum album* L. is distributed throughout drier parts and often cultivated in naturally occurring areas as well as other areas.

Santalum album L., Sp. Pl. 349. 1753 & 2: 497. 1762 & Syst. Veg. 14:164.1784; Lour., Fl. Cochinch. 2: 87. 1790; Roxb., Fl. Ind. 1:462. 1820; J. Graham, Cat. Bombay Pl. 177. 1839; Miq., Fl. Ned. Ind.1, 1:776. 1856; Dalzell & Gibson 224. 1861; Drury, Handb. Indian Fl. 3:93. 1869; Hook. f., Fl. Brit. India 5: 231. 1886; Bedd., Fl. Sylvat. t. 256. 1873; Kurz, Fl. Brit. Burma 2: 329. 1877; Watt, Dict. Econ. Prod. India 6(2): 461. 1890; Woodr., J. Bombay Nat. Hist. Soc. 12:368. 1899; Talbot, Trees, Bombay ed. 2, 293. 1902; Prain, Bengal Pl. 914. 1903; T. Cooke, Fl. Bombay 2:555. 1906; Gamble, Fl. Madras 1261. 1925; Pilger in Engl. & Harms. Nat. Pflanzenfam. 16b:81. 1935; Fl. Assam 4:129. 1940; Engl., Syllbus Pflanzenfam.: 186, t.184. 1964; Backer, Fl. Java 278. 1965; Manilal & Sivar., Fl. Calicut 254. 1982;George, Fl. Australia 22:61. 1984. B. D. Sharma et al., Fl. Karnataka Anal. 243. 1984; Mohanan, Fl. Quilon Dist. 351. 1984; Ansari, Fl. Kasaragod Dist. 328. 1985; R. S. Rao, Fl. Goa, Diu Daman & Nagarhaveli 2:376. 1986; Kumai in A. N. Henry et al., Fl. Tamil Nadu Anal. 2:219. 1987; Bole & J. M. P athak Fl. Saurashtra 2: 258. 1988; Ramach. & Nair, Fl. Cannanore Dist. 402. 1988; Antony, Fl. Kottayam Dist. 350. 1989; Vajr., Fl. Palghat Dist. 414. 1990; Parmar in B. V. Shetty & V. Singh et al., Fl. Rajasthan 2:

761. 1991; Mohanan & Henry, Fl. Thiruvananthapuram Dist. 401. 1994; Subram., Fl. Thenmala Division 321. 1995; Sasidh. & Sivar., Fl. Pl. Thrissur For. 388. 1996; R. C. Srivasat. in V. Mudgal et al., Fl. Madhya Pradesh 2:516. 1997; Sasidh., Fl. Shenduruny Wildlife Sanctuary 277. 1997; Sivar. & Mathew, Fl. Nilambur 598. 1997; Sasidh., Fl. Periyar Tiger Reserve 360. 1998; Sasidh., Fl. Chinnar Wildlife Sanctuary 276. 1999; Philcox in Dassan. & Clayton, Rev. Handb. Fl. Ceylon 13:201. 1999; Sunil, Fl. Pl. Alappuzha Dist. 786. 2000; A. Godbole & Lakshmin. in N. P. Singh et al., Fl. Maharashtra 2: 850. 2001; Sasidh., Fl. Parambikulam Wildlife Sanctuary 277. 2002; Manilal, Rheede's Hort. Malab. 4: 23, t. 8. 2003. *Santalum verum* ligno citrino & albo, foliis Laurinis" in Breyn., Prodr. Fasc. Rar. Pl. 1: 94. t. 5, f.1. 1739; L., Mat. Med. 102.1749. ***Type***: Timor, Breynius, Prod. Fasc. Rar. Pl. 1: t. 5. 1680 (Lecto: BM), Fig. 1**A**; Timor, 5 km from Soe, *Kartiwinata* 1738 (Epi: BO). Both were designated by Macklin and Parnell (2002). Although the iconotype is referable only to Fig. 1 of the two on the plate, it was not specified by them. Figure 2 named as *Solanum arborescens* belongs to *Strychnos nux-vomica* L. Sa'ad (in *Taeckholmia, Add. Ser.* 2: 16. 1983) indicated 161.1 (LINN) as type, but it is noted that this sheet lacks a *Species Plantarum* number (i.e. '1') and is not original material for the name (Figs. 3 and 4).

Malla-katou-tsjambou Rheede, Hort. Malab. 4: 17, **t. 8.** 1683 (Plate 1b).

Sandalum album Rumph., Herb. Amboin. 2: 42, 47, **t. 11**. 1741.

Sirium myrtifolium L., Mant. Pl. Alt.: 200. 1771 & Syst. Veg. 14: 160. 1784. *Santalum myrtifolium* (L.) Roxb., Pl. Coram. 1: 2, t. 2, 1795 & Fl. Ind.1: 443. 1820. ***Type***: Linn 138.1 (LINN).

Chandana Jones, Asiat. Res. 4: 257. 1799.

Santalum ovatum R. Br., Prodr. Fl. Nov. Holl.: 355. 1810. ***Type***: Australia, Melville Bay, 13 Feb. 1803, *R. Brown s.n.* (holo, BM; iso, BRI, MEL, PERTH).

Santalum ellipticum Zipp. ex Span., Linnaea 15: 335. 1841. ***Type***: not seen.

Evergreen, glabrous, hemiparasitic trees, 5–10 m tall; branches slender drooping; trunk up to 2.5 m in diameter, bark brownish when young turning dark grey to nearly black, rough with short vertical fissures on old trees; blaze reddish; the sap wood white and odourless, the heartwood yellowish-brown, strongly scented (in old trees). Leaves simple, opposite to subopposite, decussate, estipulate; petiole 1–2.2 cm long, slender, glabrous, grooved above; lamina (2.5–5–12 × (1–)2–4.5 cm, elliptic, elliptic-ovate or ovate-lanceolate, obtuse to round or attenuate at base, obtuse, acute to shortly acuminate at apex, entire to somewhat undulate at margin, glabrous, light to dark green and shiny above, dull green and glaucous beneath, coriaceous, midrib prominent, lateral nerves faintly 8–15 paired and intercostae obscurely reticulate. Flowers bisexual, 5–6 mm across, very mild scented, greenish-creamy white turning pale pinkish- to dark red, in axillary and terminal paniculate thyrasoid cymes, 3–5 cm long, shorter than leaves; lateral branches opposite, upper ones subopposite the leaves much reduced in terminal panicles; peduncles 0–5 mm (stalks of lateral branches 5–8 mm long; elongating in fruits from 10 to 12 mm), slender, angular, sulcate; pedicels 1–1.5 mm, slender, angular, glabrous; bracts subulate, 1–1.5 × 0.5 mm, caduceus leaving a distinct scar, minutely ciliate; receptacle 1–1.5 mm long, green. Perianth usually 4, rarely 5 or 6, petaloid, basally connate into a campanulate 1.5–2 mm long tube, shortly connate to the basal part of the ovary; lobes 2.5–3 × 1.5 mm, ovate-triangular or deltoid, obtuse, thin, fleshy, reflexed, glaucescent outside, a tuft white glandular hairs arising from base with tips attached to anther base; nectarial disc prominent concave, adhering to the receptacle and bottom of the perianth, deeply 4-lobed, rarely 5 or 6 with one lobe much smaller, lobes tongue-shaped, pinkish, ca. 1 mm long, thick, fleshy, alternates with perianth lobes (disc produces copious amounts of nectar, main attractant of pollinators). Stamens 4, rarely 5 or 6, exerted, basally adnate to and opposite perianth lobes; filaments 1–1.5 mm long, slightly dilated at base; anthers less than 1 mm, ovoid, 2-celled, dehiscent longitudinal by a single cleft, a tuft of white hairs present behind each anther emanate from base of perianth lobe (known to produce a viscous oily fluid is reported to act as secondary pollinator attractant); pollen mass yellow, sticky, often seen attached to the tuft hairs below anthers, grains triangular in polar view, subprolate in equatorial view, 3-zonoporate with granulate, exine sculpturing. Ovary superior becoming half inferior at the time of flowering and inferior in fruit, globose, ca. 1 mm, unilocular, ovules 2–6, central, pendulous from below the long, acuminate, central column, only one ovule develops into a seed; style 1–1.5 mm, terminal, broader at base, white turning pinkish after pollination, somewhat angular; stigma (2–)3(–4)-lobed, obscurely papillate. Fruit a drupe, 8–12 mm across, globose to obovoid, green turning bright reddish and finally shining blackish-purple or black when ripe, crowned with ring like collar of fallen perianth and minutely beaked at centre with the basal part of the style, 1-seeded; exocarp smooth, pulpy; endocarp hard, whitish, prominently 3-ribbed with short ribs between them at apex, rounded at base. Seed globose to obovoid, perisperm white with short trident mark and irregular one between them at the tip; embryo inverse, cylindric-fusiform to subulate, radicle superior, tapering, much longer than the 2 unequal, linear-lanceolate cotyledons; plumule minute, straight to semi-lunate.

Flowering and Fruiting: June–December; two flashes flowers recorded during March–April and September–December, in some trees throughout the year.

Habitat: Tropical dry deciduous and scrub forests in plains and hills up to 1200 m altitude.

Distribution: India (tropical deciduous and moist semi-deciduous forests of south of Vindhya Mountains, ascending to 1500 m altitude. Andhra Pradesh, Karnataka, Kerala, Madhya Pradesh, Maharashtra, Odisha, Rajasthan, Tamil Nadu. Uttar Pradesh; elsewhere cultivated), Australia (Northern Territory), Indonesia (Java: Bondowoso District eastwards to Timor, Sulawesi and the Maluku Islands).

It is cultivated on commercial scale in India, Indonesia, China and Australia. Cultivation trials have been made in southern Africa, Philippines and several Pacific Islands (where local indigenous species of *Santalum* are distributed).

IUCN Red list Status: Vulnerable: **A2de** (www.iucnredlist.org—downloaded on 29 October 2020) [7].

Chromosome Number: $2n = 20$ [14] $n = 10$ [8], 20 [18], 20 and 40 [9]. $2n = 40$ in haustorial cells [20]. $2n = 2x = 20$ and $2n = 4x = 40$ in shoot meristems and karyotypic formulae $2n = 20 = 18m + 2sm$ and $2n = 40 = 32m$ (2SAT) + 8sm. Karyotypes assigned to 2B type of Stebbins' karyotypic symmetry suggesting primitive status of *S. album*-based cytology [22].

Embryology: The embryo-sac is of the normal eight-nucleate type with general tendency to grow out of the ovule both in the anterior and extensively in the posterior directions forming haustoria. The endosperm formation is at first free-nuclear in *Santalum (album)* unlike in *Osyris, Scleropyrum* and *Thesium* which is cellular, and further development is uniform and distinctive of the family. The pollination and (double) fertilization are reported to be normal [14].

Pollination: The flowers of *Santalum album* are self-incompatible and are strictly adapted for cross-pollination by insects [3]. While occurrence of both self and cross-pollination has been demonstrated in *S. album* [19]. Perhaps, intensive pollination biological studies are needed to correctly understand the breeding system.

Diseases and Pests: The sandalwood 'spike disease' is the most dreaded disease caused by a mycoplasma-like organism spread by insects. The trees of all ages are susceptible to this disease. It is considered to be transmitted by insect species like *Coelidia indica*, *Moonia albimaculata*, *Cocostirphus tuberculatus*, *Nezara viridula*, *Redarator bimaculatus*, etc. The spike disease can be easily recognized by shortened internodes, reduced leaf size which change colour yellow and reddish before falling, but these symptoms appear in the advanced condition of the disease and nothing can be done to save the trees. Several fungal diseases like mottled sponge rot, spongy or butt rot, sooty mould and leaf-gall disease are known to be caused by fungal pathogens, and a leaf curl by virus is also recorded. All of them cause damage but not the extent of 'Spike disease'. In nurseries, the fungal infections by Fusarium and *Phytophthora* species and root nematodes are well known. The adult trees serve as hosts for a few known species insects are not reported to cause serious damage.

***Vernacular Names/Common Names/Local Names*:**
Indian Languages [1]:

Bengali	*Chandan, Pitchandan, Sandal, Sufaid Chandan.*
Kodava (Coorgi)	*Chandana.*
Gujarati	*Suket, Sukhud.*
Hindi	*Chandan, Chandal, Chandoie, Safed Chandan, Sandal.*
Kannada	*Agarugandha, Bavanna, Bhandarsiri, Cercanda, Chandana, Gandha* (meaning fragrant)*, Gandhada chakke, Gandada mara, Srigandha* (meaning holy incense).
Konkini	*Sriganda.*
Malayalam	*Catu-tsjambu, Catu-chandanam, Catu Tsjandanam, Malla-katou-tsjambou, Chandana cotta, Chandana-chala Chandanam, Chandanamutti, Kajoe tjindana, Tsjandana-maram.*
Marathi	*Chandan, Gandha chakoda.*
Odiya	*Chondano, Gondhassaro, Srigandha.*

Punjabi	*Chandan.*
Sanskrit	*Anaditam, Bhadrasari, Bhudrushree, Chandana (meaning refreshing), Chunduna Ghandhasara, Guadhasaru, Harichandana, Krishna Chandanm, Malayaja, Molayuyu, Mocha, Mochata, Pitachandana Tailaparnam.*
Sindi	*Sukhad.*
Tamil	*Kulavuri, Sandanam, Sundel, Shandanak-kattai, Ulocidam.*
Telugu	*Chandanmu, Chandanam, Chandanpu chettu, Gandhapu chakka, Gandhataravu, Harichandanam, Pitachandanmu, Rakta Krishna Chandanamu, Srigandhamu, talia-Parnam, Tella chandanamu, Tella chandanpu chettu, Srigandhamu.*
Tulu	*Chandana, Gandha.*

Non-Indian Languages:

Arabic	*Sandal* (considered as corrupted name of *Chandam*), *Sandali aswad, Sandal abiyae.*
Biblical	*Algum or Almug* (meaning 'Sandalwood').
Burmese	*San-ta whu, Ka-ra-mai, San-da-ku or san-ta-ku, Nasaphiyu, Nanttha hpyu, Natha hpyu, Sandakoo, Santagu, Mawsanku* (Shan).
English	*Sandalwood, East Indian Sandalwood, Indian Sandalwood, White Sandalwood, Yellow sandlwood.*
Chinese	*Tan muh, Tan-heong, Tou hehong.*
Dutch	*Sandalhout.*
French	*Bois de santal or Bios santal, Santal blanc.*
German	*Weisses Sandelholz, Weisser Sandel (holz) baum.*
Hawaiian	*Iliahi.*
Indonesia	*Ayasru* (Maluku), *Cendana,chandan, Chandam, Chendana, Ai nitu Ai salun, Gundala, Suket, Ai sarun, Ai kamelin* (Sumba: *which was once called Sandlwood Island*), *Hau meni* (Timor).
Italian	*Sandalo bianco.*
Latin	*Sandalum, Santalum* (Medieval Latin); *Santal, Santalum* (New Latin).
Persian	*Sandal sufed.*
Malaya	*Chendana.*
Polynesia	*Ahi, Kouina, Pauhi, Pauhi kua, Pauhi fiti, Pauhi ava ava.*
Sinhalese	*Rat-hihiri, Suduhandun.*
Spanish	*Sandalo, Sandalo blanco.*
Thai	*Chantana.*
Vietnamese	*Bach dan.*

Common names ending with sandalwood and their botanical identity:

African sandalwood or East African sandalwood = *Osyris lanceolata* Hochst. & Steud.

Bastard sandalwood = *Eremophila mitchellii* Benth. (Scrophulariaceae); *Erythroxylon monogynum* Roxb. (Erythroxylaceae)

False sandalwood = *Ximenia americana* L. (Olacaceae); *Adenanthera pavonina* L. (Leguminosae: Caesalpinioideae); *Myoporum platycarpum* R.Br. (Scrophulariaceae); *Myoporum tenuifolium* G.Frost. (Scrophulariaceae)

Nepalese sandalwood = *Osyris wightiana* var. *rotundifolia* P.C. Tam.

New Zealand sandalwood = *Mida salicifolia* A.Cunn. (syn.: *Santalum cunninghamii* Hook.f.; *Santalum salicifolium* (A.Cunn.) C.A.Gardner)

Red sandalwood = *Pterocarpus santalinus* L.f. (Leguminosae: Papilionoidea); *Adenanthera pavonina* L. (Leguminosae: Caesalpinioideae)

Uses: Sandalwood tree species produce very hard, close grained, yellowish-brown, strongly sweet scented heartwood. Sapwood is white to whitish-yellow and unscented, and heartwood is light yellowish-brown strongly scented when freshly cut, turn dark brown and ultimately dark reddish-brown on curing.

The heartwood is in great demand for extraction of essential oil, wood carvings (of Indian Gods and Goddesses, animals, card-cases, work-boxes, trays for cards, walking-sticks, fly-flaps, pen handles), doors and windows of palaces, ornamental boxes, burning in religious places and functions as a perfume, the preferred wood for funeral pyres of wealthy Hindus [1]. It is reported that four tonnes of Sandalwood were used in cremating Mahatma Gandhi [15]. Formerly, in China, most expensive coffins were made from sandalwood. The wood paste in water is applied on the forehead as part of sacred ceremonies and also offered in some temples. The powdered heartwood and sapwood, sawdust, wood residue after oil distillation and wood shavings from carvings are made into agarbattis or incense sticks or joss sticks. Fine sawdust put in cotton sachets used to scent stored clothes particularly silks and also to keep them free from insects and mites. An emulsion of wood or paste in water is applied to local inflammations, to the temples and forehead in fevers, skin diseases to dispel heat and pruritus, cooling application to the skin in erysipelas, prurigo and sudamina. The wood paste in water is also a diaphoretic, alexipharmic and aphrodisiac, also used in cases of gonorrhoea. Wood powder with honey and rice water is given for diarrhoea, and paste with turmeric paste reduces pimples on face.

A valuable essential oil is obtained by steam distillation from the heartwood and roots. The volatile oil with principal component Santalol, occurring in two isomer forms viz., the alpha-santalol and beta-santalol has outstanding fixative properties, excellent tenacity, blending ability and fragrance is an ingredient in the manufacture of a variety of highly attractive and expensive perfumes, scented candles, soaps and incense. The roots contain comparatively higher percentage of oil. The sandalwood oil has been approved for food use and 'generally recognized as safe' (GRAS No

3005) by the Food and Drug Administration (FDA) of the United States under paragraph 172.510. The oil is used in herbal/folk medicine (as astringent, bitter, cooling, useful against biliousness, vomiting, fever, thirst and heat of the body). Presently, it is widely used in aromatherapy. Inferior quality essential oil is also obtained by acid hydrolysis of sapwood, spent heartwood and sawdust.

It is reported that a compound extracted from the bark exhibits effective chemosterilant activity in insects [13]. The bark is reported to contain about 12–14% tannin.

The seed kernels are edible, yield thick and viscid oil used as lamp oil in homes in olden days and also used for treating skin diseases.

The lopped branches are used as fodder (for goats and other livestock) and as green manure. It is also reported as a good host plant for the larvae of some Lepidoptera insect species like *Endoclita malabaricus*.

Surprisingly, the wood was used for making charcoal by cutting dead sandal tree near charcoal making site, during which the whole village filled with fragrant smoke (observed by senior author during early 1960s).

Note on nativity: *Santalum album* is considered to have been introduced to India from Indonesia (Timor) centuries ago [4–6], and most authors follow this view till date. The prehistoric use of the sandalwood in India with innumerable references to it in ancient classical Indian literature, its cultural and religious use in India even today, however, suggests that it must have been native. In addition, based on the distribution of the species in wild throughout drier parts of India more commonly in southern India and occurrence of allied genera like *Osyrus* and *Scleropyrum,* the authors are of the view that it should be indigenous to India. Therefore, an earlier analysis of literature suggesting the hypothesis of its introduction in India is not tenable; Fischer too takes the support of circumstantial evidence. Although the bird dispersal of *Santalum album* is well known, its distribution across multiple oceanic islands and continents is still unclear, but presumed or possibly due to ocean currents and migratory birds. However, an in-depth study and analysis of all the available ancient and modern Indian literature on the species, molecular phylogeography/phylogenetic study of extant materials from all *S. album* growing localities and fossil evidence if any, likely to throw new light on its nativity in India.

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Annexure 1: Global List of *Santalum* Species (Updated)

Currently recognized species and varieties with their updated nomenclature citations, synonymy, type specimens, geographical distribution, common/local names, literature pointers to description, illustrations/photographs and distribution maps. Type specimens of a few names could not be traced and for some herbarium where they are located. It is hoped that this list will greatly help taxonomist to undertake a global revision of the genus, an urgent need and others in knowing all species and infraspecific taxa of genus *Santalum*. Presently, **20** species and **13** varieties are accepted out of 58 species, 35 varieties and seven forma (a total **100** names) published so far.

1. ***Santalum acuminatum*** (R. Br.) A. DC. in DC., Prodr. 14(2): 684. 1857; A. S. George, Fl. Australia 22: 65. 1984. *Fusanus acuminatus* R. Br., Prodr. Fl. Nov. Holland.: 355.1810; *Eucarya acuminata* (R. Br.) Sprague & Summerh., Bull. Misc. Inform. Kew 1927: 196.1927. *Mida acuminata* (R. Br.) Kuntze, Revis. Gen. Pl. 2: 589.1891. ***Type***: Australia, South Australia, Fowler Bay, 29 Jan.1802, *R. Brown s.n.* (Iso: MEL); Memory Cove and Port Lincon, *R. Brown* 3214 (K Barcode: K000880522-23), Australie, *R. Brown s.n.* (Iso: P00756405); 1 Jan. 1802–1 Jan. 1805, *R. Brown* 20008 (E, NSW).

Santalum preissianum Miq. in Lehm., Pl. Preiss. 1: 615.1845. ***Type***: Australia, Western Australia, Sussex District, near seashore, 25 Dec. 1839, *J. A. L. Preiss* 2102 (Iso: BR; BG; LD; MO; P; MEL); Nov. Holl, Riv. des Cygnes, 1843, de Preiss 2102 (Iso: P, Barcode: P00756402), Nov Holland, Preiss 2102 (B, Iso: B, Barcode B100296058).

Santalum lanceolatum auct. non R. Br. 1810; Schltdl., Linnaea 20: 579. 1847.

Santalum angustifolium A. DC. in DC., Prodr. 14:685.1857. *Fusanus acuminatus* var. *angustifolia* (A. DC.) Benth., Fl. Austral. 6:216.1873. ***Type***: Australia, Western Australia, *J. Drummond* 3:218 (Syn.: BM, K, MEL, NSW); *J. Drummond* 4:430 (Syn: BM, BRI, K, MEL).

Santalum preissii F. Muell., Fragm. 2: 179.1861. ***Type***: not seen.

Santalum cognatum Miq. in Lehm., Pl. Preiss. 1: 616.1845. ***Type***: Australia, Western Australia, near Perth, 31 Jan. 1839, *L. Preiss* 2098 (Syn.: LD, MEL, P); S of Perth, Peel District, Feb. 1841, *L. Preiss* 2100 (Syn.: LD. MEL).

Santalum densiflorum Gand., Bull. Soc. Bot. France 66: 232.1919. ***Type***: Australia, South Australia, Mt Lyndhurst, Nov. 1898, *M. Koch* 47 (Holo: LY; Iso: K, Bar code: K000880521).

Fusanus acuminatus var. *typicus* Hochr., Candollea 2: 355.1925, nom. Illeg.

Description: A. S. George, Fl. Australia 22: 65. 1984; Fl. S Australia ed. 5, 10. 2012.

Illustration: A. S. George, Fl. Australia 22: Fig. 10, 19A–B, 1984; Fl. N. S. W. 3: 58. 1992; Fl. Victoria 4: 34, Fig. 4E. 1996; Fl. S Australia ed. 5: Fig. 5A–C, Pl. 4B–H, 5K.

Distribution: Australia (West, South, New South Wales, Northern Territory, Victoria and Queensland), endemic.

Distribution map: A. S. George, Fl. Australia 22: Map. 73. 1984.
Conservation status**:** Not assessed.
Common/Local names**:** Burn-burn, Desert quandong, Katunga, Nakala, Native peach, peach tree, Quandong, Sweet quandong and Western quandong.

2. ***Santalum album*** L., Sp. Pl. 1: 34. 1753; A. S. George, Fl. Australia 22: 61. 1984. ***Type***: Timor, *Breynius*, Prodromus fascicule rariorum plantarum 1: t. 5. 1680 (Lecto: BM); Timor, 5 km from Soe, Kartawinata 1739 (Epi: BO), designated by Macklin & Parnell in Thai Forest Bull., Bot. 30: 100. 2002.

Sirium myrtifolium L., Mant. Pl. 2: 200. 1771. *Santalum myrtifolium* (L.) Roxb., Hort. Bengal.: 83. 1814; Fl. Ind., ed. Carey & Wall., 1: 464. 1820 & ed. 1832, 1: 444. 1832. *Santalum album* var. B *myrtifolium* (L.) A. DC., Prodr. 14(2): 683. 1857. ***Type***: Herb. Linn. No. 138. 1 (LINN).

Santalum ovatum R. Br., Prodr. Fl. Nov. Holland.: 355. 1810. ***Type***: Australia, Northern Territory, Melville Bay, 13 Feb 1803, *R. Brown s.n.* (Iso: BRI, MEL, PERTH). Arnhem's Land, *R. Brown s.n.* K000880539); Northern Territory, Groote Eyland, *R. Brown* 3216 (K000880537), 1 Jan 1802, *R. Brown s.n.* (BM); 1 Jan 1863, *R. Brown s.n.* (P).

Santalum album var. *anciteum* Meurisse, Bull. Mens. Soc. Linn. Paris 2:1026. 1892, nom. nud.

Santalum album var. *ellipticum* (Gauidch.) Meurisse, Bull. Mens. Soc. Linn. Paris 2:1026. 1892, nom. nud.

Santalum ellipticum Zipp. ex Span., Linnaea 15: 335. 1841, pro syn.

Description: In this publication above.
Illustration: In this publication above.
Distribution: Australia (Northern Territory, Western Australia), Indonesia (Java, Lesser Sunda Islands) and India (peninsular states, cultivated elsewhere).

Introduced into: Bangladesh, China, Cook Islands, Mauritius, Myanmar, Nepal, Rodrigues, Réunion, Sri Lanka, Taiwan, Thailand, USA (Florida, Hawaii) and Vietnam.

Distribution map: In this publication.
Conservation assessment: Vulnerable: **A2de** (www.iucnredlist.org—downloaded on 29 October 2020).
Common/Local names**:** See the detailed list under species dealt.

3. ***Santalum austrocaledonicum*** Vieill., Ann. Sci. Nat., Bot. sér. 4, 16: 61. 1861. ***Type***: Hills of Arma, Northern extremity of Grande-Terre, 1855–60, *E. Vieillard* 1090 (Holo: P; Barcode: P00645808; G, K, MPU)

Santalum homei Seem., Fl. Vit. 210. 1867, in obs. ***Type*****:** Isle of Pines, off New Caledonia, Dec 1852, *E. Home* (Holo: BM, Catalogue No.: BM001015666); Isle of Pines, Dec 1853, *J. Mac Gillivray* 818B (Syn.: K:Barcode:K000880514).

var. **austrocaledonicum**

Description: T. Page et al., ACIAR Monograph No. 151:9–10. 2012.
Illustration: A. J. Thomson, *Santalum austrocaledonicum* & *Santalum yasi* (Sandlwood), Santalaceae photo p. 3, 5.
Distribution: New Caledonia (Grande-Terre, Isle of Pines, Loyalty Islands and Vanuatu (Erro mango, Espiruto Santo), Tanna, Aniwa, Futuna, Malakula, Efate, Anityum), 5–800 m altitude; endemic.
Conservation assessment: Near Threatened: **B2b (i, ii, iii, iv, v)** (www.iucnredlist.org—downloaded on 29 October 2020).
Common/Local names**:** Coral Sea sandalwood, New Caledonian sandalwood, Vanuatu sandalwood, Sandalwud (Vanuatau: Bislama), Bis de Santal (French) and Sandalo (Spanish).

var. **glabrum** Hürl., Mém. Mus. Hist. Nat., ser. B, Bot. 15(1): 15. 1964, emend. Butaud & P. Firmenich, PhytoKeys 56: 113. 2015. ***Type:*** New Caledonia, Loyalty Islands, Maré, près de Rawa, 21° 31′ 13.044″ S; 167° 58′ 34.536″ E. 7–8 m, en fl eurs et en fruits, forêt mésophile, 17 July 1951, *M. G. Baumann-Bodenheim* 14762 (Holo: P, Barcode: P00639106; Iso: G, Z).

Description: Butaud & P. Firmenich, PhytoKeys 56: 114. 2015.
Illustration: Butaud & P. Firmenich, PhytoKeys 56: Figs. 2 & 3. 2015.
Distribution: New Caledonia: Loyalty Islands (Mare, Ouvea, Lifou), endemic.
Distribution map: Butaud & P. Firmenich, PhytoKeys 56: Fig. 1. 2015.
Conservation status**:** Not assessed.
Common/Local names**:** Loyalty Islands sandalwood, tapakae, tapakai, wekesi and wahata.
Note: Butaud (Phytokeys 56:115.2015) after amending and reinstating var. *glabrum* stated that 'high variability in *Santalum austrocaledonicum* still demands for further investigation on the taxonomy of the species'.

var. **minutum** N. Hallé, Fl. Nouv.-Calédonie & Dépend. 15: 110.1988. ***Type:*** New Caledonia, Montagne de poum, 25 March 1982, *J. M. Veillon* 4852 (NOU, Barcode: NOU006525).

Description: Butaud & P. Firmenich, PhytoKeys 56: 114. 2015.
Distribution: New Caledonia (Grand Terre: NW side), endemic.
Distribution map: Butaud & P. Firmenich, PhytoKeys 56: Fig. 1. 2015.
Common/Local names**:** New Caledonia sandalwood.

var. **pilosulum** N. Hallé, Fl. Nouv.-Calédonie & Dépend. 15:110. 1988. ***Type:*** Nouvelle Caledone, Noumea Uen Toco base SW, 50 m, 29 Dec. 1971, *H. S. Mackee* 24766 (Holo: P; Barcode: P00639107; Iso: G, Barcode: G00358262).

Description: Butaud & P. Firmenich, PhytoKeys 56: 114. 2015.
Distribution: Distribution: New Caledonia (Grand Terre: SW side, Noumea, Karaka), endemic.
Distribution map: Butaud & P. Firmenich, PhytoKeys 56: Fig. 1. 2015.
Conservation status**:** Not assessed.
Common/Local names**:** New Caledonia sandalwood.

4. ***Santalum boninense*** (Nakai) Tuyama, Bot. Mag. (Tokyo) 52: 467. 1938.

Exocarpos boninensis Nakai, Bot. Mag. (Tokyo) 43: 440. 1929. ***Type***: Japan, Bonin: in rupibus Kita-fukurozawa insular Chichishima, 2 May 1928, *H. Toyoshima s.n.* (Holo: TI, Specimen ID: 00703; Para: Specimen ID 00704).

Description: Nakai, Bot. Mag. (Tokyo) 43: 440. 1929 (under *Exocarpos boninensis*).
Distribution: Japan (Bonin & the Volcano Islands: Ogasawara-shoto Chichijima, Hahajima), endemic.
***Conservation status*:** Not assessed.
***Common/Local names*:** Japanese sandalwood, Munin-b yakudan (Japnese name) and Ogasawara sandalwood.

5. ***Santalum ellipticum*** Gaudich., Voy. Uranie, Bot. Part11: 442. 1829. *Santalum freycinetianum* var. *ellipticum* (Gaudich.) Hillebr., Fl. Hawaiian Isl. 390. 1888. ***Type***: Iles Sandwich, Oahu, Voyage Uranie, 1817–1820, *Gaudicahaud s.n* (P; Barcode: P00641562).

Santalum freycinetianum var. *cuneatum* Hillebr., Fl. Hawaiian Isl. 389. 1888. *Santalum cuneatum* (Hillebr.) Rock, Bull. Div. Forest. Board Commiss. Agric. Forest. Hawaii 3: 37. 1916. ***Type***: United States of America, Hawaii Islands, Lanai, July 1870, *Hillebrand s.n.* (BISH; B).

Santalum freycinetianum var. *littorale* Hillebr., Fl. Hawaiian Isl. 390. 1888. *Santalum littorale* (Hillebr.) Rock, Bull. Div. Forest. Board Commiss. Agric. Forest. Hawaii 3: 41. 1916. *Santalum ellipticum* var. *littorale* (Hillebr.) Skottsb., Bull. Bernice P. Bishop Mus. 43: 55. 1927. ***Type:*** United States of America, Hawaii Islands, Kailuna, 1869? *Hillebrand s.n.* (B, Barcode: B100158688).

Santalum cuneatum var. *laysanicum* Rock, Bull. Div. Forest. Board Commiss. Agric. Forest. Hawaii 3: 39.1916. ***Type:*** United States of America, Hawaii Islands, Laysan Island, Ander Uferzone der Insel, am uppigsten an der Nordwerseite, 1 Jan.1896, *H. H. Schauinsland* 20 (Holo: BISH; Iso: B, Barcode: B 100158689); *W. A Bryan s.n.* (BISH).

Santalum freycinetianum auct. non Gaudich. 1829; Bitter, Abh. Nat, Ver, Bremen 16:3, 433. 1900.

Santalum cuneaum f. *gracilius* Skottsb., Acta Horti Gothob. 2: 222.1926 & Bull. Bernice P. Bishop Mus. 43: 55.1927. *Santalum ellipticum* var. *gracilis* (Skottsb.) O. Deg., Fl. Hawaiiensis. fam. 100. 1932. ***Type***: United States of America, Hawaii Islands, Oahu, *C. J. F. Skottsberg* 118 (Syn.: BISH); *Forbes* 2442 ().

Santalum ellipticum f. *annectens* O. Deg., Fl. Hawaiiensis. fam. 100. 1932. ***Type***: United States of America, Hawaii Islands, Maui, dry *aa* forest NE of Kaalualu, 13 Sept. 1929, *O. Degener* 5319 (BISH; Iso, US, Barcode: 00441804).

Santalum ellipticum f. *physophora* O. Deg., Fl. Hawaiiensis. fam. 100. 1932. ***Type***: SW Hawaii, Oahu, Waimanalo, *O. Degner* 5297(BISH).

Description: J. F. Rock, Bull. Div. Forest. Board Commiss. Agric. Forest. Hawaii 3: 41.1916. 25, 37, 39.41.1916. M. D. Merlin et al., Spec. Prof. Pace. Is. Agrofor. 3–6. 2016.
Illustration: Sinclair, I., Indig. Fl. Hawaii Isl. t.35.1885; Skottsb., Bull. Bernice P. Bishop Mus. 43: Fig. 19–20. 1927; M. D. Merlin et al., Spec. Prof. Pace. Is. Agrofor. 3–6. 2016.
Distribution: United States of America (Hawaii Isl.: Hawai'i, Kauai, Kaena, Kahoolawe Isl., Kailua, Lanai, Laysan Isl., Maui, Moloka'i, Ni'ihau, O'ahu), endemic.
Conservation status**:** Not assessed.
Common/Local names**:** Coast sandalwood, Iliahi, Iliahi Aloe.
Note**:** Degner (1932) recognized formae annectens and physophora under *Santalum ellipticum.* However, Egler (1939) stated that 'until more complete material is available it is impossible to evaluate these segregates'.

6. ***Santalum fernandezianum*** F. Phil., Anales Mus. Nac., Santiago de Chile 9: 5, pl. 1. 1892 & Bot. Abhandl. Leipzig, 3, t. 1. 1893. *Mida fernandeziana* (F. Phil.) Sprague & Summerh., Bull. Misc. Inform. Kew 1927: 197.1927. ***Type***: Chile, Juan Fernández Islands, 1 Jan. 1888, *G. Fluhmann s.n.* (Holo: SGO) Masatierra (Now extinct, the last known tree having died between 1908 and 1916).

Description: Anales Mus. Nac., Santiago de Chile 9: 5, pl. 1. 1892; Skottsb., Bull. Bernice P. Bishop Mus. 43: 55. 1927.
Illustration: Hooker's Icon. Pl. 25: t. 2430. 1896; Skottsb., Bull. Bernice P. Bishop Mus. 43: Fig. 16. 1927.
Distribution: Chile (Juan Fernández Islands), endemic.
Conservation status**: Extinct** (www.iucnredlist.org—downloaded on 29 October 2020).

7. ***Santalum freycinetianum*** Gaudich., Voy. Uranie, Bot. Part 11: 442. t. 45. 1829. ***Type***: United States of America, Hawaiian Islands: Insulis Sandwichensibus, Wahou, alt. 350–400 hex. 1817, *C. Gaudichaud-Beaupré s. n.* (Holo: P; Iso: B, K).

Santalum longifolium Meurisse, Bull. Mens. Soc. Linn. Paris 2:1026. 1892, nom.nud. *Santalum freycinetianum* var. *longifolium* O. Deg., Flora Hawaiiensis: Fam.100. 1932. ***Type***: United States of America, Iles Sandwich (Hawaiian Islands), O'ahu, 1851–55, *M. J. Remy* 510 (Holo: P, Barcode: P00641560).

Description: *J. F. Rock,* Bull. Div. Forest. Board Commiss. Agric. Forest. Hawaii 3: *19. 1916;* D. T. Harbaugh et al., Syst. Bot. 35(4): 833. 2010. M. D. Merlin et al., Spec. Prof. Pace. Is. Agrofor. 3–6. 2016.
Illustrations: Gaudich., Voy. Uranie, Bot. Part 11: 442. t. 45. 1829; Harbaugh et al., Syst. Bot. 35(4): Fig. 3F-G. 2010. M. D. Merlin et al., Spec. Prof. Pace. Is. Agrofor. 3–6. 2016.
Distribution: United States of America (Hawaii Islands: 400–600 m altitude; Muai, Lanai, Molokai, Oahu), endemic.

***Common/Local names*:** Citron sandalwood, forest sandalwood, Freycinet sandalwood, Iliahi, Lauhala.
***Conservation status*:** Endangered: **B1ab (iii) + 2ab (iii)** (www.iucnredlist.org—downloaded on 29 October 2020).

8. **Santalum haleakalae** Hillebr., Fl. Hawaiian Isl. 390. 1888. ***Type***: United States of America, Hawaiian Islands: Maui, Haleakala, 2440–3050 m, May 1872, *W. Hillebrand & J. M. Lydgate s. n.* (Holo: B, reported destroyed; lecto: BISH-581851 (designated by Harbaugh et al., *Syst. Bot.* 35(4): 833. 2010; Isolecto: K, Barcode: K000880511).

var. **haleakalae**

Description: *J. F. Rock,* Bull. Div. Forest. Board Commiss. Agric. Forest. Hawaii 3: 23. 1916; D. T. Harbaugh et al., Syst. Bot. 35(4): 833. 2010. M. D. Merlin et al., Spec. Prof. Pace. Is. Agrofor. 3–6. 2016.
Illustrations: D. T. Harbaugh et al., Syst. Bot. 35(4): Fig. 3D. 2010. M. D. Merlin et al., Spec. Prof. Pace. Is. Agrofor. 3–6. 2016.
Distribution: United States of America (Hawaii Islands: 1800–2700 m; Haleakala on East Maui), endemic.
***Common/Local names*:** Haleakala sandalwood, Iliahi.
***Conservation status*:** Not assessed for IUCN; See conservation status notes in D. T. Harbaugh et al., Syst. Bot. 35(4): 833. 2010.

var. **lanaiense** (Rock) Harbaugh, Syst. Bot. 35: 834. 2010. *Santalum freycinetianum* var. *lanaiense* Rock., Indig. Trees Haw. Isl. 129 1913. *Santalum lanaiense* (Rock) Rock, Bull. Div. Forest. Board Commiss. Agric. Forest. Hawaii 3: 21. 1916. Type: United States of America, Hawaiian Islands: Lana‘i, Haalelepakai, on the highest ridge, 3000 ft., July 1910, *J. F. Rock* 10061(Holo: BISH-579847; Iso: GH, HUH, Barcode: 00035908).

Santalum freycinetianum var. *auwahiense* Stemmerm., Pacific Sci., 34(1): 47. 1980. Type: United States of America, Hawaiian Islands: Maui, Auwahi Forest Reserve, 1 June 1977, *R. L. Stemmermann &. J. Kjargaard* 2149 (Holo: BISH-430709; Iso: BISH).

Description: *J. F. Rock,* Bull. Div. Forest. Board Commiss. Agric. Forest. Hawaii 3: *21. 1916;* D. T. Harbaugh et al., Syst. Bot. 35(4): 834. 2010.
Illustrations: D. T. Harbaugh et al., Syst. Bot. 35(4): Fig. 3A–C, E.2010. M. D. Merlin et al., Spec. Prof. Pace. Is. Agrofor. 3–6. 2016.
Distribution: United States of America (Hawaii Islands: 550–135 m altitude: Lanai, Maui), endemic.
***Common/Local name*:** Lana‘i sandalwood.
***Conservation status*:** Not assessed for IUCN; See conservation status notes in D. T. Harbaugh et al., Syst. Bot. 35(4): 834. 2010.

9. ***Santalum insulare*** Bertero ex A. DC., Prodr. 14 (2): 685. 1857. ***Type***: French, Polynesia, Marquesas, Navarch, *Du Petit-Thours* (P); “Bertero O Taiti rec. par

M. Moerenhout 1835" (lecto.:G-DC). [Tahiti] "Ea i," 5. *coll.* (sterile branch and piece of wood). "Taiti, *M. Moerenhout'm* 1834, Eai" (incol.); Taiti, *Moerenhout,* dedit D. Guillemin in 1836; Taiti, *Bertero & Moerenhout'm*ill (Herb. Richard); Taiti, M. l'Amiral *Dupetit-Thouars.*

Santalum freycinetianum var. *insulare*; Meurisse, Bull. Mens. Soc. Linn. Paris 2: 1026. 1892, nom.nud.

Santalum multiflorum J. W. Moore, Bull. Bernice P. Bishop Mus. 102: 27. 1933. ***Type***: French Polynesia, Raiatea, Island of Raiatea, East path to Mount Temehani, on the northeast exposure of mountain, 355 m, 16 Sept. 1926, *J. W. Moore* 87 (Holo: BISH; Iso: MIN).

var. **insulare**

Description: Fosberg & Sachet, Candollea 40: 460. 1985.
Illustration: Nil.
Distribution: Cook Islands, Marquesas Islands, Tahiti (Society Island), Tubuai Island.
***Conservation status*:** Not assessed.
***Common/Local name*:** ahi.

var. **alticola** Fosberg & Sachet, Candollea 40: 463. 1985. ***Type***: French Polynesia, Tahiti, Mt. Aorai (Society Island), 11 Sept. 1997, B. H. Gagné 1552 (Holo: US Catalog No.: 3037917, Barcode: 00105704; Iso.: BISH).

Description: Fosberg & Sachet, Candollea 40: 463. 1985.
Illustration: Fosberg & Sachet, Candollea 40: Fig. 1. 1985.
Distribution: Tahiti (Society Islands), endemic.
***Conservation status*:** Not assessed.
***Common/Local name*:** Tahiti or Society Island sandalwood.

var. **deckeri** Fosberg & Sachet, Candollea 40: 463. 1985. ***Type***: French Polynesia, Marquesas, Hiva Oa Island, Crest above Taaoa, 15 Jan. 1975, *M.-H. Sachet* 2113 (Holo: US Catalog No.: 2981822, Barcode: 00105705; Iso.: BISH, L).

Description: Fosberg & Sachet, Candollea 40: 463. 1985.
Illustration: Fosberg & Sachet, Candollea 40: Fig. 3. 1985.
Distribution: Marquesas Islands, endemic.
***Conservation status*:** Not assessed.

var. **hendersonense** (F. Br.) Fosberg & Sachet, Candollea 40: 463. 1985. *Santalum hendersonense* F. Br., Bull. Bernice P. Bishop Mus. 130: 66. 1935. ***Type*:** Henderson Island (details of collection not given by original author), Pitcairn, 1 Jan–12 Dec, 1922, *E. H. Quayle & F. Brown* 10? (BISH).

Description: F. Brown, Bishop Mus. Bull. 130: 62. 1935; Fosberg & Sachet, Candollea 40: 470. 1985.
Illustration: F. Brown, Bishop Mus. Bull. 130: Fig. 12l–s. 1935.
Distribution: Henderson (Pitcairn) Island, endemic.

Conservation status**:** Not assessed.
Common/Local name**:** Henderson sandalwood.

var. **marchionense** (Skottsb.) Skottsb., Bishop. Mus. Occ. Pap. 14(1): 33. 1938.
Santalum marchionense Skottsb., Acta Horti Gothob. 5: 142.1930. ***Type***: Iles Marquises, *Du Petit-Thours s.n.* (P, Barcode: P00646136, P00646137). Marquesas, Nukuhiva, locality?, August 1922, *E. H. Quayle* 1313 (BISH)?; Hivaoa, Mokovau, 700–800 m, 1 March 1929, *Mumford & Adamson* 51 (BISH); Hivaoa, Tepehi, 465 m, June 1929, *Mumford & Adamson* 421 (BISH); French Polynesia, 15 Feb. 1921, *F. B. H. Brown* 985 (Lecto.: BISH); *F. B. H. Brown* 984 (Syn.: BISH); *F. B. H. Brown* 931 (Syn.: GB); *F. B. H. Brown* 523 (Syn.: GB).

Description: F. Brown, Bishop Mus. Bull. 130: 64. 1935.
Illustration: F. Brown, Bishop Mus. Bull. 130: 62. 1935.
Distribution: Marquesas Islands.
Conservation status**:** Not assessed.
Common/Local name**:** Marquesas sandalwood.

var. **margaretae** (F. Br.) Skottsb., Occ. Pap. Bishop Mus. 14(4): 34. 1938.
Santalum margaretae F. Br., Bull. Bernice P. Bishop Mus. 130: 62. 1935. ***Type***: Austral Islands, Rapa, Tanga, 240 m, 31 Oct. 1921, *A. M. Stokes* 392 (Holo: BISH; Iso.: BISH).
Santalum margaretae f. *Pauhi* F. Brown, Bishop Mus. Bull. 130: 65. 1935.
Santalum margaretae f. *Pauhi kua* F. Brown, Bishop Mus. Bull. 130: 65. 1935.
Santalum margaretae f. *pauhi* fiti F. Brown, Bishop Mus. Bull. 130: 65. 1935.
Santalum margaretae f. *pauhi ava ava* F. Brown, Bishop Mus. Bull. 130: 65. 1935.

Description: F. Brown, Bishop Mus. Bull. 130: 62. 1935; Fosberg & Sachet, Candollea 40: 469. 1985.
Illustration: F. Brown, Bishop Mus. Bull. 130: Fig. 12a–k. 1935.
Distribution: Astral Islands (Rapa), endemic.
Distribution map: not seen.
Conservation status**:** Not assessed.
Common/Local names**:** Pauhi, Pauhi kua, pauhi fiti, pauhi ava ava.
Note: Brown (Bishop Mus. Bull. 130: 65. 1935.) reports that like Hawaiians, the Marquesans recognize five different forms based on colour and odour of the wood, viz. *Pauhi, Pauhi kua, pauhi fiti and pauhi ava ava.*

var. **mitiaro** Sykes, Pacific Sci. 34: 79. 1981. Type: Cook Islands, Mitiaro, inland makatea, 15 Aug. 1974, *W. R. Sykes* 1045/CI (Holo: CHR); Cook Islands, Mitiaro, *makatea,* 15 Aug. 1974, *W. R. Sykes*1036/CI (CHR); Mitiaro, Atai, *makatea, 22* Jan. 1980, *W. H. Hambuechen* 243, 401 (CHR); Mitiaro, Vaiai sector, *makatea, 22* Jan. 1980, *W. H. Hambuechen,* 243, 299 (CHR).

Description: W. R. Sykes, Pacific Science 34(1): 79. 1980.
Illustration: W. R. Sykes, Pacific Science 34(1): Fig. 2. 1980.
Distribution: Cook Islands (Mitiaro), endemic.

Distribution map: W. R. Sykes, Pacific Science 34(1): Fig. 1. 1980.
Conservation status**:** Not assessed.

var. **raiateense** (J. W. Moore) Fosberg & Sachet, Candollea 40: 465. 1985.
Santalum raiateense J. W. Moore, Bull. Bernice P. Bishop Mus. 102: 27. 1933. ***Type:*** French Polynesia, Raiatea, Island of Raiatea, on ridge, south end of island, 200 m, 16 Feb. 1927, *J. W. Moore* 615 (Holo: BISH; Iso: BISH, L, MIN, U, US Catalog No.: 3575382, Barcode: 01097440; MINN).

Description: J. W. Moore, Bull. Bernice P. Bishop Mus. 102: 27. 1933; Fosberg & Sachet, Candollea 40: 465. 1985.
Illustration: not seen.
Distribution: Tahiti (Society Islands: Raiatea, Mo 'orea), endemic.
Conservation status**:** Not assessed.

var. **raivavense** F. Br., Bishop Mus. Bull. 130:62. 1935. ***Type***: Austral Islands, Raivavae, Taniora, 900 m, 10 June 1921, *A. M. Stokes* 100 (Holo: BISH; Iso.:BISH).

Description: F. Brown, Bishop Mus. Bull. 130: 62. 1935; Fosberg & Sachet, Candollea 40: 4639. 1985.
Illustration: F. Brown, Bishop Mus. Bull. 130: 62. 1935.
Distribution: Austral Islands (Raivavae), Marquesas Islands, Tahiti (Society Islands).
Conservation status**:** Not assessed.
Common/Local name**:** Raivave Sandlwood.

10. ***Santalum involutum*** H. St. John, Phytologia, 55(4): 220. 1984. ***Type***: United States of America, Hawaiian Islands: Kaua'i, between Ke'e and Hanakapiai, ridge top on NE side of last stream, NE of Hanakapiai, 25 July 1976, *C. Christensen* 38 (Holo: BISH-498267!; iso's: BISH).

Description: Harbaugh et al., Syst. Bot. 35(4): 835. 2010.
Illustrations: Harbaugh et al., Syst. Bot. 35(4): Fig. 3H. 2010.
Distribution: United States of America (Hawaiian Islands: Kauai), endemic.
Conservation status**:** Not assessed for IUCN; See conservation status notes in Harbaugh et al., Syst. Bot. 35(4): 835. 2010.
Common/Local name**:** Involute sandalwood.

11. ***Santalum lanceolatum*** R. Br., Prodr. Fl. Nov. Holland. 356. 1810; A. S. George, Fl. Australia 22: 63. 1984. ***Type***: 17 Nov. 1802, *R. Brown* 3218 (BM); Queensland, Sweers Island, 18 Nov. 1802, *R. Brown s.n* (MEL); Northern Australia, Islands of the Gulf of Carpentaria, 1862, *R. Brown s.n.* (P: Barcode: P00756409); 1 Nov. 1802, *R. Brown s.n* (NSW).

Santalum venosum R. Br., Prodr. Fl. Nov. Holland. 355. 1810. ***Type***: Australia, Northern Territory, Arnhem land, South Bay, 4 Feb. 1803, *R. Brown* 3215 (Holo: BM, K, E; Iso: K, P, Barcode: P00756408).
Santalum lanceolatum var. *venosum*; Bull. Mens. Soc. Linn. Paris 2:1026. 1892.

Santalum lanceolatum var. *venosum* F. M. Bailey, Comp. Cat. Queensland Pl. 469. 1913, nom. Illeg. non F. M. Bailey 1902. ***Type*:** Australia, Queensland, Somerset, *F. L. Jardine s.n.* (BRI).

Santalum oblongatum R. Br., Prodr. Fl. Nov. Holland. 355. 1810. *Santalum lanceolatum* var. *oblongatum* (R. Br.) Domin, Biblioth. Bot. 89: 47. 1928. ***Type***: Australia, Queensland, Endeavour River, 17 iv–3 viii, 1770, *Banks & Solander s.n.* (Holo: BM; Iso: BM, P, Barcode P00756411, P00756412).

Santalum lanceolatum var. *typicum* Domin, Biblioth. Bot. 89: 607. 1928, nom. inval. ***Type***: same as that of *Santalum lanceolatum* R. Br.

Description: D. T. Harbaugh, Australian Syst. Bot. 20:412. 2007. Fl. S Australia ed. 5: 11. 2012.
Illustrations: A. S. George, Fl. Australia 22: Fig. 18E–G. 1984. Fl. N. S. W. 3: 58 (1992); Fl. Victoria 4: 34, Fig. 4D. 1996; Fl. S Australia ed. 5: Fig. 5D–F, Pl. 4I–K.
***Distribution*:** Australia (Sea coast to 700 m: Northern Territory, Queensland, Western Australia), endemic.
Distribution map: A. S. George, Fl. Australia 22: Map. 1984; D. T. Harbaugh, Australian Syst. Bot.20: Fig. 3. 2007.
***Conservation status*:** Not assessed.
***Common/Local names*:** Australian sandalwood, Blue bush, Bush Plum, Cherrybush, Commercial Sandalwood, Native plumbush, Northern Sandalwood, Northern Sandalbox, Lanceleaf Sandalwood, plumbush, Plumwood, Tropical Sandalwood, True Sandalwood and Queensland Sandalwood.

12. ***Santalum leptocladum*** Gand., Bull. Soc. Bot. France 66: 232. 1919. ***Type***: Australia, South Australia, Mt. Lyndhurst, May 1900, *M. Koch s.n.* (Holo: LY); 1 Aug. 1899, *M. Koch s.n.* (P); Dec. 1899, *M. Koch* 27 (Iso: P, Barcode P00756410; K: Barcode: K000323057)

Santalum megacarpum Gand., Bull. Soc. Bot. France 66: 232. 1919. ***Type*:** Australia, New South Wales, Cobar, 1 July 1903, *J. L. Boorman & Maiden s.n.* (Holo: LY; Iso: NSW).

Santalum lanceolatum var. *angustifolium* Benth., Flora Austral. 6:214. 1873. ***Type*:** Australia, New South Wales, from the Darling river to Cooper's creek, *Dallachy & Goodwin s,n.*; Neilson; New England, *C. Stuart* (Syn.).

Description: D. T. Harbaugh, Australian Syst. Bot. 20: 414. 2007.
Illustration: Not seen.
***Distribution*:** Australia (Queensland, New South Wales, Northern Territory, South, & Western Australia), endemic.
Distribution map: D. T. Harbaugh, Australian Syst. Bot. 20: Fig. 3. 2007.
***Conservation status*:** Not assessed.
***Common/Local names*:** Southern Sandalwood Harbaugh (Australian Syst. Bot 20: 416. 2007), Mundaworra (Dieyerie tribal name).

Note: Based on molecular phylogeneti analysis, Harbaugh (Australian Syst. Bot 20: 415. 2007) considered *Santalum leptocladum* Gand., as cryptic lineage within *S. lanceolatum* and treated it as distinct species).

13. ***Santalum macgregorii*** F. Muell., Bot. Centralbl. 15(60): 227. 1894. ***Type***: Nova Guinea, i Jan. 1893, *W. Macgregori s.n* (Holo: K, Iso: P, Barcode P00756413; BRI; MEL);

Distribution**:** Papua New Guinea, endemic.
Conservation status**:** Endangered: **A1cd, C1** (www.iucnredlist.org—downloaded on 29 October 2020).

14. ***Santalum murrayanum*** (T. L. Mitch.) C. A. Gardner, Enum. Pl. Austral. Occ. 35.1931; A. S. George, Fl. Australia 22: 66. 1984. *Eucarya murrayana* T. L. Mitch., Three Exped. Australia 2: 100. 1839. ***Type:*** Australia, New South Wales, below Lake Benanee, Murray river, 27 May 1836, *T. L. Mitchell s.n.* (Holo: K).

Fusanus diversifolius Miq. in Lehm., Pl. Preiss. 1(4): 617. 1845. *Santalum diversifolium* A. DC., Prodr. 14(2): 684. 1857. ***Type***: Australia, Swan River (York, Aoon River), 9 Sept. 1839. *L. Preiss* 2111 (LD, U, Barcode: U0006464).

Santalum mitchellii F. Muell., Fragm. 2: 179. 1861. nom.illeg.

Santalum persicarium F. Muell., Trans. & Proc. Victorian Inst. Advancem. Sci. 1: 41. 1855. *Fusanus persicarius* (F. Muell.) F. Muell. ex Benth., Fl. Austral. 6: 216. 1873. *Mida persicaria* (F. Muell.) Kuntze, Revis. Gen. Pl. 2: 589. 1891. ***Type:*** Australia, Victoria, Near Murray River, Dec. 1853, *F. Mueller s.n.* (Iso: MEL).

Description: A. S. George, Fl. Australia 22: 66. 1984; Fl. S Australia ed. 5: 12. 2012.
Illustrations: *A. S. George,* Fl. Australia 22: 19 C–D. 1984; Fl. N. S. W. 3: 58. 1992; Fl. Victoria 4: 34, Fig. 4F. 1996; Fl. S Australia ed. 5: Fig. 5G–J, Pl. 5A–F, L.
Distribution**:** Australia (New South Wales, South, Western, Victoria), endemic.
Distribution map: A. S. George, Fl. Australia 22: Map 74. 1984.
Conservation status**:** Not assessed.
Common/Local names**:** Bitter quandong, Quandong, Ming.

15. ***Santalum obtusifolium*** R. Br., Prodr. Fl. Nov. Holland. 356. 1810; A. S. George, Fl. Australia 22: 63.1984. ***Type***: Australia, New South Eales, Hawkebury River, Jan. 1805, *R. Brown s.n.* (Iso: MEL; P, Barcode P00756414, P00756415; K).

Fusanus crassifolius R. Br., Prodr. Fl. Nov. Holland.: 355. 1810. *Santalum crassifolium* (R. Br.) A. DC., Prodr. 14: 585. 1857. *Mida crassifolia* (R. Br.) Kuntze, Revis.

Gen. Pl. 2: 589. 1891. *Eucarya crassifolia* (R. Br.) Sprague & Summerh., Bull. Misc. Inform. Kew 1927: 196. 1927. ***Type***: Australia, New South Wales, Parramatta and Hunter's river, Dec. 1804, *R. Brown* 3212 (BM, K); Hawkesburry river, *R. Brown s.n.* (?).

Fusanus glaucus Gaudich. ex A. DC. in DC., Prodr. 14: 685. 1857. ***Type***: not seen.

Description: A. S. George, Fl. Australia 22: 63. 1984.
Illustration: A. S. George, Fl. Australia 22: Fig. 18D. 1984.
Distribution: Australia (New South Wales, Queensland and Victoria), endemic.
Distribution map: A. S. George, Fl. Australia 22: Map 71. 1984.
Conservation status**:** Not assessed.
Common/Local name**:** Blunt sandalwood.

16. ***Santalum paniculatum*** Hook. & Arn., Bot. Beech. Voy. 94. 1832.

Santalum freycinetianum var. *latifolium* A. Gray, Proc. Amer. Acad. 4:327. 1860 & Fl. Hawaiian Isl. 389. 1888. ***Type***: United States of America, Hawaii, Lua Pele (Hale-Maumau), 1 Jan. 1838, Wilkes Explor. Exped.s.n. (US Catalog No. 0055061, Barcode: 00105703; Iso: HUH, Barcode: 00035907; GH; NY).

Santalum latifolium Meurisse, Bull. Mens. Soc. Linn. Paris 2:1026.1892, nom.nud.

Santalum paniculatum var. *chartaceum* O. Deg. & I. Deg., Phytologia 27(3): 146. 1973. ***Type***: Hawaii, Puna, Forest estates, East of belt Road, 2000 ft., 5 June 1972, *I. Degner & O. Degner* 32769 (Iso: G, Barcode: G00358263; B, Barcode: B100158692).

var. **paniculatum**

Description: *J. F. Rock,* Bull. Div. Forest. Board Commiss. Agric. Forest. Hawaii 3: 33. 1916; M. D. Merlin et al., Spec. Prof. Pace. Is. Agrofor. 3–6. 2016.
Illustration: M. D. Merlin et al., Spec. Prof. Pace. Is. Agrofor. 3–6. 2016.
Distribution: United States of America (Hawaii Islands: 450–2000 m altitude: Hualalai, Kilauea, Maui, Mauna Loa, Molokai), endemic.
Conservation status**:** Vulnerable: **B1ab (ii, iii, v); D2** (www.iucnredlist.org—downloaded on 29 October 2020).
Common/Local name**:** Iliahi.

var. **pilgeri** (Rock) Stemmerm., Pacific Sci. 34(1): 52. 1981.

Santalum pilgeri Rock, Bull. Div. Forest. Board Commiss. Agric. Forest. Hawaii 3: 29. 1916. ***Type***: United States of America: Hawaii Islands, Kona, 1862, *Hillebrand s.n.* (B); S Kona, Pulehua, on *aa* lava flows above Kelakekua, boardering the great Central plain, 5000 ft, 10 Feb. 1912, *J. F. Rock* 10033 (HAW; Iso: GH; HUH; barcode-00035909) Hawai'i, Kona, 1862, *Hillebrand s.n.* (B; labelled as *Santalum freycinetianum* var.*gaudichaudi*).

Santalum pilgeri var. *luteum* Rock, Bot. Bull. Div. Forest. Board Commiss. Agric. Forest. 3: 31. 1916. *Santalum ellipticum* var. *luteum* (Rock) O. Deg., Fl. Hawaiiensis. fam. 100. 1932. ***Type***: United States of America: Hawaii Islands, On the lava flows of South & North Kona, Huehue to Puuwaawaa North Kona, slopes of Mt Hualalai, 2–3000ft., June 1909, *J. F. Rock* 3728 (HAW; Iso: HUH, Barcode: 00035910): Kapua, South Kona, Jan. 1912, *Rock* 12515 (HAW).

Santalum affine Pilg. ex Skottsb., Bull. Bernice P. Bishop Mus. 43: 55. 1927. pro syn. Type: United States of America: Hawaii Islands, 1862, *Hillebrand s.n.* (B).

Description: J. F. Rock, Bull. Div. Forest. Board Commiss. Agric. Forest. Hawaii 3: 29. 31. 1916.
Illustration: Skottsb., Bull. Bernice P. Bishop Mus. 43: Fig. 24. 1927.
Distribution: United States of America (Hawaii Islands: Haehue, Kona, Puuwaawaa), endemic.
Conservation status**:** Not assessed.
Common/Local name**:** Iliahi.

17. ***Santalum papuanum*** Summerh., Bull. Misc. Inform. Kew 1929(4): 125. 1929. ***Type:*** Papua, Rigo, 9 Dec. 1925, *L. J. Brass* 819 (Holo: K, Barcode K000880540; Iso: P, Barcode P00756420).

Description: Bull. Misc. Inform. Kew 1929(4): 125. 1929.
Illustrations: Not seen.
Distribution: Papua New Guinea, endemic.
Conservation status**:** Not assessed.

18. ***Santalum pyrularium*** A. Gray, Proc. Amer. Acad. Arts 4: 327. (1859?) 1860. *Santalum freycinetianum* var. *pyrularium* (A. Gray) Stemmerm., Pacific Sci., 34(1): 48. 1980. ***Type:*** United States of America, Hawaiian Islands (Sandwich Islands): Kaua'i, 1838–42, *US Exploring Expedition s. n.* (Holo: US-00055059; Barcode: 00105706; Iso: GH; HUH, Barcode:00035911; P, Barcode: P00646139).

Santalum majus H. St. John, Phytologia, 55(4): 223. 1984. ***Type:*** United States of America, Hawaiian Islands. Kaua'i, Kumuela Ditch Trail, along border between Koke'e State Park and NaPali-Kona Forest Reserve, 13 Aug 1964, *M. R. Crosby & S. Anderson* 2024 (Holo: BISH-68301).

Santalum pyrularium var. *sphaerolithos* Skottsb., Acta Hort. Gothoborg. 4: 359. 1944. ***Type:*** United States of America, Hawaiian Islands, Kaua'i, Alakai, 16Aug 1938, *L. M. Cranwell & C. Selling* 2979 (Holo: BISH-579831).

Description: *J. F. Rock,* Bull. Div. Forest. Board Commiss. Agric. Forest. Hawaii 3: 27. 1916; D. T. Harbaugh et al., Syst. Bot. 35(4): 836. 2010.
Illustrations: Skottsb., Bull. Bernice P. Bishop Mus. 43: Fig. 17. 1927. D. T. Harbaugh et al., Syst. Bot. 35(4): Fig. 3I–J. 2010.
Distribution: United States of America (Hawaii Islands: Kaua'i), endemic.
Conservation status**:** Not assessed for IUCN; See conservation status notes in D. T. Harbaugh et al., Syst. Bot. 35(4): 836. 2010.
Common/Local names**:** Kauai sandalwood, Iliahi, Sandwich sandalwood.

19. ***Santalum spicatum*** (R. Br.) A. DC. in DC., Prodr. 14(2): 685. 1857; A. S. George, Fl. Australia 22: 65. 1984. *Fusanus spicatus* R. Br., Prodr. Fl. Nov. Holland. 1: 355. 1810. *Eucarya spicata* (R. Br.) Sprague & Summerh., Bull.

Misc. Inform. Kew 1927: 196. 1927. ***Type***: Australia, South Australia, Spencer Gulf, 11 March 1802, *R. Brown s.n.* (Iso: MEL, NSW).

Santalum cygnorum Miq. in Lehm., Pl. Preiss. 1: 615. 1845. *Mida cygnorum* (R. Br.) Kuntze, Revis. Gen. Pl. 2: 589. 1891 ('cignorum). ***Type***: Australia, Western Australia, York, 29 Mar. 1839, *J. A. L. Preiss* 2103 (Iso: MEL, LD); Novae Hollandiae., Riv. des Cygnes, 1843, *J. A. L. de Preiss* 2103 (Iso: P, Barcode: P00756406).

Fusanus spicatus var. *frutescens* Hochr., Candollea 2: 355. 1925. ***Type:*** Australia, Western.

Australia, Boorabbin, 15 Feb. 1905, *B. Hochreutiner* 2938 ().

Description: A. S. George, Fl. Australia 22: 65. 1984. Fl. S Australia ed. 5: 12. 2012.
Illustrations: A. S. George, Fl. Australia 22: Fig. 19E. 1984; Fl. S Australia ed. 5: Fig. 5K–M, Pl. 5G–J.
Distribution: Australia (South and Western), endemic.
Distribution Map: A. S. George, Fl. Australia 22: Map 72. 1984.
Conservation status**:** Not assessed.
Common/Local names**:** Australian sandalwood, bois de santal australien, fragrant sandalwood and santal australien.

20. ***Santalum yasi*** Seem., [Bonplandia 9: 258. 1861, nom.nud.] Fl. Vit. 210. t. 55. 1867. ***Type***: Fiji, Mbua or Sandalwood Bay, Vanua Levu, 1860, *B. Seemannn* 385 (Lecto: K, Barcode: K000880513; isolecto: BM; Isolecto: P, P00646144; B, Barcode: B100158703; G, GH, MEL); Sandalwood Bay Mission station at Buxa, Oct.1852, *E. Home s.n.* (Syn: P, Barcode: P00646142-43).

Description: Seem., Fl. Vit. 1: 210. t. 55. 1867; A. C. Smith, Fl. Vit. Nova 3: 738. 1985.
Illustration: A. C. Smith, Fl. Vit. Nova 3: Fig. 187. 1985; A. J. Thomson, *Santalum austrocaledonicum* & *Santalum yasi* (Sandlwood), Santalaceae 2006, photo p. 3, 4, 14, 17.
Distribution: Fiji, Tonga, Vanuatu (New Hebrides); endemic.
Conservation status**:** Endangered: **A2cd + 3d + 4cd** (www.iucnredlist.org—downloaded on 29 October 2020).
Common/Local names**:** Yasi, Yasi ndina, yasi mboi, yasiyasi, Fiji sandalwood (Fiji), Ahi (Tonga), Asi Manogi (Samoa).

Excluded species:

Santalum capense Spreng. ex A. DC., Prodr. 14(2): 635, 686. 1857 = ***Rhoiacarpos capensis*** (Harv.) A. DC.

Santalum cunninghamii Hook. f., Fl. Nov.-Zel. 1: 223. 1853 = ***Mida salicifolia*** A. Cunn.

Santalum preissianum Miq. in Lehm., Pl. Preiss. 1: 615. 1845 (cited as synonym of *Fusanus emarginatus* Miq. in Lehm., Pl. Preiss. 1(4): 617. 1845 by F. mull., Frag.

1:86. 1861) = ***Daviesia emarginata*** (Miq.) Crisp, Austral. Syst. Bot. 8: 1191. 1995. Type: Preiss 2112 (Leguminosae).

Santalum lanceolatum var. *typicum* Domin, nom. inval. = ***Santalum lanceolatum*** var. ***lanceolatum***.

Santalum lanceolatum var. *rugosum* Meurisse, Bull. Mens. Soc. Linn. Paris 2:1026. 1892, nom. nud.

Santalum lanceolatum var. *multinerve* Meurisse, Bull. Mens. Soc. Linn. Paris 2:1026. 1892, nom. nud.

Santalum lanceolatum var. *vulgare* Meurisse, Bull. Mens. Soc. Linn. Paris 2:1026. 1892, nom. nud.

Santalum mida Hook., Hooker's Icon. Pl. 6: t. 563. 1843 = ***Mida salicifolia*** A. Cunn.

Santalum mida Hook., Ic. Pl. tt. 563, 575. 1843, nom.nud. = ***Mida salicifolia*** A. Cunn.

Santalum pyrularium var. *neo-caledonicum*; Meurisse Bull. Mens. Soc. Linn. Paris 2:1026. 1892, nom.nud.

Santalum salicifolium Meurisse, Bull. Mens. Soc. Linn. Paris 2:1026. 1892, nom.nud.

Santalum yasi var. *acutum* Meurisse Bull. Mens. Soc. Linn. Paris 2:1026. 1892, nom.nud.

Santalum salicifolium auct. non Meurisse, 1892; (A. Cunn.) C. A. Gardner, Bull. Woods Forests Dept. Western Australis 44: 9. 1928 = ***Mida salicifolia*** A. Cunn.

Names listed without reference to earlier publication or taxonomically validated.

Santalum lanceolatum var. *angustifolium*; Bull. Mens. Soc. Linn. Paris 2:1026. 1892.

Santalum lanceolatum var. *ovatum*; Bull. Mens. Soc. Linn. Paris 2:1026. 1892.

Annexure 2: Global Distribution of *Santalum*

Sl. No.	Species	Australia						Chile	Fiji	India	Indonesia		Japan	New Caledonia				Papua New Guinea	Polynesia							USA	Vanuatu							
		New South Wales	Northern Territory	Queensland	South	Victoria	West	Juan Fernández Is		Peninsular States	Java	Lesser Sunda Is	Bonin Is	Grande-Terre	Isle of Pines	Loyalty Islands	Noumea		Austral Is	Cook Is	Marquesas Is	Pitcairn Is	Society Is	Tonga	Tubuai Is	Hawaii Is	Aneityum	Aniwa	Efate	Erromango	Futuna	Malakula	New Hebrides	Tanna
1	*S. acuminatum*	+	+	+	+	+	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	*S. album*	-	+	-	-	-	+	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	*S. austrocaledonicum* var. *austrocaledonicum*	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	-	+
3a	*S. austrocaledonicum* var. *glabrum*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3b	*S. austrocaledonicum* var. *minutum*	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3c	*S. austrocaledonicum* var. *pilosulum*	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	*S. boninense*	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	*S. ellipticum*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
6	*S. fernandezianum*	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	*S. freycinetianum*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
8	*S. haleakalae*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
8a	*S. haleakalae* var. *lanaiense*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
9	*S. insulare* var. *insulare*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	+	-	+	-	-	-	-	-	-	-	-	-
9a	*S. insulare* var. *alticola*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
9b	*S. insulare* var. *deckeri*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
9c	*S. insulare* var. *hendersonense*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-

Sl. No.	Species	Australia						Chile	Fiji	India	Indonesia		Japan	New Caledonia					Polynesia							USA	Vanuatu							
		New South Wales	Northern Territory	Queensland	South	Victoria	West	Juan Fernández Is		Peninsular States	Java	Lesser Sunda Is	Bonin Is	Grande-Terre	Isle of Pines	Loyalty Islands	Noumea	Papua New Guinea	Austral Is	Cook Is	Marquesas Is	Pitcairn Is	Society Is	Tonga	Tubuai Is	Hawaii Is	Aneityum	Aniwa	Efate	Erromango	Futuna	Malakula	New Hebrides	Tanna
9d	*S. insulare* var. *marchionense*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
9e	*S. insulare* var. *margaretae*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9f	*S. insulare* var. *mitiaro*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9g	*S. insulare* var. *raiateense*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
9h	*S. insulare* var. *raivavense*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-
10	*S. involutum*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
11	*S. lanceolatum*	-	+	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	*S. leptocladum*	+	+	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13	*S. macgregorii*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14	*S. murrayanum*	+	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15	*S. obtusifolium*	+	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16	*S. paniculatum*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
16a	*S. paniculatum* var. *pilgeri*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
17	*S. papuanum*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
18	*S. pyrularium*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19	*S. spicatum*	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20	*S. yasi*	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	+	-

See Figs. 1, 2, 3 and 4.

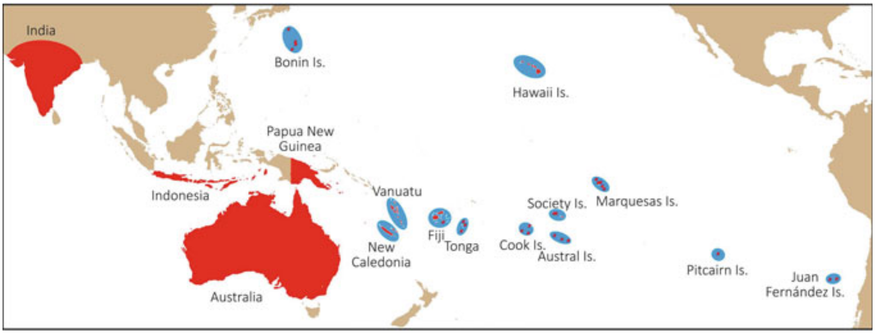

Fig. 1 Global distribution of genus *Santalum* L.

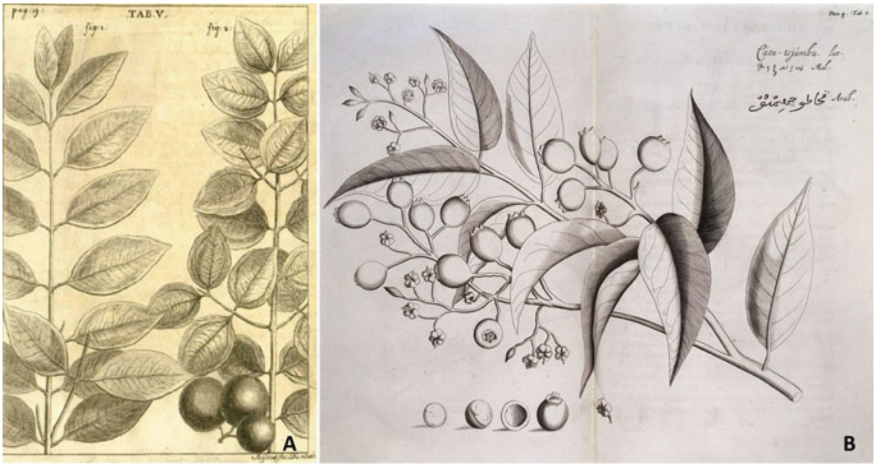

Fig. 2 *Santalum album* L. **a** Lectotype (Fig. 1 only), 1680; **b** Illustration in Hortus malabaricus (Rheede 1683)

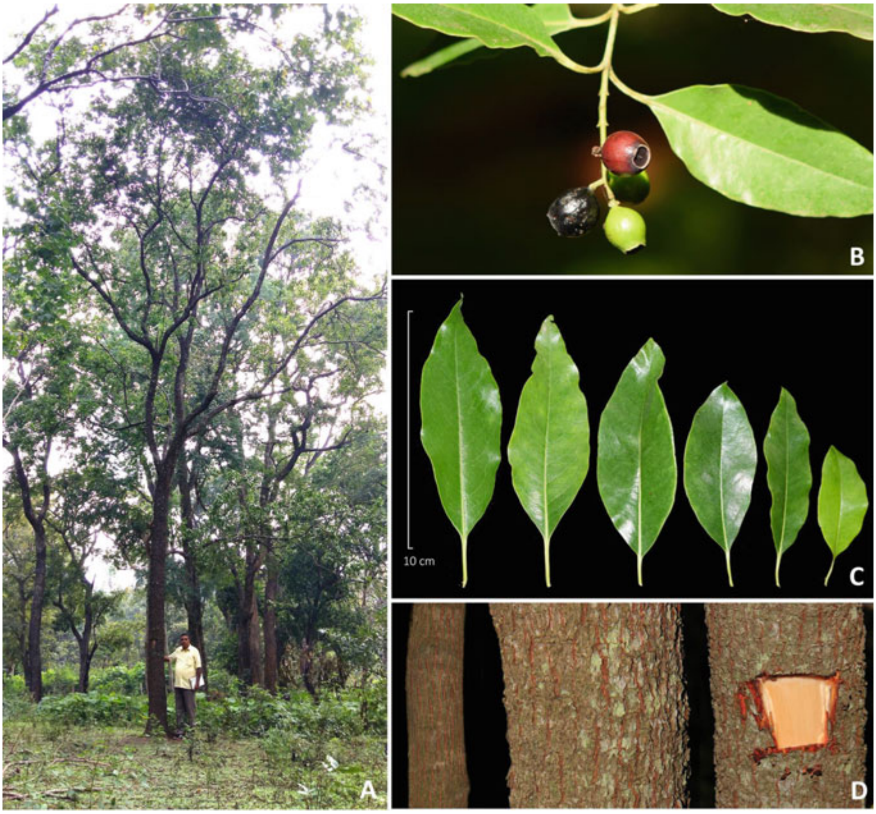

Fig. 3 *Santalum album* L. **a** Habit; **b** Fruiting twig showing fruits of three different stages and colours; **c** Variations in leaf size and shape; **d** Young and mature bark and blaze

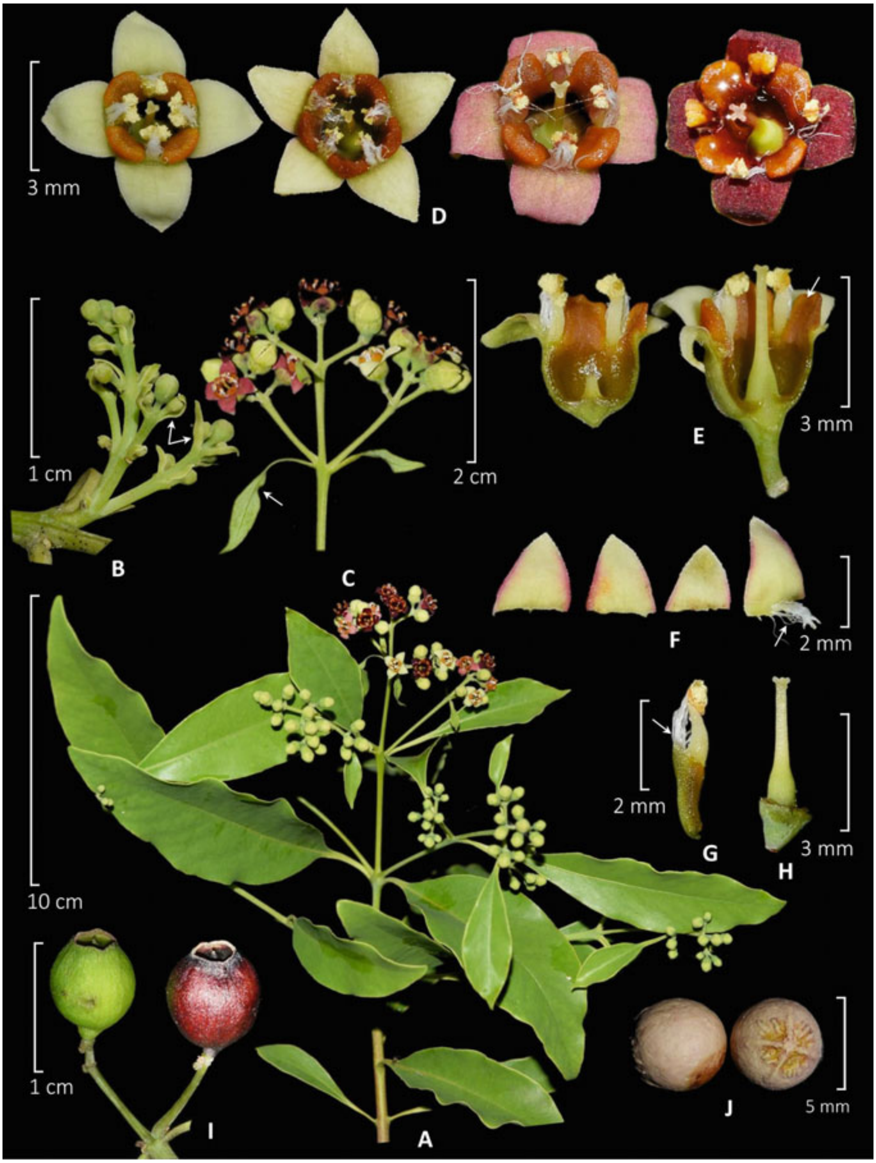

Fig. 4 *Santalum album* L. **a** Flowering twig; **b** Young inflorescence showing bracts (arrows); **c** Mature inflorescence showing reduced leaf at the base (arrow); **d** Different stages of flowers from freshly opened (greenish white) to older flowers (pink to dark red), also showing varation in tapels from 4 to 5 and stigmatic lobes from 3 to 4; **e** L. S. of Flower showing nectary lobes (arrow) and epitepalous stamens; **f** Perianth lobes showing post-staminal hairs attached at the base of the perianth lobe (arrow); **g** Stamen showing post-staminal hairs attaching from the base of perianth lobe to base of the anther lobes (arrow); **h** Carpel; **i** Fruits; **j** Seeds (side and top view)

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Chapter 12
Anatomy of Indian Sandalwood (*Santalum album* L.)

Satish Kumar Sinha and R. Vijendra Rao

1 Introduction

Santalum album L. commercially known as Indian sandalwood is an evergreen, small to medium-sized semi-root parasitic tree species of the family Santalaceae. The second most valuable tropical hardwood species globally, next to the African blackwood (*Dalbergia melanoxylon*), is known for its scented heartwood and oil present in stem and root both [1]. The scented wood is mainly suited for fine carving, whereas the oil is extensively used in soaps, perfumes, cosmetics, incenses, aromatherapy and medicine [2]. In the present scenario, the global supply of Indian sandalwood has reached critical levels due to over harvest, vandalization and smuggling of mature trees in past that resulted this species to be categorized as 'Vulnerable' by the International Union for Conservation of Nature's (IUCN) Red List of threatened species [3].

The increased demand and the high market price of sandalwood oil have always been a reason for frequent adulteration and importing cheaper substitutes of this prized material [4]. For instance, the import of such substitute, the 'African sandalwood' (*Osyris lanceolata* Hochst.& Steud) from Tanzania, was more than 3000 MT in 2006 that started flooding into our Indian sandalwood oil industry and affected the superior oil quality [4, 5]. Consequently, the government had to compel a ban on the import of sandalwood in India. Due to the presence of a unique and large number of essential oil molecules in Indian sandalwood, it is challenging to replace them with a synthetic substitute [6]. The common fragrant sandalwood adulterants commercially available in the Indian market are Nepal sandalwood (*Osyris*

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wightiana Wall. exWight), bastard sandalwood (*Mansonia gagei* J.R. Drumm) and Indian bastard sandal (*Erythroxylum monogynum* Roxb.) [7]. Furthermore, some non-fragrant timbers that are adulterated with sandalwood due to their fine texture are Himalayan box (*Buxus wallichiana* Baill), Indian Drypetes (*Drypetes porter* (Gamble) Pax & K. Hoffm.), Indian boxwood (*Gardenia latifolia* Ait.), Haldu (*Haldina cordifolia* (Roxb.) Ridsdale) and Kalam (*Mitragyna parvifolia* (Roxb.) Korth). These species are passed through the temporary application of sandalwood oil to make them fragrant [8]. Due to these adulteration problems, wood anatomical experts are often consulted to identify wood/timber to resolve legal disputes.

The macroscopic and microscopic structures of wood and general features are the common basis of timber identification. Some timbers can be identified at the macro-level, while most timbers are identified by examining the detailed anatomical structures using a microscope [8]. Like wood anatomy, the study of bark anatomy can provide an important clue in understanding the forensic forestry of sandalwood. However, sandalwood's haustorial anatomy study can be useful to know the functional attributes of haustorial–host interactions to grow successful sandalwood plantations. Although most studies are conducted on stem wood anatomy of *S. album* [4, 8–10] followed by haustorial anatomy [2, 11, 12] and root wood anatomy [8], no detailed information is available on the bark anatomy of sandalwood. In this chapter, the detail of the bark, stem wood, root wood and haustorial anatomy is described based on the investigation carried out on the availability of sandalwood trees and xylarium samples.

2 Sampling

Three *S. album* trees (mean girth, 30 cm; mean height, 5.9 m) located at three different places within the main campus of Navsari Agricultural University (20.95°N; 72.93°E), Navsari, Gujarat, India, were selected for the present investigation. General properties and anatomical features of stem wood, including growth rings, were studied using two core samples (width 5 mm) per tree collected by increment borer at the breast height (1.37 m above ground level) during October 2020 and one wooden disc sample available at forestry museum of the university (Fig. 1a, b). However, the general and anatomical bark and root features were determined by collecting bark samples (5 cm × 5 cm) from opposite sides of stem and wood samples from lateral roots of each tree, respectively (Fig. 1c, d). Haustorial anatomy was studied by randomly selecting five host roots of 3–4 months old *Alternanthera* sp. grown along with *S. album* in the same polybag at college farm nursery (Fig. 6a).

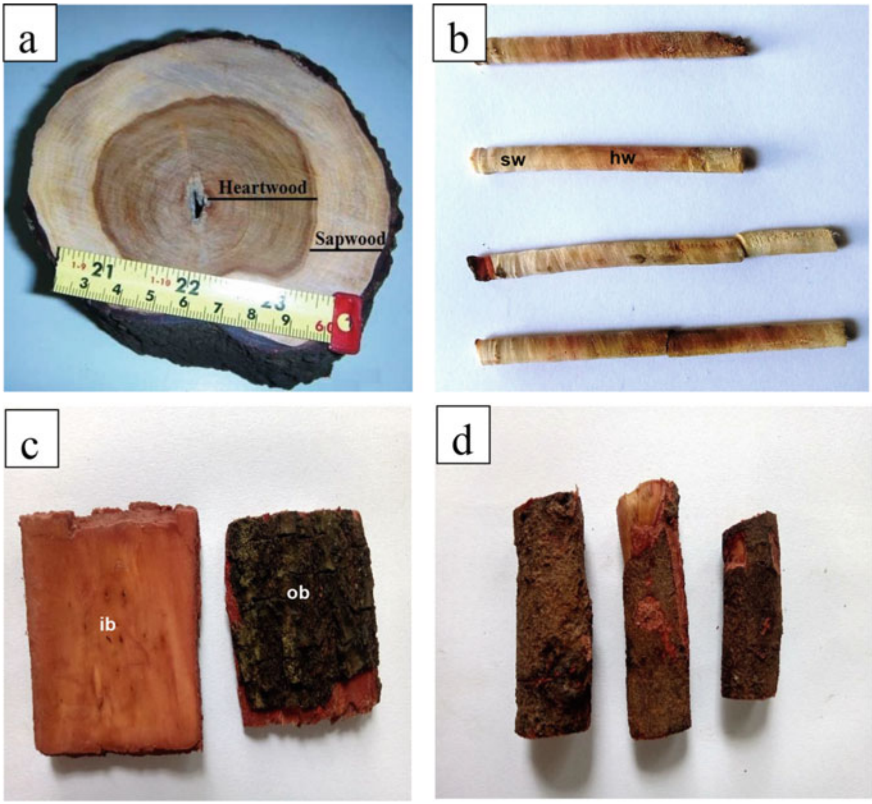

Fig. 1 **a** and **b** Sandalwood disc and core samples showing yellowish-brown to dark brown heartwood (hw) and pale yellow sapwood (sw) in the periphery, **c** sandalwood outer bark (ob) and inner bark (ib), **d** sandalwood root wood billets harvested from secondary roots

3 Sample Preparation and Measurements

For the measurement of general properties and anatomical features, bark, stem wood and root wood samples were initially cut into 3-cm-long billets or blocks depending upon the samples' size and shape. The air-dry volume of each sample was determined by the mercury displacement method, and air-dry density was calculated by taking the ratio of air-dry weight and volume [13]. The thickness of harvested bark was measured by a screw gauge.

For exploring the anatomical features of growth ring in stem wood, core samples collected from sandalwood were mounted in a grooved wooden block with waterproof glue (Fig. 4a). The surface of cores was planed using different grades of sandpapers to expose growth rings. The arrangement of different cells and growth rates was examined under a Leica stereo-zoom microscope. The anatomical features of haustoria were observed by taking the longitudinal section at sandalwood haustorium and host root interface (Fig. 6c).

Anatomical measurements of bark, stem wood and root wood samples were carried out under the microscope equipped with an image analysis system by maceration technique and sectioning 25-μm-thick samples in transverse, radial and tangential directions using a sliding microtome. Vessel parameters (tangential vessel diameter and vessel frequency) of stem wood and root wood and ray parameters (ray height, width and frequency) of bark, stem wood and root wood were measured at 10x objective under Leica trinocular microscope with a LAS measurement software using the slides of transverse and tangential sections, respectively. Ray compositions of bark, stem wood and root wood were recorded in radial section. The microscopic features of bark such as thickness and composition of various cells in phellem, phelloderm and secondary phloem were observed and recorded using the slides of transverse, radial and tangential sections according to the International Association of Wood Anatomists (IAWA) committee guidelines for bark anatomy [14].

To determine fibre parameters (fibre length, diameter and cell-wall thickness) of bark, stem and root wood and vessel parameters (vessel length and intervascular pit size) of the stem and root wood, small slivers of wood and bark were taken into test tubes and macerated by Schultz's method using 50% HNO_3 and few crystals of $KClO_3$ [15]. Fibre length was measured at 4x objective and vessel length at 10x objective, while fibre diameter, cell-wall thickness and intervascular pit size were measured at 40x objective under a Leica trinocular microscope. At least, 25 measurements were recorded for each anatomical characteristic to derive mean and range values according to IAWA committee guidelines [14, 16].

4 General Features of Wood and Bark

The sapwood colour of stem and root of *S. album* is white to pale yellow, unscented and sharply differentiated from yellowish-brown to dark brown, strongly scented heartwood [8]. The heartwood colour turns darker reddish-brown over time [10]. It has a pleasant characteristic odour due to aromatic oil (popularly known as Indian sandalwood oil or sandalwood oil), which lasts for many years [17]. Wood is moderately hard, heavy (sp. gv. 0.87–0.92 air dry), dull to lustrous with oily feel, without characteristic taste, straight-grained to slightly wavy, very fine and even-textured [8, 10, 17]. In the present study, similar general features were also recorded in our sandalwood samples (Fig. 1a, b). We reported the presence of scented heartwood (avg. 40.4% on an area basis) in stem wood only; however, heartwood was absent in root wood. The average air-dry density of stem and root wood was recorded to be 0.89 gcm^{-3} and 0.79 gcm^{-3}, respectively.

The stem's outer bark is reddish-brown or dark brown, while the inner part of the bark is red. Young trees have smooth bark that develops into rough with deep vertical cracks as the tree matures [1]. In the current investigation, we reported that the sandalwood stem's outer bark was dark brown to black with rough vertical cracks

(Fig. 1c), whereas the outer bark of the root was dark reddish-brown (Fig. 1d) and comparatively smoother than the stem bark. The inner part of bark in both stem and root was red (Fig. 1c). There was no scent in the bark of sandalwood. The average air-dry density and bark thickness in the stem were reported to be 0.48 gcm^{-3} and 5.1 mm, respectively.

5 Bark Anatomy

The anatomical structure of bark has remained relatively poorly studied because it is composed of both very soft and hard and both permeable and impermeable tissues, creating a problem in sectioning [14]. No detailed information is available so far on the anatomical features of sandalwood bark. For the first time in the present study, we are reporting the detailed anatomical characteristics of sandalwood bark, which is summarized in Table 2. In the microscopic study of sandalwood bark, two distinct layers, i.e. periderm (phellem, phellogen and phelloderm) and secondary phloem, were observed (Fig. 2a). Phellem (cork) cells were compactly arranged in radial files, square and rectangular in shape, non-stratified, evenly thick-walled and sclerified. Phelloderm (secondary cortex) cells were parenchymatous, square and rectangular in shape, non-stratified, thick (more than 3 cell layers), lacking lenticels. Starch grains were present in parenchyma cells, crystals occasional in cortical cells either solitary or in tangential line. Secretory cells with coloured contents were observed in the cortical region of bark.

In secondary phloem, sieve tube was arranged in tangential bands of 2–3 layers alternate with tangential bands of fibres (Fig. 2b) and companion cells were present in strands of 2 cells as seen in transverse and tangential sections, respectively (Fig. 2d). Axial parenchyma was diffuse to diffuse in aggregate occasionally filled with cubical- or cuboidal-shaped crystals in chambered cells. Rays were fine to very fine, 5–9 per mm, homogeneous, uniseriate to biseriate (1–2 seriate), composed of procumbent cells, 30–48 μm in width and 110–309 μm in height. Generally, the course of phloem rays was straight in the transverse section. However, dilatation (ray cells tangentially expanded) in the central region of wedge-shaped rays was observed through a dilatation meristem (Fig. 2b). Ray dilatation occurs when bark increases in circumference to adjust to the xylem's secondary growth [18]. Crystals were lacking in rays and fibres. Interestingly, in the sandalwood bark, distinct oil cells were reported without oil globules associated with ray parenchyma (Fig. 2d). Fibres were libriform, non-septate and tangentially elongated in transverse section, 591–1266 μm in length, 12–25 μm in diameter with 3–6 μm cell-wall thickness.

6 Stem Wood Anatomy

The anatomical characteristics of stem wood of *S. album* are summarized in Table 1.

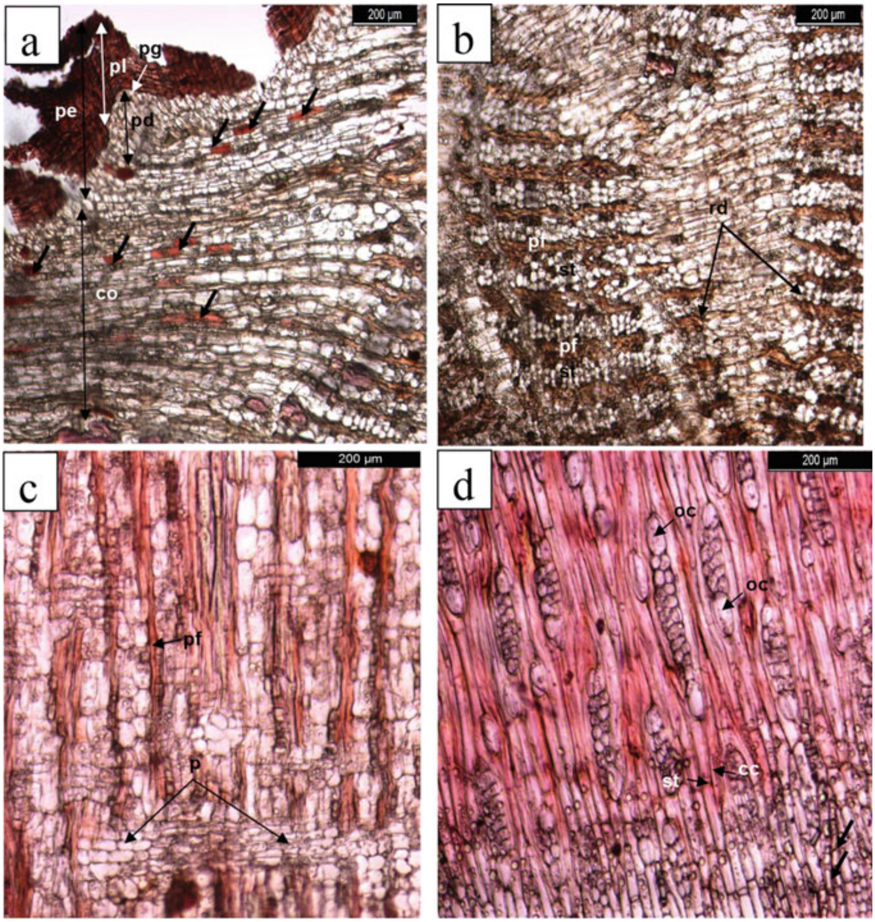

Fig. 2 **a** Transverse section of sandalwood outer bark showing periderm (pe) with phellem (pl), phellogen (pg), phelloderm (pd), cortical cells (co) and secretory cells with colour contents (arrows), **b** transverse section of inner bark (secondary phloem) representing ray dilatation (rd) and alternate bands of sieve tubes (st) and phloem fibres (pf), **c** homogeneous rays composed of procumbent cells (p) along with vertical bands of phloem fibres (pf) in radial section, **d** tangential section of inner bark showing oil cells (oc), strands of sieve tube (st), companion cell (cc) and crystals in locules of axial parenchyma (arrows)

Our results indicate that sandalwood's stem wood was diffuse-porous with very small to extremely small pores/vessels, 26–50 μm in diameter, 30–57 per mm^2, mostly solitary and circular to oval in shape in transverse sectional view (Fig. 3a). Vessel members were 226–491 μm in length, intervascular pit size 2–7 μm, perforation simple, empty or occasionally contained tyloses (Fig. 3d). Axial parenchyma was mostly apotracheal, diffuse to diffuse in aggregate, infrequently filled with rhomboidal crystals either solitary or in 4–6 locules (Fig. 3c). Rays were fine to very fine, 7–11 per mm, heterogeneous, uniseriate to biseriate (1–2 seriate), composed of

Table 1 Anatomical characteristics of stem wood and root wood of *Santalum album* L. (values presented are minimum–maximum and mean ± standard deviation in parenthesis)

Anatomical characteristics	Stem wood		Root wood	
	Results from present study	Results from other studies	Results from present study	Results from other studies
Vessels				
1. Type of perforation	Simple	Simple [4, 10, 8]	Simple	Simple [8]
2. Length (μm)	226–491 (380 ± 68.2)	100–500 [8] 100–570 [10]	144–512 (301 ± 84.7)	180–450 [8]
3. Tangential diameter (μm)	26–50 (38 ± 4.8)	50–70 [4] 50–80 (65) [8] 70–85[10] 20–76 [9]	24–80 (46 ± 10.9)	36–72 [8]
4. Frequency (per mm^2)	30–57 (41 ± 7.6)	40–50 [8] 25–30 [10] 27–61 [9]	50–90 (66 ± 14.1)	66–71 [8]
5. Intervascular pit size (μm)	2–7 (4 ± 0.9)	4–5 [8] 3–5 [10]	3–6 (4 ± 0.8)	4 [8]
Axial parenchyma				
1. Type	Diffuse and diffuse in aggregate	Diffuse and diffuse in aggregate [4, 10, 8]	Diffuse and diffuse in aggregate	Diffuse and diffuse in aggregate [8]
2. Crystals	Present	Present [10, 8]	Present	Present [8]
Rays				
1. Type	Heterogeneous	Heterogeneous [10, 8]	Heterogeneous	Heterogeneous [8]
2. Height (μm)	107–373 (192 ± 69.3)	350 [8] 200–335 [10] 160–360 [9]	140–272 (193 ± 36.5)	324 [8]
3. Width (μm/cell number)	22–41 (31 ± 4.5)/ 1–2 seriate	20–30 (1–3 seriate) [8] 25–30 (1–2 seriate) [4, 10] 8–36 [9]	24–41 (31 ± 4.4) 1–2 seriate	36 (1–2 seriate) [8]
4. Frequency (per mm)	7–11 (9 ± 1.1)	7–10 [10, 8] 6–10 [9]	4–8 (5 ± 1.4)	9–11 [8]
5. Oil cells	Absent	Absent [10, 8]	Absent	Absent [8]
6. Crystals	Absent	Absent [4, 10, 8]	Present	Present [8]
Fibres				
1. Type	Libriform and non-septate	Libriform and non-septate [4, 10, 8]	Libriform and non-septate	Libriform and non-septate [8]

(continued)

Table 1 (continued)

Anatomical characteristics	Stem wood		Root wood	
	Results from present study	Results from other studies	Results from present study	Results from other studies
2. Length (μm)	909–1517 (1194 ± 148.0)	500–1500 [8] 490–1490 [10]	661–1632 (1030 ± 184.4)	990–1512 [8]
3. Diameter (μm)	13–22 (17 ± 2.2)	15–20 [8] 17–20 [10]	12–20 (17 ± 1.8)	13–23 [8]
4. Cell-wall thickness (μm)	3–6 (4 ± 0.8)	3–6 [10]	2–5 (4 ± 0.6)	–
5. Crystals	Absent	Absent [10, 8]	Absent	Absent [8]

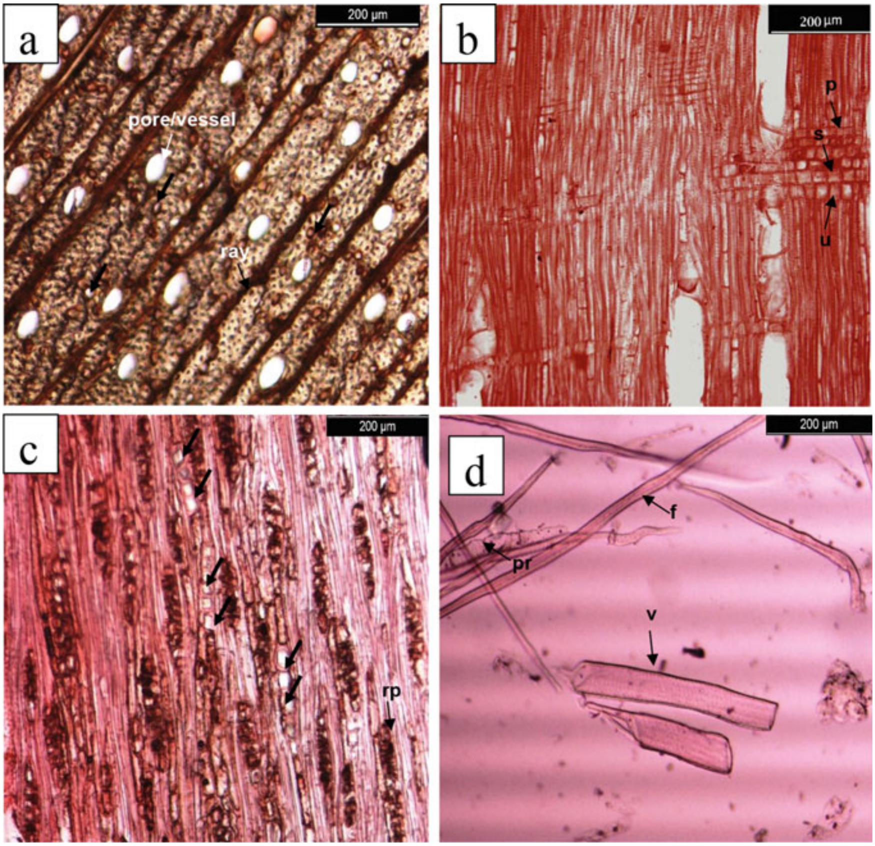

Fig. 3 **a** Diffuse-porous stem wood of sandalwood showing diffuse to diffuse in aggregate axial parenchyma (arrows) and fine rays in transverse section, **b** heterogeneous rays composed of procumbent (p), upright (u) and square (s) cells in radial section, **c** uniseriate to biseriate ray parenchyma (rp) and rhomboidal crystals (arrows) in chambered cells of axial parenchyma in tangential section, **d** maceration of stem wood showing vessel members (v), fibres (f) and parenchyma (pr)

procumbent cells, square and upright cells, 22–41 μm in width and 107–373 μm in height (Fig. 3b, c). Fibres were libriform and non-septate, 909–1517 μm in length, 13–22 μm in diameter with 3–6 μm cell-wall thickness (Fig. 3d). Crystals were absent in rays and fibres both. The anatomical features reported in the present study confirm the findings of many authors [4, 8–10]. However, some variations in our anatomical measurements were observed from earlier findings that may be due to change in the tree's locality factors and age [19] (Table 1). In contrast to the common anatomical observations, the occurrence of triseriate and huge multiseriate rays in some sandalwood specimens was also reported by Rao et al. [8] and Rajan [20], respectively (Table 2).

Growth rings in stem wood of *S. album* were distinct or indistinct from pith to the periphery; when distinct, most evident at low magnifications, the growth rate was about 8–10 rings per inch (Fig. 4a). Growth rings were delimited either by a band of darker, thick-walled fibrous tissue towards the outer margin or consisting of zones with relatively crowded pores of small diameter alternating with zones with comparatively scattered pores of large diameter (Fig. 4b–d). Cross-dating of growth rings in sandalwood was challenging to estimate accurately from a dendrochronological point of view due to the presence of frequent false and missing rings. Similar observations were also reported by Pearson and Brown [10]. They recorded 6–8 growth rings per inch in sandalwood, frequently fluctuating in diameter at various points throughout the circumference.

Sandalwood oils usually are secondary metabolites, biosynthesized in developing heartwood tissues [21, 22]. In our analysis, no distinct oil cells were observed in association with radial or axial parenchyma and fibres in sandalwood's heartwood to store oil. However, brownish-yellow, fine oily infiltration globules were observed in lumens of axial parenchyma and procumbent ray cells. Oil globules in axial parenchyma and ray cells were also reported by Pearson and Brown [10], whereas oil globules in vessels were recorded by Susikumar et al. [23].

7 Root Wood Anatomy

Very scanty information is available on the root wood anatomy of the *S. album*. The anatomical features of root wood are presented in Table 1. The present study shows that sandalwood's root wood was diffuse-porous with very small to extremely small pores/vessels, 24–80 μm in diameter, 50–90 per mm^2, mostly solitary and round to oval in shape in cross-sectional view (Fig. 5a). Vessel members were 144–512 μm in length with simple perforation, intervascular pit size 3–6 μm, lacking tyloses and other deposits (Fig. 5d). Growth rings in root wood were inconspicuous. Axial parenchyma was mostly apotracheal, diffuse to diffuse in aggregate, occasionally filled with rhomboidal crystals in chambered cells (Fig. 5b). Rays were fine to very fine, 4–8 per mm, heterogeneous, uniseriate to biseriate (1–2 seriate), composed of procumbent and upright cells, 24–41 μm in width and 140–272 μm in height

Table 2 Anatomical characteristics of bark of *Santalum album* L. (values presented are minimum–maximum and mean ± standard deviation in parenthesis)

Anatomical characteristics	Observation recorded during this study
Phellem (cork)	
1. Type	Phellem cells evenly thick-walled and sclerified
2. Cell Shape	Square and rectangular (radially elongate)
3. Stratification	Non-stratified
Phelloderm (secondary cortex)	
1. Thickness	Thick (more than 3 cell layers)
2. Cell type	Parenchymatous
3. Stratification	Non-stratified
4. Cell shape	Square and rectangular (radially elongate)
5. Lenticels	Absent
6. Organic inclusions	Starch grains in parenchyma cells
7. Crystals	Occasionally present in cortical cells either solitary or in tangential line
8. Secretory cells	Coloured contents present
Secondary phloem	
1. Sieve tube in TS	Arranged in tangential bands with 2–3 layers of sieve tubes alternate with tangential bands of fibres
2. Companion cells in TLS	Present in strands of 2 cells
3. Axial parenchyma	Diffuse to diffuse in aggregate
(i) Crystals	Occasionally filled with cubical- or cuboidal-shaped crystals in chambered cells
4. Phloem ray	Fine to very fine
(i) Course of rays in TS	Straight
(ii) Ray dilatation	Dilatation (ray cells tangentially expanded) in the central region of wedge-shaped rays by means of a dilatation meristem
(iii) Ray width (μm/cell number)	30–48 (37 ± 4.3)/1–2 seriate
(iv) Ray height (μm)	110–309 (186 ± 46.6)
(v) Frequency (per mm)	5–9 (7 ± 1.2)
(vi) Ray composition in RLS	Homogeneous and procumbent type
(vii) Secretory cells	Oil cells observed in TLS
5. Phloem fibres	Libriform and non-septate
(i) Shape in TS	Tangentially elongate
(ii) Length (μm)	591–1266 (971 ± 175)
(iii) Diameter (μm)	12–25 (19 ± 3.8)
(iv) Cell-wall thickness (μm)	3–6 (5 ± 1.1)

TLS Tangential longitudinal section; *RLS* radial longitudinal section; *TS* transverse section

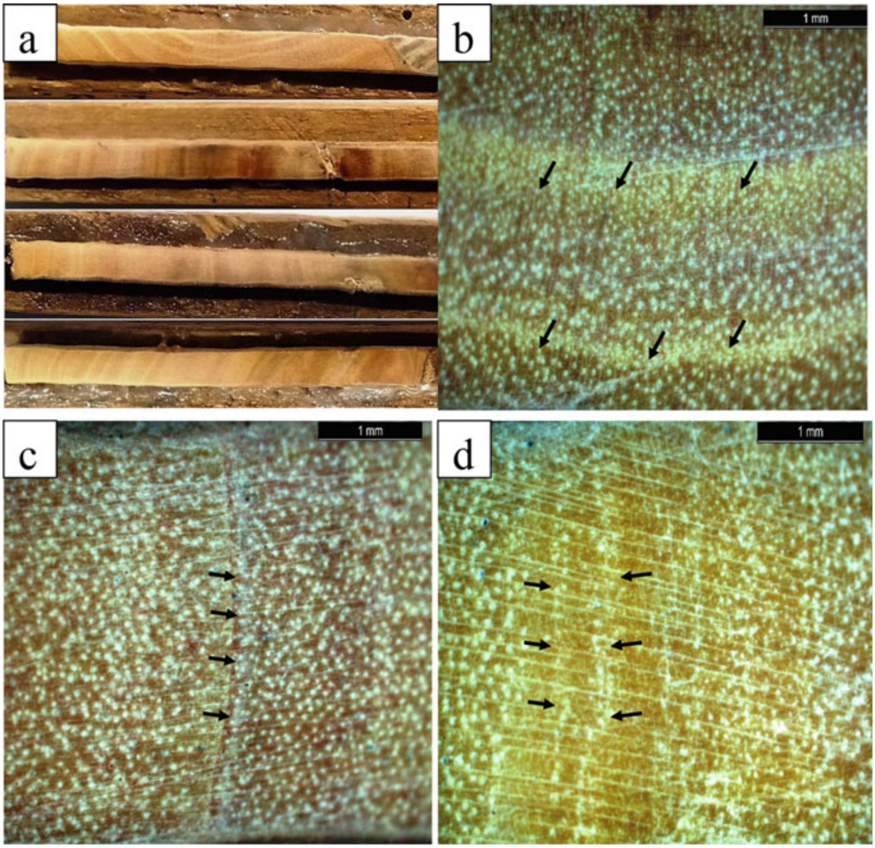

Fig. 4 **a** Growth rings visible in core samples of sandalwood stem, **b** growth rings towards pith delimited by zones of small diameter crowded pores (arrows) alternating with zones of large diameter pores (arrows), **c** growth ring in middle of core sample delimited by dark thick-walled fibrous tissue, **d** growth rings towards periphery delimited by thick bands of fibres alternating with narrow band of pores (arrows)

(Fig. 5b, c). Fibres were libriform and non-septate, 661–1632 μm in length, 12–20 μm in diameter with 2–5 μm cell-wall thickness. Crystals were absent in both rays and fibres. Like stem wood of sandalwood, no distinct oil cells associated with radial or axial parenchyma and fibres were observed in the heartwood of root wood. Rao et al. [8] also reported similar kinds of anatomical observations in root wood of *S. album* except for some variations in anatomical measurements, which may be due to change in the locality factors and age of the tree (Table 1). They reported smaller vessel diameter in root wood than stem wood of *S. album*. On the contrary, we reported a slightly bigger vessel diameter in root wood.

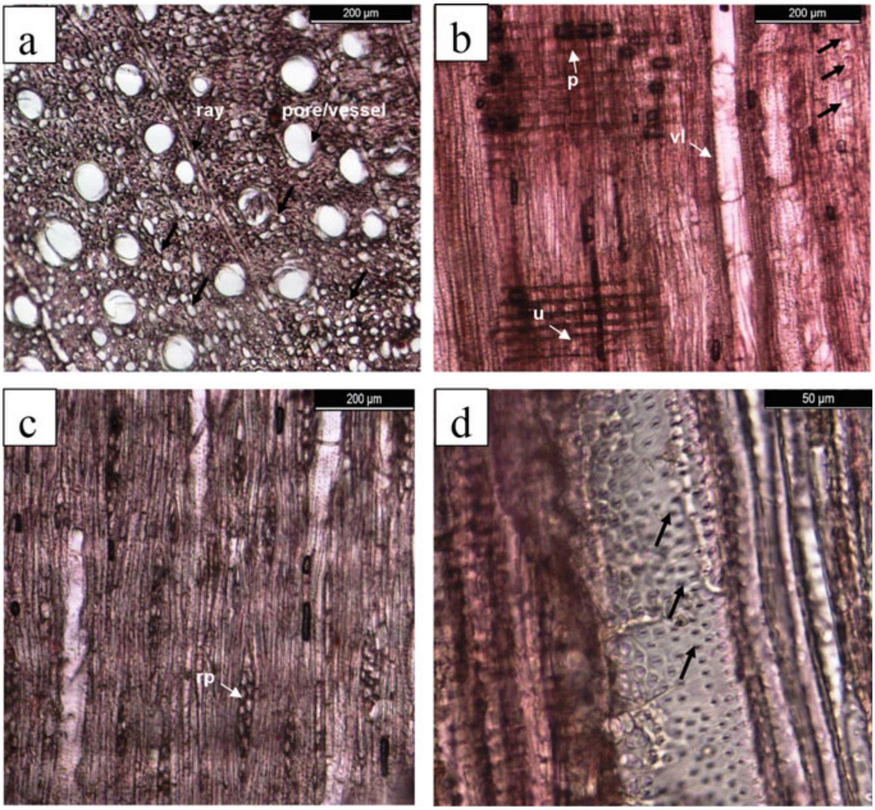

Fig. 5 **a** Diffuse-porous root wood of sandalwood showing diffuse to diffuse in aggregate axial parenchyma (arrows) and fine rays in transverse section, **b** radial section representing vessel linings (vl), rhomboidal crystals in axial parenchyma (arrows) and heterogeneous rays composed of procumbent (p) and upright (u) cells, **c** uniseriate to biseriate ray parenchyma (rp) in tangential section, **d** maceration of root wood showing vessel member with intervascular pits (arrows)

8 Haustorial Anatomy

Sandalwood is a partial root parasite that relies on the host for mineral nutrients (mainly nitrogen, phosphorous and potassium) and water [2]. It is reported that lateral roots of sandalwood may extend up to more than 20 m from the mother tree in search of suitable host plants for its survival [24]. The parasitic root absorbs the host resources through an organ known as haustorium, which provides a physical and physiological connection between the parasite and host [12]. The mature haustorium of sandalwood consists of an external hyaline body and the penetration peg composed of parenchyma cells that makes the initial contact with the host root and penetrates the host root xylem to access nutrients and water [12]. A schematic diagram of vascular connectivity between sandalwood and the host through haustorium is shown

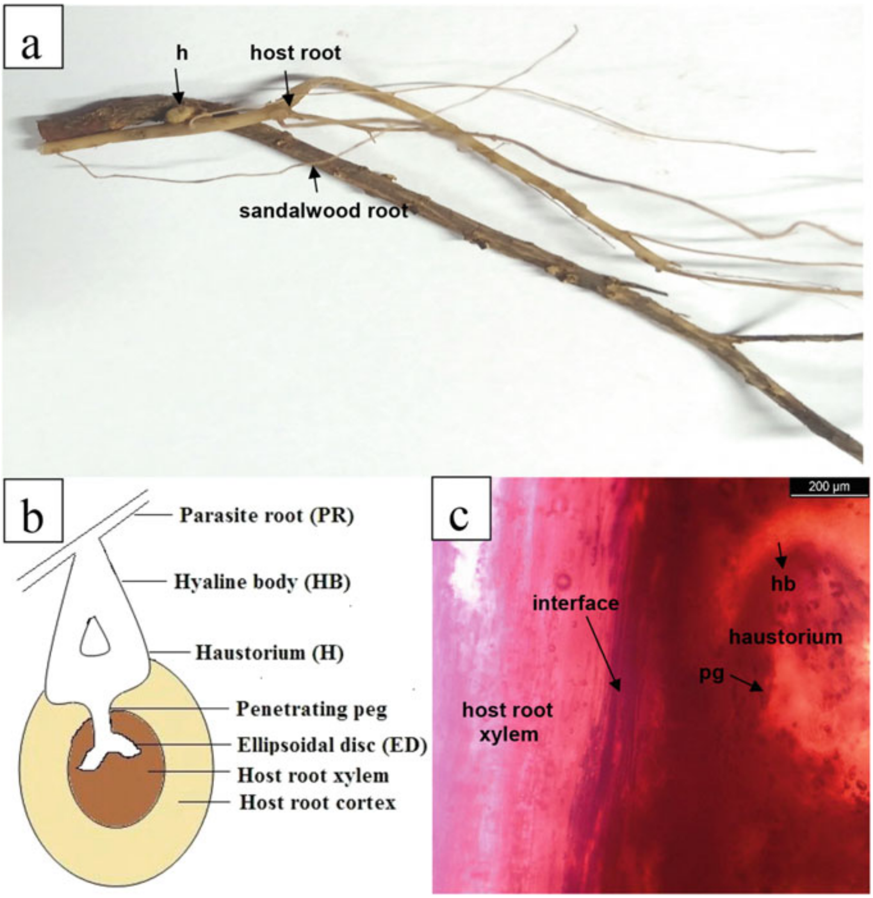

Fig. 6 **a** Sandalwood haustorium (h) formed on host root (*Alternanthera* sp.), **b** schematic diagram representing vascular connectivity between sandalwood and host through haustorium, **c** longitudinal section taken at host root and sandalwood haustorium interface showing hyaline body (hb) and initiation of penetration peg (pg) towards host root xylem

in Fig. 6b. The penetration peg of sandalwood haustorium is connected with the pits of host root xylem elements, but phloem connections and lumen-to-lumen xylem connections between the parasite and host root are absent [11, 12]. In the current study, 2–3 bud-shaped haustoria connections were observed between the taproot of sandalwood and the lateral root of the host plant (Fig. 6a). Anatomically, the hyaline body and penetration peg initiation were examined at host root and parasite haustorium interface of *S. album* with *Alternanthera* sp. (Fig. 6c). The initiation of penetration peg indicates the transition phase of young haustoria to mature haustoria. Our result is supported by the findings of Tennakoon and Cameron12 , who reported that initiation of penetration peg at the host root–haustorium interface of *S. album* only occurred when there were close connections with compatible mature hosts.

9 Conclusions

Anatomically, both stem wood and root wood in the *S. album* look similar except that in root wood, vessel diameter was slightly bigger and more frequent than vessel diameter in stem wood, while ray frequency and fibre length in stem wood were higher than root wood. No distinct oil cells were observed in the stem and root wood of the *S. album*. The oil globules in stem wood were observed in lumens of parenchyma cells. However, distinct oil cells were reported in bark without oil globules. Heterogeneous type of ray cells was reported in both stem and root woods, while the homogeneous type was observed in the bark. Rhomboidal crystals were present occasionally in chambered cells of axial parenchyma in stem wood and root wood both, whereas cubical- or cuboidal-shaped crystals were present in axial parenchyma of bark. The initiation of penetration peg during sandalwood's haustorial anatomy confirmed the transition of young haustoria to mature haustoria. These conclusions are based on the study of limited bark samples, stem wood, root wood and haustoria; however, many samples are needed to be studied for the above propositions to be confirmed.

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Chapter 13
Seed Biology

Geeta Joshi, A. N. Arunkumar, and Rekha R. Warrier

1 Introduction

Sandalwood trees have considerably reduced in their natural habitat, and the International Union for Conservation of Nature has categorized *Santalum album* as 'vulnerable' [6]. In the recent past, great interest is being shown for its propagation because numerous plantations are being established. This has increased the demand for seeds to raise quality planting material. Seeds are the primary source of regeneration of plants. They are channels for transfer of genetic material across generations. Basic understanding of the biology of the seed, its formation and development are necessary for collection, germination and improved nursery techniques. This chapter reviews information on flowering, fruiting, seed germination, pretreatment and storage.

2 Flowering

Sandalwood flowers occur in axillary or terminal cymose panicles that are shorter than leaves. The floral organs develop in acropetal succession [80], and an inflorescence comprises 20–40 single flowers [73]. Krishnakumar and Parthiban [38] observed that flowering proceeds top to bottom and initiates on the crown's Southern and South–Eastern sides. A similar sequence of flowering has been reported by Ratnaningrum and Indrioko [70] and Ratnaningrum et al. [73].

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Sandalwood flowers are straw yellow coloured at the initiation stage and turn deep purplish-brown on maturation [80]. The perigonium begins to bloom (white colour) during early anthesis, coinciding with mature pollen (yellow) dehiscence from yellowish anthers. It is followed by a change of perigonium colour from reddish white into maroon; when the stigma becomes receptive, the anthers gradually shrink and pollen starts to lose viability [73].

The bud undergoes various stages before developing into a fruit. Srinivasan et al. [80] state that it takes 30–35 days from the initiation of bud stage to the anthesis and 84–95 days from the initial stage to the ripe fruit. Veerendra and Padmanabha [86] report the existence of significant differences in flowering biology. Ratnaningrum et al. [73] describe three phases from flowering to anthesis, starting from flower buds initiation and development before anthesis (4–7 weeks), followed by early anthesis (2–4 days) which overlaps with the pollen maturity and finally complete anthesis which coincides with stigma receptivity (5–7 days). They further describe three more stages until fruit maturity, 5–10 days to develop pollinated flowers into young fruit, 4–6 weeks to attain maximum size and 3–4 weeks until fruit maturity. Krishnakumar and Parthiban [38] observed that flowering biology varied from 94 to 112 days.

Reports on flowering in sandalwood dates back to more than a century. It starts flowering at an early age of 4–5 years [84]. The flowering season in India was reported by Brandis [18] from February to July; Bourdillon [16] observed flowering and fruiting around the year. As per Hutchins, the flowering was observed at the end of hot weather or early rains [84]. Srimathi et al. [77] stated that flowering appears once, twice or throughout the year in a single population. Ananthapadmanabha et al. [3] categorized sandalwood trees into three distinct groups (i) flowering twice a year during March to May and September to December (ii) flowering once a year in September to December and (iii) No flowering even after 15 years. Srimathi [76] reported that most trees usually flower and fruit twice a year. The first flowering begins in May—end of the dry season, with fruit maturity commencing in September—end of the wet season; and the second flowering commences in November. Krishnakumar and Parthiban [38] reported two flowering seasons in July to October and December to March. In Indonesia, Haryanto et al. [30] and Prasetyaningtyas [60] and Ratnaningrum and Prehaten [72] reported flowering time from June to October, while Ratnaningrum and Indrioko [70, 71] reported flowering twice a year, at the beginning of the dry season in May up to September, and at the beginning of the rainy season in November up to March. Baskorowati [13] observed flowering twice a year, which reaches a peak in June and November, varying with the locality. In Australia, flowers appear twice—from December to January and also June to August. Mature fruit is available from June to September [56]. In Sri Lanka, flowering is observed from August to October and February to April and fragmentary flowering occurs in other months [83]. In China, the species flowers between March and May [40]. Flushes of flower production are observed to overlap, and at a time in a tree, all stages of flower and fruit development can be observed. Flowering period in different regions is given in Table 1.

Table 1 Variations in flowering recorded in different countries

Country	Flowering period	Author
India	February–July	Brandis [18]
	Flowering and fruiting around the year	Bourdillon [16]
	December–April	Matthew [45]
	July–September and fragmentary flowering in other months of the year	Srimathi [77] Veerendra and Padmanabha [86]
	July–October and December–March	Krishnakumar and Parthiban [38]
China	June–August with fragmentary flowering occurs in other months	Ma et al. [40]
Indonesia	June–October	Haryanto et al. [30]; Prasetyaningtyas [60]; Ratnaningrum and Prehaten [72]
	May–September and November–March	Ratnaningrum and Indrioko [70, 71]
	April–June and November–January	Baskorowati [13]
Australia	December–January and June–August	Orwa et al. [56]
Sri Lanka	August–October and February–April and fragmentary flowering occurs in other months of the year	Tennekoon et al. [83]

Ananthapadmanabha et al. [3] attributed the difference in flowering to variations in the levels of gibberellic acid-like substances in the shoots; before flowering, it increased in the shoots.

Flowering is affected by both genetic and climatic factors. Provenances from similar origin and progenies from the same genotypes report similar flowering characters. Among provenances, asynchrony and plasticity have been observed [71]. Provenances from Eastern Indonesia flowered early compared to those of central Java. Eastern Indonesia had a shorter flowering span, while Bromo had a longer one [70]. Prevailing local weather conditions affect flowering and seed production in the species [83]. Temperature variation results in differences in flowering frequency and reproductive outputs also [73]. In the dry season, the production of flowers and mature fruits is high compared to the rainy season [71]. The flowering time differs according to altitude. Sandalwood growing in low altitudes start flowering about one month earlier than those growing in higher altitude [81]. Early flowering and shorter flowering period were recorded for plants from a lower altitude, lower rainfall, highest temperature, lowest relative humidity and lowest soil moisture in Indonesia [73].

3 Fruit and Seed

Sandalwood fruit is a single-seeded succulent drupe with moderately hard brown endocarp. The shape of fruit may vary from round to oblong and occasionally

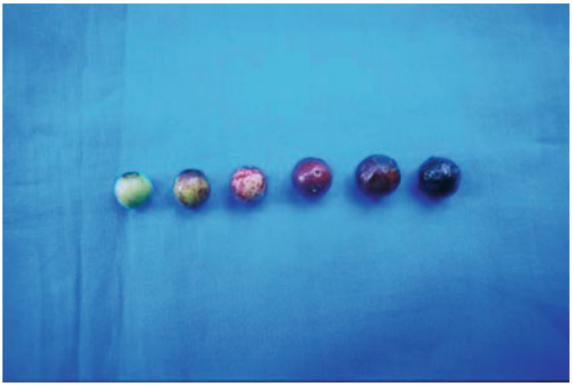

Fig. 1 Different stages during maturity of *S. album* fruits

with tapering ends [80]. During fruit development, the colour gradually changes from green to red to dark purple at maturity (Fig. 1). Black fruits have increased germination, seedling vigour, and higher viability and vigour in storage [42, 43].

Fertile seed production starts in 3 or 4 years old trees, the amount of seed and quantity of fertile seed increases with the age of the tree [54]. Age of tree age does not affect seed quality, as seeds from trees of different age groups had similar viability, germination and plant percentage [51]. Variation in fruiting is observed with season [62] fruiting being highest in December to March and low in July to October season [38]. However, the viability and germination of seeds collected at different seasons do not vary [80]. The mature fruits of *S. album* are dispersed by bird-based endozoochory [7, 11, 14]. The albuminous seed typically comprises a massive endosperm with an elongated dicotyledonous embryo devoid of testa [69]. The seed has stony endocarp, which is the false seed coat [80]. It contains 50–60% of drying oil composed of poly saturated fatty acids [32].

Mature fruits are plucked directly from the trees or collected from the ground. The fruits are depulped as pulp makes it susceptible to fungal infection. The seeds collected directly from the crown showed better germination and storage capacity than those collected from the floor [42]. Utomo et al. [85], comparing seeds collected directly from the trees and seeds from bird droppings, reported that germination was 70% and 85% respectively. For depulping the fruits are soaked in water and rubbed on the rough surface, and dull white or light purple coloured seeds are obtained (Fig. 2). The excess of moisture in the depulped seeds is removed by drying in the shade. Setiadi and Komar [75] suggested avoiding direct sun drying as it causes a reduction in seed viability. The germinability is more in depulped and dried seeds than in the seeds with pulps.

The seeds have polymorphic characters with varied shape and size. On average, nearly 6000 seeds are found in one-kilogram of seed [47]. The seeds at the micropylar have three or four ridges, it is either spherical/ovoid/conical, and diameter varies from 5 mm to 1 cm and the weight ranges from 0.10 g to 0.20 g. Based on the size and weight Nagaveni and Ananthapadmanabha [47], grouped seeds into small, medium and big. They observed that 82–87% were medium-sized with a weight of 0.1–0.2 g and size

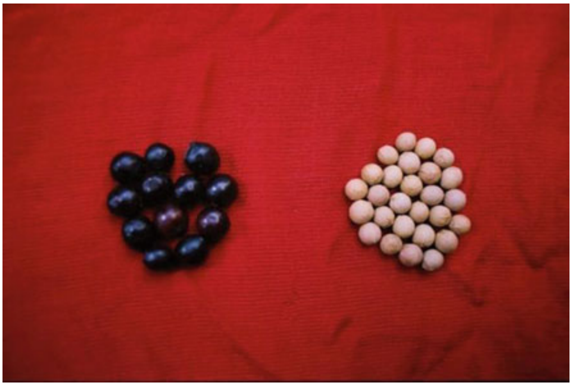

Fig. 2 Mature fruit with pulp and depulped seeds

7–8 mm. Veerendra and Sarma [89] reported that seed weight is inversely proportional to the rate of germination and directly proportional to seedling vigour. Seed weight was found to have a positive correlation with viability and germination percentage [63]. Large-sized seeds had better germination and germination percentages [17] and seedling height [40].

Seed traits are significantly affected by seed source, variation in seed traits for seed collected from different trees, provenances [23, 87, 88], plus trees [9] and clones [5] have been reported. From a single clone or family, uniform seedlings can be obtained by eliminating seeds of extreme sizes. However, rejecting the small-sized seeds from bulked seed lots of different clones can narrow down genetic diversity [5].

4 Germination and Pretreatment

Sandalwood seed shows epigeal germination. The cotyledons remain underground. The upper portion of hypocotyl appears above the ground as a loop while the lower portion swells and becomes fleshy—referred to as 'carrot' of the seedling. The hypocotyl straightens due to translocation of nutrients from seed albumen, raising the cotyledons above the ground, and the shrivelled seed either falls off or dries later (Fig. 3).

According to Hutchins [33] Sandalwood seeds germinate poorly and irregularly and takes six weeks to germinate and if proper soil is available germination continues for several months. He opined that only 50% of the seeds might germinate and mentions '*it requires on an average a small handful of Sandal seeds to produce a dozen plants or to stock two tile-pots*'. Various aspects related to seed germination had to be studied to rapidly and uniformly obtain seedlings in the nursery. Seeds were dibbled in soil or strewn in forest reserves anticipating germination on its own. However, germination always remained poor [67]. An extensive study carried out by Rao [47, 68] on germination and growth of Sandalwood seedlings mentions that the minimum time required for the emergence of the first germinated seed is one month

Fig. 3 Stages during seed germination

and continues beyond three months. Bahadur and Raghavan [10] mention that as per the Mitchell Sandal Scheme for Coorg, germination percentage was higher in Coorg seeds than that of Mysore or Salem seed. Inferior seeds were removed by floatation process, wherein seeds were immersed in water for 24 h, and the floating seeds were removed. The remaining seeds were used after shade-drying. They opined that artificial regeneration was more difficult than natural, although sandalwood seeds germinate easily. The Coorg Forest Department (1940–41) mentions that seeds collected from plantations failed to germinate while 19–25% of those from natural forests germinated. A comparative germination test on the seeds from Chittoor and Timor island revealed that the seed weight and germination percentage were higher in Chittoor seeds. Ramaswami and Gowda [65] used coconut water to enhance germination, but with no results.

Troup [84] reports that Sandalwood seeds require 30–90 days for germination extending to almost a year in some cases because of dormancy. Sandalwood seeds have post drop dormancy of 50–60 days, and it takes more than 140–150 days for obtaining 80% germination, due to the impenetrable seed coat [50–52]. Ananthapadmanabha et al. [2] reported that leachates of sandalwood seed inhibited germination revealing dormancy. Mahdi [41] reported that leachate of the black pericarp of *S. album* was more inhibitory for seed germination than the red pericarp. Germination is also dependent on the stage of fruit development and source and size of seed [44].

According to Srinivasan et al. [80], the dormancy is due to the seed coat or chemical substances in the seed coat. Breaking of seed coat resulted in rapid germination and reduced germination time to 15 days, showing inhibitory principles in the seed coat [79]. Sandalwood seed has physiological dormancy or morphophysiological dormancy and the minute embryo elongate inside the seed during or after losing physiological dormancy [12]. After extensive studies, Jayawardena et al. [34] proved that seeds have non-deep morphophysiological dormancy.

To enhance seed germination, studies have been carried out since later part of the nineteenth century. Srimathi and Rao [79] studied the effect of soaking, scarification and hard mesocarp removal on germination. At the end of 70 days, maximum germination (94%) was observed after 10 days in seeds without hard mesocarp. Removal of the testa and dipping of naked seed in fungicide Dithane™ M45 for 5 min resulted in 67% germination [31]. Biopriming using *Pseudomonas fluorescens* at varying concentrations and time durations revealed that the process for 8 days resulted in high germination (88%) within 21 days with low energy period (15 days) and high germination energy (62.98%) with a significant increase in growth attributes of the seedlings also [19].

Different treatments were conducted by Nagaveni and Srimathi [50, 51] to hasten the germination of Sandalwood seeds. Seeds devoid of seed coat germinated in 9–12 days and reached a maximum (90%) at the end of 40 days. Though seeds without seed coat had maximum germination, some of the inherent difficulties in this treatment are that the seeds tend to get damaged, is laborious, time-consuming, seeds are susceptible to fungal and insect attacks. Therefore, it may not be a viable option to use this method for large-scale seedling production. In acid-scarified seeds (soaked for 50 and 60 min), 80% germination was observed at the end of 70 days. However, handling acid needs care and caution. The authors used chemicals namely potassium nitrate, ammonium nitrate, sodium nitrate and potassium nitrite at concentrations of 10^{-1} and 10^{-2} M. They also used gibberellic acid (GA_3) at different concentration of 0.2, 0.1 and 0.05%. In both cases, the germination medium was initially fed by 10 ml solution after every 48 h. The seeds were also pre-soaked for 8, 16, 24 and 48 h in GA_3 solution of concentrations 0.1, 0.05 and 0.025%. Pre-soaked seeds responded well. Germination was initiated in 10 days and reached 90% by 35–37 days; 16 h soaking in 0.05% GA_3gave the best results. GA_3 500 ppm as best pretreatment has also been reported from West Bengal [20, 61], Kerala [37, 82] and Orissa [46] in India and also from Indonesia [85] Sri Lanka [25, 34, 83], Pakistan [8] and Australia [26, 57]. Jin et al. [35] soaked sandalwood seeds in 0.08, 0.1 and 0.12% GA_3 solution for 6, 12 and 24 h. Seeds soaked in 0.8% GA_3 for six hours showed 67.3% germination. Gunaga et al. [29] reported that soaking seeds in 0.3% GA_3 resulted in 68% germination. Ramaraoji [64] observed that germination was significantly high in seeds primed with GA_3 100 ppm solution for 24 h and sown in sand at 30 ± 2 °C for germination. Polaiah et al. [58] studied the effect of GA_3, cow urine, cow dung slurry, HNO_3, KNO_3, Thiourea and H_2SO_4 on seed germination and reported GA_3 1500 ppm as the best treatment for breaking the seed dormancy. However, Biradar [15] found that removal of seed coat followed by treating with GA_3 recorded the highest germination of 63.22%.

Nagaveni and Srimathi [53] tested the floatation technique and found that both floating and sunken seeds germinated, but the germination percentage of floating seeds was lesser than sunken seeds. Nagaveni et al. [49] also soaked seeds in $ZnCl_2$ (1%); NaOH (0.5%); cytozyme (5%); thiourea (0.5%); HCl (0.1 N); IBA (0.1%); IAA (0.1%); methanol extract of Sandalwood leaves, H_2O_2 (1%) and kinetin (0.01%). Germination initiated by 15 days in seeds soaked in the methanol extract and H_2O_2 (1%) while in others, it took 45 days. At the end of 60 days, more than 50% germination was obtained in all treatments. The group summarized that treating the seeds with gibberellic acid was better for quick and uniform germination. However, chemicals such as H_2O_2 (1%), thiourea (0.5%), methanol extract of Sandalwood leaves and IAA (0.1%) could be used as a substitute due to less soaking period. Dutt and

Verma [22] and Mohapatra et al. [46] reported that seeds devoid of mesocarp gave maximum germination (70%). Prasetyaningtyas [59] reported that germination could be enhanced by soaking the seeds for 12–24 h in water before sowing. Sutheesh et al. [82], in a study with 16 different treatments suggested soaking seeds in cow dung slurry for 24 h as it yielded 70% germination. It can be used as an alternative to GA_3, considering the cost and ease of operation. For large-scale seed germination, Lu et al. [39] recommended soaking *S. album* seeds in 0.1% GA_3 for 12 h using the protocol of Radomiljac [61] followed by surface sterilization with 3% NaOCl for 5 min and washing with distilled water before germination in sterilized sand at 28–30 °C.

In vitro studies carried out by Rangaswamy and Rao [66] using White's medium supplemented with coconut milk (20%) and casein hydrolysate (0.4%) resulted in germination within 10 days. Sahai and Shivanna [74] germinated sandalwood seeds on agar (0.6%) as a medium and achieved 40% germination. Nikam and Barmukh [55] used sandalwood seeds pretreated with GA_3 of different concentrations—0.6, 1.2, 1.8 and 2.4% for 12 h and subsequently inoculated in Murashige and Skoog's medium fortified with or without 2.0 or 4.0 μM benzyl amino purine. At the end of 30 days, germination was 80.67% in seeds pre-soaked in 1.2% GA_3—twice the germination observed in the control seeds.

To overcome seed dormancy and extended germination period, Anandalakshmi et al. [1] conducted seed encapsulation. GA_3-pretreated Sandalwood seeds were encapsulated in sodium alginate. Seeds encapsulated in 6 and 8% sodium alginate concentration had high germination capacity of 60 and 55%, respectively compared to untreated seeds (38.2%).

With Sandalwood cultivation being extensively taken up, based on the information collected, it can be concluded that till a low-cost pretreatment method is identified, over-night pre-soaking of Sandalwood seeds in gibberellic acid (0.5%) solution is the best pretreatment. This treatment has consistently proved successful because of easy handling and obtaining quick and uniform germination.

5 Seed Storage

S. album is commonly propagated by seeds [21, 27]. Therefore, it is essential to ascertain factors affecting seed viability. The viability of sandalwood seeds varies between individual trees [24], populations [17, 81] and is also dependent on the storage method [83]. Storage temperature and seed moisture content play a critical role in retaining the viability of seed in storage. Generally, the seeds are stored in gunny bags; the seeds gradually lose viability by 8–9 months [78] due to moisture absorption. Viability can be retained up to one year by storing in airtight containers like polythene bags or tin containers. For storing seeds beyond 12 months, dry cold storage can be adopted [78]. By treating the seeds with carbon dioxide, nitrogen and iodine vapour, the viability can be extended beyond 24 months [48]. For long-term storage, seeds should be air-dried in the shade until the moisture content is approximately 5–8% and stored at 4 °C in plastic bags [75]. Viability can be retained for more than two years by storing seed with 4.5–9% moisture content at 5–15 °C temperature [36]. Viability decreases in seeds with high moisture content due to metabolic changes in the fat reserves. Gamage et al. [28] reported a negative relationship of germination with storage time, viability reduced to 50% after seven weeks and was completely lost after 28th week of storage. Low storage temperature and reduced moisture content slow down the metabolic activity, thereby retaining the seed viability. Ananthapadmanabha et al. [4] reported depletion of food reserve and low total protein content in non-viable seeds compared to viable seeds.

6 Conclusion

Growing demand for large-scale planting stock necessitates the need for developing seed-handling protocols for the long-term viability of seeds. Sandalwood seeds pose various problems in germination and storage. It is also influenced by various factors such as locality, temperature and size. Natural populations with a proven record of germination over time can be delineated as seed sources. Seedlings and clonal seed orchards established with identified genotypes can serve as seed sources in future. Seed certification is a crucial pending decision in forestry. This process will ensure the deployment of quality planting stock in all plantations raised hitherto.

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Chapter 14
Pollination Biology of Sandalwood

A. S. Hareesha, V. V. Belavadi, and K. B. Tharini

1 Introduction

Pollination, an essential ecosystem service, is considered as the basis for sustaining biodiversity. It is the transfer of pollen grains from anthers to the stigma of the same flower (self-pollination) or to a different flower of the same plant or from a flower on another plant of the same species (cross-pollination). Plants benefit when the pollen grains are received from another plant, as it increases variability. Hence, majority of plant species tend to be either completely or partially cross-pollinated. Since plants are stationary, they need a vector for cross-pollination. Diversification in angiosperms began about 130 mya, when some species of insects started visiting flowers to feed on pollen, accidentally dropping some pollen grains on the stigma of another flower, thus effecting cross-pollination. Plants soon 'learnt' the benefit of these flower visitors and started attracting them. Species of flower visitors differ in their perception of floral signals, leading to a coevolutionary relationship between the plant and its pollinator, since floral traits get selected in response to the most frequent flower visitor and its efficiency in transferring pollen [7, 8, 11, 33, 37]. With the arrival of bees, which became efficient pollen vectors, around 120 mya, there was a spurt in plant speciation, mainly because of competition for pollinators [10].

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Presently, over 87% of all flowering plant species depend completely or partially on flower visitors for pollination and seed set [23]. In the present chapter, we make an attempt to review the available literature on pollination biology of sandalwood, *Santalum album*. Under the genus *Santalum,* 53 species are listed. However, only 12 of them are accepted, including the Indian sandalwood, *S. album* (http://www.theplantlist.org/tpl1.1/search?q=Santalum; accessed on 10.11.20) [35].

2 Floral Biology of *Santalum album*

2.1 Flowering Phenology

The flowering phenology in sandalwood is a bit confusing in terms of seasonality, number of flowering cycles per year and the duration of each cycle. Srimathi [32], while discussing flowering behaviour, mentioned that flowering in sandalwood may appear once, twice or even throughout the year in a single population. Flowering has been recorded from June to October [4, 36], and Krishnakumar and Parthiban [19] observed flowering from July to October and again from December to March. In Bangalore north, we noticed flowering from June to September and also observed that a population that is regularly irrigated and supplied with nutrients flowered and set fruits almost throughout the year. When we analysed the published information from India [4, 19, 36] and Indonesia [27], on flowering time and duration of flowering, it appears there is an indication of sandalwood flowering throughout the year in one or the other population depending on the genotype and weather conditions (Fig. 1).

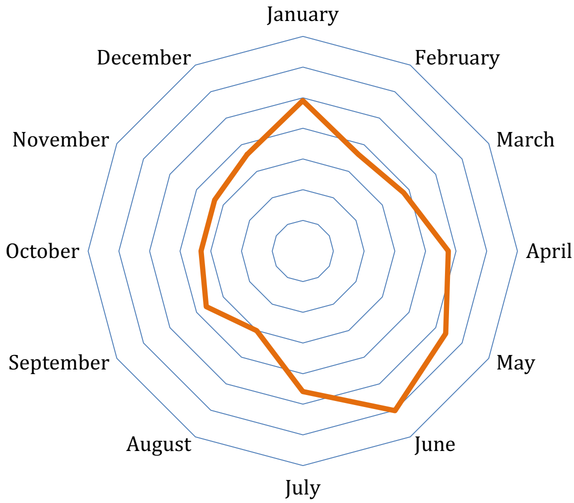

Fig. 1 Flowering frequency of sandalwood trees month-wise

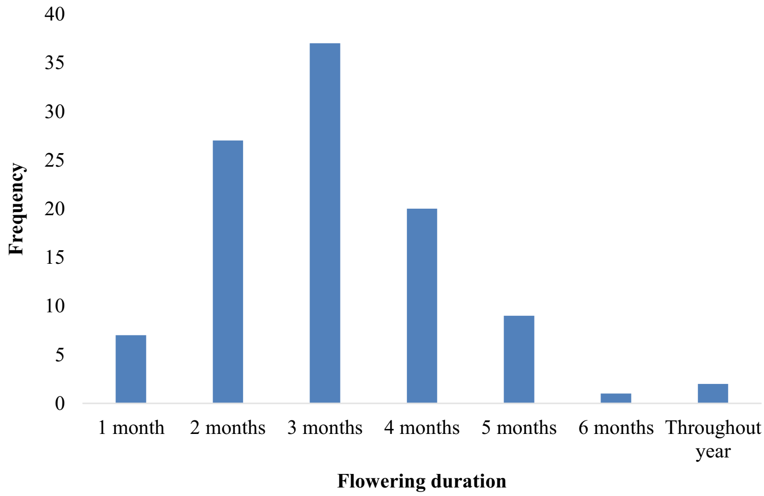

Fig. 2 Duration of each flowering window

The duration of flowering ranges from one to six months with a duration of three months being more common (Fig. 2).

Sandalwood flowers twice a year with varied flowering periods in Indonesia [27], but flowering duration is prolonged during extreme temperatures often resulting in mass flower abortion and an incomplete flowering period. It is argued that an additional flowering period sets in under such conditions [27]. Delayed and prolonged flowering was observed in rainy season also. Sandalwood produces more flowers in the rainy season, but the seed set is very low compared to a dry season when the reproductive success will be higher, resulting in higher fruit set [27, 28].

2.2 Anthesis and Duration of Flowering

The buds take 18–20 days to attain maturity and majority of the mature buds open in the early hours of the day, between 3 and 6 a.m., though a few flowers continue to open till 12 noon. During anthesis the perianth lobes split open one by one [4]. The total duration of a flowering cycle lasts between 89 and 150 days with a mean of 105 days [27]. Anther dehiscence occurs at the time of flower opening or soon after [22]. Pollen mass is yellow and sticky. Pollen grains are triangular with granular exine [4].

2.3 Flower Structure

There have been several studies on flower morphology and floral biology of *S. album* [4, 5, 15, 17, 21, 22, 24–26, 36] (Fig. 3).

Sandalwood trees start flowering when they are 4–6 years old [4]. Flowers are bisexual, actinomorphic and epigynous, borne on axillary or terminal panicles. They are odourless or may emit very little fragrance. The just-opened flowers are pale green or white in colour and turn pale pink, red and dark red gradually after approximately 24, 48 and 72 h, respectively, [4], and according to Tamla et al. [34], the colour change starts at 19 h and completes by 53 h. Inflorescence size varies from 40 to 50 flowers [22]. The overall life of an inflorescence ranges from 18 to 25 days, and the longevity of a single flower is 7–9 days [34].

The total length of the flower varies from 6 to 7 mm and width from 5 to 6 mm [22, 34]. The flower is not differentiated into calyx and corolla. The number of tepals, though usually 4, may vary from 4 to 6. The number of stamens varies in accordance with the number of tepals. They may or may not possess staminal hairs. The length of stamens varies from 1.5 to 2.5 mm [34] and borne on short, < 1 mm long, filaments. The perianth tube varies in shape from tubular to conical. The gynoecium is epigynous and differentiated into style, stigma and ovary. Ovary appears free in the beginning, but later, the perianth tube encloses the ovary resulting in a perigynous condition [4]. Ovary is inferior [4] or partially so [34] with a short style that bears a trilobed stigma almost at the level of or slightly below the level of anthers [4, 34]. Flowers are classified based on position of stigma into three types: flowers with stigma above anther level (pin), flowers with stigma below anther level (thrum) and stigma and anther at the same level (homostylous) [36]. The colour of style and stigma change from white to red synchronous with the change in colour of tepals [34]. The cup-like

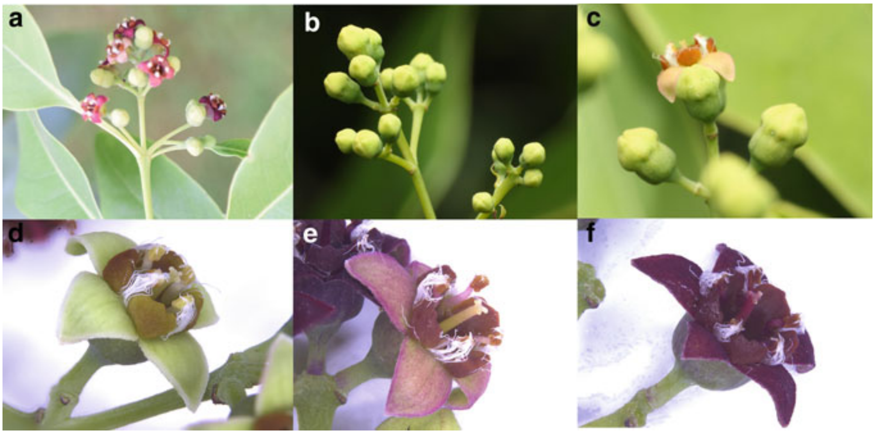

Fig. 3 **a** Inflorescence; **b** flower buds; **c** just-opened flower; **d** white/greenish coloured flower; **e** intermediate pink flower; **f** reddish flower. (Photos by H.M. Yeshwanth)

disc secretes nectar around the base of the ovary which glistens when seen from top. Maximum nectar is found in the pale green and pale pink flowers, and it is completely absent in red and dark red flowers [4]. The ovary has three to four carpels fused to form a unilocular ovary. Usually, three to four 'ovules' are differentiated in a basal or lateral position but invariably a single seed develops [22].

As in other members of family Santalaceae, the gynoecium in *S. album* has a single ovarian cavity enclosing a long and straight 'placental column', partly projecting upwards into the style. There is no ovule as such since the female gametophyte does not show any distinction into integuments and nucellus. The gynoecium has 2 to 4 'S'-shaped embryo sacs which grow out freely into the ovarian cavity from the base of the placental column towards the protruded tip of the placental column [4]. The process involved in the embryonic development, seed set and fruit development has been worked out in detail [22].

The embryo sac is reported to be 8-nucleate or 'polygonum' type [5, 15]. Out of 2 to 4 embryo sacs, only one matures into an embryo. The development of the endosperm may be initiated in more than one embryo sac in an ovary but only one reaches maturity and the remaining embryo sacs invariably degenerate [4].

3 Pollination

Some earlier studies have shown that the flower structure of *S. album* is designed for self-pollination, taking into consideration the position of stigma at the same level or below the level of anthers [36]. There was no sign of fruit development in unpollinated flowers, but when the flowers were artificially self-pollinated, the per cent seed set was 3.1 in *S. album* [24], and the species is found it to be a predominantly out-breeding species and is self-incompatible [36]. Many subsequent workers have supported that *S. album* is an obligate outcrossing species [4, 17, 29].

The developmental difference between the mature embryo sac and pollen in the same flower is approximately 10 days, whereas pollen germination and the entry of pollen tubes into the embryo sac last for only 2 to 4 days, and hence, natural self-pollination resulting in self-fertilization is unlikely [4, 17, 29]. But one study concluded that *S. album* appears to have self-compatible characteristics to some extent, but only if the development of pollen and embryo sac is made coincidental (i.e. through intervention via artificial pollination), self-fertilization may be achieved [22]. However, because of inherent dichogamy, *S. album* avoids self-pollination, virtually assuming heterozygosity under 'normal' conditions. Unfertilized flowers will stop growth and fall off spontaneously. Fertilized flowers develop into fruit [22].

In pollination experiments, there was no fruit set in the treatment where flowers were bagged, 14% fruit set with artificial pollination and only 3% fruit set with open pollination [22].

3.1 Flower Visitors

One of the common misconceptions in pollination biology is treating all flower visitors as pollinators, which is often not true. Available records on pollinators of *S. album* are very few. However, there are several records of flower visiting insects and birds. In addition to the published records, we also looked into a Citizen Science Platform (efloraofindia [6]) from which we extracted the names of flower visitors of sandalwood (Table 1; Fig. 4). In all 46 species of flower visitors have been recorded, of which one species is a bird (Purple sunbird, *Cinnyris asiaticus*). Of the species of insects that visited sandalwood flowers, majority represent Lepidoptera (73.33%) followed by Diptera and Hymenoptera (13.33% each). Nearly 88% of records are from photographs of butterflies visiting sandalwood flowers, posted on efloraofindia Website, which may not be by professional biologists, and hence may need validation for their role in pollination. Ignoring these records, we are left with a few dipterans (four species of Syrphidae and two of Calliphoridae) hymenopterans (three species of honeybees, one carpenter bee and two species of ants).

Though sandalwood flowers are visited by flies, bees and ants, flies were the most common visitors [4]. The syrphid flies, *Phytomia argyrocephala, P. (Dolichomerus) crass* and *Eristalinus arvorum* were the most frequent flower visitors. Honeybee species (*Apis cerana, A. dorsata* and *A. florea*) were both less frequent and less abundant, though bees dominated in the early period of flowering season. *Dolichomerus crass* was observed to insert its proboscis in the space between anther and stigma to suck nectar. Such flies also carried plenty of pollen on their mouthparts. Bhaskar [4] concludes that syrphids are pollinators of sandalwood. He also observed ants and some beetles visiting flowers with pollen sticking to their body as well and suggests that these also could be effecting pollination. Unfortunately, these conclusions are not supported by hard data with any controls.

Apis mellifera was recorded as the most frequent visitor of sandalwood flowers in Indonesia [2] where, under open pollination conditions, the fruitset was 9.3%, while it was just about 1% when the flower visitors were excluded.

A more detailed study on flower visitors of *S. album* was carried out in Tamil Nadu [20], in which the species of flower visitors, time of visit, frequency and time spent by an individual of each species on a flower were recorded. Two species of ants (*Monomorium destructor* and *Camponotus* sp.), the Indian honeybee (*A. cerana*), a blue bottle fly (*Calliphora vomitoria*) and a nymphalid butterfly (*Vanessa cardui*) were recorded as flower visitors. Frequency of visits by *M. destructor* and *A. cerana* was high compared to *C. vomitoria* and *V. cardui*. The authors also made observations on 'stigma touch behaviour' by the flower visitor and recorded it to be 'good' by *M. destructor* and *A. cerana*, compared to other visitors and concluded that these species are the efficient pollinators of *S. album*. Again, the results appear to be subjective and not supported by data.

Table 1 Flower visitors of sandalwood

Common name	Scientific name	Order	Family	Location	Reference
Blue bottle fly	*Calliphora vomitoria*	Diptera	Calliphoridae	Tamil Nadu and Karnataka	[20] H*
Blow fly	*Lucilia* sp.	Diptera	Calliphoridae	Karnataka	H
Hoverfly	*Phytomia crassa*	Diptera	Syrphidae	Karnataka	[4]
Hoverfly	*Eristalinus arvorum*	Diptera	Syrphidae	Karnataka	[4]
Hoverfly	*Ischiodon* sp.	Diptera	Syrphidae	Karnataka	H
Hoverfly	*Phytomia argyrocephala*	Diptera	Syrphidae	Karnataka	[4]
Indian honey bee	*Apis cerana*	Hymenoptera	Apidae	Tamil Nadu and Karnataka	[4, 20] H
Giant honey bee	*Apis dorsata*	Hymenoptera	Apidae	Karnataka	[4] H
Dwarf honey bee	*Apis florea*	Hymenoptera	Apidae	Karnataka	[4] H
Carpenter bee	*Xylocopa sp.*	Hymenoptera	Apidae	West Bengal	[6]
Camponotus sp.	*Camponotus sp.*	Hymenoptera	Formicidae	Tamil Nadu and Karnataka	[20]
Singapore ant	*Monomorium destructor*	Hymenoptera	Formicidae	Tamil Nadu	[20]
Common spotted flat	*Celaenorrhinus leucocera*	Lepidoptera	Hesperiidae	West Bengal	[6]
Chestnut bob	*Iambrix salsala*	Lepidoptera	Hesperiidae	West Bengal	[6]
Common pierrot	*Castalius rosimon*	Lepidoptera	Lycaenidae	West Bengal	[6]
Gram blue	*Euchrysops cnejus*	Lepidoptera	Lycaenidae	West Bengal	[6]
Tajuria	*Tajuria sp.*	Lepidoptera	Lycaenidae	West Bengal	[6]
Commander	*Moduza procris*	Lepidoptera	Nymphalidae	West Bengal	[6]
Colour sergeant	*Athyma nefte*	Lepidoptera	Nymphalidae	West Bengal	[6]
Red lacewing	*Cethosia biblis*	Lepidoptera	Nymphalidae	West Bengal	[6]
Leopard lacewing	*Cethosia cyane*	Lepidoptera	Nymphalidae	West Bengal	[6]
Plain tiger	*Danaus chrysippus*	Lepidoptera	Nymphalidae	West Bengal	[6]
Striped tiger	*Danaus genutia*	Lepidoptera	Nymphalidae	West Bengal	[6]
Common crow	*Euploea core*	Lepidoptera	Nymphalidae	West Bengal	[6]

(continued)

Table 1 (continued)

Common name	Scientific name	Order	Family	Location	Reference
Great eggfly	*Hypolimnas bolina*	Lepidoptera	Nymphalidae	West Bengal	[6]
Danaid eggfly	*Hypolimnas misippus*	Lepidoptera	Nymphalidae	Karnataka	H
Peacock pansy	*Junonia almana*	Lepidoptera	Nymphalidae	West Bengal	[6]
Grey pansy	*Junonia atlites*	Lepidoptera	Nymphalidae	West Bengal	[6]
Lemon pansy	*Junonia lemonias*	Lepidoptera	Nymphalidae	West Bengal	[6]
Common sailor	*Neptis hylas*	Lepidoptera	Nymphalidae	West Bengal	[6]
Common leopard	*Phalanta phalantha*	Lepidoptera	Nymphalidae	West Bengal	[6] H
Common Jester	*Symbrenthia lilaea*	Lepidoptera	Nymphalidae	West Bengal	[6]
Blue tiger	*Tirumala limniace*	Lepidoptera	Nymphalidae	West Bengal	[6]
Vagrant butterfly	*Vagrans egista*	Lepidoptera	Nymphalidae	West Bengal	[6]
Painted lady	*Vanessa cardui*	Lepidoptera	Nymphalidae	Tamil Nadu	[20]
Common four-ring	*Ypthima huebneri*	Lepidoptera	Nymphalidae	West Bengal	[6]
Tailed jay	*Graphium agamemnon*	Lepidoptera	Papilionidae	West Bengal	[6]
Common jay	*Graphium doson*	Lepidoptera	Papilionidae	West Bengal	[6]
Common bluebottle	*Graphium sarpedon*	Lepidoptera	Papilionidae	West Bengal	[6]
Common rose	*Pachliopta aristolochiae*	Lepidoptera	Papilionidae	West Bengal	[6]
Common mormon	*Papilio polytes*	Lepidoptera	Papilionidae	West Bengal	[6]
Striped albatross	*Appias libythea*	Lepidoptera	Pieridae	West Bengal	[6]
Common gull	*Cepora nerissa*	Lepidoptera	Pieridae	Karnataka	H
Red-spot jezebel	*Delias descombesi*	Lepidoptera	Pieridae	West Bengal	[6]
Indian cabbage white	*Pieris canidia*	Lepidoptera	Pieridae	West Bengal	[6]
Purple sunbird	*Cinnyris asiaticus*	Passerine	Nectariniidae	West Bengal	[6]

*H: Hareesha unpublished

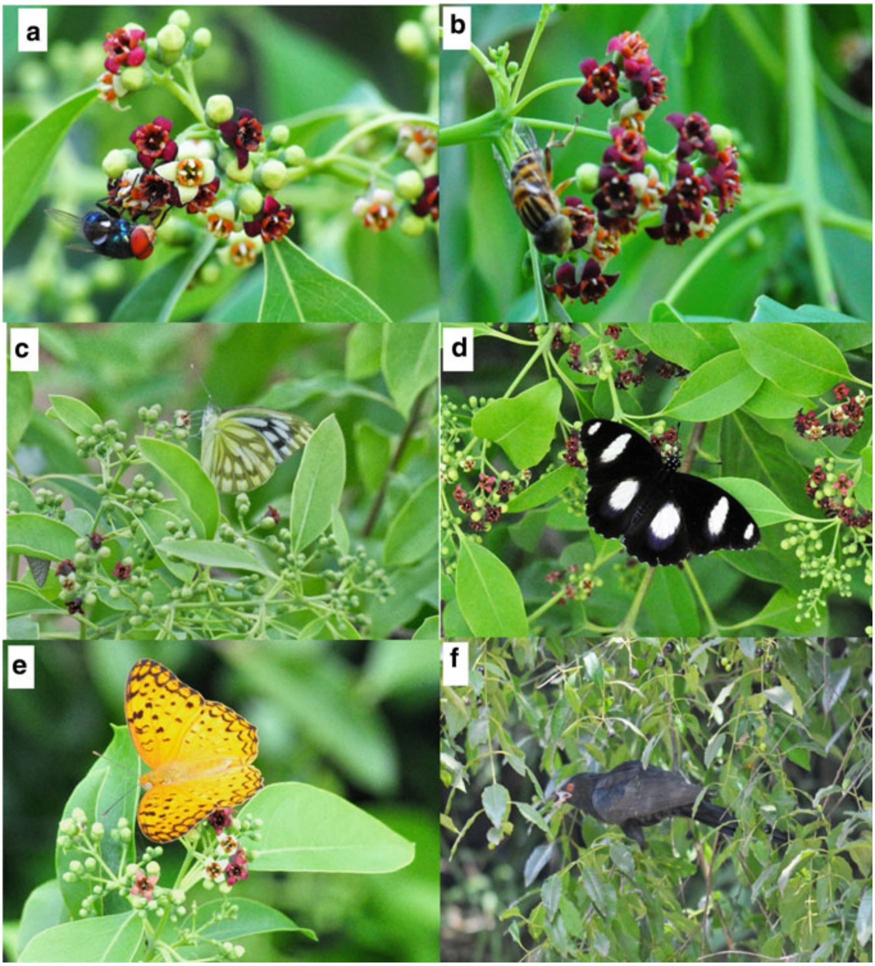

Fig. 4 a–e Floral visitors, **f**-seed dispersal from GKVK campus, Bengaluru, India **A**. Blow fly (*Lucilia* sp.) **b**. Syrphid fly (*Ischiodon* sp.) **c**. Common Gull (*Cepora Nerissa*) **d**. Danaid Eggfly (*Hypolimnas misippus*) **e**. Common Leopard (*Phalanta phalantha*) **f**. Asian Koel (*Eudynamys scolopaceus*) (Photos by A.S. Hareesha)

3.2 Need to Overcome Research Gaps in Pollination Studies

It appears we need more detailed studies to understand the complete pollination biology of *S. album*. We outline here some of the basic methodology for future studies, for anybody who is interested.

Some basic things about floral biology to be reworked are the following.

1. Anthesis—At least 100 mature buds should be labelled and observed for the time of opening. Time range at which maximum number of flowers are open may be considered as the time of anthesis.
2. Flower longevity: The marked flowers may be further observed till the set or drop off.
3. Time of anther dehiscence: At least 30 mature buds should be labelled and observed from anthesis till the anther lobes split and pollen grains come out. Time of dehiscence to be recorded.
4. Pollen viability: From the time of dehiscence samples of pollen grains (minimum 100) to be tested for viability at different time intervals.
5. Stigma receptivity: From the time of anthesis receptivity of stigma should be studied at definite time intervals with at least 10 flowers per sample. (For procedures, see references given above)
6. Flower visitors: All insects visiting flowers in different times of the day should be recorded and properly identified—most frequent visitor should be identified based on initial observations.

    a. Rewards taken by the flower visitor—whether it is taking nectar or collecting pollen
    b. Foraging behaviour of most frequent visitor—Time of activity, number of flowers visited per visit, movement pattern, time spent per flower (may have to mark the forager)
    c. A few foragers may be collected and observed in the laboratory for number of pollen grains sticking on the body—if it is a bee, pollen in pollen baskets of hind legs need not be considered.

7. Pollination studies: With the most frequent visitors, the following can be done

    a. Pollen removal efficiency index (PREi)

$$\text{PREi} = Ri - N/V - N$$

    where

    Ri is the mean number of pollen grains removed from a flower on a single visit by a species *i*;

    N is the mean number of pollen grains missing from a flower which has received no visitation; and

    V is the mean number of pollen grains removed per flower receiving unlimited visitations.

    PREi ranges between 0 (poor pollen remover) and 1 (excellent pollen remover).

    b. Pollination efficiency index (Pei)

$$\text{PEi} = \text{Pi} - Z/U - Z$$

where

Pi is the mean number of seeds set per flower by a plant population receiving a single visit from species *i*;

Z is the mean number of seeds set per flower by a plant population receiving no visitations; and

U is the mean number of seeds set per flower by a plant population receiving unlimited visitations.

The above indices should be worked out independently for each species of flower visitor that is recorded as frequent visitor to identify the most efficient pollinator.

c. Controlled pollinator visitation experiments

Once the most efficient pollinator is identified,

i. Six sets of 30 flowers each (of same age/stage) should be labelled
ii. Set one is left for open pollination
iii. Set two: flowers are bagged to prevent flower visitors
iv. Set three: flowers are hand pollinated with pollen from same flower
v. Set four: flowers are hand pollinated with pollen from a different flower of the same plant
vi. Set five: flowers are hand pollinated with pollen from a flower from a different plant
vii. Set six: Flowers are bagged and allowed known number of visits (~10) by the efficient pollinator species. Any other species trying to visit should be chased away, and after the allowed visits, the flowers should be again bagged.
viii. Percent fruit and seed set in each treatment should be recorded.

[For more details on methodology, See 3, 9, 18, 30].

The above studies will give a clear picture about self-pollination (if any), the presence or absence of self-incompatibility and the efficiency of the pollinator species and will help in developing strategies to improve overall seed set and in taking measures to conserve or enhance the population of the pollinator.

Since pollination studies will not be complete without information on the fruit and seed set in *S. album,* we continue our review on available literature on this aspect. We include the mechanisms of seed dispersal as well.

4 Fruit Set and Seed Dispersal

From flowering to complete maturation of fruit, it takes 80–85 days [22]. Though a relatively high fruit set, up to 31% was recorded [29], very low set (0.3–1.5%) has also been recorded [22]. Information on fruit set under similar or different pollination conditions observed by different workers varies greatly (Table 2) and need clarification.

Table 2 Relationship between fruit set and mode of pollination

Pollination type	Fruit set (%)	Reference
Artificial pollination	14	[22]
Artificial selfing	40	[36]
Artificial selfing	3.46	[36]
Artificial selfing	1.7	[36]
Cross-pollination	7.2	[29]
Free outcrossing	5.2	[36]
Free outcrossing	5.3	[36]
Free outcrossing	9.4	[21]
Hybrid with cover bag	12	[22]
Inbred with cover bag	**0**	[22]
Natural outcrossing	**93**	[36]
Obligate self-pollination	0.8	[36]
Natural outcrossing	3	[22]
Parthenocarpy and apomixis	0	[36]
Selfing among flowers	0.25	[29]
Selfing same flower	**0**	[29]

The mature, dark berries, are often eaten by birds, especially Asian Koel (*Eudynamys scolopacea* L.) [4] which may also disperse the seeds. We observed the Asian Koel (*E. scolopacea*), Rufus treepie (*Dendrocitta vagabunda*), Red-whiskered Bulbul (*Pycnonotus jocosus*), and White-browed Bulbul (*Pycnonotus luteolus*) feeding on sandalwood fruits in Bengaluru (GKVK campus) between 2017 and 2020. Bimal Sarkar, a volunteer, who contributes his observations to Citizen Science platform 'efloraindia', also has recorded Asian Koel (*E. scolopacea*), Blue-throated Barbet (*Megalaima Asiatic*), Red-vented Bulbul (*P. cafer*), Red-whiskered Bulbul (*P. jocosus*), Black-hooded Oriole (*Oriolus xanthornus*) and Rufus treepie (*D. vagabunda*) feeding on sandalwood fruits in Cooch Behar, West Bengal, India. (Table 3). After eating the ripened fleshy pulp, the seeds are dropped by the birds. The seeds usually take three months to germinate, and by September–October, a large number of recruits will form on the ground [4]. A frugivorous bird is benefitted by the total pulp reward that it gets for it to be an efficient seed disperser. It has been suggested that pulp-to-seed ratio and the cost–benefit ratio of handling fruits are important criteria [12, 16, 31]. In case of *S. album*, selection based on dispersal efficiency favours small seeds, while that based on seedling establishment favours larger seeds, and it has been argued that seed size is shaped by a trade-off between these two, opposing, selective forces [13].

Sandalwood, *S. album,* is recognized by the International Union for the Conservation of Nature (IUCN) [14] as '*Vulnerable*' species. It is important to not only to conserve the natural habitats of sandalwood, but also its pollinators, seed dispersers and their natural habitats.

Table 3 Frugivorous bird visitors on sandalwood fruits

Common name	Scientific name	Locations	Reference
Common myna	*Acridotheres tristis*	Pachaimalai, Tamil Nadu	[1]
Rufus treepie	*Dendrocitta vagabunda*	Cooch Behar, West Bengal, Bangalore, Karnataka	[6] H*
Asian koel	*Eudynamys scolopacea*	Pachaimalai, Tamil Nadu; Bangalore, Karnataka; Cooch Behar, West Bengal	[1, 6, 13] H
Three-striped palm squirrel	*Funambulus palmarum*	Pachaimalai, Tamil Nadu	[1]
Blue-throated barbet	*Megalaima asiatic*	Cooch Behar, West Bengal	[6]
Brown-headed barbet	*Megalaima zeylanica*	Parali Hills, Tamil Nadu	[1]
Indian grey hornbill	*Ocyceros birostris*	Hasanur, Tamil Nadu	[1]
Black-hooded oriole	*Oriolus xanthornus*	Cooch Behar, West Bengal	[6]
Small green-billed Malkoha	*Phaenicophaeus viridirostris*	Anaikatty, Tamil Nadu	[1]
Rose-ringed Parakeet	*Psittacula krameri*	Pachaimalai, Tamil Nadu	[1]
Red-vented Bulbul	*Pycnonotus cafer*	Anaikatty, Tamil Nadu; Cooch Behar, West Bengal	[1, 6]
Red-whiskered Bulbul	*Pycnonotus jocosus*	Anaikatty, Tamil Nadu; Bangalore, Karnataka; Cooch Behar, West Bengal	[1, 6] H
White-browed bulbul	*Pycnonotus luteolus*	Anaikatty, Tamil Nadu, Bangalore, Karnataka	[1] H
Brahminy starling	*Sturnus pagodarum*	Anaikatty, Tamil Nadu	[1]
White-headed babbler	*Turdoides affinis*	Anaikatty, Tamil Nadu	[1]

*H: Hareesha unpublished

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Chapter 15
Host Plant Influence on Haustorial Growth and Development of Indian Sandalwood (*Santalum album*)

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The first evidence of the hemiparasitic nature of the *Santalum album* was reported by Scott [1], and the subsequent discovery that a suitable host as the single most important factor influencing sandalwood survival and growth has remained the central research theme on the silviculture of sandalwood. It was subsequently discovered that sandalwood parasitizes the roots of almost all plants, but it shows an inclination for certain host species [2]. The sandalwood has over 150 host plants reported across the world. Host plants with the nitrogen-fixing ability and light shade appear to be the most suitable for good sandalwood growth [3, 4]. A suitable host plant helps in the survival and growth of sandalwood even in the pot stage and in field conditions as well. In India, suitable host recorded from various parts of India is *Azadirachta indica, Cassia fistula, C. siamea, Dalbergia latifolia, Ficus benghalensis, Pithecellobium dulce, Pongamia pinnata, Syzygium cumini, Wrightia tinctoria, Zizyphus mauritiana, Acacia nilotica, Bauhinia biloba, Casuarina equisetifolia, D. sissoo, Melia dubia, Terminalia arjuna, T. alata, Cajanus cajan, Eucalyptus camaldulensis* and *Tectona grandis,* while *Butea monosperma, Dodonaea viscosa, Gmelina arborea, Melia azedarach, Tamarindus indica, Artocarpus integrifolia, Acacia auriculiformis and Swietenia mahagoni* were reported as unsuitable hosts [5–9].

1 Host Preference of Sandalwood

Fast-growing species are commonly better hosts than slow growing, as they provide their parasitic plants with more/higher-quality organic resources through an enhancement of photosynthesis [10]. The growth rate of parasitic plants is reported to be strongly coupled with the rate of host growth [11]. Activities like nutrient addition which increases the sink strength of fast-growing hosts that are responsive

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to improved nutrient supply reduce their quality as a host species [12]. Alternatively, since additional nutrients would have a limited effect on the sink strength of slow-growing hosts, they can be better as hosts too.

Fabaceae members, due to their N-fixing nature that improves soil improvement, are commonly used host species [13, 14]. In general, *S. album* associated with N-fixing hosts has significantly greater growth and more haustoria apparently due to their ability to supply greater N than leguminous hosts compared with non-leguminous species [13, 15–18]. A sixfold increase in the amount of N transferred by the nodulated host than the non-nodulated plant has been observed [19]. Higher foliar nitrogen concentration, chlorophyll contents and photosynthetic rate and larger leaf area have been observed consequent to legume host in sandalwood [20]. Host characteristics such as thin and watery lateral root system, sparse crown, slow-growing nature, translocation of nutrients, sap flow of xylem tissue and higher water use efficiency of the parasite in an association with legume host too have been observed to decide the performance of sandalwood [21].

Close resemblances have been observed between *S. album* and legume hosts in the concentration and composition of xylem sap amino acids [22]. Host species that carries a C- and N-rich xylem stream ranks in terms of supporting the parasitic plant growth. The studies of net gains of C and N of sandalwood and C:N ratios of xylem solutes of parasitic plant–host associations showed greater heterotrophic gains of C from the leguminous host's xylem than non-legumes or a parasitic plant without a host [22, 23]. Generalization may not be possible since several N_2-fixing species belonging to Mimosaceae (e.g. *Albizia lebbeck*, *Acacia auriculiformis*, *Leucaena leucocephala*) and Caesalpiniaceae (e.g. *Cassia fistula*, *Delonix regia, Bauhinia blakeana* and *C. surattensis*) were found to be inferior to numerous non-N_2-fixing host species [13, 24]. For example, quite a similar rate of net photosynthesis, transpiration, stomatal conductance and *S. album* height was noticed in two suitable host species, *Dalbergia sissoo* (leguminous tree) and *Lonicera japonica* (non-leguminous vine) [25].

Considerable differences in parasitic xylem stream in the composition of amino acid, sugar and organic acid occur when sandalwood is associated with different hosts, and these differences along with the growth rates of sandalwood can be used to explain why certain host species are distinctly superior to other hosts in terms of parasitic overall benefit [20]. The strength of elements like Ca, K, P and Na in sandalwood is observed to depend on the presence of the corresponding element in the associated host. Lack of clear association in the content of these elements as evident from the net losses or only lesser gains of these elements is associated with a poor host. Biomass production per haustoria and overall haustorial biomass production, which combines many such measures, are considered as the best index of host suitability in sandalwood.

2 Developmental Stages and Host Specificity in Sandalwood

Sandalwood is a sciophile in its seedling stage [26] and becomes more heliophilic in nature once they are established. Full sunlight is harmful to the survival of *S. album* germinants, and they need to be grown under shade. The canopy of *S. album* grown in the open area produces often nearly bare, whereas in dense shade, also in association with a host, it produces darker green large and thicker larger leaves [26]. However, the phenomenon may not be related to shade as a sparse sandalwood canopy when grown without a host is the result of high water and nutrient deficits it experienced, whereas when hosts associated, it develops a strong crown by using the host roots, consequently, lowering root:shoot ratio of sandalwood. Contrary shreds of evidence are also reported on the heliophilic nature of *S. album* seedlings [27–30] which becomes stunted under the host's heavy shade. This in turn suggests that the sciophilic or heliophilic nature of sandalwood is a function of the strength of association with the host.

Robust *S. album* seedling growth with a host species is attributed to the supplement of nutrients for growth and development by its host [31–34]. Sandalwood exhibits host specificity at different developmental stages of the plant, and the hosts are classified into the pot (primary), intermediate and long-term host [20, 35]. Pot enhances the survival and growth rate of sandalwood seedling by supplementing primary nutrients and water and by reducing planting out stress [20, 34–42]. The poor growth rate of sandalwood seedlings without a primary host despite supplementing nutrients indicates that a pot host is essential for vigorous and healthy sandalwood seedling production. Propagation of *S. album* with a nursery pot host can increase the field survival rate of *S. album*. Most of the sandalwood seedlings develop haustoria within a month of planting with a pot host [43]. Sandalwood seedlings with abundant and advanced haustorial connections on the pot host are observed to endure outplanting stress. Suitable seedlings for outplanting are 6 to 8 months old with a height of 30 cm and a woody stem [32, 34]. Conversely, field survival of sandalwood seedlings can be achieved when associated with efficient pot hosts, thus effectively reducing the nursery period.

Pot host species has the greatest influence on the survival and growth of sandalwood seedlings after field establishment. Ideal pot host characteristics include abundant fine root growth which is evenly spread in the pot, ability to withstand top pruning, low competition with sandalwood seedlings, low allelopathic impacts, minimum growth structure, ability for the establishment of favourable osmotic gradient between host and parasite and hemiparasitic compatibility. Planting of the host sufficiently early with sandalwood seedlings will enhance early parasitism in nursery conditions, and such seedlings have considerably higher growth rate when planted in the field than plants parasitized to host immediately before outplanting. Sandalwood seedlings not associated with the host before field establishment perform poorly. In India, *Cajanus cajun* seed is sown into a pot containing germinating sandalwood seed and grown together till field planting [32]. Some of the other pot hosts reported from India are *Desmanthus virgatus*, *Alternanthera* species, *Crotalaria* *juncea* [34], *Calotropis procera, Cassia siamia* and *Calliandra calothyrsus* [29]. *Desmanthus virgatus*, *Alternanthera* species and *Acacia villosa* [4, 35] in Indonesia, *Phaseolus mungo* and *Cosmos sulphureus* in Sri Lanka [44], and *Alternanthera nana* and *Sesbania formosa* in Australia [20] are some other good pot hosts reported. Some species like *Atalaya hemiglauca, Acacia hemignosta* and *Crotalaria retusa* were poor pot hosts [20].

Appropriate levels of sandalwood field survival and growth are ensured by the selection of appropriate pot hosts. Pot host growth rate understanding is vital in choosing an ideal pot host. For example, *Sesbania formosa* requires top pruning owing to its profligately apical growth and *A. nana* can smother minor sandalwood seedlings. Subsequently, a suitable pot host ‘pricking in’ management is essential. The pot host competes with sandalwood within the pot if they are sown too early, while a delay in sowing results in poor haustorial connections and resultant outplanting stress. In south China, *Kuhnia rosmarinifolia* was recorded as a good pot host plant [13, 45, 46]. It is a good host as it is propagated by plant cuttings, roots easily and produces no seeds which avoid its dispersal. Even after transferring seedlings to the field, *K. rosmarinifolia* functions as a good host for 1–2 years until the host dies.

The pot host acts as the initial host and also reduces sandalwood outplanting stress at the field establishment stage. Sandalwood is a debilitating parasite while growing as a single parasite:host association causes early mortality of smaller and weaker hosts. Early mortality of host disrupts parasite:host association subsequently resulting in reduced sandalwood survival and/or growth [31]; however, larger host plants are favourable to sandalwood survival and growth subsequent establishment in the field. *S. album* can survive without a host for one year [2] or between 2 and 3 years [43] with poor survival after that though hosts were provided. During this initial planting time, shrubs and small trees need to be cultivated alongside sandalwood trees to serve as intermediate hosts. Until the intermediate host has parasitized the sandalwood, the pot host is maintained.

Intermediate hosts are generally a fast-growing, short-lived perennial which acts as hosts between pot host and field host. They serve to stimulate the early growth rate of sandalwood plantations [6, 47]. An intermediate host seedling is usually planted up to 2 m from sandalwood seedling and usually parasitized within a year of field planting. Intermediate hosts result in considerable stimulation in sandal growth [47]. Intermediate hosts ultimately die or become insignificant following sandalwood’s association with long-term hosts, which must continue as the final host for the entire field growth [18]. *Cajanus cajan* and *Crotalaria juncea* are ideal intermediate hosts for sandalwood [6, 47]. *Emblica officinalis* and *Macrotyloma uniflorum* were found to be suitable hosts for sandalwood in agroforestry in southern India [48]. *Citrus aurantium* being a woody long-term host of sandalwood caused greater mortality of the hosts, maybe due to the greater parasitic nature of sandalwood on *C. aurantium* [49]. Timely screening of appropriate host trees for sandalwood plantations is desirable to improve the returns [18, 50].

3 Haustorial Physiology

Haustoria are structures common to all parasitic plants that make physical connections with the roots of host plants and form a transportation channel [51] that transfers water and nutrients from host to parasitic plant. The number of haustorial connections made by sandalwood on roots of different hosts however poorly correlated with host quality [18]. Morphological and anatomical characters of haustorium are extensively studied in sandalwood [8, 23, 45, 46, 52–55]. Haustorium has an inverted conical shape, and its head is horizontally round before contacting its host root. Haustorium develops laterally from the pericycle of sandalwood. The haustoria are directly associated with the parasitic plant to access to host resources either through direct vascular continuity or through interfacial parenchyma or a combination of both [56]. Haustorium is composed of the hyaline body (a structure rich in nuclei believed to be involved in resource translocation and processing), the endophyte or penetration peg (the projection of which enters the host root tissue), and the ellipsoidal disc (laterally flattened, relative to the host root, against the host's stele and the point of contact between the parasite and its host's vascular system) [55]. The haustorial gland is a distinctive feature of the haustorium in the family Santalaceae, and the gland commonly develops in the inner haustorium in sandalwood once the haustorium makes contact with the host root system [46] (Zhang et al. 2012).

Proto-haustoria of sandalwood has a bell-shaped structure and flattened against the host root surface on contact and starts the conversion to young haustorium. Sometimes, haustorial commencement is elicited by contact with inert materials like stones or walls of plant pots or even with the same plant roots. The penetration peg deployment occurs only when a close connection is made with a compatible mature host root system. Strong connections form through well-coordinated grafting of tissue between the true host root and haustorium. A darkly stained mucilaginous hemicellulose material is formed by the contact surface of the haustorium [57]. This material plays a significant part in sandalwood host connection establishment. Association between the parenchymal cells of the haustorium and the host root cell is firm in case of good hosts, and it is linked to the occurrence of this prominent darkly stained mucilaginous constituent while it is thin in poor host plants [25]. After host root attachment, intrusive cells of haustorium penetrate the host epidermis and root cortex. Along with the development of endophytic development, the cortical foldings of haustorium partly enfold the host root [58]. During the initial stage of haustorial establishment, projections of the endophyte extend up to the host root's thin-walled parenchyma cells of cambial tissue. The cells of endophytic projections and host root xylem entangle with each other giving a tubular appearance to the cells. Clear evidence on the role of pressure or cell wall degrading enzymes in the development of sandalwood haustoria lacking. Extracellular enzymes are involved as the parasite penetrates the cortex and gains access to the host conducting tissues. After the successful establishment of vascular connections and reaching the host root cambium, the penetration peg flattens out laterally to form a thin ellipsoidal disc closely pressed against the centrally located host root xylem.

An enormous concentration of parenchyma cells and considerably fewer xylem elements typically short tracheary elements are normally associated with the haustorial interphase region. Sandalwood haustoria lack phloem connections with its hosts. There is no direct lumen-to-lumen xylem connections between the host and parasite xylem, and hence, direct flow of water and nutrients from host to xylem through tracheary connections is quite unlikely. Hence, movement of xylem sap from a host could only occur primarily via host xylem element pits to the interfacial parenchyma of the parasite.

Phytohormones play a significant role in haustorial development as the endogenous levels of IAA, CK, GA_3 and ABA were noted greater in haustorium than in seedling roots [46, 59]. Haustorial initiation is required by the auxin signal transduction, whereas throughout haustorial developmental processes it is supported by GAs [59]. Application of plant growth regulators in an in vitro environment can artificially increase the number of haustoria, for instance, xenognosin application, the active fraction of tragacanth gum, sandalwood seedlings, haustoria effectively induced in the absence of the host [60].

S. album is principally a xylem feeding hemiroot parasite [55]. There exists a variety of opinions on the nutrients that are absorbed by sandalwood from the host through haustoria and from the soil through its root system [32, 39, 61]. It is true that despite its parasitic nature, sandalwood roots are quite capable of absorbing nutrients from the soil like any other plant [7]. Sandalwood seeds have large seed reserves, and the seedlings in their initial stages derive most of their nutrient requirements from these reserves. The seed kernels provide balanced nutrition for up to three months which supports the growth of seedlings. At about three-month stage, the seedling growth is limited by lack of N, K and P, while such a limitation is not experienced in seedlings deficient Ca or S. Establishment of a host connection becomes essential for its survival and growth beyond this stage [62]. The growth and vigour of the seedling increased after sandalwood host connections are formed [42, 63]. Independent seedlings are capable of acquiring nutrients without host support as supported by the observation of higher K, P and Ca concentrations in seedlings supplied with all-nutrients than mature *S. album* with hosts [32]. It has been suggested that a host association is essential for sandalwood as a source of N and P [39]; K, P and Mg [42]; Ca and Fe [54]; and K, Ca, Mg, Fe, Cu and Zn [41]. Deficiencies in the nutrient supplements by the hosts create significant morphological development effects, and some of these may directly prevent the formation of host associations; hence, sandalwood is not able to parasitize and survive. Increased growth of sandalwood is associated with improved K and low levels of P and Na as well as a relatively constant N concentration of the foliage. One monovalent osmoticum replacement for another and decline in sandalwood foliar Na with increasing concentration of K is observed with a longer duration of sandalwood host association [33]. However, longer host association does not seem to considerably affect the parasites' nitrogen status.

The dissimilarities between parasites mainly depend on the host xylem sap and which depend on substances derived from the phloem become manifested in K:Ca ratio [64]. Potassium and calcium are phloem and xylem mobile elements, respectively, indicating the xylem and phloem connectivity between the hosts and parasite.

A high K:Ca ratio is a feature of many parasitic angiosperms [33, 65]. Higher ratio suggests a phloem-feeding parasite [66]. *S. album* seedlings parasitized to suitable host for extended periods before the establishment in the field have a greater K:Ca ratio [33]. Sandalwood is not exclusively dependent on xylem absorption. Similar to all photoautotrophs, sandalwood has leaf chlorophyll and can synthesize carbohydrates [67]. A significantly higher rate of carbon assimilation rate (photosynthesis) is observed in sandalwood trees growing with the host than the parasite growing without a host. The chlorophyll level of *S. album* increases when attached to a suitable host [8]. This may be due to the alleviation of solar radiation by host plants resulting in less photodestruction of chlorophyll in *S. album* [8, 44], whereas low chlorophyll content was observed with poor host, e.g. *Ailanthus* and teak [62, 68]. Among the different agroforestry crops (coconut, black pepper, cashew, cocoa, rubber, teak, casuarina), the maximum rate of photosynthesis was recorded in sandalwood grown with casuarina as host and with the combinations of sandalwood–teak-casuarina and sandalwood–teak associations. The lowest rate of photosynthesis in sandalwood was observed in plants with rubber, coconut or cashew as host. The studies thus indicate that with a favourable host, the photosynthetic capacity of sandalwood seems to be improved.

In general, tissue water relations of sandalwood are not significantly altered by the quality of hosts and it has been observed that sandalwood always maintains transpiration rate through a favourable water potential gradient compared to the host [18]. It was observed that the plant water potential in sandalwood decreases significantly after the removal of the host plant and developed leaf wilting and leaf fall indicating the contribution of the host in maintaining higher water potential [8].

Parasitic plants generally have lower values of water use efficiency (WUE) compared to the associated host [2, 69–71]. However, in sandalwood, the rate of photosynthesis rate and WUE is usually found greater than their corresponding hosts [25]. Sandalwood can maintain a lower leaf water potential gradient through transpiration ensuring continuous water and nutrient uptake as indicated by the close match between the gas exchange, water potential and stomatal responses of hosts and parasites [18]. The close resemblances in transpiration of sandalwood and its associated host reveal the capability of sandalwood to recognize the stomatal responses of its associated host coordinate the response to ensure the uptake of xylem fluid from the host [18]. Sandalwood plants have a lower ability to adjust and coordinate the stomatal response when the N level in the xylem sap is low. For example, transpiration in sandalwood is significantly lower when attached with non-N_2-fixing hosts. In sandalwood grown with various agroforestry crops, higher water stress was observed for sandalwood in the absence of a preferred host [68].

The structure and function of the parasitic haustoria are possibly related to its endogenous plant growth regulators (PGRs) present in it. The highest quantity of endogenous ABA is observed in the haustoria of the parasite/host association of parasitic angiosperms [72]. Among the PGRs, indications of auxins and cytokinins control the differentiation of vascular tissue [73–75]. It has been observed that in the case of sandalwood, higher levels of GAs, IAA and cytokinins are involved in the differentiation of xylem elements in the haustoria [55, 76, 77]. The substantial presence of hormones like cytokinins including zeatin, zeatin riboside and zeatin nucleotide was also observed in the haustoria of the parasite associated with a host [78, 79]. The sandalwood haustorial development goes through considerable physiological as well as structural modifications. Moreover, levels of endogenous hormones, cytokinins (zeatin and zeatin riboside), IAA, GAs and ABA of the sandalwood haustoria differ significantly from the rest of the plant. ABA significantly increases the permeability of cell membrane [51, 80, 81], whereas phytohormones function in the regeneration of xylem elements [74, 82]. Increased cytokinin levels are reported during infection by sandalwood, but the source of the increased cytokinins and their biological relevance remains unknown. Higher levels of cytokinins and IAA and lower levels of GAs and ABA phytohormones are always observed haustoria, even non-attached, than the normal roots. The higher cytokinins and auxin levels in the haustoria before host attachment indicate that these two phytohormones may play a vital role in the initial ontogeny of the sandalwood haustoria. The cytokinins and auxin levels show a consistent increase with the attachment of the haustorium of sandalwood. Haustorial structural changes mostly take place after the young haustorium comes into contact with the root surface of the host. The higher levels of cytokinins and IAA in haustoria attached to the host probably correspond to more division and differentiation of meristematic tissue, signifying the active rate of metabolism. These levels of cytokinins, GAs and IAA in haustoria of sandalwood are always higher than the normal roots of the parasite as well as the host. These PGRs have an important function in starch metabolism during the growth and development of the plant [83–85]. Sandalwood haustoria synthesize these phytohormones, essential for the cell division and differentiation of the meristematic regions, during the development of haustoria. A higher ratio of cytokinin:auxin level induces the formation of the root [74], and this ratio is always higher than one in sandalwood haustorium indicating its actively growing nature.

Since transpiration rate in parasitic plants is normally higher than their host plants [86, 87], a greater ABA concentration [88, 89] is required to keep the stomata closed and maintain a high hydraulic conductivity of parasitic roots. While higher ABA levels in the roots are due to the biosynthesis of ABA in its root tips, a higher level of ABA is encountered in post-attachment haustoria compared to the root tissues of parasite and host [90]. Hence, it can be assumed that the high ABA found in the haustorium might be linked with the water and inorganic solute transportation from the host into the sandalwood haustorium.

Considerable information is available on the solute transfers between the xylem of host and parasitic plants [91]. To maintain high growth rates, *S. album* has to access large quantities of organic solutes from the host plant. Substantial differences in organic solutes in terms of sugar, organic acid and amino acid composition of the xylem stream occur when the parasitic plant is connected with various host species, and this along with parasitic growth data can explain the host preference of parasitic plants. Nitrogen can decide host suitability in sandalwood, and the effects of extra N, when associated with an N_2-fixing host, are evident as better dry matter production consequent to enhanced parasitic foliage and photosynthesis. In addition to C and N richness in the xylem stream, the xylem of hosts contains variable concentrations of sucrose, glucose and fructose, while sandalwood is dominated by fructose [31]. When associated with legume hosts, asparagine, glutamate, aspartate and glutamine are the major amino acids transferred from the host to sandalwood. Even while significant quantities of proline are encountered in the foliage of sandalwood, proline is not detected in the xylem stream of sandalwood or its host plants. The proline has an osmoprotective function and helps to lower the water potential of the parasite; in that way, it helps in the transfer of water from the host to sandalwood. High proline accumulation is often an indication of high water or salt stress experienced by the plant [30, 92–94]. Significant differences between solute concentrations between the host and parasite xylem stream suggest that the uptake and initial processing of the solute happen in the parenchyma of the haustorium. Haustorial tissue seems to have a significant role in solute processing. This includes its ability to utilize nitrate or ammonium and the processing of a variety of solutes from different hosts. Even when the source of xylem sap differs from diverse hosts, there seems to be a remarkable consistency in the set of nitrogenous solute that is passed on to the parasitic shoot via the xylem stream. Large amounts of starch granules that accumulate in the parenchyma cells around the meristematic region near the haustorial gland and on both sides of the endophyte tissue are used to generate energy for various cellular activities such as cell division and elongation, penetrating the host cortex as well as to access water and inorganic solutes from the host.

4 Host Response to Parasitism

The host root system acts as an extension of the parasitic root system by supporting the biomass of the parasite. Mostly, hemiroot parasites are always smaller than the hosts [50, 56, 95], whereas sandalwood often develops larger than their associated hosts and can be a crippling parasite. It can negatively affect host growth through its enormous size, faster growth, metabolic rate and higher levels of heterotrophic dependence [96]. The parasite is an additional sink for the host plant and therefore reduces its capacity for its carbon fixation [97, 98]. The amount of assimilates that sandalwood can access is host-dependent. Even when the hosts are of similar biomass, the sandalwood can substantially differ in their growth indicating the difference between hosts in allowing access to its xylem stream [20].

The reduced host's growth when associated with parasites is due to the water, and solute loss due to parasitic effect [99, 100] also results in a reduced rate of host photosynthesis [101, 102]. In the comparatively small root system of the parasite, there can be only limited direct water and nutrient uptake from the soil parasite. Reduction in host growth due to light competition by the parasite shoots is not substantial [92]. The host damage increases with the parasitic biomass, considering that better hosts are more negatively affected than poor, indicating a stronger source–sink relationship with a better host. Small biomass reduction of hosts with a high relative growth rate indicates that fast-growing hosts are able to compensate for the loss to the parasite than slow-growing hosts [103].

Hemiparasite infection significantly influences host biomass production. The pooled of hemiparasitic and its host's biomass is generally lower than the hosts growing without parasitic plants [11, 104–107]. This productivity reduction is attributed to lower parasitic resource efficiency [108]. Hemiparasites have a much higher rate of transpiration [70, 100, 109] as well as higher concentrations of tissue nutrients [56, 100, 110], but have comparable or lower photosynthesis rates [70, 109] than their associated hosts. The parasitic plant's direct and indirect negative effects extensively influence host-parasitic growth and survival.

Parasitic plants alter the growth and allocation patterns of their associated host plants, particularly the amount of biomass allocated to their root. Stem parasite (e.g. Cuscuta) increases biomass allocation pattern to host shoots [111, 112], whereas root parasites reduce the availability of the resources by the roots such as water and nutrients to the hosts. Thus, root hemiparasite influences the host shoots more than the roots, which results in a lower host shoot:root ratio of hosts compared with uninfected plants. This altered higher biomass allocation to roots resulting from root parasitism follows the functional equilibrium hypothesis of plant growth that proposes an increased allocation to the plant organs to gain more access to the limiting resource [93]. This altered allocation pattern is an indication of the control exhibited by the parasite on the hosts by increasing the proportion of host organ useful to the parasite and reducing light competition by the host. High root:shoot ratio of sandalwood seedling increases survival rate following the establishment in the field [113], whereas a low root:shoot ratio will lead to either higher mortality or reduced growth rate if the host perishes. Water deficit [114, 115] and nutrient deficiency [116–122] too can increase in root:shoot ratios by favourably partitioning biomass to roots.

5 Conclusion

The research spanning over 150 years on the parasitic nature of sandalwood has revealed several important aspects of the nature of dependence of sandalwood over host species. Attempts to elucidate the morphological, anatomic and physiological relationship have helped to standardize cultivation practices of sandalwood. The research efforts on the parasitic nature of sandalwood are almost at the far end of research attention. However, there are some important areas that need further research. Physiological alterations of the commercially important hosts after successful parasitization as well as the use of sandalwood as an intercrop for agroforestry and suitable crop combinations for various situations need to be worked out more for finding best candidate to provide a brand new mixed plantation pattern of host and *S. album*. Tree management practices for the host species like optimum spacing of the host based on growth habit and end use, fertilization schedules, etc., are areas needing research attention. Use of arbuscular mycorrhizal fungi (AMF), an important tool that is gaining importance in tree husbandry, has attracted little attention in sandalwood cultivation and would probably need more research efforts.

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Part IV
Propagation and Cultivation

Chapter 16
Nursery Practices, Plantation Technology and Hosts of Sandalwood (*Santalum album* L.)

T. S. Rathore, D. Annapurna, and Geeta Joshi

1 Introduction

Natural regeneration of *S. album* is mainly by seed and root suckers. Artificial propagation vegetatively is by root cuttings [1], air layering and cleft grafting [2] and micropropagation. Though micropropagation through various methods has been standardized (detailed in Chap. 22 of this book), the major bottleneck is hardening and commercial level production. Production of planting material by seed is most common, economical and maintains genetic variability for better adaptation and tolerance/resistance against insect-pest attack. In India, before till 2000, *S. album* plantations were raised by State Forest Departments. The 'Royal Tree' tag for sandalwood, cumbersome rules/policies against farmers and industries, was the biggest setback for taking up plantations in private land. The implementation of relaxed policies in the year 2001 and 2002 by the Karnataka and Tamil Nadu state governments, respectively, permitted the grower with ownership rights for cultivating sandalwood trees, their harvest and sale which resulted in large scale cultivation of sandalwood in private lands. This has escalated the demand for quality planting material of *S. album* in India. Research work carried out on nursery practices, plantation technology and hosts of *S. album* is elaborated here. .

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2 Nursery Practices

2.1 Seed Collection, Processing and Storage

Sandalwood produces flowers and fruits twice a year—during September–October and March–April. It is highly desirable to collect seeds from identified trees, seed stands, seed production areas and clonal seed orchard as sources of genetically superior seeds. Seed stands and seed production areas have been identified in Tangali, Yedehalli, Rayalpad (Karnataka), Javadis, Chitteri (Tamil Nadu) and Marayoor (Kerala) during the past. However, today only Marayoor is well protected as a source of improved seeds. Ripened purple colour fruits are collected and depulped by rubbing. It is essential to remove the pulp thoroughly to avoid chances of fungal and bacterial attack on seeds. Depulped seeds are dried on the clean floor under the shade until moisture levels reach 6–8%. Dried seeds are dressed with fungicide (Bavastin or Diathane) to avoid seed deterioration due to fungus. Normal viability of the seed is up to 9 months at room temperature. Seed storage in airtight containers at 5 °C can prolong viability for about 2 years [3]. It is essential to test the viability and vigour of seeds before sowing. Detailed review is presented in Chap. 13 of this book.

2.2 Sowing

Two types of beds are used for the sandalwood seed germination—sunken and raised. Raised beds are suitable in high rainfall zones. Seedbeds of size 1 × 10 m can be prepared using sand and red earth mixture in 1:3 ratio mixed with nematicide (Ekalux or thimet). Sand bed is drenched with 0.1% (w/v) Bavastin to avoid chances of fungal contamination. Seeds soaked in 0.02% Agallol solution (Agrosan/Cerasan) for 30 min. help to prevent surface contamination. Seeds are sown at 500 g per m^2 and covered with 2 cm sand [2]. Annapurna et al. [4] report a high rate of seed germination in nursery beds of sieved sand and soil (2:1) compared to traditional bed consisting of sand and soil (1:3). They also observed that seed density of 400 g m^{-2} resulted in a high rate of germination. To identify the best seed germination medium, various media combinations were evaluated. Among the nine treatments, it was found that (i) sand, (ii) soilrite and (iii) cocopeat, soilrite, charcoal and neem cake in the ratio of 10:6:3:1 were the best. Based on availability, any one of these three can be used to obtain high rate of germination [5]. Since sand is available at all places at low cost, it can be used for large-scale seedling production. In raised or sunken beds, the lower 5 cm is gravel; this is covered by sand up to 10–15 cm height. To get early and uniform seed germination, soaking in 500 ppm of GA_3 for 16 h is essential [6, 7]. As a prophylactic measure, fungicides can be applied at 15 days interval. Daily irrigation is required to ensure sufficient moisture in the bed. Under favourable temperature and moisture conditions, germination is initiated within 20 days, and seedlings of two leaf stages can be obtained within 30–40 days. This stage is ideal for transplanting in containers. Profuse fibrous secondary roots are developed in sand medium, which supports early establishment and survival of plants in containers. In south India's climatic conditions, seed sowing in sand bed should be in middle of November so that transplanting can be done in December–January. Depending on the climatic conditions, there can be flexibility in timing for seed sowing.

2.3 Potting Media and Its Ingredient

Traditionally, *S. album* is grown in soil, sand and FYM in the ratio of 1:2:1 (v/v) in 1500 cc polybags and *Cajanus cajan* as a primary (pot) host. Seedlings 15 inches tall with a well-developed bark established in 6–8 months [8]. Annapurna et al. [5, 9] carried out studies on the effect of potting media and sieve size on *S. album* root trainer seedling growth. The potting medium ingredients, viz sand and soil, compost, cocopeat, burnt rice husk and charcoal, were used in 14 combinations in 270 cc block type root trainers with *C. cajan* as a primary host. The medium comprising sand, soil, compost, burnt rice husk (BRH) and charcoal in the ratio of 25:15:50:5:5 proved the best for the overall growth of seedlings, followed by sand, soil and compost in the ratio of 35:15:50 (v/v). Since burnt rice husk and charcoal are not commonly available, sand, soil and compost (35:15:50) sieved through 6 × 6 holes per sq. inch sieves can be used to produce quality seedlings. Xiao-jin et al. [10] carried out studies on different culture media on the growth of *S. album* and revealed that out of six treatments used, medium consisting of burnt soil, peat and coconut dust in the ratio of 1:1:1 plus 2% calcium superphosphate as basal manure proved the best for most of seedlings growth parameters. Mohapatra et al. [11] used sand, red soil, FYM, perlite, vermicompost, neem cake and pongamia cake in 19 different combinations in 9″ × 5″ size black polythene bags with *C. cajan* as a primary (pot) host. Potting mixture comprising sand, red soil and vermicompost in 1:1:1 (v/v) ratio was best for overall seedling growth.

2.4 Primary Host Species

Primary host or pot host is essential for the survival and growth of *S. album* seedlings at the nursery and field condition to establish the plant up to one year [12–14]. The pot host plays a dual role in nutrition and water relation and also reduces out planting stress. Radomiljac and McComb [15] used five-pot host species, viz., *Alternanthera nana*, *Sesbania formosa*, *Atalaya hemiglauca, Acacia hemignosta* and *Crotalaria retusa* and found significant variation in seedling growth with different pot host. Host species *A. nana* and *S. formosa* significantly increased survival, height and diameter of sandalwood seedlings. In another study, Radomiljac et al. [16] used *Sesbania formosa*, *Acacia trachycarpa*, *A. ampliceps* (nitrogen-fixing) and *Eucalyptus camaldulensis* (non-leguminous). *S. formosa* proved the best host, followed by *A. ampliceps* and *A. trachycarpa*. They concluded that there was no improvement in growth with *E. camaldulensis* compared to control (without host). Assays of leaf, stem, bark and root tissues of *S. album* and its host revealed a net gain in Ca, K, P and Na with a leguminous host after 33 weeks. In contrast, net losses or only small increases were observed without host or with *E. camaldulensis*. Annapurna et al. [12] carried out the studies on the stage of host requirement and screening of primary (pot) host by using *C. cajan*, *Iresine herbstii*, *Pilea microphylla*, *Cassia fistula*, *Casuarina equisetifolia*, *Alternanthera sessilis*, *Mimosa pudica*, *Calopogonium mucunoides*, *Macroptilium atropurpureum* and *Phaseolus vulgaris*. Out of these, six species were leguminous and five non-leguminous. In general, sandalwood seedling growth was better with a leguminous host. *M. pudica* proved the best host, based on growth and nutrient (NPK) status of seedlings. Among the non-leguminous hosts, best growth of sandalwood seedlings was with *A. sessilis*. Host species influenced haustorial number, connection, size and chlorophyll content. The maximum number of haustoria and haustorial connections was with *A. sessilis*, whereas large haustoria developed with *C. cajan* and *M. pudica*. Xiao-jin et al. [17] reported the effect of pot host configuration on Indian sandalwood seedling growth in China. They observed pot host requirement after transplanting the seedlings into containers. *Kuhnia rosmarinifolia* as pot host improved the height, diameter, biomass and number of haustoria of *S. album* seedlings after five months of growth.

2.5 Biofertilizers

Biofertilizers such as *Arbuscular mycorrhizae* (AM), PSB (phosphate solubulizing bacteria), *Azotobacter*, *Azospirillum* and *Rhizobium* play an important role in growth of plants at nursery and field by providing NPK, better root growth, and preventing water stress and pathogen infestations.

Nagaveni et al. [18] studied the effect of vesicular arbuscular mycorrhizae (VAM) and composite cultures on the survival and growth of *S. album* seedlings in root trainers and polybags. They reported that out of four treatments of biofertilizers, viz *Glomus fasciculatum*, *G. aggregatum*, *G. caledonicum* and composite spores, seedlings treated with composite spore were the best in terms of survival and seedling growth. Other three treatments also favoured better growth of seedlings as compared to control. Rathore et al. [16] conducted studies on VAM, VAM helper bacteria and N_2 fixing bacteria on seedling growth. *G. fasciculatum*, *G. mosseae*, composite spores, *Bacillus coagulaus* (VAM helper bacteria), *Azotobacter chrocoocum* and *Azospirillum brasilense* were used either alone or in combinations as an inoculum. The combined use of *G. fasciculatum* and *G. mosseae* exhibited best growth performance in terms of height, collar diameter, total dry weight and quality index of seedlings.

Nagaveni and Vijayalakshmi [19] reported that sandalwood seedlings inoculated with composite culture of VAM exhibited resistance against *Fusarium oxysporum* wilt as well as better growth performance of seedlings as compared to control. Binu et al. [20] carried out studies on the effect of different arbuscular mycorrhizal (AM) fungi and different levels of shade on the growth of *S. album* seedlings. Out of the three VAM fungi, viz *Glomus mosseae*, *G. fasciculatum* and *G. intraradices*, the best overall growth of sandalwood seedlings under 50% shade was observed with *G. mosseae*. In seedlings inoculated with AM fungi kept under 100% light, survival and growth were less than seedlings kept under shade.

2.6 Supplementary Nutrition

Supplementary nutrition is important to support seedling growth in sandalwood after 3–4 months of transplanting from mother beds to containers. At this stage, the nutrient level in potting mixture is depleted, and supplementary nutrients, viz macro- and microelements, support continuous growth. Supplemental nutrition can be provided in liquid or solid (slow release of nutrients) form. Radomiljac [13] conducted studies on the influence of supplementary nutrition on seedling growth and reported that slow-release fertilizer favoured growth at nursery and field planting. Annapurna et al. [21] conducted studies on the effect of supplementary nutrition on seedling growth of sandalwood to reduce nursery gestation period and better growth of seedlings in 270 cc block type of root trainers. They used various commercially available fertilizers, viz multiplex, polyfeed, manusol 60, nitriplex, neem cake and single superphosphate (SSP) in 12 treatments. Supplementary nutrition was provided in two forms, viz slow-release (in solid form mixed in potting medium) and liquid form as a foliar spray in various dosages at different intervals of time. There was a significant effect of supplementary nutrition on the growth of the seedlings. Slow-release fertilizer (Osmocote) or foliar spray of macro-nutrients at 15 days intervals after three months of nursery period proved the best treatment to boost seedlings growth in terms of height (25 cm), collar diameter (3.6 mm) and quality index (0.3).

2.7 Quality Seedling Parameters

Identification and fixing of quality seedlings parameters are essential before large-scale production of planting material to ensure a high survival rate and better growth after planting in the field. Quality of seedlings are attributes of genetically superior source of seed or propagules and physically robust seedlings. Annapurna [6] and Annapurna et al. [21] identified collar diameter as an important physiological indicator of the quality of seedlings. It correlated positively to height, woody portion, the number of leaves, dry weight (root, shoot and total) and root growth. Culling of seedlings less than 2.5 mm collar diameter of *S. album* seedlings reduces the coefficient of variation. Quality seedlings of > 3 mm diameter, 25 cm in height with a quality index of 0.3 can be raised within 5–6 months in 270 cc block type root trainers with a potting mixture consisting of sand, soil and compost in the ratio 35:15:50 with

10 kg/cum^2 neem cake + 400 g ssp/cum, sieved with 6 × 6 holes/sq inch sieve, *M. pudica* or *Alteranthera nanna* as a primary (pot) host, *Glomus fasiculatum* + *G. mosseae* as biofertilizers and application of slow-release or foliar spray of macro-nutrient at the interval of 15 days after three months of transplanting in containers. Similarly, 600 cc polybags with sand, soil and compost in the ratio of 40:20:40 with other ingredients as above were best for the production of QPM in 5–6 months. QPM raised in 270 cc root trainer had 95% survival rate in the field. Early establishment of plants was better for root trainers plants than polybags, possibly due to more secondary and tertiary root development in root trainers [6].

3 Plantation Technology

Plantation technology plays a vital role in the early establishment and growth of outplanted saplings. It involves land preparation, spacing, layout, pitting, fertilizer and pesticide application, irrigation, etc. Type of soil and topography of land are important factors in the selection of site. *S. album* is sensitive to waterlogging conditions; therefore, the land should have proper drainage. Sandy, sandy loam, alluvial red and deep soil are suitable for better growth. Ideal spacing is crucial in the success of the plantation. Spacing depends on the fertility of the soil, type of intermediate and long-term host. The ideal spacing is 5 × 5 m, but under certain situations, 4 × 6 m or 4 × 4 m spacing can also be adopted. Narrow spacing (4 × 4 m) may lead to competition between sandalwood and it's intermediate and long-term host for light, water and nutrients. As a result, growth may get hampered at later stages of the plantation.

The pit size for may vary from 2 to 3 cu.ft depending upon the soil. If soil is compact and hard, a 3 cu.ft. pit will be beneficial, otherwise 2 cu.ft. can be used. Pit size for intermediate host can be 1 cu.ft., and for long-term host, it can be 2 cu.ft. Each pit should be provided with compost 10–15 kg + neem cake 250–500 g + phorate 10 g + Bavastin 2.0 for sandalwood and long-term host. For an intermediate host, 5 kg compost + 250 g neem cake + 5 g phorate + 1 g Bavastin per pit can be used. Pit refilling work should be completed before the onset of monsoon.

Irrigation schedule depends on climatic conditions, soil type and soil depth. Initially, single line drip irrigation @ 8 L/h can be used for the first year. Once plants are well established, then from the second year onwards, a double line of drip can be installed, and water discharge rate can be double due to double dripper (@ 8 L/h single dripper). If the site is sandy or sandy loam, then alternate day irrigation can be given during summer. During summer, daily or alternate day, irrigation will be ideal, whereas, in winter, irrigation once in 3–4 days will also be sufficient. During summer, in water scarce areas, mulching with a mulching sheet can be used to check water evaporation and maintain soil moisture. There should not be any water stress for sandalwood for the initial 6–8 years. This will help in the development of good girth, height and canopy. After 8 years, irrigation can be reduced to develop water stress to trigger heartwood formation at a greater rate. Cultural operations—weeding and soil working—are essential to eliminate competition for nutrient, water and light (at an early stage). During the rainy season, minimum 2–3 times weeding will be useful. Soil working will allow better root aeration and break capillary action through which water evaporates. Soil working, three to four times in a year, will benefit both *S. album* and host.

After one year of planting, 5 kg/plant compost + 250 g/plant neem cake + 25 g/plant NPK (19:19:19) can be provided to the soil at six-month intervals. Every year, the application of fertilizers in February and June will allow continuous supply of nutrients to *S. album* and host to maintain growth phase. The dose levels can be increased with the age of the plantation. To boost growth, biofertilizers *G. fasciculatum* + *G. mosseae* + PSB can be applied at early stages of establishment. As a biocontrol agent, *Trichoderma viride* can be used to prevent wilt disease (*Fusarium* spp.) at the early stage of the plantation.

As such no systematic studies are conducted in *S. album* on pruning. Based on field experiences, it has been observed that pruning of 1/3rd canopy of *S. album* can be initiated from the second year to give proper shape to the saplings. Bordeaux mixture/paste can be applied on the wounded surface or copper oxychloride, and 0.1% (w/v) can be sprayed. The damaging main stem may pose problems of insect attack and stem borers. Therefore, pruning should done very carefully.

4 Intermediate and Long-Term Host

The requirement of a suitable host plant for the successful establishment of sandalwood is widely recognized. Sandalwood requires intercropping with host species from which it derives nutrients for growth and development—especially Ca, Fe, N, P, K, Mg, Cu and Zn [22]. The sandalwood hosts have been classified as primary/pot, intermediate and long-term hosts [15]. Though *S. album* parasitizes almost all the plant species, the best growth can be achieved with a compatible host. Host plants are considered good, medium and poor depending on growth, biomass and number of haustoria produced by sandalwood when associated with them [23]. Leguminous or nitrogen-fixing plant species are considered the best intermediate and long-term host of sandalwood. Fast-growing hosts pose competition for light, moisture, nutrient, and growth, which will adversely hamper sandalwood growth. Therefore, the host must be of moderate growth, narrow crown and compatible with sandalwood. Primary hosts support the growth of sandalwood up to one year. Parallelly, intermediate host and *S. album* develop a haustorial connection and support growth for 3–4 years. After four years, the long-term host develop haustorial connections and support until sandalwood's gestation period. Based on field observations, *Sesbania grandiflora*, *S. farmosa* and Citrus spp. can be used as intermediate hosts. For better growth, the host can be planted on both sides of 1½ to 2 ft away from sandalwood. In a study in Timor, *Desmananthus virgatus* was found as an efficient intermediate host [24]. Preferred species as a long-term host are *C. equisetifolia*, *Acacia nilotica*, *Zizyphus mauritiana*, *Phyllanthus emblica*, dwarf variety of *Mangifera indica, Punica* *granatum,* etc. Ananthapadmanabha et al. [23] carried out field trials with and without host to determine sandalwood's host requirement. The best growth was recorded for *S. album* planted at 3 m × 3 m spacing and in the centre of four *Pongamia glabra.* Singh et al. [25] reported the effect of long-term host on the growth of *S. album* under agroforestry condition. A field trial was established in 2008 at Mesana in Gujarat at a spacing of 5 × 5 m with three host—*Citrus aurantium, P. granatum* and *C. equisetifolia.* Initially, *C. cajan* was provided as a primary host and intercrop for the second year. Survival of *S. album* was 93–97% with all the host species. Survival of *C. equisetifolia* was highest, followed by *P. granatum* and *C. aurantium.* At the end of six years, sandalwood growth was maximum with *C. aurantium* (height 5.95 m, dbh 10.01 cm and crown diameter 4.19 m) followed by *P. granatum* (4.79 m height, 8.67 cm dbh and 3.19 m crown diameter). The possible reason for the poor growth with *C. equisetifolia* might be the overgrowth of host and greater competition for light, moisture and nutrient. Again, high mortality of *C. aurantium* could be due to excess drawing of sap and nutrient by *S. album.* Balasubramanian et al. [26] reported the influence of host species on sandalwood's early growth when grown in farm settings. Field trials were conducted in Tamil Nadu (India) with three host species *Alternanthera sessilis, Sesbania grandiflora* and *Casuarina* under drip irrigation in five treatments. After eight months of planting, the best growth was observed with the combined use of *A. sessilis* and *S. grandiflora.*

5 Prospects

It is estimated that about 20,000 ha *S. album* plantations have been established in India since 2002 in various states by the farmers, industries and State Forest Departments. Commercial plantations of sandalwood have also been established in Australia and China. Unfortunately, most of the private and public nurseries raise planting material from undefined seed sources. Therefore, there is a need for

(i) Seed certification and certified nurseries for the production of QPM
(ii) Identification of trait-specific genotypes and establishment of seedling, seed and clonal seed orchards as a source of quality seeds
(iii) Systematic trials on spacing, host species and management practices
(iv) Studies on heartwood and oil percentage in plantations over 15 years of age at different locations in various agroclimatic conditions.

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Chapter 17
Insect Pests of Indian Sandalwood

John Prasanth Jacob

1 Introduction

Santalum album (Santalaceae) is a commercially and culturally important species. Oil extracted from the heartwood is used in traditional and pharmaceutical medicines as well as in perfumery while the wood powder is used for various cultural and religious purposes. The wood is used for carving handicrafts and idols. All these make Sandalwood one of the most expensive woods in the world [2]. The species is distributed in India, Indonesia, Australia, Taiwan and Hawaii. In India, Sandalwood is naturally distributed mainly in the states of Karnataka and Tamil Nadu. *S. album* is a hemiparasite absorbing specific nutrient from the host trees via root connections.

Overexploitation of the species has resulted in categorizing this species as vulnerable by IUCN. The Government of India has liberalized rules to encourage Sandalwood cultivation. There is an increase in agroforestry and in private lands with quality planting material from the known sources. Pests and diseases are observed in both monoculture plantations and agroforestry, which has become a limiting factor for the successful establishment of the species on a large scale. This review attempts to consolidate information on the insect pest problems associated with Sandalwood feasible management measures identified so far as well as the research gaps which need addressing in the future.

Due to its highly destructive nature, Sandalwood spike disease has been a topic of discussion since the nineteenth century. Sandalwood spike disease was reported in 1900 by Mc Carthy [48] and later by Barber [5]. Even after extensive studies for an extended period, the exact cause of the disease could not be determined. Insect transmission of spike disease was suspected by Coleman [28, 29]. Thereafter, series of works into the entomological investigation on the spike disease of Sandalwood to analyse the role of different orders and families of insects like sap feeders, defoliators and wood borers had been initiated [7] and carried forwarded by many authors

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in insect groups like Brenthidae and Lycidae [43], Anthribidae [42], Cerambicydae [32], Carabidae [1], Neuroptera [4], Fulgoridae, Cicindelidae, Jassidae and Pentatomidae [12–16], Lepidoptera [17], Cicadidae, Coreidae and Reduviidae [18–20], Lygaeidae [21], Heteroptera [22], Coccidae [25], Chrysomelidae [26], Membracidae and Cercopidae [23], Fulgoridae [24], Dermaptera and Orthoptera [27], Elateridae [34], Membracidae [35], Anthicidae [38], Coccinellidae [44], Cercopidae [45], Formicidae [49] and Jassidae [52]. It has been confirmed that Sandalwood spike disease can be transmitted by insect vectors [55] like *Monia albimaculata* [31, 63, 64] and leafhopper *Jassus indicum* [56]. The presence of mycoplasma in the phloem sap of Sandalwood was doubted initially [30]; later it was confirmed that the mycoplasma is the causative agent [40, 87]. With biotechnological tools, the detection of Sandalwood spike disease became easy [39]. Chemical treatment using tetracycline has been reported with the most positive effect in managing Sandalwood spike disease [50] but with practical difficulties associated with its application in large areas. Proper management of insect vector has been suggested for control of phytoplasma-induced disease [36, 89] by developing disease-free superior genotypes through tissue culture [3], application of plant growth-promoting microbes to enhance nutrient levels and to protect against microbial and insect vectors [84].

Many insects and mites attack Sandalwood. Although some effect in nearly all locations, many others are of only local significance. Relatively few species cause significant injury and are only a problem when the population exceeds damaging thresholds. The raising of large quantities of Sandalwood seedlings in nurseries and the establishment of extensive Sandalwood plantations has been progressively increasing in the recent past. The successful establishment is based on the survivability of the seedlings and planted saplings in the field. Insect pests affect the growth of the Sandalwood sapling in the nursery and the field plantation beside the economic loss of wood in storage also. Insect pests have been documented in almost all parts and stages of the Sandalwood plants. Some of the earliest documentation include those by Fletcher [33], Ramakrishna Ayyar [53] and Brown [10]. At the same time, documenting insects associated with different plant genera in India and adjacent countries in a series of publications, an attempt was made to bring out the spectrum of pests associated with Sandalwood [47]. However, the Sandalwood cultivation pattern changed later on with the inclusion of Sandalwood in agroforestry as well as extensive cultivation in private lands outside forests. There has been a high demand for raising of nursery seedlings for the establishment of Sandalwood plantations by state forest departments and tree-growing farmers. It has led to an increase in frequency, intensity and incidence of different groups of insects in on Sandalwood.

2 Insect Pests

The majority of studies are on the insect pests associated with Sandalwood in nurseries and plantations. A checklist of 1049 insects associated with Sandalwood, along with information on the nature of incidence and location of the reported problem, is an exhaustive one with additional inputs from old records [75]. However, information on the pest status and extent of the injury is not available. Documentation by Jag Ram et al. [41] provides lucid information on some of the potential Lepidopteran, Coleopteran, Orthopteran and Hemipteran pests of Sandalwood. The paper details about *Paralutis olivenscens* and *Cryptothelia crameri* larvae, which cut the seedlings at ground level in nurseries, white grubs *Adoretus latirostis* and *Apogenia ferruginea*, which feed on the roots in nursery beds, and discolouration of leaves due to phytophagous mite infestation. Injury to seedling roots by nematodes species like *Aphelenchus arenae, Helecotyienchus indicus, Botyienchus reinformis* and *Scutteloriema bangaloriensis* paves the way for infection by soil fungi [51]. Among the Lepidopteran defoliators, *Nipila conferata* is a commonly observed species on Sandalwood. Nymphs and adults of Tettigonid *Lantana inflate* and Acridid *Orthacris simulana* defoliate nursery seedlings. Coleopteran defoliators reported were the Anthecid *Formicamus sulcipes* and Curculionid *Astycus aurovittatus.* Weevil *Sympiezomias cretaceous,* a polyphagous species, defoliates Sandalwood in nurseries [61]. Orthopterans *Holochlora albida* (Locustidae), *Teratodes monticollis* (Acrididae), *Letana inflata* (Tettigonidae) and the bagworms *Cryptothelia cramerii, Acanthopsyche moorei, Pteroma palgiophleps* (Psychidae) also defoliate seedling in the nursery. *Amata passalis*, a defoliator occurring on pulses like cowpea and ornamentals also defoliates Sandalwood [86].

Sap-feeding coccids like *Sassietia nigra, S. coffeae, Pulvinaria psidii, P. maxima, Ceroplastes actiniformis, Ignis bivalvata, Tachardina lacca* and *Aspidotus* sp. result in failure of grafted twigs in the nursery [61]. *Inglisia bivalvata* was responsible for die-back and death of Sandalwood [58] as well as Indian wax scale *Ceroplastes ceriferus* [59] and *Saissetia* sp. [60]. Incidence of leafhopper, treehoppers, froghoppers [72], whiteflies [73] and leafhopper was also frequent [88]. An epidemic outbreak of lac insect was observed on Sandalwood [62]. However, the species was later confirmed as *Paratachardina silvetrii* [11].

The population dynamics of *Ferrisia virgata* on Sandalwood was found to continue for an extended period due to monsoon failure associated with climate change effects [65]. High temperatures had a negative impact on coccid *Aonidiella orientalis* infesting Sandalwood. Low temperatures showed a positive correlation with the population level of *Cardiococcus bivalvata.* None of the weather factors tend to have an influence on the incidence and build-up of *Ceroplastes actiniformis* and *Parasassetia nigra* [79].

Flowers of *S. album* are self-incompatible and are cross-pollinated by insects like flies *(Phytomia argyrocephala, Eristalinus arvorum, Dolichomerus crassa)* and bees (*Apis florea, A. cerana, A. dorsata*) [9]. However, *Mylabris pustulata*, the flower-feeding coleopteran, was recorded as a pest of Sandalwood [69]. Two species of bugs *Saissetia nigra* and *S. coffeae* were recorded, damaging immature fruits that fall off and do not germinate [70].

The earliest note on Sandalwood boring insects was by Stebbing [71]. The heartwood borer *Aristobia octofasciculata* Aurivillius and red stem borer *Zeuzera coffeae* Nietner were more prevalent infesting Sandalwood in natural forest areas of Karnataka. In Sandalwood plantations, *Z. coffeae* was the major stem borer, while the infestation of stem borer *Purpuricenus sanguinolentus* was limited. Two cerambycid beetles, viz. *Ceresium gracile* (Perroud) and *Stenodryas nigromaculatus* (Gardner), were reported to infest Sandalwood for the first time [82]. Fungal spores carried by insects that enter through wound result in wood rot in Indian Sandalwood in Australia. After degradation of the inner region of wood, the hollow formed provides an entry point for other pathogens and pests like ants and termites [6]. The Biodeterioration of Sandalwood logs by termites severely lowers the log quality, particularly those used for carvings [57].

3 Pest Management Measures

Along with the pest complex of Sandalwood, possible control measures have been suggested way back in 1941 [8]. Judicious planting of Sandalwood associates, which are not the alternate hosts of insect pests, was attempted. Chemicals like Dieldrin and BHC had been suggested but banned later due to concerns created by the chemicals' persistent presence in the environment. Systemic pesticides like Quinalphose were recommended for sap feeders and borers [74]. At the time of preparation of mother beds, soil mixing with pesticides and nematicides was recommended before sowing seeds.

Certain species of sucking pests vary in their prevalence on Sandalwood based on their seasons. Lots of reports on the abundance of natural enemies associated with various Sandalwood pests have been reported. Identified parasitoids associated with *Cardiococcus bivalvata* are reported to be efficient in managing the sap-feeding Coccid [54]. Deploying or conserving the potential chalcid parasitoids in the field, which can attack Coccoidea infesting Sandalwood, is suggested [37]. The Braconid *Glyptapanteles* sp. is an important biocontrol agent regulating the population of defoliator *A. passalis* to acceptable limits in Sandalwood stands [85]. When Sandalwood is established along with horticulture tree species, infestation by *Ferrisia virgata* can be suppressed with the predator *Cryptolaemus montrouzieri* [65]. Abundance and diversity of natural enemies like coccinellids [80], predatory insects [76], parasitoids [78], odonates [67], spiders [77], mantids [66] in various Sandalwood provenances highlight the importance of exploiting these natural enemies for development of ecologically and environmentally sound insect pest management strategies in Sandalwood plantations. Habitat diversification in growing Sandalwood has been suggested as an ideal option to manage an insect pest problem. More diversified areas recorded more species of insects and natural enemies with a less severe infestation. In contrast, less diversified areas showed severe sapsucker and stem borer incidence resulting in undertaking control measures [81]. Silvicultural practices like pruning and other mechanical injuries by farmers in farmlands were found to attract insect infestation, mainly stem and wood bores [83].

Based on the association of ants and honeydew-producing sucking pests in Sandalwood, positive species interaction in food web dynamics and greater predictability of direct and indirect effects of herbivores and natural enemies could benefit attempts of biological control of Sandalwood insect pests [68]. However, there is a need to apply pesticides shortly after planting to protect young Sandalwood seedlings from generalist insects like grasshoppers [46]. Control of termites problem in the field also needs the use of some pesticides [74].

4 Gaps and Challenges

With the various government programmes which support tree cultivation in private lands through state forest departments and non-governmental agencies, the rate of Sandalwood plantation establishment through large-scale multiplication of seedlings in the nursery has increased. When the species is introduced to different environments, the insect pest spectrum tends to change by the transformation of minor pests to major ones and the emergence of new species exploiting Sandalwood. The present review shows that the works so far carried out were on the identification of insect groups responsible for the transmission of spike disease, isolated reports of recurrence or the emergence of species of defoliators, sap feeders and wood borers in Sandalwood nurseries and plantations. Information on the extent of area under infestation, periodicity of incidence and intensity of the attack by key pest species of Sandalwood is not available. Pesticide application has been practised for defoliators, sap feeders and borers. However, reports suggest the prevalence of biocontrol agents associated with Sandalwood pests. Attempts for the conservation or augmentation of potential biocontrol agents have also not been looked into. In natural forest stands with Sandalwood and in plantations, pesticide treatments for Sandalwood pests is a remote possibility due to the high cost involved in the application and associated environmental hazards. Therefore, the present review underscores the need for further systematic studies for identification of changing/emerging insect pest complex of Sandalwood and identification of combinations of feasible, need-based strategies for employing integrated pest management methods, particularly in Sandalwood outside forests. The key tactic is prevention. For this, information on pests and methods to prevent or reduce the pest incidence is required.

Systematic, continuous or regular monitoring and early detection of Sandalwood pests in different agro-climatic zones is required. Information gathered from these studies such as pest abundance levels, periodicity of incidence, the extent of the area infested in relation to biotic and abiotic factors would help in the development of a Pest Calendar for Sandalwood that would go a long way in planning and undertaking prophylactic management measures for the key pests.

The possibilities of a combination of insect trap for pest monitoring, cultural and physical methods like weed clearing, disposal of infested plant parts or plants, handpicking or net collection of pests and destruction, pruning of affected plants that can minimize incidence and spread of the pest need investigation. All these would help in the selection of the right pest management strategies well before pest incidence. Delaying pesticide applications can go a long way in allowing the build-up of the natural enemy population. Applying commercially available bacterial, viral, fungal formulations for various groups of insect pests can also limit the use of chemical pesticides. Identification of extracts from commonly available plants with insecticidal properties through cost-effective methods would be useful to minimize pest incidence and spread if insect abundance is at low to medium levels. A package of need-based, safe and less persistent insecticides would be the last option in the event of an outbreak situation. Identification of pest tolerant varieties of Sandalwood, if any, with sufficient oil yield may also be explored. Finally, dissemination or updating of information on the pest spectrum and critical use of different pest management options to tree growers through periodic training and interactions is required for the successful establishment of the Sandalwood plantations.

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Chapter 18
Diseases, Diagnosis and Their Management of Indian Sandalwood

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1 Introduction

Indian sandalwood is vulnerable to several diseases caused by fungal, viral and phytoplasmal pathogens. The most important diseases of sandalwood include collar rot, wilt and leaf spot caused by different fungal species, leaf curl disease caused by virus and the spike a phytoplasmal disease [1].

2 Nursery Diseases

The establishment of plantation involves raising of seedlings in containers under nursery conditions [2–7]. Sandalwood being a partial root parasite requires a host which enhances seedling growth by providing nutrients particularly nitrogen, phosphorus and potassium [8–11]. Sandalwood can parasitize the roots of almost all plants, but it shows preference for and exhibits the best growth with certain host species [12].

Sandalwood seedlings are susceptible for damping off and seedling wilt which can destroy the entire nursery stock during damp seasons. Highest incidence of these diseases was recorded in Karnataka and Tamil Nadu, India. Fungal genera, viz., *Pythium, Phytophthora, Fusarium* and *Rhizoctonia* are commonly associated with the infected seedlings [13].

Wilt is a systemic disease caused by *Fusarium oxysporum* in sandalwood seedlings. The entire plant or its branches exhibit wilting of foliage in acropetal succession, and the leaves become yellow, lose turgidity and fall off. The affected seedling or branch dies with necrotic symptoms [14]. *Fusarium oxysporum* Schlecht.

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is the most common and virulent fungus that spreads rapidly in the tissues and seedlings causing either complete wilting or rotting at ground level. Synergistic association of nematode with *Fusarium* enhances the vascular wilt at seedling stage [15]. The root rot caused by *Fusarium moniliforme* [*Gibberella fujikuroi*] is reported as serious disease in Bangladesh. The typical symptom is gradual browning of top leaves of the seedlings, and the brown spots appear on the branch and tap roots which later turn black. The leaves of infected seedlings lose their freshness and begin to die with the stem standing erect [16].

3 Tree Diseases

3.1 Fungal Diseases

Canker disease caused by *Lasiodiplodia* sp. was first reported in sandalwood from western Australia. Symptoms of canker appear as small areas of dead tissue which grow slowly over years. Cankers can kill branches of trees by choking them off [17].

In India, the first report of canker disease on sandalwood was made by Nagaveni et al. [18]. The plants grown under the canopy of banyan tree where water logging condition was more prevalent showed sudden death and the collar region of the dead plants showed canker-like structure caused by the pathogen *Fusarium oxysporum* (Table 1).

During the year 2013 and 2014, powdery mildew disease was recorded on sandalwood in Mandsaur and Indore districts of Madhya Pradesh, India. The causal agent was identified as *Pseudoidium santalacearum* on the basis of symptoms, morphological characters and host range [19]. Circular white patches were seen on both sides of leaves in initial stage and these spots increase in size and spread all over the surface of leaves. The mycelium of *P. santalacearum* is epiphytic, amphiphyllous, thick walled, hyaline and conidia are formed singly [20].

3.2 Sandalwood Spike Disease

Sandalwood spike disease (SSD) is the most serious disease of *S. album* among all the diseases reported. Sandalwood spike is found to be significantly most destructive and more prevalent where sandalwood is grown in India and Indonesia. In 1903, the disease was first reported by Barber from Coorg district of Karnataka state, India [24]. During 1969, Varma et al. [28] reported the causal organism as phytoplasma. Typical symptoms of SSD are ‘rosette spike or spike inflorescence’ and ‘pendulous spike’. Rosette spike is characterized by the extreme reduction in size of leaves and internodes resulting in crowding of leaves on branches. Further, the size of emerging leaves gets reduced and becomes stiff, thereby standing out as spikes. In infected trees,

Table 1 Diseases of sandalwood caused by fungi and phytoplasma

Disease	Causal organism	Symptoms	References
Canker	*Fusarium oxysporum/Lasiodiplodia* sp.	Bulged canker-like structure in the collar region	[18]
Anthracnose	*Colletotrichum fructicola*	Leaves with purple or purple-brown spots in the early stage of the disease leading to the defoliation of leaves. Round lesions on the stem and shoots with a black dot surrounded by pale brown margin. Most parts of leaves become black and dead	[21]
Powdery mildew	*Pseudoidium santalacearum*	Small floury patches on lower and upper side of leaves and later spread all over the surface of leaves	[19, 22, 20]
Sandalwood spike disease	*Phytoplasma*	Chlorosis, reduction in leaf size and shortened internodes, causing leaves to become crowded on twigs with a ‘bushy’ appearance and stems stand out stiffly, acquire a ‘spike-like’ appearance. Spiked plants do not bear flowers or fruits and trees generally die within 1 to 2 years if infected at young age	[23–27]

flowers become leaf like and do not bear fruits and the ends of roots of spiked plants die out resulting in loss of haustorial connection with the host plants. Symptoms of ‘pendulous spike’ include continuous apical growth of individual shoot without proper thickening and result in drooping of shoots. The dormant buds do not grow and no rosettes are produced. In this symptom, the roots and haustorial connection are not damaged [29].

4 Etiology of SSD

The history on sandal spike research has been over a century. Initially, the spike disease was suspected to be a root disease and a physiological disorder caused by unbalanced sap circulation brought about by adverse factors such as forest fires [25]. Latham [30] was of the opinion that the disease was due to a fungus, whereas Fischer [31] thought that the disease was caused by some ultramicroscopic bacteria. Coleman [32, 33] attributed the disease to a virus. The viral theory of sandalwood spike disease was disproved during 1969 when three groups of researchers showed the phytoplasma in the phloem tissues of spike-diseased plants through transmission electron microscopy studies [28, 34, 35]. The morphology was described as the pleomorphic bodies with 40–750 nm size devoid of cell wall; the cytoplasm was bound by a unit membrane of 10–12-nm thickness with a fibrillar network of DNA and ribosomal bodies. The reduction of spike disease symptoms after the treatment with antibiotic tetracycline further confirmed the phytoplasmal etiology [36]. Phytoplasmas survive in sieve tubes (phloem) of the host plants and are capable of replicating without utilizing the host machinery. The limiting factor in research of phytoplasma disease is that this pathogen cannot be cultured under laboratory condition [37].

5 Transmission and Ecology of SSD

The disease is transmitted naturally through root contact and dodder [33, 38, 70]. In nature the transmission is also possible through the insect vectors which feed on phloem and hence the insects are responsible for transmission of phytoplasma under field [38] (Table 2). The insect vectors while feeding puncture the phloem cells, thereby tearing the cells. The plant cells around the punctured cells become hypertrophied due to the injection of the salivary secretion by the insect vector. The phytoplasmas multiply within the vectors and circulate through a sequence of tissues and organs of vectors when the latent period of pathogen is long [39].

Insect vectors such as *Moonia albimaculata* [40], *Jassus indicus* [41, 42] and *Nephotettix virescens* [39, 43–46] were suspected to be involved in transmission of sandalwood spike disease in the field. Ghosh et al. [47] reported *Redarator bimaculatus* as the insect vector. Eggs of *Moonia albimaculata* are laid on leaf edges by making slits in tissues and reproduce for three generations in a year. *Jassus indicus* lays eggs on tender leaves, and duration of life cycle is 12–14 weeks. *Nephotettix virescens* is phototropic in nature, thereby hiding during day time. Its population declines during February to May in the sandalwood ecosystems and reaches peak during October to November [39]. Laboratory transmission of the disease is achieved mainly through grafting and dodder. Coleman [32, 33] was the first to demonstrate the graft transmissibility of the disease to healthy trees. The establishment of the scion was found to be a prerequisite for disease transmission [41]. Nayar and Srimathi

Table 2 Transmission characteristics of sandalwood spike disease

Transmission	Mode of transmission	References
Dodder transmission (*Cuscuta subinclusa*)	*Cuscuta subinclusa*, a dicot, is an annual herb or vine parasitei, dodder forms haustoria on the 'spiked' shoots and branches. The disease could be transmitted five weeks after attaching the dodder from the diseased sandalwood trees to healthy seedlings	[33, 70]
Seed transmission	The seeds obtained from an artificially grafted plant, whose fruit-bearing branch manifested symptoms of SSD when the fruits were in advanced stage of maturity. These seeds on germination gave rise to two spiked plants	[70]
Bud, bark and twig grafting	By inserting parts of fresh, diseased leaves between wood and bark of branches or stems of healthy plants	[32]
Patch grafting	The ordinary patch of bark tissue including the cortex can be easily skinned from a scion and might, on grafting, induce the disease in healthy stocks	[71]
Insect transmission	Leaf hopper, *Jassus indicus* (Walk)	[39]
	Nephotettix virescens Distant	[39]
	Moonia albimaculata Dist., *Lodiana indica* (Wlk.)	[40]

[48] were of the opinion that incidence of SSD was higher in areas where *Lantana camera* is the dominant host species because of (i) inadequate supply of nutrients to sandalwood, *Lantana* being a xerophytic type, (ii) increase in the incidence of insect vectors due to paucity of insectivorous birds and (iii) greater build-up of inoculum, *Lantana* being a symptomless carrier of the disease pathogen. The most important ecological factor of sandalwood spike pathogen is the occurrence of several collateral hosts in the natural sandalwood forests. The plants showing identical 'yellows' symptoms are *Allamanda cathartica, Acacia* spp., *Catharanthus roseus, Dendrocalamus strictus, Dichrostachys cinerea, Dodonaea viscosa, Stachytarpheta indica, Ziziphus oenoplia,* etc. [42, 47].

6 Diagnosis and Detection of SSD

Spike disease of sandalwood is generally diagnosed by the manifestation of external symptoms. Attempts have been made to detect the diseased plants by determining the length/breadth ratio of leaves [49]. The diseased plants can be diagnosed by light and fluorescent microscopic techniques. The detection of abnormal levels of wound callus produced in response to injury to phloem cells has been suggested as an indirect method of diagnosis of phytoplasma. Ghosh et al. [47] used Shigometer to diagnose the spike-diseased sandalwood, and the electrical resistance of the inner bark of diseased trees was correlated with the intensity of visual symptoms.

Histochemical tests carried out using Mann's stain [50], Dienes' stain [51], Aniline blue, a DNA binding fluorochrome and Hoechst 33258 [47, 52] showed large number of fluorescent spots throughout the phloem tissue giving evidence of the presence of phytoplasma. Thomas and Balasundaran [53] used Giemsa and Dienes stain through light microscopy and aniline blue, Hoechst 33258 and DAPI stain by fluorescence microscopy for the detection of phytoplasma.

7 Immunological Techniques for SSD

Immunoassays are used in plant pathology for diagnosis of disease, identification and quantitation as the antigen–antibody reaction is highly specific [54]. The antigens are substances that can elicit immune response when injected into animals in the appropriate manner which initiates the synthesis of specific antibodies [55]. Immunological techniques are most valuable and simplest to use and interpret for diagnosis of diseases with inconsistent and undeveloped symptoms [4]. The most sensitive immunoassays in use include enzyme-linked immunosorbent assay (ELISA), dot immunobinding assay (DIBA), immunomicroscopy and immunoblotting (Western blotting) [56]. Nayar and Ananthapadmanabha [57] purified sandalwood spike phytoplasma by ammonium sulphate precipitation method to raise polyclonal antibodies in rabbit. Other methods of purification include differential centrifugation method, celite pad filtration technique and Percoll density gradient centrifugation. Various laboratories have reported the production of polyclonal antibodies to selected phytoplasma derived from sandalwood tissue extracts [58–61] which could be used for distinguishing phytoplasma-affected diseased plants from healthy ones. The use of monoclonal antibodies [62] circumvents many of the problems encountered with polyclonal antibodies, but the production of suitable monoclonal antibodies requires specialized laboratory and considerable time [58].

8 Nucleic Acid-Based Techniques for SSD

Sandalwood spike disease associated with sandalwood can be detected by direct polymerase chain reaction (PCR) using universal phytoplasma-specific primers, viz., P1/P7 and R16F2n/R2 with PCR amplicon size of 1.8 kb and 1.25 kb, respectively. Amplicons obtained through direct PCR can also be subjected to restriction fragment length polymorphism (RFLP) analysis with different restriction endonucleases to detect SSD [37]. Phytoplasmas could also be detected by variants of PCR, viz. real-time PCR and nested-PCR for which 16S rDNA primer is essential [63]. Nested-PCR-based system also facilitates detection of SSD in insect vectors [64]. Based on the DNA amplification, the causal agent is designated as *Phytoplasma cynodontis* belonging to 16SrI, which is one of the major groups of phytoplasmas associated with different plant species reported to be infected worldwide [63, 65–67]. The sequence similarity analysis showed that the phytoplasma infecting sandalwood spike is similar to aster yellows subgroup 16SrI-B [26].

9 Management Practices

The nursery diseases can be managed by the selection of seeds free of fungi, controlled watering, maintaining good drainage in containers and drenching the potting medium with copper fungicides (copper oxychloride/Bordeaux mixture) and nematicide (quinalphos/phorate) [14].

9.1 Management of SSD

Production of disease-free plants through tissue culture is the most effective method for the management of SSD, and transgenic strategies to derive disease-resistant trees may be the only realistic solutions for ridding the limited *S. album* forests of SSD [23]. Development of phytoplasma-resistant and insect-resistant plants is another possible permanent option for the management of sandalwood spike disease. Planting of a hybrid of *Eucalyptus tereticornis* (Mysore gum trees) at a distance of 10–20 m from the sandalwood trees keeps the latter free of SSD infection [50].

Raychaudhuri et al. [36] attempted using the chemotherapeutic agents such as antibiotics (dimethyl chlortetracycline 9 hydrochloride and tetracycline hydrochloride), systemic fungicides (benlate (methyl 1-(butylcarbaucyl)-2-benzimidazole carbamate) and toxins (arsenic) to treat the phytoplasma-infected sandalwood. However, use of other antibiotics such as achromycin, aureomycin and ledermycin was not found to be effective [68]. Nevertheless, tetracycline antibiotics—tetracycline hydrochloride, oxytetracycline HCl, ledermycin, aureomycin and doxycycline—showed temporary recovery of the disease in various degrees through injection method [69].

10 Conclusion

Sandalwood being a high-value wood tree suffers from various diseases, and the major production constraint is the sandalwood spike, an insect-transmitted phytoplasmal disease. The early detection and timely management of the seedling and adult plant diseases is utmost important to harvest the economic part of the sandalwood. Various advanced serological techniques such as ELISA and immunoblotting and DNA-based techniques such as real-time PCR and nested-PCR are available for the detection of the phytoplasmas infecting sandalwood; however, further standardization of the techniques is required. The use of antibiotics is considered as the possible way to manage the spike disease along with the vector control. However, further studies on the host–pathogen interaction and sensitive detection methods are to be focused with respect to the spike disease for the early detection and effective management.

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Chapter 19
Indian Sandalwood Cultivation Prospects in India

S. Viswanath and Sandeep Chakraborty

1 Introduction

Since ages, farmers have been growing trees on their farmlands for sustained production of food, fuel, timber and also maintain healthy soil environment. This has now been recognized as agroforestry. In India, agroforestry has special importance considering the limitations in the agriculture sector and the population dependent on agriculture as the mainstay for food security and livelihoods. The National Agroforestry Policy launched in 2014 in India has recognized this and seeks to address some of the policy constraints identified in the agroforestry sector. It is also being recognized that agroforestry practices can enhance the resilience of farming systems to cope up with even adverse impacts of climate change [11]. Trees like sandalwood have a huge potential in agroforestry and can play a major role in providing ecological, economic and social security to farmers especially in semi-arid region where incidentally most of the increase in average of sandalwood cultivation is being reported [6]. Considering the huge demand for the wood and the oil commercial cultivation of *S. album* has been taken up since 2002 and by 2014, India had 20,725 ha of sandalwood plantation, mainly concentrated in Karnataka, Tamil Nadu and Kerala [5]. It is reported that the local consumption of sandalwood products in India amounts to 50%, suggesting that in the future, India will have to struggle for getting this resource to supply in the international market, notwithstanding the tremendous demand internally [3, 13].

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2 As a Multipurpose Tree Species (MPT)

In agroforestry, a tree is ranked high as an MPT species if it has multiple uses like timber value, edible products, fodder value, nitrogen fixing ability, fast growing nature and an ideal ideotype to be integrated with associated component woody species. In the case of Sandalwood, the most notable feature which makes it attractive to farmers is the high-value heartwood from stem and roots. More or less, all parts of the tree have some use value. The mature leaves have fodder value and are relished by sheep and goats. The tender leaves are used to make a tasty 'chutney' paste which is regarded as traditional knowledge in the Malnad region of Karnataka. The dried flowers are also marketed as tea in some south Asian countries. Many bird species predate the dark purple drupe while the oil from seeds has a cosmetic value. Sandalwood seeds have been reported as a source of oil with nutritional, industrial and pharmaceutical values. *S. album* is also reported to be an excellent source of ximenynic acid as well as oleic acid which has been less exploited commercially [16].

The value of a sandalwood tree for commercial purposes primarily depends on the quantity and quality of heartwood and oil.

3 Nursery Management and Quality Planting Material (QPM) Production

A significant problem that has emerged in recent times is regarding the low quality of planting stock available to sandalwood growers which may be realized by the farmer only 15 years later when sandalwood is harvested. The quality of planting stock used/procured by farmers is mostly of dubious quality and from unknown sources. There is a severe dearth of certified quality planting stock while private nurseries have mushroomed all over, especially in southern India, where seeds of unknown origin are used. The nursery, seed handling, pretreatment and raising of Quality planting stock in the nursery have been well standardized at the Institute of Wood Science and Technology (IWST), Bangalore [2].

Most nursery owners still rely on traditional nursery practices rather than expensive root trainer technology for raising seedlings. Polythene bags of 1500 ml capacity (13 cm $\times$ 30 cm size) using a potting mixture of soil, sand and farmyard manure (FYM) in 2:1:1 ratio are conventionally used as a potting medium. The drawback is that there is the possibility that such mixtures may produce seedlings with good shoot development but poor root systems. By the end of six months, healthy seedlings of 30 cm height having dark green leaves can be used for field planting. Traditionally, *Cajanus cajan* has been used as a primary host. *Mimosa pudica* is also considered a good alternative primary host. To a certain extent, good primary host selection can offset the poor root formation noticed when sandalwood seedlings are raised in cost-effective polybag containers.

4 Agroforestry Combinations with Sandalwood Across India

It is generally observed that in semi-arid landscapes, farmers are prone to experiment and take more risks as compared to humid tropical landscapes due to vagaries of nature being more common in semi-arid and arid landscapes. Since the spectre of agricultural crop failure due to monsoon failure is a probability that needs to be factored into cropping practices, farmers tend to adopt a diversified cropping pattern. The addition of a long-term lucrative woody component in the cropping system tends to lend a greater degree of economic stability in rain-fed agricultural practices besides the animal component. Hence, the area under sandalwood cultivation in semi-arid areas have shown an exponential increase over the past decade [5].

Sandalwood has excellent agroforestry potential due to its many intrinsic properties like its hemiparasitic nature, adaptability to thrive in adverse soil and climatic conditions, resilience to pests/diseases, multipurpose uses besides the high economic value of heartwood. The potential of sandalwood in agroforestry practices can be primarily attributed to the following factors.

- Hardy and grow in a wide range of agroclimatic conditions.
- Not demanding in respect of nutrients and moisture.
- Not a light demander in the initial stages which enhances the chances of underplanting sandalwood in existing horticultural plantations.
- Ability to grow in dry and degraded lands.
- As a multipurpose tree, every part of the tree is useful.
- Ability to recover quickly from browsing and hacking in the initial stages.
- Ability to regenerate through root suckers.
- Besides the high-value heartwood from stem and roots, even the sapwood has an economic value in the handicraft sector.
- Requires primary, secondary sometimes intermediate hosts which allow the possibility of integrating a multitude of annuals and perennials during its cultivation period in farmlands.

Sandalwood cultivation in private lands has shown a spurt from 2002 to 2003 onwards due to post liberalization of sandalwood rules [8]. Farmers have shown a willingness to take up sandalwood cultivation, and this has seen a corresponding increase in the total area under sandalwood cultivation. States like Gujarat, Rajasthan, Maharashtra, Telangana, Andhra Pradesh and Madhya Pradesh have taken an early lead in acreage under cultivation. The farmers in traditional natural sandalwood distribution areas like Karnataka and Tamil Nadu have been mostly cautious in their early response to sandalwood cultivation, primarily out of fear of theft and protection problems at later stages. There has also been tremendous interest in sandalwood cultivation in North-east states like Assam, Tripura and Manipur, besides states like Punjab and Himachal Pradesh [5, 10].

In sandalwood cultivation, selecting an appropriate host plant right from the nursery stage is of utmost importance because it is xylem tapping obligate root hemi-parasite and requires host plants during its life span. Being an aggressive hemiparasite, it can develop haustoria within 30 days from germination [1, 13]. Quantitative studies done previously to evaluate the right primary host plant have identified species like *Cajanus cajan, Alternanthera* spp., *Mimosa pudica* and some forestry species like *Pongamia pinnata, Acacia nilotica, Azadirachta indica, Casuarina* spp, etc., as good hosts depending on root cation exchange capacity [1]. However, farmers tend to prefer *Cajanus cajan* (Fig. 1) as the primary host inside the same pit as the sandalwood seedling in the first year when establishing sandalwood plantations. If intensive management is not possible, then preference is for secondary woody species that are fast growing, leguminous, hardy perennials at relatively close spacing to the sandalwood sapling like *Casuarina equisetifolia* (Fig. 2). Species like *Pongamia pinnata* and *Melia dubia* have also been successfully tried out. In general, the perception is that leguminous plants seem to be a more efficient host than non-leguminous plants.

However, currently, farmers who opt for sandalwood cultivation have a distinct preference for horticultural species like grafted mango (*Mangifera indica*), drumstick (*Moringa oleifera*), pomegranate (*Punica granatum*) (Fig. 3) ber (*Zizyphus mauritiana*), custard apple (*Annona squamosa*), lemon (*Citrus limon*), gooseberry (*Emblica officinalis*) (Fig. 4), etc. (Table 1). However, these secondary horticultural species performances are to be scientifically documented and validated. Nevertheless, it needs to be appreciated that this approach is quite in contrast to how sandalwood plantations have been raised in the past by the state forest departments when sandalwood tree was considered a 'royal tree' or a state tree before 2002. At that time, the long-term secondary hosts preferred were trees like *Pongamia pinnata, Azadirachta*

Fig. 1 Sandalwood seedling with *Cajanus cajan* as primary host

Fig. 2 Sandalwood with *Casuarina equisetifolia* as host

Fig. 3 Sandalwood with *Punica granatum* as host

Fig. 4 Sandalwood with *Emblica officinalis* as host

Table 1 Preferred horticultural species used by farmers as secondary hosts for sandalwood cultivation in agroforestry practices across India

S. No.	Long-term horticultural species as secondary hosts observed	Agroclimatic zone	Type of management adopted
1	*Emblica officinalis* (amla/Indian gooseberry)	Semi-arid zone	With drip irrigation
2	*Mangifera indica* (mango)	Semi-arid and subhumid	Grafted mango preferred with drip irrigation
3	*Psidium guajava* (guava)	Semi-arid	With drip irrigation
4	*Punica granatum* (pomegranate)	Semi-arid	With drip irrigation
5	*Annona squamosa* (custard apple)	Semi-arid	With drip irrigation
6	*Zizyphus mauritiana* (ber)	Semi-arid	With drip irrigation
7	*Citrus limon* (lemon)	Semi-arid	With drip irrigation
8	*Moringa oleifera* (curry leaf)	Semi-arid	With drip irrigation
9	*Coffea robusta* (robusta coffee)	Humid	Under shade trees

indica, Casuarina equisetifolia (Fig. 3), etc., and the seedlings of these species used to be planted very close to the sandalwood seedling, often inside the same pit [14]. The minimum rotation age was not less than 30 years under natural forest conditions as sandalwood was considered a very slow-growing tree.

The early stage of sandalwood cultivation also offers immense inter cultivation scope, especially short statured annuals or biennials. Crops like *Glycine max* (soya bean), *Citrullus lanatus* (watermelon), *Vigna unguiculata* (cowpea), *Vicia faba* (field bean/broad bean), *Curcuma longa* (turmeric) have been tried out as intercrops in *S. album* up to even 10 years in states like Madhya Pradesh in Central India (Plate 3). Available data and observations indicate that if sufficient space of at least a minimum of 4 m is available between the sandalwood rows as interspace, it may be possible to take various annual or biennial crops/vegetables as intercrop even up to 10 years of sandalwood plantation without any significant reduction in crop yields. The key to the model's success may depend on spacing, silvicultural management of the sandalwood tree and long-term secondary host, and management inputs like drip irrigation, soil working, etc. Generally, a spacing of 5 × 4 m in sandalwood agroforestry is deemed optimum. The long-term intermediate host may be accommodated within the sandalwood rows keeping a minimum distance of 2.5 m from the sandalwood tree inside the row. However, farmers generally prefer a variety of horticultural species over forestry species as long term secondary hosts depending on availability, market accessibility of produce and availability of management inputs like labour, drip irrigation, plant growth regulators, intercropping and weeding, etc. Farmers have often suggested that horticultural species like *Citrus limon* and *Punica granatum* do not survive beyond five years when accommodated at a 2.5 m distance between the sandalwood trees in a row, possibly due to intense parasitizing sandalwood roots on these host species. However, these hosts apparently provided an incremental boost to sandalwood growth compared to some other long-term horticultural species. Preliminary observations on growth data on sandalwood plantations with different horticultural species in field conditions show that certain horticultural species like Indian gooseberry/amla, pomegranate and citrus may have apparently boosted the growth of sandalwood trees as compared to some other species as mango or guava in the short term (Table 2) [7]. Screening of these horticulture species in pot culture studies using N15 stable isotopes may provide a scientific explanation for these observations.

5 Economic Returns from Sandalwood Agroforestry Models

Due to the perceived lucrative price of heartwood and oil, sandalwood cultivation on a commercial basis has picked up in recent times. The cost of cultivation, maintenance and protection cost can consume nearly 40–50% of the estimated returns from Sandalwood at final harvest [15, 17]. As this expenditure has to be incurred ahead, only the large farmers with access to resources could invest in this venture rather than resource strapped poor farmers. Though an accepted package of practice for cultivation is yet to be made available by State Agricultural departments or ICAR institutions, Institute of Wood Science and Technology (IWST) Bangalore and Karnataka Soaps and Detergents Ltd (KSDL), Mysore, Karnataka had come out

Table 2 Assessment of growth performance of sandalwood trees in association with various horticultural species as secondary host over a 5 year period

S. No.	Sandalwood in combination with various horticulture species as secondary host	Incremental growth parameters of sandalwood		
		Height (m)	GBH (cm)	Basal girth (cm)
1	Sandalwood without host (Control)	$0.73^{ab} \pm 0.63$	$2.5^{ab} \pm 0.68$	$4.8^{c} \pm 0.84$
2	Amla (*Phyllanthus emblica*)	$1.04^{a} \pm 0.29$	$4.4^{a} \pm 0.70$	$6.3^{a} \pm 0.42$
3	Mango (*Mangifera indica*)	$0.75c^{ab} \pm 0.63$	$2.5^{ab} \pm 0.68$	$3.7^{ab} \pm 0.84$
4	Pomegranate (*Punica granatum*)	$0.90^{ab} \pm 0.09$	$2.5^{a} \pm 0.34$	$3.1^{c} \pm 0.43$
5	Lemon (*Citrus limon*)	$1.42^{ac} \pm 0.97$	$5.8^{bd} \pm 0.85$	$9.3^{ab} \pm 1.57$
6	Guava (*Psidium guajava*)	$0.74^{ab} \pm 0.10$	$3.1^{ab} \pm 0.25$	$6.0^{ab} \pm 0.21$
p value		0.0077	5.1×10^{-6}	8.62×10^{-6}
LSD*		1.90	2.76	3.50

Value with similar alphabets are not significantly different (Source: 8)

with some data on cultivation costs as early as 2008 when only guesstimates were available. However, over the last few years, data on the actual yield of heartwood, sapwood and mixed wood have started to emerge from farmers' fields.

Sandalwood trees are generally harvested at 30–60 years when grown under natural forest conditions. Sandalwood cultivation had so far been restricted to government-controlled lands, reserve forests and protected areas, and hence data is lacking on growth behaviour and heartwood formation when grown on private lands under intensively managed conditions. The economic viability of Sandalwood intercropped with amla (*Phyllanthus emblica*) and horse gram (*Dolichos uniflorus*) was analysed in different rotation period of 15 and 20 years through indicators such as NPV (Net Present Value), Benefit-to-Cost ratio (B/C), Equivalent Annual Income (EAI) and Land Expectation Value (LEV) indicated that Sandalwood-based agroforestry is financially viable [15]. Sandalwood cultivation appears to be lucrative at current market rates, as indicated by a B/C ratio of 3.3 in 15 years and 1.9 in 20 years (at a 15% discount rate). The IRR of 33% in 15 years and 21.62% in 20 years also indicate the financial viability of Sandalwood cultivation. Overall financial indicators at 15 and 20 years indicate that it would be more economical if trees were harvested in the 15th year instead of 20 years. However, field data to support such conclusions are still awaited. Of the total cost, nearly 50% turned out to be protection costs in private plantations [15].

6 Challenges in Sandalwood-Based Agroforestry Models

The effect of external management inputs on sandalwood growth and subsequent heartwood formation has also not been documented in sandalwood agroforestry practices across different agroclimatic zones in the country. Silvicultural management practices like spacing, pruning and thinning affect the rate of growth and heartwood formation. However, to what extent the impact will be is still to be documented. This could also be a reason for variation in heartwood and oil, even among similar age trees in the same plantation. Thus, it is essential to document scientific data for developing a package of practices on developing cultivation in India.

Currently, there exists a monopsony situation in buying sandalwood [8] in Karnataka. Government agencies like Karnataka State Handicraft Development Corporation (KSHDC) and KSDL are authorized to procure and deal with Sandalwood private cultivators in addition to the State forest department in Karnataka. However, the high retail price of Sandalwood has not translated into matching remunerative profits for farmers when grown in farmlands is sold to such Government agencies. During 2016–2017, the average procurement price from farmers by KSDL was Rs 6400/kg of heartwood. In 2017, in an instance of direct purchase from a farmer in Nelamangala near Bangalore, KSDL had procured around 75 mature sandalwood trees (18 years age) having a GBH ranging from 60 to 75 cm. On average, the trees yielded 15 kg heartwood and around 6 kg mixed wood and were valued at Rs 22,000/tree. KSDL valued the trees after fixing a rate of Rs 6400/kg for heartwood, Rs 2000/kg for mixed wood, Rs 80/kg for sapwood and Rs 30/kg for bark and chips. There appears to be a considerable gap between the procurement price by government agencies and retail price sold by them through their outlets which is certainly a disincentive for sandalwood farmers. Despite this anomaly, there is an increasing demand for sandalwood seedlings over the past decade. The National Medicinal Plant Board (NMPB), through its subsidiary State Medicinal Plants Boards (SMPBs), have initiated various schemes to promote sandal cultivation.

Along with spurt in cultivation came other problems like an increase in the incidence of pests and diseases. Some of the pests like coffee white stem borer *(Xylotrechus quadripes)* commonly seen associated with secondary hosts have been a problem in young sandalwood plantations. Phytoplasma caused disease like 'Sandalwood Spike' which was thought to have been controlled in the mid half of the twentieth century, also showed signs of resurgence. Some diseases like downy mildew and powdery mildew, usually seen in early nursery stages, are a significant cause for concern even in the first year of planting in the main field especially in the current climate change scenario [5]. Silvicultural practices like pruning and canopy management generally associated with fast growing trees like *Tectona grandis* or *Melia dubia* seem to have adversely affected young Sandalwood trees growth. The injury marks left on the main stem after improper pruning of lower sandalwood sapling branches are often entry points for stem borers *Xylotrechus quadripes*.

Challenges in the physical protection of mature trees from theft have proven to be the major challenge for farmers. Lack of tree insurance schemes for Sandalwood has compounded the problem. Farmers are discouraged by investing heavily in securing the plantations to install tamper-proof boundary walls, engaging armed security for patrolling along with trained dogs, especially in large commercial plantations. Unmanned aerial vehicles and remote surveillance systems are still in the experimental stages, and a low-cost fool proof system adapted to Indian climatic conditions is yet to emerge. Due to the long gestation period of 15–20 years advocated in Sandalwood agroforestry, the challenge is in choosing an appropriate crop combination with proper spacing of the components. Farmers across India have tried out various horticulture crops with varying degrees of success depending on the agroclimate, market access and QPM availability. Clear scientific evidence on the compatibility of Sandalwood with appropriate horticultural species is lacking. Secondary horticultural host that can support sandalwood parasitization without succumbing halfway through the sandalwood gestation period is another problem that has been noticed in *Citrus lemon* and *Punica granatum*. The opportunities in sandalwood agroforestry to introduce horticulture species as secondary hosts and short-term primary hosts and annual intercrops are manifold and can sustain the farming system's maintenance during the long gestation period.

7 Future Perspectives on Sandalwood Cultivation in India

It is interesting to note that with the liberalization of rules regarding sandalwood cultivation in 2001 and 2002 in the traditional sandalwood zones in southern India like Karnataka and Tamil Nadu, the initial enthusiasm and spurt in sandalwood cultivation was in the western states like Gujarat, Rajasthan and Maharashtra. Later on, states like Andhra Pradesh and Telangana picked up the baton. It is only in the past one decade that farmers in Karnataka and Tamil Nadu followed suit. In the meantime, farmers of the north eastern states like Assam especially the lower region in Karbi Amlong have shown an interest in sandalwood cultivation while in the southernmost state of Kerala, the cultivation of sandalwood is yet to pick up. Farmers have recognized the potential of this tree in agroforestry in less favourable climate and soil regimes especially in the semi-arid zones. The choice of long-term secondary host for sandalwood has also been selected based on local demand and agroclimate with a distinct preference for horticultural crops. Farmers have also realized the importance of quality planting material (QPM), silvicultural management including appropriate spacing between secondary host and sandalwood while primary hosts like redgram are accommodated in the sandalwood pits in initial stages.

Sandalwood-based agroforestry are set to become more popular and are increasingly being adopted by farmers in semi-arid areas where low rainfall, poor soils and high temperatures during summer are major limitations in growing high value plantation crops. In the relatively high rainfall areas straddling the western ghats and in the high rainfall areas in North east India where plantation crops like tea, coffee, pepper and spices dominate in shaded perennial agroforestry systems, sandalwood is unlikely to replace any of the high-value plantation crops. Also, the agroclimate especially high rainfall does not seem favourable for the natural growth and establishment of sandalwood.

Relatively long gestation period (15–20 years), current monopsony situation existing in harvest, sale and marketing of final end product, investment in protection from theft and pilferage are some of the deterrents existing in sandalwood cultivation irrespective of the state or geographical region in India. These issues and other concerns raised by sandalwood farmers are being addressed through interactive training programmes for farmers by various R&D organizations like Institute of Wood Science and Technology, Bangalore. It is also suggested that setting up a statutory Sandalwood Board under the Ministry of commerce on the lines of existing Spices Board or Coffee board can address the marketing issues to some extent. Extending a credit line for sandalwood cultivation, tree insurance schemes and other policy incentives can also help farmers to a great extent.

8 Conclusion

Commercial cultivation of Sandalwood in the private sector is a recent development in India, primarily due to unimaginative government policies. In the meantime, the natural growing stock of Sandalwood in protected and reserve forest has decreased drastically due to illegal extraction. Since tree cultivation in farmlands was not encouraged previously, this has resulted in low or non-availability of quality heartwood. However, increased interest in Sandalwood cultivation by farmers and private investors has been noticed since the past one and a half decades. Encouraging sandalwood-based agroforestry practices through policy incentives programmes and supply chains can enhance heartwood production without compromising the area under horticultural and agricultural crops, especially in semi-arid areas will be the ideal approach to promote sandalwood cultivation in India to meet the domestic and international demand. This should be augmented with certified QPM supply, package of practices for cultivation and proper training to farmers. Sandalwood cultivation has only come to stay, and the acerage is only set to increase since the Indian farmer has realized the opportunity in it for providing financial security and stability.

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Part V
Tree Improvement and Biotechnology

Chapter 20
Tree Improvement of Sandalwood in India with Special Emphasis on Heartwood and Oil—An Analysis

A. N. Arunkumar and A. Seetharam

1 Introduction

Santalum album L., or Indian sandalwood (Family Santalaceae), is the lone representative of the genus *Santalum* in India [42]. A partial root parasite tree, it is valued for the scented heartwood and the aromatic essential oil in its heartwood. Having earned several epithets such as green gold, dollar earning parasite, queen of essential oil, vegetable gold, the etymology of the generic name *Santalum* is believed to come from '*Chandal'*—a Persian word derived from the Sanskrit *Chandana* meaning fragrant. *Chandal* was later adopted as *Shandal* by the Arabs and subsequently named *Santalon* by the Greeks. The specific epithet *album* means 'white' in Latin which refers to the sapwood colour [45]. Sandalwood and India have a very significant religious and cultural binding, as is evident from its extensive use both during auspicious and inauspicious occasions. Therefore, sandalwood has been given a divine status. The Nobel Laureate Rabindranath Tagore describes what a sandalwood tree is —'*The sandalwood tree as if to prove, how sweet to conquer hate, love, perfumes the axe that lays it low*'.

Tree improvement for any tree species is a continuous programme which enables researchers to identify and develop genotypes with superior traits of commercial importance. To achieve this, various steps and processes are involved running into many years depending on the objectives and the species targeted [50, 51]. An important aspect to be remembered in this entire programme is maintaining a high level of genetic diversity in the base population so that future selection processes continue and the chances of inbreeding are reduced [10]. All these factors should also support the fundamental aspect of forest and ecosystem sustainability. The programme should

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ultimately result in a proper convergence of species improvement and domestication processes so that the targeted species is not only conserved in its natural habitat but also utilized sustainably outside its habitat.

As the first step of tree improvement, an extensive countrywide survey on Indian sandalwood was conducted during 1977–78 by a team of researchers from the erstwhile Sandal Research Centre, Bangalore (presently merged with the Institute of Wood Science and Technology, Bengaluru). Most of the states in India were covered, and around 125 locations comprising nearly 5000 trees were documented. During the survey, commercial traits and health status were given priority. The health status was assessed as the presence/absence of spike disease and heartwood borer infestation. Apart from these, natural regeneration status was also documented. From each population stand density, leaf shape, size and colour, fruit, seed shape and size, flower shape and size, sapwood width, heartwood colour and oil content were recorded. Details of tree characters are provided in Table 1.

Of the 118 locations surveyed (Table 2), 78% were from Karnataka (40 locations) and Tamil Nadu (52 locations). Only 22% of these population were dense, while 42% had medium density (Fig. 1). This indicates that population density was not high even in the states proclaimed to be sandalwood-rich.

The percentage of trees having heartwood ranged from 0 to 100%. It was also observed that in ~50% of the locations heartwood was found in more than 70% of trees. Between Karnataka and Tamil Nadu, trees from nine locations from Tamil Nadu and one from Karnataka did not have heartwood. Among the nine locations in Tamil Nadu, trees without heartwood were found in 3, 4 and 2 populations having dense, medium and sparse populations.

The average percentage of trees with heartwood was 73.08, 72.73 and 64.56%, for the dense, medium and sparse populations, respectively. It is interesting to note that the minimum percentage of trees having heartwood for the dense, medium and sparse population was 28, 17 and 4% (Table 3). There were certain locations in dense (3), medium (4) and sparse (4) populations having trees without heartwood and 46% of the locations had trees with >80% heartwood content (Fig. 2).

From the survey data, it can be deduced that sandalwood is distributed in 9044 km^2 in different parts of India. The different states and the areas accordingly are estimated as follows—Karnataka (5245 km^2); Tamil Nadu (3040 km^2); Andhra Pradesh (175 km^2); Kerala (63 km^2); Madhya Pradesh (33 km^2); Orissa (25 km^2); Maharashtra (08 km^2); Uttar Pradesh (01 km^2); Uttar Pradesh (01 km^2); Rajasthan (8962 ha); Himachal Pradesh (30–35 ha) [49]. Considering pockets of population in different states such as Bihar, Gujarat, West Bengal, Tripura, Manipur, Pondicherry, Goa and Andaman and Nicobar Islands, it is estimated to be in a cumulative area of 5 km^2 and including the private lands across the country accounts for 500 km^2. The survey also provided evidence that sandalwood can be distributed from sea level to 1800 m above sea level. The predominant soil types in which the sandalwood population occurred varied from red loamy to red laterite sometimes extending up to black soil.

Table 1 Details about tree characters along with different criteria used during the first sandalwood survey carried out in India in case of sandalwood trees [49]

Sl No	Tree Characters	Criteria for different characters
1	Density	Dense— > 200 trees/ha Medium—between 50 to 200 trees/ha Sparse— < 50 trees/ha
2	Leaf	Shape—ovate, elliptic, linear, lanceolate, big, small and normal Normal—standard leaf size—length 6.00 to 8.00 cm Small— < L/B: 6.00 to 8.00/2.00 to 3.00 cm Big— > L/B: 6.00 to 8.00/2.00 to 3.00 cm Leaf colour—green, yellow-green, light green, copper green and dark green
3	Flower	Shape—companulate, cylindrical and obconical Medium—normal flower L/B: 5.00/3.00 cm Small— < L/B: 5.00/3.00 cm Big— > L/B: 5.00/3.00 cm
4	Fruit	Globose, fusiform, with elongated base Medium—medium normal fruit L/B: 1.00/0.80 cm Small— < L/B: 1.00/0.80 cm Large— > L/B: 1.00/0.80 cm
5	Seed	Round, oval Medium—seed diameter 6.00 to 7.00 mm Small—seed diameter < 6.00 to 7.00 mm Large—seed diameter > 6.00 to 7.00 mm
6	Sapwood width	Very narrow (below 1.00 cm) Narrow (between 1.10 and 2.00 cm) Broad (between 2.10 and 4.00 cm) Very broad (above 4.10 cm) All sap
7	Heartwood colour	Yellow, yellow–brown, light brown, brown, dark brown, pink
8	Oil content	Very rich—6.10 to 7.00% Rich—4.50 to 6.00% Moderately rich—2.00 to 4.40% Poor—below 2.00%

2 Variability for Morphometric Traits

Variation has been documented for flower, leaf, seed, bark, heartwood and oil. An attempt was also made by Srimathi et al. [43] to identify distinct phenotypes available in the natural populations. Based on their survey, three distinct phenotypes were identified, namely Thindlu, Chickballapur and Robust types.

Thindlu phenotype: This phenotype was first recorded in Thindlu Reserve, located in Hoskote Range, Bangalore Forest Division. A similar phenotype was also observed in Kolar (Vakkaleri Reserve) and Hassan Division (Ammanakatte Forest) in Karnataka and in Valliyur Reserve Forest of Kalakkad Wild Life Division in Tamil Nadu. A typical slow growing, 4 to 8 cm diameter (8 cm diameter tree having 25

Table 2 Sandalwood population density across different states estimated during the survey [49]

Sl. No	Name of the state	Number of locations	Density status
1	Tamil Nadu	50	Dense (10), Medium (25), Sparse (15)
2	Karnataka	42	Dense (11); Medium (14); Sparse (17)
3	Kerala	6	Dense (1), Medium (1), Sparse (4)
4	Andhra Pradesh	5	Dense (1), Medium (4)
5	Maharashtra	4	Dense (1), Medium (1) Sparse (2)
6	Rajasthan	3	Sparse (3)
7	Madhya Pradesh	3	Dense (1), Sparse (2)
8	Orissa	3	Dense (2), Sparse (1)
9	Uttar Pradesh	1	Sparse
10	Punjab	1	Sparse

Dense— >200 trees/ha; Medium—Between 50 to 200 trees/ha; Sparse— <50 trees/ha

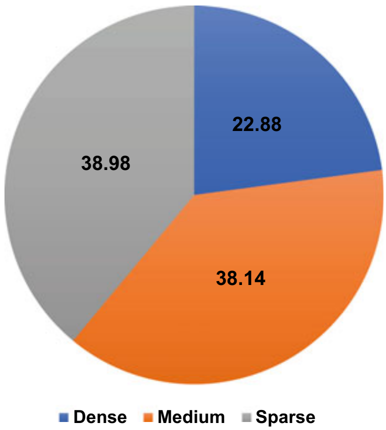

Fig. 1 Pie chart showing the dense, medium and sparse populations of Sandalwood as reported in the first all India sandalwood survey carried out during 1977–78 [49]

Table 3 Basic statistics for the percentage of trees having heartwood in the dense, medium and sparse populations

Population	n	Population with 100% heartwood	Mean	SD	CV(%)	Minimum	Maximum
Dense	27	5	73.08	22.35	30.57	28	100
Medium	45	10	72.73	22.70	31.21	17	100
Sparse	46	8	64.56	27.25	42.21	4	100

to 30 annual rings) trees with dark brown heartwood and narrow sapwood of 2 to 10 mm thickness.

Chickballapur phenotype: The uniqueness of this tree type is that the leaves are small which resembles a spiked tree; however, the leaf colour is bluish-green. Unlike

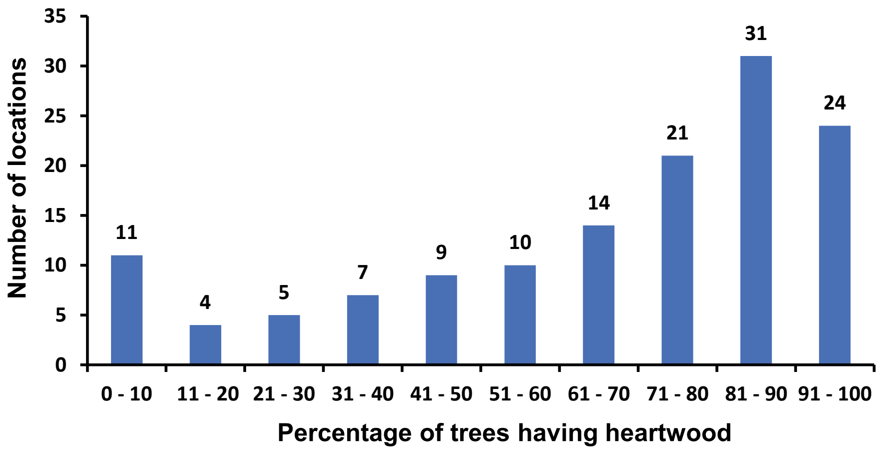

Fig. 2 Number of locations having trees with varied heartwood content percentage in the first all India survey [49]

Thindlu biotype, the sapwood is thicker. These trees were observed in the Shimoga and Kolar Divisions of Karnataka.

Robust phenotype: As the name suggests, it is fast-growing, with a straight and cylindrical bole and a typical rust-brown coloured smooth bark. The crown is compact with lush green coloured leaves and the sapwood is thick. It was predominantly observed in Srinivaspura Forests of the Kolar Division of Karnataka.

Flowering: Flowering starts as early as between two and four years [1, 23, 44], and during flowering, all stages from buds to fruits are seen. Considerable variation has been observed in the flowering pattern of sandalwood, and three distinct patterns have been identified–those that flower once a year, twice a year and throughout the year. Considering the data from the all India Sandalwood Survey, 48.30% of the population flowered twice a year while only 4% of the population flowered exclusively once a year. It was reported that sandalwood trees flowering once in a year produces flower during September–December, while it is once in March–May and the other in September–December in those tree flowering twice a year. Accordingly, 60% of the trees flower twice a year, 36% flowers once a year and only 4% of trees produce flowers throughout the year [1].

Bark: Preliminary assessment of the bark indicated that the colour varies from reddish-brown or dark brown. The brown bark which was also indicated as rust brown is associated with fast growth [21]. However, distinct morphological appearance considering bark as a trait has not been categorized yet.

Leaves: *S.album* has considerable variation, especially for leaf traits. Initially, some of the variations depicted were probably due to the spike disease which at various stages of infection can result in different leaf sizes [5]. An extensive study on biometric analysis of leaf shape and size. Data were arrived at after collecting leaf samples from 14 different locations situated in Karnataka, Tamil Nadu, Andhra

Fig. 3 Variation in leaf shape and size in sandalwood

Pradesh and Kerala. They designated four leaf types, ovate, lanceolate, elliptic, linear and big and small leaf type. A standard leaf varies from 4 to 9 cm in length and 1.8 to 3.7 cm in breadth. Leaves having lesser/higher length and breadth than the standard leaf was considered as small/big leaf, and these leaves were either ovate or elliptic. Based on length: breadth ratio, the leaf shape of spike and healthy leaves were differentiated. However, the authors cautioned before using these differences. The average leaf length: leaf breadth ratio for various leaf types were as follows–ovate (2.30); elliptic (1.71); lanceolate (2.55); linear (5.15); small (1.93) and big (2.12) [21]. Variation in leaf shape and size is shown in Fig. 3.

3 Tree Improvement Trials and Their Status

Extensive research on sandalwood tree improvement was carried out from 1978 to 1985–which can be considered as the 'golden period' of sandalwood research in India. Various trials such as seed stands/seed production areas, clonal banks, biotype germplasm banks, provenance trials, clonal/seedling seed orchards, progeny trials were established in different parts of sandalwood growing areas during this period which have been summarized along with its present status (Table 4).

It is evident from Table 4 that most of the trials established did not provide conclusive results and most of the trials ceased to exist. Clonal germplasm bank established at Gottipura, Hoskote, (Karnataka) was assessed for its seed, germination, heartwood and oil traits. The details are provided elsewhere in this book. Seeds from

Table 4 Various tree improvement field trials of sandalwood established during 1980–1984

Activity	Location	Year	Area (ha.)	Present status
Seed Stands	Marayoor (Kerala)	1980	3.00	Seed collection is regularly carried out
	Chitteris (Tamil Nadu)	1980	5.00	No information
Provenance trials	Nallal at Hoskote (Karnataka)	1981	3.14	No information regarding any data that has been collected and the trial does not exist
	Kuderu at Anantapur (Andhra Pradesh)	1982	0.24	Preliminary observations on growth were recorded for three years and the trial does not exist
Clonal germplasm banks	Gottipura at Hoskote (Karnataka)	1980–82	1.00	This germplasm bank was assessed for variability in seed, heartwood and oil content. However, the number of accessions in the germplasm bank has reduced from 60 to 35 accessions including a reduction in the number of ramets per clone
	Karvatnagar at Chittoor (Andhra Pradesh)	1983	0.10	Information regarding any data being collected is not there. The trial does not exist
	Kurumbapatty at Salem (Tamil Nadu)	1983	0.50	Germplasm bank exists
Biotype germplasm bank	Gottipura at Hoskote (Karnataka)	1982	0.75	No data were collected from this germplasm bank and the trial does not exist
Clonal seed orchards	Nallal at Hoskote (Karnataka)	1982	1.35	Assessed for seed variability. The trial does not exist
	Akkarampalli at Tirupati (Andhra Pradesh)	1983	1.00	The trial does not exist
	Jarakabande at Bangalore (Karnataka)	1984	1.50	The trial does not exist
Half sib progeny trials	Nallal at Hoskote (Karnataka)	1980 1981 1983	0.20 0.65 1.20	The trial does not exist

the clonal seed orchard established at Nallal, Hoskote (Karnataka), were collected until 2002, and the seedlings obtained were also distributed. The clonal germplasm bank and seed orchard served as a source material for establishing seedling seed orchard and clonal seed orchard during the World Bank Project. The provenance trial established at Kuderu consisted of seeds collected from 10 different provenances, and a preliminary assessment was carried out by the end of three years. The results revealed that there was no significant difference between the provenances for survival percentage and height growth [23].

Srimathi and Kulkarni [42] carried out a progeny trial of selected trees to assess variation in seedlings. From 16 sources mostly from southern and central India, seeds were collected from 60 individual trees and seedlings were raised. As depicted in Fig. 3, the average maximum and minimum germination percentage of seed sources varied from 33.20 (Madras) to 84.09% (Jamnamarthur). The authors also reported segregation, variegation, albinism and pleiocotyly in seedlings. Twin and triplet seedlings were recorded, and twin seedlings were found in 50 per cent of the seeds (0.6 to 4.6 per tree). Twin seedlings were also reported by [6, 16]. Variability was evaluated among the clones in the clonal seed orchard for two consecutive years for seed morphometric and germination traits. A significant variation was observed among the clones for the seed and germination traits [2].

Status of various tree improvement activities and trials established from 1995 onwards by Institute of Wood Science and Technology

During 1994 to 2001, sandalwood research again gained impetus in one of the research components 'Research on Sandal' by the World Bank Aided Forestry Research Education and Extension Project (FREEP).

Under this project, an extensive survey of sandalwood population was carried out during 1995–97. The survey was carried out especially in some of those Forest

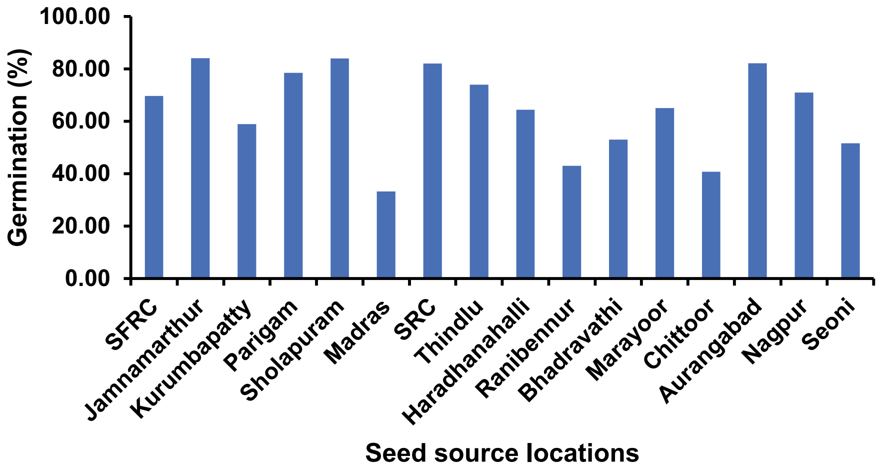

Fig. 4 Variability for germination percentage in seed sources collected from different locations [42]

Divisions known for sandalwood populations. In Karnataka, Forest Divisions of Shimoga and Chickmagalur had dense and Sagar and Mysore had a sparse population. In Tamil Nadu, two Forest Divisions, Harur and Tirupattur, had dense population, and Munnar division in Kerala had a dense population. Paderu Forest Division in Andhra Pradesh had a sparse population, while Rayagada and Seoni Forest Divisions representing Orissa and Madhya Pradesh had medium dense populations. The general observation was that in most of the areas mentioned in the first sandalwood survey the population density had drastically reduced across all the states. The reduction in population was more extensive in Karnataka and Tamil Nadu.

Based on the survey and the population density, nine potential provenances were identified. In Karnataka three potential provenances, namely Bangalore, Thangali (Chickmagalur Forest Division), Mandagadde (Shimoga Forest Division); from Tamil Nadu two potential provenances, namely— Chitteri (Harur Forest Division) and Javadis (Tirupattur Forest Division); one each potential provenance from Kerala—Marayoor (Munnar Forest Division), Orissa—Koraput (Rayagada Forest Division), Madhya Pradesh—Seoni (Seoni Forest Division) and Andhra Pradesh—Horsely Hills. [17, 18]. The first author was a part of the team that carried out this survey. Subsequently, during 2004–2006, the author conducted an extensive survey in most of the sandalwood bearing areas in Karnataka, Tamil Nadu and Kerala. Except for Marayoor in Kerala, which has a considerable population even now, in most areas, the sandalwood population had dwindled and economically viable trees; *i.e.,* trees above 30 cm girth were more or less absent. Interestingly, the first sandalwood survey carried out extensively during 1978–80 remains to be the only comprehensive survey to date in India.

Under this project, provenance trials, seedling seed orchard, clonal seed orchard of sandalwood were also established. The status of those are provided in Table 5.

4 Progress of Research on Heartwood and Oil Variability

Information about variation in heartwood can be traced to Hutchins [14] who mentioned that the scent in the wood varied due to soil conditions and the tree attains maturity by 27 to 30 years. Lushington [25], based on his studies conducted on 12 trees in Srivilliputtur forests and two billets obtained at North Coimbatore suggested that the quality of heartwood and oil is dependent on elevation and exposure and is not based on the soil. Lushington [26] further segregated the trees based on girth and the availability of scented wood (heartwood) from the stem and roots in different coupes at varied elevations such as Mavihalla (1220 m; n = 192), Kotadai (1220 m; n = 150), Talakarai (915 m feet; n = 1445), Karlia (700 m; n = 823) and Kodampalli (700 m feet; n = 128). Scented wood was available in very few trees having a girth less than 30.48 cm. Even though Mavihalla and Kotadai were at the same elevation, the quantity of scentwood obtained was different. Similar variation in outturn was also recorded in Karlia and Kodampalli which were of the same elevation but 20 miles away. He opined that '*there is an immense variation of Sandal even when*

Table 5 Tree improvement trials established by the Institute of Wood Science and Technology, Bengaluru

Activity	Location	Year	Clones/families	Area (ha.)	Present status
Seedling seed orchard	Siddalagandi farm (Bhakrapet Range, Andhra Pradesh)	1998	25	4.0	The trial does not exist
	Kuchuvarapalli VSS (Bhakrapet Range, Andhra Pradesh)	1998	25	1.0	The trial does not exist
Clonal seed orchard	S. V. University, Tirupathi	1998	25	4.0	No data on seed collection
Seedling seed orchard/progeny trial	Gottipura (Hoskote Range), Karnataka	2004	20	1.0	No data have been recorded. A small quantity of seed is being collected
Germplasm bank (Seedling origin)	Gottipura (Hoskote Range), Karnataka	2007	20	1.0	No data have been recorded

grown under similar conditions'. Rao [32] consolidated heartwood yield from the fellings carried out during 1902–1904 at different elevations (~2000 to 3200 feet) on the Salem Javadis. There was considerable variation within and between girth classes for heartwood content in trees with girth above 91 cm girth. Rao also suggested that factors like tree density, associated host species, growing conditions can impact the heartwood formation. Based on small sample of sandalwood collected from Madras ($n = 15$), Singh [38] concluded that trees growing in poor rocky/gravelly soils had higher oil content (3.75 to 5.02%) than trees growing in fertile soils (3.26 to 4.24%) based on a small sample of sandalwood collected from Madras. Singh [39] later conducted a similar study on the roots and stems obtained from 44 trees. The oil percentage from the Madras samples varied from 3 to 6 per cent irrespective of the plant part. However, it was categorically mentioned earlier that locality, elevation or age had relationship with heartwood and the essential oil in it. The author was of the firm opinion that soil is the only factor responsible for high heartwood and oil content in sandalwood. Troup [47] and Fischer [13] opined that there is a need for detailed study in the case of heartwood and oil formation. Sreenivasaya and Rangaswami [40] reported that conditions not favouring profuse vegetative growth would enhance heartwood formation. They also documented variation in heartwood content in trees recorded from different localities (Fig. 5). In the 5th Silviculture Conference, 1941, held at Dehra Dun, three important papers on sandalwood exclusively about heartwood and oil were presented. Mitchell [29] reported that trees with similar girth growing in deciduous forests had higher heartwood content compared to that of trees growing in evergreen forests. Laurie [24] mentioned that there was

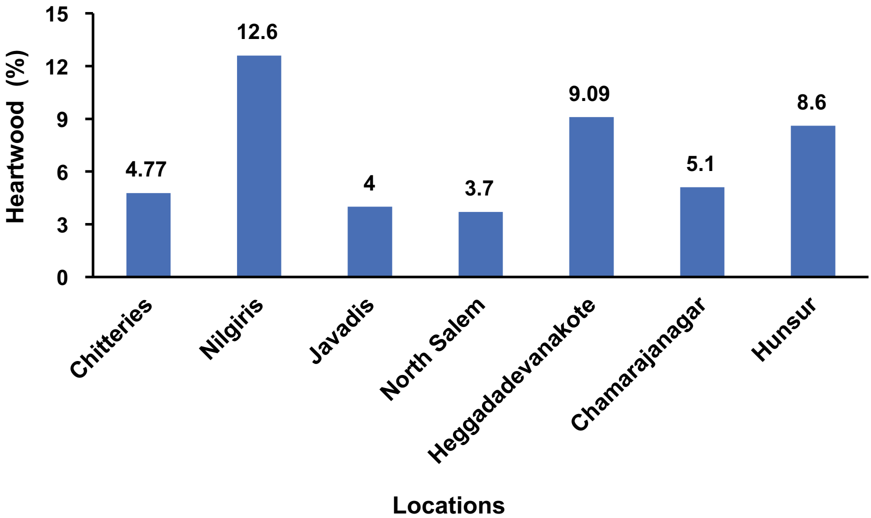

Fig. 5 Heartwood percentage in trees grown in different sandalwood locations [40]

a high degree of variation in heartwood quantity for a given sized tree. Venkata Rao [32] was of the view that heartwood formation occurs when the tree is 15 to 20 years old. All of them urged that scientific evaluation is to be further carried out to understand the heartwood and oil variation. In his article, Rao [31] addresses the issues of forest plant breeding categorically mentioning that heartwood formation in sandalwood trees needs to be critically addressed.

Bhatnagar [6] opined that even though a sandalwood tree reaches physiological maturity, the heartwood may not have been formed and the tree reaches full maturity at the age of 50–80 years. Even in the first and second All India Sandal Seminar held in 1977 and 1981, respectively, information related to heartwood and oil remained unexplored. Kaikini [20] and Shanmuganathan [37] had a similar opinion and stressed that growth rate and yield have to be intensified. An empirical table depicting girth and heartwood yield based on personal observations was published by Venkatesan [48] which mentioned that a tree of 15 cm girth would yield 2.4 kg of heartwood while it would be 127 kg from trees with girth class 75–90 cm. The average yield mentioned included stem and root wood. Another study was carried out in Belgaum, Karnataka, by Rai and Sarma [30] with the trees DBH ranging from 6.8 cm to 23.6 cm. Trees with DBH class of 6.8–9.2 cm yielded 1.814 kg of heartwood while DBH class of 21.2–23.6 yielded 54.431 kg. Considering various factors playing a role in heartwood formation and its variation, a study was carried out by Srimathi and Kulkarni [41] to assess the variation in the 50 trees growing in a similar area (Sandal Research Centre) falling between the girth class of 10.65–11.7 cm (Fig. 6). It was found that in three trees heartwood had not formed. The radial heartwood proportion deduced from the original data indicated that it varied from 0.91 to 86.21%. There was no correlation between girth and radial heartwood proportion ($r = 0.13$).). Considering

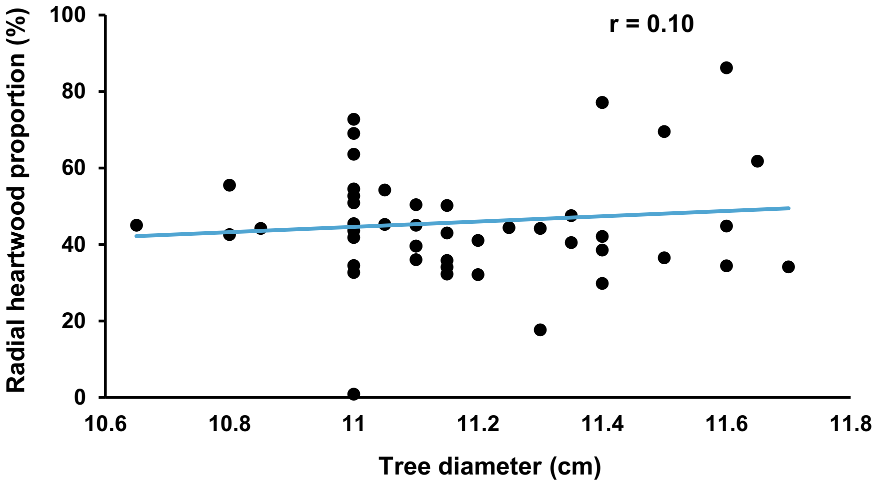

Fig. 6 Relationship between tree diameter (10.65 to 11.7 cm) and radial heartwood proportion in trees grown at Sandal Research Centre (modified from [41])

the heartwood colour, 64% of the trees had brown or yellowish-brown heartwood. The authors concluded that heartwood formation can occur in some trees at an early age of five to six years and can extend as late as 15 years in some others. The study proved that emphasis on the tree age is also important and can play a significant role in heartwood formation.

Various working plans, unpublished information were reviewed to collate information pertaining to variation for heartwood (%) and tree diameter in different locations in 10 trees. One of the criteria used was that the average tree diameter was between 10 to 20 cm. Heartwood had not yet developed in two trees out of ten trees from Kurumbapatti having an average diameter of 20.08 cm, and in all the ten trees from Seoni with an average diameter of 10.17 cm. The heartwood percentage varied from 24.69% (average diameter of 20.08) in Kurumbapatti to 49.94% (average diameter of 11.80 cm) in Kollapur (Table 6).

Variability for oil content (%) and its constituent α and β Santalol (%) was estimated by Jayappa et al. [19], and root samples had the highest content. They collected root wood samples and two categories of heartwood (*Jaj* and *Milwa*) from various locations of Karnataka and Tamil Nadu. The minimum and maximum oil content for the root samples, *Jaj* and *Milwa,* were from Mysore (6.56%), Satyamangalam (4.22%) and Tarikere (2.42%), respectively. The maximum oil content was from the samples collected from Hassan—8.43% for roots, 5.79 and 3.52% for *Jaj* and *Milwa*, respectively. Interestingly, α and β Santalol (%) was minimum in the root samples from Hassan–88.07; 89.09% from *Jaj* and 88.62% from *Milwa.* Maximum α and β Santalol for root sample was from Dharwad (95.16%), Tarikere for the *Jaj* sample (94.98%), and the *Milwa* samples from Mysore (94.12%). Shankaranarayana and Parthasarathi (1984) reported that oil percentage ranged from 0.7 to 2.5%, while

Table 6 Consolidated information from different sources showing variability in the heartwood at different locations

Location	Average diameter (cm)	Trees without HW	Average HW depth (cm)	HW (%)
Seoni	10.17	0	2.21	44.27
Dindigul	10.77	5	1.48	26.49
Coimbatore	11.33	3	1.85	32.01
Puttur	11.67	2	2	34.7
Kollapur	11.8	2	2.92	49.94
Courtallum	12.59	2	2.24	35.57
Wynad	12.89	4	2.8	36.12
Chamarajnagar	13.21	2	2.58	36.44
Hyderabad	13.87	3	3.26	47.24
Kuchnahalli	14.62	0	2.69	37.43
Guindy Park	14.97	2	3.02	39.92
Janiguda	14.98	0	3.53	47.65
Kurumbapatti	20.08	2	2.55	24.69
Kushalnagar	20.76	0	3.97	42.42

HW: Heartwood

santalol varied from 76 to 80% in 10-year-old trees. In trees aged 20 years and above, the oil value ranged from 2.5 to 6.3 per cent, while the santalol varied from 88 to 92 per cent. Light brown heartwood had 2.5–6.2% oil per cent with 90% santalol. Yellow heartwood had 2.0–3.5% oil and 90% santalol. Dark brown and brown heartwood had 2.5% oil and ~85% santalol [35].

From most of the studies mentioned earlier, it is evident that age was never a common factor. It is difficult to estimate age in sandalwood, and the error involved while estimating the age is very large [11]. A study carried out by Arunkumar [3] assessed 111 trees in a 20-year-old clonal germplasm bank established at Gottipura, Hoskote (Karnataka). In 14% of trees, heartwood had not formed. Heartwood proportion varied from 29.34 to 65.77%. Similarly, oil yield varied from 0.62 to 2.29%. To elucidate the inherent variability in a better way, trees with 11 cm diameter were segregated and variation for heartwood proportion and oil content is depicted in Table 7. The study revealed a significant positive relationship between girth and heartwood proportion. It clearly demonstrated that genetics plays a significant role in heartwood formation and experiments under controlled conditions are needed for a better understanding of the variation for heartwood and oil in sandalwood. Similar observations have also been recorded in Australia by Brand et al. [5], McComb [27] and Brand [9]. Recently, few other studies have reported variability for heartwood and oil content in India [7, 28, 34].

Extensive studies have been carried out on sandalwood in India for more than 150 years. Though predominant work has been on spike disease, sufficient studies

Table 7 Variability for heartwood proportion (%) and oil yield (%) in 20-year-old trees having ~11 cm diameter [3]

Tree diameter (cm)	Heartwood proportion (%)	Oil yield (%)
11.03	42.52	1.81
11.09	42.11	2.29
11.14	65.77	1.19
11.19	59.78	2.04
11.41	41.63	1.85
11.57	36.56	2.09
11.62	29.34	0.62
11.67	43.44	1.86
11.67	46.78	1.16
11.99	30.10	0.88

report that sandalwood has substantial morphological and genetic diversity. Considerable variability has been documented for morphological traits, however, studies on variability for heartwood and oil are still not conclusive. It is essential to understand the role of genetics and the environment on heartwood and oil formation. Now that sandalwood is cultivated in large areas in India, it is hoped that there would be a better understanding of many of the grey areas. Sandalwood has already been categorized as 'Vulnerable' by the International Union for Conservation of Nature [4]. To reinitiate tree improvement studies, another extensive all India Survey of Sandalwood has to be carried out. The status of its presence/absence across the country needs to be updated. Unlike other tree species, further tree improvement studies on sandalwood will not necessarily be initiated from its natural habitats as the population has dwindled. As numerous plantations are being raised in different parts of India, these plantations would be the future base population for developing tree improvement programmes on Indian sandalwood.

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Chapter 21
Heartwood and Oil Content Variation in Sandalwood Accessions from Diverse Origins

A. N. Arunkumar, Geeta Joshi, Y. B. Srinivasa, and A. Seetharam

1 Introduction

Cultivation of Indian sandalwood (*Santalum album*) extensively in different states of India is increasing. Two reasons attributed to this trend are—reduced availability of trees in natural habitat and increased value in the global market for heartwood and essential oil. The two states in India, Karnataka and Tamil Nadu which had the most extensive natural population of sandalwood, had also designated this tree as government property. Apart from various issues associated with this rule, one of the major drawbacks was the non-availability of basic data related to growth and heartwood. Several researchers conducted studies on heartwood and oil variation (detailed in the Chapter 20 of this book). In most cases, the impact of age and associated management practices could not be delineated as they can have serious implications on the results. Understanding the extent of variation related to growth data across various ages and locations becomes essential for successfully strategizing cultivation practices.

Heartwood is found in the trunk's innermost part and is considered deadwood as it lacks living cells in it [3, 7]. One of the important issues concerning studying heartwood is the non-availability of easily operative devices without damaging the trees, clearly depicting its time and formation rate. Also, in case of other tree species

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wherever the age is known, there is a definite relationship between age and heartwood formation [2, 7]. Other associated factors influencing heartwood are the rate of growth, site and management practices [6]. However, factors controlling heartwood quantity and quality remain poorly understood in most tree species [10] and sandalwood is no exception.

Both traits, *i.e.* heartwood and oil, are highly variable in sandalwood, and to understand the extent of variation, accessions from the diverse origin assembled in one location were assessed. The age of these accessions was 20 years—considered apt for harvesting the tree. The information thus obtained provides a baseline for selecting superior genotypes, help in better plantation management, and ultimately forecasting the yield for heartwood and oil.

2 Details of Study Material and Methodologies Adopted

Under an *ex situ* conservation programme, a clonal (cleft grafted) germplasm bank of sandalwood was established with ramets of various clones/plus trees identified by the Sandal Research Centre [presently, Institute of Wood Science and Technology (IWST)], Bangalore, during 1981–1982 at Gottipura Field Research Station, Hoskote (13º6'N; 77º48'E). The clonal trial does not exist today, due to various anthropogenic interferences. This germplasm bank consisted of 51 accessions selected from the natural habitat of sandalwood, *i.e.* four southern states of India—Karnataka, Tamil Nadu, Andhra Pradesh and Kerala. These mother trees were selected based on girth, heartwood and oil content. Each accession was represented by 25 ramets planted in blocks of 5×5 at a spacing of 3×3 m. *Pongamia pinnata* served as the host. The germplasm bank was irrigated for the first two years, with regular weeding and protection from grazing and fire. Thirty-seven accessions (Table 1) were measured for basal girth (cm) one inch above the grafted union. Two core samples from each ramet were drawn using Pressler's increment borer, just above the graft union at right angles to each other to obtain the correct dimension of heartwood radius, sapwood thickness and bark thickness. The core samples were wrapped in blotting paper and kept in a desiccator (to avoid absorption of moisture) for further experimentation. Sapwood and bark thickness was measured using a scale. By converting the tree girth into radius using the formula $2\pi r$ (where $\pi = 3.1415$ and $r =$ radial length), heartwood radius (cm) was calculated.

Sandalwood oil was estimated through solvent extraction [9]. To estimate the extractive content, the finely chopped heartwood portion was divided into three replicates of 100 mg each and was extracted thrice with 10 ml of benzene: alcohol (2:1 v/v) mixture. The mixture was boiled in a water bath at 80 °C for 15 min. The solution was cooled, filtered and evaporated to dryness. The residue was vacuum dried and weighed.

$$\text{Extractive}(\%) = (\text{Final weight after extraction}/\text{Initial weight before extraction}) \times 100$$

Table 1 List of plus trees used in the study and their origin

Sl. no.	Accession code	Origin
1	AP4	Nehru Zoological Park, Hyderabad, Andhra Pradesh
2	K2	Thindlu, Hoskote, Bangalore, Karnataka
3	K4	PWD guest house, Vani Vilasa Sagara, Chitradurga, Karnataka
4	K5	IWST, Bangalore, Karnataka
5	K6	IWST, Bangalore, Karnataka
6	K7	IWST, Bangalore, Karnataka
7	K8	IWST, Bangalore, Karnataka
8	K9	IWST, Bangalore, Karnataka
9	K10	IWST, Bangalore, Karnataka
10	K11	Haradanahalli, Chamarajanagar, Karnataka
11	K13	Haradanahalli, Chamarajanagar, Karnataka
12	K14	Rayalpad (SF, Srinivaspur), Kolar, Karnataka
13	K16	Haradanahalli, Chamarajanagar, Karnataka
14	K23	Honehatti MF, Bhadravathi, Karnataka
15	T1	Sholavaram Research Garden, RR Pudukkottai, Thanjavur, Tamil Nadu
16	T2	Forest College, Coimbatore, Tamil Nadu
17	T3	Forest Guest House, Anchetty, Hosur, Tamil Nadu
18	T4	Komateri, Polur, Vellore, Tamil Nadu
19	T5	Inner Javadhis RF, Alangayam, Tirupattur, Tamil Nadu
20	T6	Veerapannur RF, Polur, Vellore (1968 plantation), Tamil Nadu
21	T7	Veerapannur RF, Polur, Vellore (1970 plantation), Tamil Nadu
22	T8	Pavanamials Farm, Patta land, Shirkali, Thanjavur, Tamil Nadu
23	T9	FRC, Kurumbapatty, Shevaroys, South Salem, Tamil Nadu
24	T11	FRC, Kurumbapatty, Shevaroys, South Salem, Tamil Nadu
25	T12	FRC, Kurumbapatty, Shevaroys, South Salem, Tamil Nadu
26	T13	FRC, Kurumbapatty, Shevaroys, South Salem, Tamil Nadu
27	T14	FRC, Kurumbapatty, Shevaroys, South Salem, Tamil Nadu
28	T19	Mundanthurai, Tirunelveli (1966 plantation), Tamil Nadu
29	T20	Mundanthurai, Tirunelveli (1966 plantation), Tamil Nadu
30	T21	Mundanthurai, Tirunelveli (1966 plantation), Tamil Nadu
31	T22	Nachikotai, Harur, Chitteri, Dharmapuri, Tamil Nadu
32	T23	Perieri Village, Pudur East, Chitteri, Harur, Dharmapuri, Tamil Nadu
33	T24	Thombakal, RF, Shanimadu, Harur, Chitteri, Dharmapuri, Tamil Nadu
34	T27	Parigam, Dharmapuri (1974 plantation), Tamil Nadu

(continued)

Table 1 (continued)

Sl. no.	Accession code	Origin
35	T28	Jirgehalli, Hanur, Tamil Nadu
36	T29	Cattle Farm, Padak—3 Hosur, Tamil Nadu
37	T30	Cattle Farm, Padak—3 Hosur, Tamil Nadu

Analysis of variance (ANOVA) was carried out on the data to assess the variation, and the means of various accessions were compared using the critical difference value at 5% level of significance.

3 Analysis of Observations

The basal girth ranged from 27.67 to 47.17 cm, with the mean girth of 36.23 cm. The coefficient of variability was 14.55% (Table 2). Highly significant differences were observed for basal girth among various accessions. The highest and lowest basal girth was recorded in and T6 accessions, respectively (Table 3). The heartwood radius ranged from 0.00 to 3.77 cm, with an overall mean of 2.10 cm and with CV of 47.91% (Table 2). In five accessions, K4, K6, T9, T14 and T27, heartwood had not yet formed. Among the accessions that produced heartwood, general mean was 2.43 cm. The highest radius was in T28 (Table 3). The oil content ranged from 0.00 to 2.42%, with a general average of 1.44%. The CV was 49.89% (Table 3). Oil content was absent in five accessions listed earlier where heartwood formation was not observed. Among the accessions that had oil, the general mean was 1.66%. The highest oil content of 2.42% was recorded in T2 (Table 2). The extractive content ranged from 0.00 to 7.31% with a general mean of 5.20% (Table 3). The clones in which oil was absent did not have extractives too. The general mean of accessions with extractive

Table 2 Summary of statistics on basal girth (cm), heartwood radius (cm), oil content (%) and extractive content (%) across various accessions

	Basal girth (cm)	Heartwood radius (cm)	Oil content (%)	Extractive content (%)
Mean	36.23	2.10	1.44	5.20
Median	35.83	2.33	1.58	5.85
Range	27.67–47.17	0.00–3.77	0.00–2.42	0.00–7.31
Variance	2.30	1.00	0.85	1.50
Standard deviation	5.27	1.01	0.72	2.25
CV (%)	14.55	47.91	49.89	43.21
Kurtosis	−0.81	0.49	−0.11	1.61
Skewness	0.33	−0.93	−0.88	−1.64

Table 3 Mean values for basal girth, heartwood radius, and oil and extractive content across various accessions

Accessions	Basal girth (cm)	Heartwood radius (cm)	Oil content (%)	Extractive content (%)
AP4	34.67	2.35	1.81	6.93
K2	34.00	1.70	1.85	6.68
K5	**47.17**	2.87	1.46	5.85
K7	31.00	2.18	1.85	6.71
K8	32.67	2.46	1.93	6.86
K9	39.67	2.44	2.08	7.10
K10	32.83	1.82	1.58	6.48
K11	34.83	2.33	2.29	6.43
K13	40.83	2.67	1.23	5.38
K14	38.00	2.61	1.25	5.40
K16	36.33	2.10	2.09	5.70
K23	43.67	3.14	1.36	5.02
T1	36.50	1.71	0.62	3.76
T2	31.17	2.07	**2.42**	7.27
T3	36.67	2.53	1.86	5.95
T4	30.50	1.63	1.26	5.45
T5	37.67	1.81	0.88	4.50
T6	**27.67**	1.54	2.30	**7.31**
T7	32.27	2.10	1.19	5.45
T8	35.17	3.34	2.04	6.82
T11	40.00	2.40	2.07	6.73
T12	32.67	2.25	1.57	6.09
T13	36.67	2.73	1.16	5.23
T19	44.67	3.27	2.05	6.66
T20	35.83	2.37	1.85	6.21
T21	42.50	2.39	1.58	5.39
T22	41.83	2.26	1.27	4.93
T23	42.83	3.18	1.02	4.69
T24	28.83	1.37	1.87	6.36
T28	35.00	**3.77**	1.19	5.29
T29	43.17	2.80	2.17	6.74
T30	45.83	3.49	2.11	7.22
K4	29.07	**0.00**	**0.00**	**0.00**
K6	32.17	**0.00**	**0.00**	**0.00**
T9	29.00	**0.00**	**0.00**	**0.00**

(continued)

Table 3 (continued)

Accessions	Basal girth (cm)	Heartwood radius (cm)	Oil content (%)	Extractive content (%)
T14	29.50	**0.00**	**0.00**	**0.00**
T27	37.67	**0.00**	**0.00**	**0.00**
Mean	36.23	2.43	1.66	6.02
SEm(±)	3.759	0.784	0.243	0.619
CD	7.368	1.537	0.477	1.214

$\alpha = 0.05$; values in bold are maximum and minimum values

Table 4 Pearson product-moment correlation on coefficients between basal girth, heartwood radius, and oil and extractive content in sandalwood accessions ($n = 37$)

	Basal girth	Heartwood radius	Oil content	Extractive content
Basal girth	1.00			
Heartwood radius	0.62*	1.00		
Oil content	0.21	0.67*	1.00	
Extractive content	0.26	0.78*	0.95*	1.00

* 0.01 < *p* 0.0.5, significant

content was 6.02%. Accession T6 (7.31%) recorded the highest extractive content (Table 2). Correlation studies revealed a significant positive correlation between girth and heartwood radius ($r = 0.62$) indicating that girth can be a selection trait for heartwood radius. However, there was a non-significant relationship between basal girth, oil and extractive content. Heartwood radius had a significant positive relationship between oil ($r = 0.67$) and extractive content ($r = 0.78$) (Table 4).

Heartwood formation, a kind of programmed cell death in the oldest sapwood issues, is the final step in living xylem cells' life cycle. In the transition zone between living sapwood and dead heartwood, parenchyma cells die genetically determined, and extractives are accumulated [4]. The heartwood extent, along with oil quality and quantity, decides the value of sandalwood [1]. Information on variation in both these traits is not yet properly understood. Age being an important criterion influencing heartwood, this study reveals the extent of variability for both these traits in 20-year-old accessions. The CV values for heartwood radius (47.91%), oil content (49.81%) and extractive content (43.31%) reveal considerable variation. Of the 37 accessions, heartwood had not formed in five accessions (K4, K6, T9, T14 and T27). A study carried on 14-year-old clones K7, LS and R32, grown in different Australian locations, revealed that in Geraldton, heartwood had not yet formed in the clones. Out of the 67 trees in which heartwood was assessed at base trunk diameter, in 23 trees heartwood had not formed at the height of 1.5 m suggesting the extent of variation. The heartwood percentage varied from 3.8 to 30.9 percentage. The oil content varied from 0.02 to 5.71% in those clones in which heartwood had formed. It was suggested that apart from the varied hosts provided, the management practices adopted may impact heartwood and oil content [5]. In another study in Australia on 16-year-old sandalwood trees ($n = 32$), in three trees heartwood had not yet formed and in six trees heartwood yield was ≤ 1.0 kg indicating the extent of variation for a given age [1]. The top three trees having 33.1, 29.3 and 27.4 cm stem diameter had the highest heartwood air-dry weight of 30.2, 24.3 and 25.3 kg. There was a strong positive relationship between stem diameter and heartwood ($r = 0.93$). However, it was cautioned that this should be used only in a narrow range of age (15–17 years). Considering the extent of variation for heartwood and yield, it was suggested that the rotation period could be reduced to 25 years to obtain a substantial yield. It was also suggested that a rotation age of 20 to 30 years might be ideal for the sandalwood trees grown in the Ord River Irrigation Area, Australia [8].

4 Conclusion

Though there was positive relationship between girth and heartwood, it is strongly recommended that further investigations on heartwood and oil at different locations and ages are essentially required. As both the commercial traits, heartwood and oil, are substantially influenced by genetic and environmental factors, cultivators growing sandalwood should tread a cautious path while projecting sandalwood yield.

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Chapter 22
Micropropagation in Sandalwood (*Santalum album* L)

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Abbreviations

2ip	6-Dimethylaminopurine
ABA	Abscisic acid
BA	6-Benzylaminopurine
BARC	Bhabha Atomic Research Centre
BM	Basal medium
CH	Casein hydrolysate
CM	Coconut Milk
CPA	Chlorophenoxy acetic acid
CW	Coconut water
2,4-D	2,4-Dichlorophenoxyacetic acid
ELISA	Enzyme-linked immunosorbent assay
FYM	Farm yard manure
GA_3	Gibberellic acid
HBsAg	Hepatitis B surface antigen
IAA	Indole-3-acetic acid
IBA	Indole-3-butyric acid
IISc	Indian Institute of Science
Kn	Kinetin
Mac	Macerozyme
PEG	Polyethylene glycol
MS	Murashige and Skoog
NAA	Naphthaleneacetic acid
NOA	2-Naphthoxyacetic acid
PCR	Polymerase chain reaction
PGRs	Plant growth regulators

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RT-PCR	Reverse transcription-polymerase chain reaction
TDZ	Thiazuron-N-phenyl-N-1,2,3 thiadiazol-5ylurea
WPM	Woody plant medium

1 Introduction

The natural populations of sandalwood have declined drastically, and it is not easy to locate trees more than 40 cm girth in forests, except maybe in Maryoor in Kerala [1, 24]. Regeneration is mainly by seed and root suckers. Vegetative propagation through air layering and root cuttings [34, 61], stem cutting and clefts grafting and air layering have also been reported [59, 60]. These traditional vegetative propagation methods are season dependant and require a large quantity of material, and the success rate is moderate, (<60%) limiting use in clonal forestry. Biotechnological tools provide the opportunity to mass multiply selected genotypes overcoming problems encountered in traditional methods. Details of research carried out on various aspects are reviewed in this chapter.

1.1 In vitro *Regeneration Through Axillary Shoot Proliferation*

This is the most common and widely used regeneration mode in forestry to produce clonal plants of desirable genotypes. Since forced axillary bud proliferation takes place from the existing lateral/apical meristems, therefore, chances of somaclonal variation are rare.

Rao et al. [38] reported numerous shoot buds from two-node shoot segments obtained from 30-year-old trees, cultured on MS medium + BAP (0.5 and 1.0 mgl^{-1}, each). The medium, which consisted of other cytokinins, namely Kn and zeatin (0.1, 0.5 and 1.0 mgl^{-1}, each) failed to induce shoot buds and resulted in necrosis. Sanjay et al. [48] obtained multiple shoots (10.9 ± 2.5) from 50 to 60-year-old trees from nodal shoot segments in 4–5 weeks on MS medium with BAP 5.0 mgl^{-1}. Shoot multiplication declined after four–five passages. Shoots of 3–4 cm were used for rooting on ½ MS basal medium with different concentrations and combinations of IAA, IBA and NAA. None of the treatment could induce roots. Meanwhile, Parthiban et al. [27] reported fewer multiple shoots (average 2.9 shoots/explants) from nodal shoot segments collected from selected plus tree of *S. album* on MS medium combined with 1.0 mgl^{-1} BAP + 2.0 mgl^{-1} Kn in 4 weeks period. They used MS medium with IAA and IBA at different concentrations, either alone or in combinations for root induction from the *in vitro* raised shoots, but none of the treatments favoured rooting. It was only in MS medium with IBA 2.0 mgl^{-1} that sporadic single roots were observed after 15 weeks.

For the first time, complete plantlet from nodal shoot segment of mature and high oil yielding trees was reported [49]. Multiple shoots (five shoots/explant) were obtained from the nodal shoot segments on MS medium with 0.1 mgl^{-1} NAA and 2.5 mgl^{-1} BA. *In vitro* differentiated shoots were multiplied on MS medium with additives (ascorbic acid + citric acid + cysteine + glutamine + 10% CM). Microshoots pulse treated for 48 h with 20 mgl^{-1} IBA followed by transfer on ¼ MS hormone-free medium favoured 41.67% rooting. A 50% rooting was observed from the shoots treated with 200 mgl^{-1} IBA for 30 min, followed by transfer to sterile soil rite medium in 400 ml culture bottles.

Detailed studies on *in vitro* cloning [15] revealed that nutrient media and genotypes had shown a significant effect on multiple shoot induction and growth. Nodal shoot segment was better than apical shoot for multiple shoot induction from plus trees and clones. Among the five genotypes/clones used, shoots induction varied from 2.13 to 4.11 shoots per explant on MS medium with 0.1 mgl^{-1} IAA + BAP 1.0 mgl^{-1} + additives in 4 weeks period. Similarly, nutrient media, PGRs, additives and genotypes significantly affect further multiplication of *in vitro* differentiated shoots. Shoot multiplication rate varied from 2.62 to 4.21-fold in five genotypes/clones on MS medium + additives + 0.1 mgl^{-1} IAA + 1.0 mgl^{-1} BAP in 4 weeks period. Among the various auxins, their concentrations and mode of treatment, polyamine concentrations, genotypes and incubation conditions tested, ¼ MS medium combined with IAA + IBA proved the best and induced 70.39% rooting in clone KL3. Hardening for 12 weeks was essential for high rate of survival in the nursery.

Rathore et al. [43] reported high frequency of multiple shoot induction from nodal shoot segments collected from the selected clones/plus trees on MS medium with additives, namely ascorbic acid 50 mgl^{-1} + citric acid 25 mgl^{-1} + cysteine 25 mgl^{-1} + NAA 0.1 mgl^{-1} + BAP 1.0–2.5 mgl^{-1} within 4 weeks period at 25 ± 2 °C temperature and 2500 lx of light intensity for 12 h photoperiod. Incorporation of TDZ in the medium did not help improve multiplication rate, but induced callus from the proliferated shoots. Further shoot multiplication rate was three–fourfold in 6 weeks period on shoot multiplication medium (MS + additives + IAA 0.1 mgl^{-1} + BAP 1.0 mgl^{-1}). *In vitro* raised shoots were multiplied for two years without loss of multiplication rate and vigour. Genotypes influenced shoot multiplication rate. *In vitro* induced shoots can be rooted under *in vitro* as well as *ex vitro* conditions. MS/4 basal medium with the combined use of IAA + IBA proved the best for rooting. An initial dark period for one week favoured early root induction. An alternative method of pulse treatment of shoots with 1000–2500 ppm IBA followed by transfer on ¼ MS basal medium also favoured rooting without callus [44], bypassing *in vitro* rooting step. *Ex vitro* rooting can be achieved by pulse treatment of 2500 ppm IBA for 30 min in soil rite medium in a greenhouse. Hardening of 8–12 weeks was found essential for good survival and growth of root and shoot (Fig. 1).

Krishakumar and Parthiban [19] reported multiple shoot induction on MS medium + 5.0 mgl^{-1} Kn + 2.0 mgl^{-1} BAP from shoot tip explants. For rooting of shoots, 3.0 mgl^{-1} IBA gave good results. Bhargava et al. [10] reported *in vitro* clonal propagation through forced axillary shoot proliferation from nodal explants of trees. Shoot initiation was observed on MS medium + 0.5 mgl^{-1} BAP + 5.0 mgl^{-1} IBA in

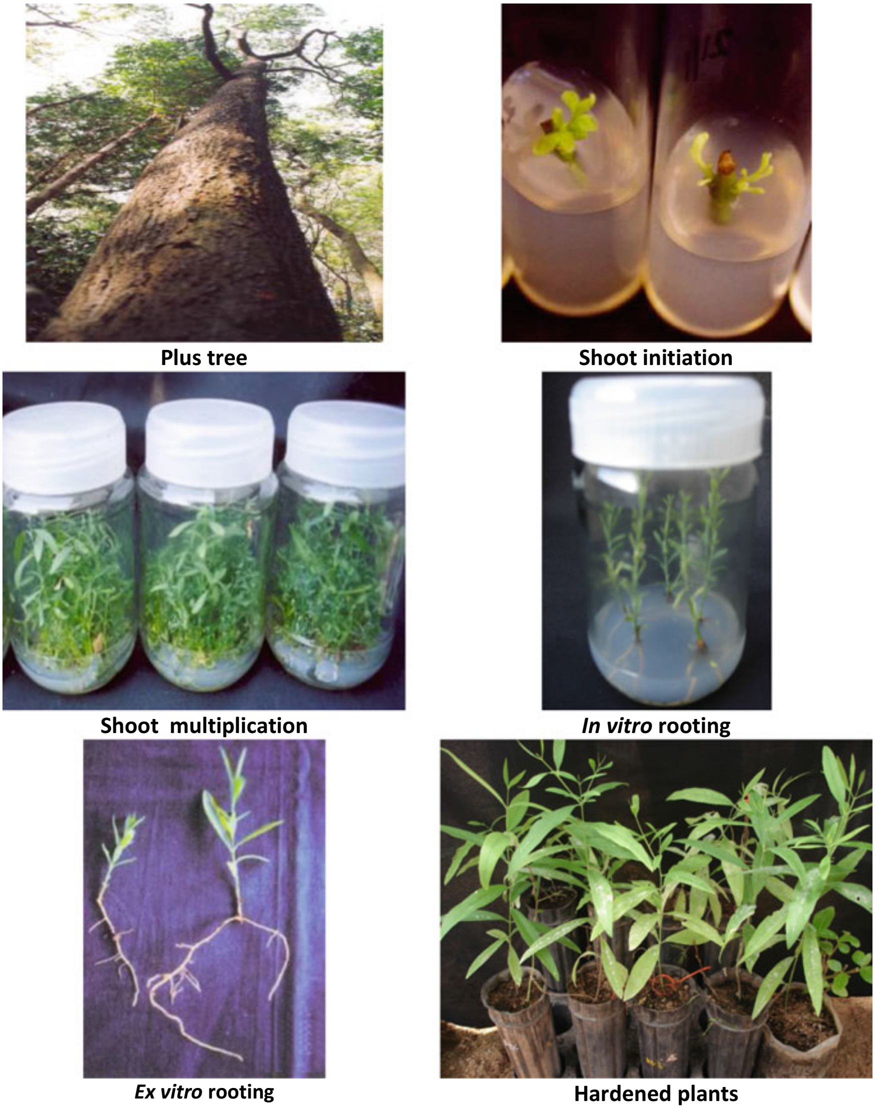

Fig. 1 Micropropagation of sandalwood

30 days period. Further shoot multiplication was carried out by subculturing on same medium up to three passages at the interval of 4 weeks. *In vitro* proliferated shoots (3–4 cm in length) treated with 50.0 mgl^{-1} IBA for 48 h produced rooting (50%) on hormone-free half-strength MS medium with initial one-week incubation in the dark and later on under light at 28 ± 1 °C temperature and 16 h photoperiod. Summary of *in vitro* propagation through axillary shoot proliferation is given in Table 1.

Table 1 *In vitro* regeneration of *S. album* through axillary shoot proliferation (chronological)

Type of explant and references	Source of explant	Shoot initiation medium	Response	Shoot multiplication medium + PGRs	Response	Rooting medium + PGRs	Response
Two-node shoot segments [38]	Mature trees (30 years old)	MS + 0.5 and 1.0 mgl^{-1} BAP	Numerous shoot buds after 3 weeks	–	–	Used various combinations of hormones and media	No root induction
Nodal shoot segments [48]	Mature trees (50–60 years)	MS + 5.0 mgl^{-1} BAP	Multiple shoots (10.9 ± 2.5) in 5 weeks	MS + BAP	Shoot multiplication declined after fourth–fifth passage	MS/4 medium with auxins (IAA, IBA and NAA alone or in combinations	No root induction
Nodal shoot segments [27]	Selected plus trees	MS + 1.0 mgl^{-1} BAP + 2.0 mgl^{-1} Kn	Multiple shoots (2.9 shoots/explants)	–	–	MS + IAA + IBA (different concentrations and combinations)	No root induction
Nodal shoot segments [49]	Mature trees (50–60 years)	MS + 0.1 mgl^{-1} NAA + 2.5 mgl^{-1} BA	Multiple shoots (5 shoots/explant) in 4–5 weeks)	MS + additives + 0.1 mgl^{-1} NAA + 2.5 mgl^{-1} BA	Multiple shoots(threefold)	20 mgl^{-1} IBA pulse treatment of shoots for 48 h, followed by transfer on MS/4 hormone-free medium	41.67% rooting
Nodal shoot segments [15]	Clones and selected trees	MS + additives + 0.1 mgl^{-1} IAA + 1.0 mgl^{-1} BAP	Multiple shoot induction (80.95%)	MS + additives + 0.1 mgl^{-1} IAA + 1.0mgl^{-1} BAP	Shoot multiplication varies with clones (2.62–4.21-fold)	MS/4 medium + IAA + IBA	70% rooting

(continued)

Table 1 (continued)

Type of explant and references	Source of explant	Shoot initiation medium	Response	Shoot multiplication medium + PGRs	Response	Rooting medium + PGRs	Response
Nodal shoot segments [43, 44]	Plus trees	MS + additives + 0.1 mgl^{1} NAA + 1.0–2.5 mgl^{-1} BAP	Multiple (3–4) shoots/explants	MS + additives + IAA 0.1 mgl^{-1} + BAP 1.0 mgl^{-1}	Three–fourfold shoot multiplication in 6 weeks	MS/4 + IAA mgl^{-1} + IBA mgl^{-1}	Rooting (72%) from fifth passage onward shoots
Shoot tip [19]	Mature plants	MS + 5.0 mgl^{-1} Kn + 2.0 mgl^{-1} BAP	Multiple shoots induction	–	–	MS + 3.0 mgl^{-1} IBA	Rooting (Not quantified)
Nodal explants [10]	Trees	MS + 0.5 mgl^{-1} BAP + 5.0 mgl^{-1} IBA	Shoot proliferation in 30 days	MS + 0.5 mgl^{-1} BAP + 5.0 mgl^{-1} IBA	Shoot proliferation up to three passages at 4 weeks interval	Pulse treatment of shoots, with 50.0 mgl^{-1} IBA for 48 h, followed by transfer on HF MS medium	50% rooting

1.2 In vitro *Regeneration Through Adventitious Shoots*

For the first time, Rao and Bapat [35] reported shoot induction from hypocotyl segments of 4-week-old *in vitro* grown seedlings on basal nutrient medium (BM). Hypocotyl explants on BM showed green protuberances in 4 weeks. Bud formation from the protuberances occurred better on NAA and IAA (1.0 mgl^{-1}) compared to IBA and NOA. The medium containing Kn (1.0 mgl^{-1}) and adenine (10 mgl^{-1}) favoured high bud formation. Maximum 15–20 buds developed on the medium with 1.0 mgl^{-1} BAP in 70% of cultures. Position of explants also influenced bud induction. Basal portion proved better than the middle and upper regions of hypocotyls for shoot induction. Very few cultures consisting of liquid BM + NAA (0.5 mgl^{-1}) + IBA (0.5–5.0 mgl^{-1}) developed roots. Rao and Bapat [36, 41] observed that shoots induced from the hypocotyl further multiplied and produced numerous shoot buds on fresh BM medium up to fifth passage of subculture. The basal portion of hypocotyls inserted in the medium exhibited 100% shoot induction, and in the opposite position, only 10% developed shoots.

Mujib [26] used leaf and leaf segments as an explant from 3–4-weeks-old *in vitro* raised seedlings of sandalwood for the direct adventitious shoot induction using woody plant medium (WPM) with Kn, BAP and 2ip and also 2,4-D and CPA. Direct shoot induction was obtained on WPM with BAP 0.5 mgl^{-1} in liquid and agar-gelled medium. Shoot induction was better in liquid medium (14–16 shoots/explant) compared to agar-gelled medium (3–4 shoots/explant). Frequency of shoot induction was more in liquid medium (18.6%) than agar-gelled medium (13.95%). Histological studies showed protuberances from the leaf surface without callus phase.

Rathore et al. [45] reported direct adventitious shoot induction from internodes of mature trees. Pulse treatment with TDZ (0.1 mgl^{-1}) in MS liquid medium for a week on a magnetic shaker (90 rpm) followed by transfer on hormone-free MS medium with additives (ascorbic acid 50.0 mgl^{-1} + citric acid 25 mgl^{-1} + cysteine 25 mgl^{-1}) proved the best for direct adventitious shoot induction in 3–4 weeks. Incorporation of TDZ with NAA in the medium resulted in the induction of callus, whereas medium with NAA and BAP resulted in fewer multiple shoots. Shoots were further multiplied on MS medium with additives + 0.1 mgl^{-1} IAA + 1.0 mgl^{-1} BAP and shoots elongated on MS medium with additives + activated charcoal (250 mgl^{-1}) + GA_3 (1.0 mgl^{-1}). *In vitro* produced shoots (3–4 cm) exhibited 80% rooting in MS/4 medium with IAA + IBA. Hardening of explants was essential in the greenhouse for 8–12 weeks.

Janarthanam and Sumati [18] obtained adventitious shoots (71.6 ± 2.8%) from internodes (0.8–1.1 cm) using two-months-old *in vitro* raised seedlings on MS medium with 1.0 mgl^{-1} 2ip in 45 days. Maximum shoot induction (4.0 ± 1) was with BAP 1.0 mgl^{-1}. Highest rooting frequency (75.0 ± 5%) was obtained on half-strength MS medium with 0.5 mgl^{-1} IBA and 0.25 mg/l NAA in 145 days. Eighty per cent plantlets survived after 3 weeks of hardening in red soil, vermiculite and FYM (1:1:1, v/v). Bele et al. [9] reported adventitious shoot induction through callus phase from the leaf disc of 4-weeks-old *in vitro* raised seedlings of *S. album*. Callus induction was observed in MS medium with 2.0 mgl^{-1} 2,4-D + 0.5 mg/l TDZ, and subsequently, 20% shoot induction was observed. The shoots rooted on MS + 1.0 mgl^{-1} TDZ + 0.5 mgl^{-1} GA_3 + 1.0 mgl^{-1}NAA were hardened and established in field.

Singh et al. [56] reported regeneration from leaves of mature trees through callus phase. Callus was induced on WP medium with 0.4 mgl^{-1} TDZ. Differentiation of shoots from callus was observed on WP medium + 2.5 mgl^{-1} BAP + 0.4 mgl^{-1} NAA. Root induction was observed in 91.67% in vitro raised shoots on WP medium + 1.5 mgl^{-1} IBA. Singh et al. [57] later reported callus from the nodal segments on WPM + 0.6 mgl^{-1} TDZ. Highest number of shoot buds were developed from callus clump on WPM medium + 2.5 mgl^{-1} BA + 0.4 mgl^{-1}NAA in 8 weeks. Further shoot proliferation was achieved with 3.0 mgl^{-1} Kn. Highest rooting (82.37%) was on WPM medium with 1.5 mgl^{-1} IBA. The *in vitro* raised plantlets were transferred into plastic pots containing sterile soil, sand and coco peat (1:1:1) and hardened in a greenhouse with 85% survival after 4 weeks.

Solle and Semiarti [58] reported shoot induction from hypocotyls from *in vitro* raised seedlings as explants. High-frequency shoot induction from hypocotyls was obtained on MS medium with 2.0 mgl^{-1} BAP after 8 weeks of culture. Comparing MS and WPM with BAP 2.0 mg/l or CW 15%, MS medium with BAP proved the best for shoot induction. Barpanda et al. [8] attempted adventitious regeneration from leaf disc from trees through callus phase, but failed to induce shoots from the callus induced on MS medium with 2.5 mgl^{-1} BAP + 1.5 mgl^{-1} 2,4-D. Greenish and compact callus subcultured on MS medium with various concentrations and combinations of BA, IAA and NAA resulted in browning and dying of callus and shoot buds. Singh et al. [55] reported regeneration via organogenesis from callus raised from leaf explants. Callus induction was obtained on WP medium supplemented with either TDZ or 2,4-D. High-frequency callus induced from leaf on WP medium with 0.4 mgl^{-1} TDZ. The WP medium with 2.56 mgl^{-1} BA + 0.4 mgl^{-1} NAA favoured the highest number of shoot buds (24.6) per callus. In vitro shoots rooted (91.6%) on WP medium with 1.5 mgl^{-1} IBA. Plantlets were acclimatized in greenhouse. The summary on adventitious regeneration in *S. album* is given in Table 2.

2 Callus Culture

In *S. album,* Rangaswamy and Rao [31] reported callus initiation and multiplication from endosperm tissues on modified White's medium incorporated with 2.0 mgl^{-1} 2,4-D + 5 mgl^{-1} kinetin (Kn) and 0.25% yeast extract. Later, Rao and Rangaswamy [33] observed callus induction from embryos on White's basal medium with yeast extract, Kn and 2,4-D, which differentiated into embryos and developed into plantlets. Lakshmi Sita et al. [22]reported callus initiation from nodal segments obtained from 20–25-years-old plants on MS medium with 2 mgl^{-1} NAA + 0.5 mgl^{-1} 2,4-D + 0.5 mgl^{-1} BAP + 15% CM and established callus, which was further multiplied on MS medium with 1.0 mgl^{-1} 2,4-D alone. Rao and Bapat [36] obtained callus

Table 2 *In vitro* regeneration through adventitious shoot induction in *S. album* (chronological)

Type of explant	Source of explants	Medium and PGRs for shoot/callus induction	Response	Medium and PGRs for shoot proliferation	Response	Medium and PGRs for rooting	Response
Hypocotyl segments [35]	4-weeks-old in vitro seedlings	BM + 1.0 mgl^{-1} BAP	15–20 shoot buds in 70% cultures	–	–	BM + 0.5 mgl^{-1} NAA + 0.5 – 5.0 mgl^{-1} IBA	In few cultures roots developed
Hypocotyl segments [41]	4-weeks-old in vitro seedlings	BM + BA	Shoot buds	BM + BA	Further multiplied up to fifth passage	–	–
Hypocotyl segment [26]	4-weeks-old in vitro seedlings	BM + BA	100% shoot induction	–	–	–	–
Leaf and leaf segments [45]	3–4-weeks-old in vitro seedlings	WPM + 0.5 mgl^{-1} BAP (liquid and agar gellel medium)	Liquid medium induced 14–16 shoots/explant)	–	–	–	–
Internode segments [18]	In vitro shoot multiplication cultures of mature trees	Explants in MS liquid medium with 0.1 mgl^{-1} TDZ for a week, followed by transfer on MS hormone-free medium	Direct shoot induction from internode	MS medium + 0.1 mgl^{-1} IAA + 0.5 mgl^{-1} BAP for shoot multiplication	Shoot further multiplied 2.5-fold every week	MS + IAA mgl^{-1} + IBA mgl^{-1}	80% rooting

(continued)

Table 2 (continued)

Type of explant	Source of explants	Medium and PGRs for shoot/callus induction	Response	Medium and PGRs for shoot proliferation	Response	Medium and PGRs for rooting	Response
Internode [9]	2-months-old in vitro seedling	MS + 1.0 mgl^{-1} 2ip	Direct adventitious shoots (71.6 ± 2.8)	MS + 10%CM	Shoot proliferation and elongation	MS/2 + 0.5 mgl^{-1} IBA + 0.25 mgl^{-1} NAA	75% rooting and 80% plant survived after hardening
Leaf disc [56]	In vitro seedlings (4 weeks old)	MS + 1.5 mgl^{-1} 2,4-D + 0.5 mgl^{-1} TDZ	Developed callus and subsequently shoots	–	–	MS + 1.0 mgl^{-1} TDZ + 0.5 mgl^{-1} GA_3 + 1.0 mgl^{-1} NAA	Plantlets developed
Leaf [57]	Mature trees	WP + 0.4 mgl^{-1} TDZ	100% callus induction	WP + 2.5 mgl^{-1} BAP + 0.4 mgl^{-1} NAA	Induced shoots (24.6)	WP + IBA 1.5 mgl^{-1}	In vitro shoots rooted (91.67%)
Nodal shoot segment [58]	Mature trees	WP + 0.6 mgl^{-1} TDZ or 1.5 mgl^{-1} 2,4-D	Developed callus	WP + 2.5 mgl^{-1} BA + 0.4 mgl^{-1} NAA	Developed 16 shoots per / inoculum of callus	WP + 1.5 mgl^{-1} IBA	Rooting in 82.37% cultures
Hypocotyl segments [8]	In vitro seedlings	MS + 2.0 mgl^{-1} BAP	100% explants induced shoots in 8 weeks	–	–	–	–
Leaf disc [55]	Mature trees	MS + 1.5 mgl^{-1} 2,4-D	Induced callus	MS + 2.5 mgl^{-1} BAP	Callus browning and died later	–	–

Table 3 Callus culture of *S. album* (chronological)

Type of explant with reference	Source of explant	Details of medium + PGRs
Endosperm [31]	Seed	White's + 2.0 mgl^{-1} 2,4-D + 5 mgl^{-1} Kn + 0.25% yeast extract
Embryo [33]	Seed	White's + Kn + 2,4-D + yeast extract
Nodal segment [22]	20–25–years-old plant	MS + 2.0 mgl^{-1} NAA + 0.5 mgl^{-1} 2,4-D + 0.5 mgl^{-1} BAP + 15% CM
Hypocotyl [36]	Seedlings	MS + 2,4-D 1.0 mgl^{-1}
Leaf [30]	cultures (five shoot multiplication clones)	MS + additives (ascorbic acid 50 mgl^{-1} + citric acid 25 mgl^{-1} + cysteine 25 mgl^{-1} + glutamine 100 mgl^{-1} + 2,4-D 1.0 $mgl^{-1)]}$

from hypocotyl on MS medium + 2,4-D, which later differentiated into somatic embryos. Rangaswamy [30] induced embryogenic callus from leaf explants of in vitro shoot culture of five clones/genotype of mature trees on MS medium with additives (ascorbic acid 50 mgl^{-1} + citric acid 25 mgl^{-1} + cysteine 25 mgl^{-1} + glutamine 100 mgl^{-1}) and 2,4-D 1.0 mgl^{-1} within 4 weeks period at 20 °C, which was further multiplied on fresh medium. Studies on callus culture in *S. album* are summarized in Table 3.

Gowda and Narayana [14] conducted studies on callus induction from nodal and intermodal segments of healthy and spike disease infected plants of *S. album*. MS and White's media were used with 2,4-D (0.1 mgl^{-1}) + BA or Kn (1.0mgl^{-1}). Callus growth of explants was better on MS medium than White's medium. Spiked segments failed to induce callus on both these media with 2,4-D + BA/Kn. Callus initiation from the spike diseased explants was observed, when GA_3 2.0 to 5.0 mgl^{-1} was added in the MS medium with 2,4-D (0.1 mgl^{-1}) + Kn (1.0mgl^{-1}). In the diseased tissues, callus differentiation to somatic embryos was observed only in the presence of GA_3.

2.1 In vitro *Regeneration Through Somatic Embryogenesis and Characterization*

Bapat and Rao [2] reported somatic embryogenesis from hypocotyls of 4-week-old *in vitro* raised seedlings through direct bud regeneration. The explants were recultured on BM + 1.0 mgl^{-1} BA, which produced callus at the cut ends, followed by extensive differentiation of numerous somatic embryos of preglobular stage in 20% of cultures. Two approaches were adopted for somatic embryogenesis. In the first approach, preglobular embryos were isolated from the callus and suspended in liquid basal medium with plant growth regulators under agitated condition using shaker for four weeks at 120 rpm. In the second approach, undifferentiated callus developed on agar-gelled BM is incorporated with various growth hormones. Callus cultured on BM + 0.5–1.0 mgl^{-1} IAA differentiated into embryos in 70% of cultures. Fully organized embryos with cotyledons developed plantlets in 30% of the cultures on BM + IAA 1.0 mgl^{-1}. Plantlets were transferred to containers with vermiculite, irrigated with Hoagland's solution. After 8 weeks, plants were established in soil.

Lakshmi Sita et al. [22] reported somatic embryogenesis through callus phase from nodal and internodal segments from 20-years-old trees of *S. album*. Callus initiation was 100% on MS medium with 2.0 mgl^{-1} NAA + 0.5 mgl^{-1} 2,4 –D + 0.5 mgl^{-1} BAP + 15% CW and after subculturing turned brown. MS medium supplemented with 1.0 mgl^{-1} 2, 4-D + 0.2 - 0.5 mgl^{-1} Kn produced friable callus, which was further maintained by subculturing on MS + 1.0 mgl^{-1} 2,4-D alone. Callus subcultured on MS medium + GA_3 developed all stages of embryos within 3–4 weeks. Embryoids subcultured on White's medium with 0.5 mgl^{-1} IAA developed plantlets with a well-developed shoot and root system.

Preglobular embryos when transferred to agar medium developed into rapidly growing colonies. This, later on, developed heart and torpedo-shaped embryos. BM medium + 0.5–1.0 mgl^{-1} IAA stimulated embryo differentiation in 70% cultures. They observed that GA had no significant effect on embryo differentiation. Basal medium (BM) + 1.0 mgl^{-1} IAA + 4% sucrose favoured callus growth and also embryo differentiation. Embryos germinated on BM + 1.0 mgl^{-1} IAA and developed plantlets (20–30%).

Rao and Raghav Ram [37] reported somatic embryogenesis from callus developed from stem segment on MS + 2,4-D 1.0 mgl^{-1} + 0.5 mgl^{-1} GA_3 + 5% sucrose. On this medium with filter paper bridge, plants were maintained for 4–6 weeks and later on transferred to paper cups with vermiculite. After hardening, plantlets were transferred to earthen pots with soil. Later, Bapat and Rao [6] observed embryogenic callus induction and regeneration of plantlets through somatic embryogenesis from nodal shoot segments of a 20-year-old tree. The MS medium with 1.0 mgl-1 2,4-D + 1.0 mgl-1 Kn produced callus from the cut ends multiplied by subculturing. High regeneration of somatic embryos was obtained on MS + 1.0 mgl^{-1} IAA + 1.0 mgl^{-1} BAP. Cultures on MS medium with IAA, NAA, IBA and GA_3 developed embryos, which were globular to mature embryos. Good suspension cultures were established from the callus raised on 2,4-D (1.0 mgl^{-1}) medium and organized embryos developed plantlets, on transfer to agar-gelled medium.

Rugkhla and Jones [47] observed somatic embryogenesis and plant development in *S. album* and *S. spicatum* from seed, nodal segments from trees and leaf from the in vitro grown shoot cultures. Somatic embryos (100%) were induced directly in MS medium with TDZ or indirectly (through callus phase) in 2,4-D + TDZ. The globular embryos and friable embryogenic callus were transferred to 1.0 mgl^{-1} IAA + 0.2 mgl^{-1} Kn. Mature somatic embryos (1–2 mm) germinated on basal medium containing 2.0 mgl^{-1} GA_3. Germinated somatic embryos (10–20 mm long) were subcultured on 1.0 mgl^{-1} GA_3 containing MS medium with casein hydrolysate (CH) and coconut milk (CM). Histological studies revealed that primary somatic embryos developed from single cell or from epidermis or cortical parenchyma. Rai and McComb [29] reported for the first time direct somatic embryogenesis without callus phase from mature embryos. MS medium with 1.0 mgl^{-1} TDZ or 1.5 mgl^{-1} BAP induced direct somatic embryos from zygotic embryos. TDZ proved better than BAP. Somatic embryos transferred on MS medium without cytokinin developed secondary embryos in repetitive cycles with or without IAA. Mature and well-developed cotyledonary stage somatic embryos germination (80%) was on MS/2 medium + 0.5 mgl^{-1} GA_3 in 6 weeks. Plantlets were transferred in plastic pots containing soil and vermiculite (1:1 v/v) and hardened in a growth chamber. Survival of plants was about 70%.

Rangaswamy [30] reported somatic embryogenesis from in vitro grown leaves obtained from shoots of mature and five selected genotypes/clones. Significant callus induction and further multiplication on MS + 2,4-D medium were observed. Somatic embryo induction was also observed on IAA medium and maturation on ABA + PEG in WP medium and germination on MS/4 + IAA + GA_3. Plantlets were hardened in greenhouse for 8–10 weeks before keeping them in open nursery (Fig. 2).

Rathore et al. [43] reported somatic embryogenesis through callus phase from leaf and internodes of mature trees. Various auxin, viz. IAA, NAA, NOA and 2,4-D (1.0–2.0 mgl-1) with or without Kn/ BAP, were tested for embryogenic callus induction and further multiplication. In order to improve texture and quality of embryogenic callus, studies were conducted using different additives. MS medium + ascorbic acid (50 mgl^{-1}), citric acid (25 mgl^{-1}), cysteine (25 mgl^{-1}), glutamine (100 mgl^{-1}), yeast extract (500 mgl^{-1}), malt extract (500 mgl^{-1}) and CM (10% v/v) with 1.0 mgl^{-1} 2,4-D favoured embryogenic callus induction and multiplication. Among the various growth hormones and additives tested, MS medium with additives + 1.0 mgl^{-1} IAA proved the best for induction of globular embryos. The medium containing ABA + PEG favoured synchronized embryo maturation in 4 weeks period. On this medium, late torpedo and bipolar embryos developed without physical contacts. MS/4 medium + IAA + GA_3 was the best combination for high rate of embryo germination into plantlets. Abnormality was very less. Plantlets were hardened in a greenhouse for 10–12 weeks and later on transferred to nursery. Plantlets were normal in growth and morphology.

Revathy and Arumugam [46] reported direct somatic embryogenesis from leaf of in vitro raised seedling on MS medium with 3.0 mgl^{-1} 2,4-D. About 60% of cultures exhibited embryo induction. Direct embryos developed from internode were subcultured on MS medium + 0.5 v BA + 1.0 mgl^{-1} GA, and it favoured shoot elongation. Rooting (60%) of in vitro shoots was observed on MS + 3.5 mgl^{-1} TBA. Plantlets on hardening in red soil, vermiculite and FYM (1:1:1) showed 60% survival. Bele et al. [31] observed somatic embryogenesis from leaf disc of 3–4 weeks in vitro seedlings. MS medium + 1.0 mgl^{-1} 2,4-D + 0.5 mgl^{-1} TDZ favoured direct somatic embryogenesis in 11.44% cultures. The somatic embryogenesis was achieved through callus phase in 54.23% of cultures, with an average 160.08 somatic embryos per explant. However, MS medium + 2.0 mgl^{-1} TDZ and 1.0 mgl^{-1} GA_3 proved suitable for plant regeneration. Regenerated plants were acclimatized and established in the field.

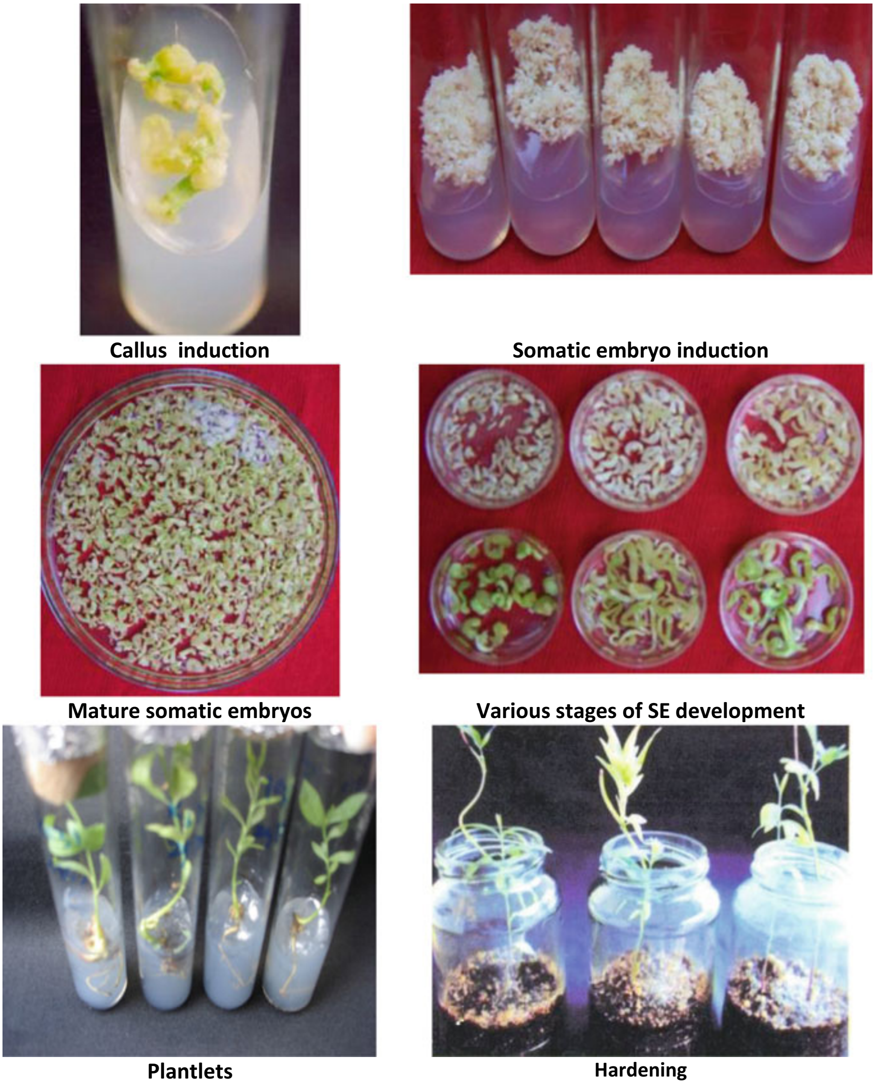

Fig. 2 Somatic embryogenesis in *S. album*

A summary of research work carried out on somatic embryogenesis in *S. album* is presented in Table 4.

Herawan et al. [16] reported somatic embryogenesis through callus phase from leaf as an explant from *S. album* clones. There was a significant effect of clones on callus induction. Callus was induced from epicormic leaf on MS medium + 2,4-D 3.0 mgl^{-1} + Kn 0.15 mgl^{-1}. About 30% callus cultures induced somatic embryos in nine clones in 8 weeks period. Among the different clones, clone K

Table 4 *In vitro* regeneration of *S. album* through somatic embryogenesis (chronological)

Type of explants	Source of explant	Medium and PGRs for callus induction	Response	Medium and PGRs for embryo induction	Response	Medium and PGRs for embryo maturation	Response	Media and PGRs for embryo germination	Response
Hypocotyl [2]	*In vitro* seedlings(4 weeks old)	Basal medium (BM) + 1.0 mgl^{-1} BAP	Callus induction from cut ends later on numerous SE of preglobular stage in 20% cultures	Liquid BM + 1.0 mgl-1 NAA or IAA at 120 rpm on shaker	Globular embryoid	Agar gelled BM + 0.5–1 mgl^{-1} IAA	SE rooted and shoot development was moderate	BM + 1.0 mgl^{-1} IAA	Plantlets developed in 30% cultures
Nodal and internodal segments [22]	Mature trees (20–25 years old)	MS + 2,4-D	Callus induction in 10% cultures	MS + GA_3	Developed embryoids within 3–4 weeks	–	–	White's medium + 0.5 mgl^{-1} IAA	Developed plantlets
Hypocotyl [37]	*In vitro* seedling	Basal medium + BA	Embryoid developed in suspension culture	Agar gelled basal medium	Developed embryoids of all stages in 7–8 weeks	BM + 0.5–1.0 mgl^{-1} IAA	Stimulated SE differentiation in 70% cultures	BM + 1.0mgl^{-1} IAA	20–30%cultures developed plants

(continued)

Table 4 (continued)

Type of explants	Source of explant	Medium and PGRs for callus induction	Response	Medium and PGRs for embryo induction	Response	Medium and PGRs for embryo maturation	Response	Media and PGRs for embryo germination	Response
Stem segments [6]	Mature plants	MS + 2,4-D1.0 mgl^{-1}	Developed embryogenic callus and embryos	–	–	–	–	MS liquid medium + 1.0 mgl^{-1} IAA + 0.5 mgl^{-1} IBA + 0.5 mgl^{-1} GA_3 + 5% Sucrose	Complete plantlet developed in 4–6 week
Nodal shoot segment [47]	Mature tree(20 years)	MS + 1.0 mgl^{-1} 2,4-D + 1.0 mgl^{-1} Kn	Callus from the cut ends	MS + 1.0 mgl^{-1}IAA + 1.0 mgl^{-1} BAP	Multiple SE developed	MS + IAA/NAA/IBA/ + GA_3	Developed globular to mature embryos	MS agar-gelled medium	Developed plantlets
Nodal segments and mature seed [29]	Mature tree	MS + 0.25 or 0.5 mgl^{-1} TDZ MS + 2,4-D + TDZ	Direct somatic embryos Fragile embryogenic callus	MS + 1.0 mgl^{-1} + IAA + 0.2 mgl^{-1} Kn	Globular and mature embryos	–	–	MS + 2 mgl^{-1} GA_3 MS + 1 mgl^{-1} GA_3 + CH + CM	SE germinated
Mature zygotic embryos [46]	Mature seed	MS + 1.0 mgl^{-1} TDZ	Direct somatic embryos induction	MS with or without IAA	Secondary embryos developed	–	–	MS/2 + 0.5 mgl^{-1} GA_3	Germination of 80% somatic embryos

(continued)

Table 4 (continued)

Type of explants	Source of explant	Medium and PGRs for callus induction	Response	Medium and PGRs for embryo induction	Response	Medium and PGRs for embryo maturation	Response	Media and PGRs for embryo germination	Response
Leaf and internode [30]	*In vitro* shoot multiplication cultures	MS + additivies + 1.0 mgl $^{-1}$ 2,4-D	Fragile embryogenic callus	MS medium + IAA/IBA	Embryo induction from surface of callus	MS + ABA + PEG	Maturation of embryos to torpedo and bipolar stage	MS/4 medium + IAA + GA_3	SE germinated and produced plantlets
Leaf/leaf segments [43]	*In vitro* shoot multiplication cultures	MS + additives + 2,4,D 1.0 - 2.0 mgl^{-1}	Fragile white embryogenic callus	WP medium with 1.0 mgl^{-1} IAA	Globular and heart shape embryo induction	WP medium 1.0 mgl^{-1} ABA + PEG	Torpedo and bipolar embryos	MS/4 + IAA + GA_3	Germination of embryos into plantlets
Leaf and internode [16]	*In vitro* seedling	MS + 3.0 mgl^{-1} 2,4-D	Somatic embryo induction	MS + 0.5 mgl^{-1} BA + 1.0 mgl^{-1} GA_3	Shoot elongation	–	–	MS + 0.5 mgl^{-1} IBA	Rooting of 60% shoots
Leaf disc [18]	*In vitro* seedlings (3–4 weeks old)	MS + 1.0 mgl^{-1}, 2-4D + 0.5 mgl^{-1} TDZ	Direct somatic embryos (11.44%) and (54.23%) through callus phase	–	–	–	–	MS + 2.0 mgl^{-1} TDZ + 1.0 mgl^{-1} GA_3	Plant regeneration

(continued)

Table 4 (continued)

Type of explants	Source of explant	Medium and PGRs for callus induction	Response	Medium and PGRs for embryo induction	Response	Medium and PGRs for embryo maturation	Response	Media and PGRs for embryo germination	Response
Leaf [28]	Clones	MS + 3.0 mgl^{-1} 2,4,D + 0.15 mgl^{-1} Kn	Callus induction and in 30% cultures SE in nine clones	MS medium + BAP + Kn	Stimulated secondary embryos	MS + 1.0 mgl^{-1} BAP + 0.01 NAA + sucrose 40 gl^{-1} in light condition	Maturation of somatic embryos	CND_2 medium	Germinated somatic embryos
Nodal segment, seed and leaf disc [63]	2-year-old plants	MS + 2.5 mgl^{-1}2,4,D + 3.0 mgl^{-1} Kn	95.64 fragile callus	MS + 0.5 mgl^{-1} BAP + 1.0 mgl^{-1} IAA + 0.5 mgl^{-1} Kn	Somatic embryo induction	–	–	MS + 2.0 mgl^{-1} GA_3 MS + 0.4 mgl^{-1} BAP + 0.2 mgl^{-1} IAA	SE germination Plantlet development
Shoot tip [51]	2-years-old plants	MS + 1.0 mgl^{-1} BAP	Callus induction in 4 weeks	MS + 1.0 mgl^{-1} + Ascorbic acid 1.0 mgl^{-1})	Somatic embryoids developed	–	–	–	–

had 60% embryo induction. Medium containing BAP stimulated the development of secondary embryos. Somatic embryo maturation was on MS medium with 2.0 mgl^{-1} BAP. Peeris and Senarath [28] have carried out studies on in vitro propagation through somatic embryogenesis from the single nodal segments of two-years-old plants and seed (mature and immature) and leaf discs (1 cm^2). Nodal shoot segments proved the best explant for embryogenic (fragile and translucent; 95.64%) callus induction on MS medium + 2.5 mgl^{-1} 2, 4-D + 3.0 mgl^{-1} Kn in 6 weeks in the dark. Somatic embryo induction was obtained on MS medium with 0.5 mgl^{-1} BAP + 1.0 mgl^{-1} IAA and 0.5 mgl^{-1} Kn under dark. Somatic embryo germination was the best in MS medium + 2.0 mgl^{-1} GA_3. Plantlets developed (76.67% ± 3.03%) on MS medium with 0.4 mgl^{-1} BAP + 0.2 mgl^{-1} IAA. Vanajah and Seran [63] reported induction of embryogenic callus from shoot tip explants of 2-years-old plants on MS medium + 1.0 mgl^{-1} BAP in 4 weeks period. After this, no response was observed, and explants turned brown. Incorporation of antioxidant (1.0 mgl^{-1}ascorbic acid) in medium + 1.0 mgl^{-1} BAP induced embryogenic callus from shoot tip and developed into somatic embryoids after 8 weeks of culture.

Shankara Rao et al. [51] characterized synchronized somatic embryogenesis in *S. album*. After callus induction, they observed three distinct stages of embryogenesis 1) preglobular, 2) globular and 3) bipolar embryos. Transition from stage 0 (callus) to 1 (preglobular) was accomplished using 2,4-D, which involves a stage-specific polypeptide of molecular weight 15 and 30 kDa. A 24 kDa polyptide detected in the primary callus was not observed in stages 1, 2 and 3. Tissue-specific 50 kDa glycoprotein decreased during transition stage 2 to 3. Glycoproteins were higher in stage 0 as compared to stage 1. The activities of protein kinase, glycosidase and xylanase increased with progressing of embryogenesis.

Somatic embryo irregularities like aggregation of pro-embryos, embryo growth arrest and browning with no or deformed development were observed in liquid medium. In solid medium, embryo swelling, callus without further embryogenesis, large-scale secondary embryo formation and root degeneration were common (Illah et al. [17]). Somaclonal variation was also observed in plants raised through somatic embryogenesis. They exhibited dark green or virescent leaves, whorled phyllotaxy and distorted and fasciated stem (Rao et al. [38]).

3 Synthetic Seed Production and Germination

Most of the research work on synthetic seed production and germination on *S. album* has been carried out at the Bhabha Atomic Research Centre (BARC), Trombay. Bapat and Rao [4] and Rao and Bapat [40] reported synthetic seed production and germination. Calcium alginate beads containing somatic embryos were kept for 40 min on a shaker (40 rpm) under light (950 lx). The encapsulated beads were washed 3–4 times with MS basal medium and placed in petriplates with filter paper for germination. The plantlets developed in 16 weeks.

Fernandes et al. [13] further improved in vitro germination of encapsulated somatic embryos. Fully matured somatic embryos were encapsulated in a 3% (w/v) sodium alginate gel prepared in MS medium + 1.0 mgl^{-1} IAA + 0.5 mgl^{-1} IBA + 0.5 mgl^{-1} GA_3 matrix. Gel matrix was provided with fungicide or a food preservative. The embryos were dipped in matrix and dropped into a 0.69% (w/v) solution of $CaCl_2$. $2H_2O$ for 30 min. The encapsulated embryos (17%) germinated in autoclaved soil. Sodium bicarbonate (25 mgl^{-1}) prevented contamination. Bapat and Rao [7] reported regeneration of plantlets from both encapsulated and non-encapsulated desiccated somatic embryos of *S. album* for 10, 20 and 30 days. Both types of embryos exhibited revival of growth when rehydrated on White's medium and developed into plantlets. Somatic embryos subjected to desiccation for 30 days exhibited revival.

4 Protoplast Culture

Two groups of researchers, viz. BARC, Trombay, and Indian Institute of Science (IISc), Banglore, carried out research work on protoplast culture and plant regeneration of *S. album.* Rao and Ozias-akins [39], Bapat et al. [3] and Rao and Bapat [40] reported protoplast isolation from leaf mesophyll, stem and hypocotyl callus and suspension cultures. Protoplast from the hypocotyl callus was obtained using a mixture of cellulase (2%) + pectinase (1%) + hemicellulase (1%). Isolated protoplasts were plated on MS medium with 1.0 mgl^{-1} 2,4-D, and division was observed after 5 days of culture. Multicellular colonies were developed at the end of 8 weeks. Callus from stem released protoplasts by incubation in enzyme mixture of cellulase (1%) + Mac enzyme (0.5%). Protoplast after culture regenerated cell wall in 36 to 48 h. About 50% of divided protoplast developed colonies. Microcalli developed on modified V47 medium in 8–10 weeks. Callus colonies subcultured on MS + 1.0 mgl^{-1} IAA, MS + 1.0 mgl^{-1} BAP, MS/2 + 1.0 mgl^{-1} IAA and MS/2 + 10% CM (v/v) + 500 mgl^{-1} casein hydrolysate differentiated to somatic embryos. Somatic embryos germinated and developed plantlets. From leaf combined use of cellulase (2%) + Mac enzyme (1%) + hemicellulase containing 0.8 M manitol produced a good yield of protoplasts. The maximum yield of protoplast was obtained after 8 h. Protoplast release increased with an increase in the osmoticum level to 1.0 M. However, leaf protoplast did not develop colonies.

Through cell suspension cultures, Rao and Ozias-Akins [39] reported plant regeneration through somatic embryogenesis from protoplasts. Protoplasts were isolated from embryogenic cell suspension cultures raised from the shoot segments of a 20-year-old tree. A combination of Mac enzyme (1%) + Driselase (1%) and cellulase (%) resulted in protoplast release. Protoplast divisions were observed on V47 medium (3 mM 2-(N-morpholino)ethane sulfonic acid + BAP + 2,4-D). At the end of third week, visible colonies developed, which differentiated into somatic embryos on MS + 1.0mgl^{-1} IAA + 1.0 mgl^{-1} BAP + 400 mgl^{-1} amino acid. Plantlets were developed after 3 weeks on MS/2 basal medium or Whites with 1.0 mgl^{-1} IAA + 0.5 mgl^{-1} IBA + GA_3 (1.0 and 3.0 mgl^{-1}). Lakshmi Sita and Shobha Rani [21] reported protoplast isolation from callus, suspension culture and leaves to develop methods for diploid and triploid protoplast fusion. Isolated protoplast divided and produced callus which regenerated into plantlets.

5 Endosperm Culture

BARC, Trombay, and IISc, Bangalore research groups worked extensively on endosperm culture and regeneration of triploid plants of *S. album.* Rao and Rangaswamy [33] for the first time attempted seed and endosperm culture to understand parasitic nature and regeneration of plants from endosperm culture. Whole seed was attempted to induce callus on the White's medium with various PGRs and natural extracts. Callus induced from split endosperm after six weeks on White's medium + 2,4-D + Kn + yeast extract. Endosperm cultures maintained for several passages, but did not differentiate into shoot, root or embryoids. Lakshmi Sita and group [20, 23] for the first time reported triploid plantlets development from the endosperm culture through embryogenesis. MS medium consisting of 2,4-D 1.0–2.0 mgl^{-1} + 0.5–2.0 mgl^{-1} BAP + 1.0 mgl^{-1} NAA induced callus. Callus was maintained in MS medium with 1.0 mgl^{-1}, 2,4-D. Callus subcultured on MS medium with 1.0–2.0 mgl^{-1} GA differentiated into numerous embryoids. Embryoids were transferred in liquid medium on shaker to separate different stages of embryoids. Medium with 0.3 mgl^{-1} BAP + 1.0 mgl^{-1} IAA + 0.3 mgl^{-1} Kn + 1.0 mgl^{-1} GA favoured maximum embryogenesis. Mature embryos on White's medium developed plantlets. Root tip squashes confirmed triploid number of chromosomes ($3n = 30$).

Rao and Bapat [40] reported endosperm culture and production of plantlets through embryogenesis from callus. Seeds were opened, and endosperm without embryo was cultured on MS medium with various growth regulators. Callus was obtained from endosperm on MS + 1.0 mgl^{-1} 2,4-D alone or with 0.2 mgl^{-1} Kn. Callus subcultured on MS + 1.0 mgl^{-1} BAP favoured embryos differentiation in 4 weeks. Embryos to plantlet (20–30%) formation were on MS medium + 1.0 mgl^{-1} IAA + 0.5 mgl^{-1} IBA + 0.5 mgl^{-1} GA + 5% sucrose.

6 Micrografting

Sanjay et al. [50] reported in vivo and in vitro micrografting and production of micrografted plants of *S. album*. Seedlings were raised in 250 and 450 cc single cell root trainers consisted compost, sand and soil (5:4:1, v/v) in greenhouse. Seedlings of 40–110 days were used as a root stock for in vivo grafting. Scion was used from the candidate plus trees (CPTs) of 50–60 years of age for in vivo micrografting. To carry out in vitro micrografting, in vitro seedlings were raised in MS basal medium under aseptic condition, and scion was used from the in vitro shoot multiplication cultures.

In vivo micrografting was successful up to 50% using 90 days root stock and 4.0–5.0 cm length of scion. Scion size, root stock age and season of scion collection were found to influence success of grafting. Grafted plants were covered with polythene bags and incubated in greenhouse for 6–8 weeks (till graft union). In vitro micrografting was carried out under aseptic conditions. Scion (1.0 to 2.0 cm long) obtained from in vitro cultures was grafted onto hypocotyl of 45–days-old rootstocks. After in vitro micrografting, plants were transferred in culture tubes containing filter paper bridge in liquid MS/2 basal medium with 2% sucrose. Success rate of in vitro micrografting was 60%. Like in vivo micrografting, success of in vitro micrografting was influenced by the scion size and root stock age. Under favourable conditions, union of scion and hypocotyls was in 6–8 weeks period. In vitro micrografted plants after 8 weeks were transferred into 450 cc single cell root trainers with soilrite moistened with 1/4 MS basal salts medium and covered with polythene bags and kept at 25 ± 1ºC temperature and light of 160 μMol m^{-2} s^{-1}. After 2–3 weeks, in vitro grafted plants were kept in greenhouse for primary hardening and later on (after 2 weeks) to shade house before keeping in open nursery.

7 Bioreactor Technology

Production of somatic embryos: Rao and Bapat [40, 42] reported establishment, maintenance of cell suspension culture and regeneration of plantlets through somatic embryogenesis. Cell suspension cultures were initiated from friable stem callus grown in MS + 1.0 mgl^{-1} 2,4-D. The cultures produced fine suspension of single cell and few cells aggregates. Cell suspension cultures were used for production of somatic embryos, synthetic seeds and production of plantlets.

Bapat and team [5, 6] used bioreactors to produce somatic embryos for the production of plants in bulk quantity in a short time. Two types of bioreactors were used. The 7 L capacity bioreactor was used to cultivate non-embryogenic cells, whereas 1 L capacity bioreactor for the conversion of embryogenic cells to mature embryos. In 7 L bioreactor, cell suspension was transferred, and final volume of the medium was kept to 4.5 L. Preglobular embryos were inoculated in 1 L bioreactor consisted 500 ml MS + 0.5 mgl^{-1} IBA + 0.5 mgl^{-1} GA_3 + 5% sucrose. Mature embryos were harvested from the bioreactor and transferred to agar-gelled medium (MS medium + 1.0 mgl^{-1} IAA), on this medium, plantlets developed. Das et al. [12] reported cell suspension culture and use of bioreactor for rapid and mass propagation of *S. album*. Embryogenic cell mass was produced by growing callus in MS medium with IAA 0.5 mgl^{-1} on agar medium for 3 weeks. Embryogenic cell mass was about 10 g per litre in medium with 3% sucrose + 0.5 mgl^{-1} BA transferred in bioreactor (12 L airlift type) and incubated for 4 weeks. Somatic embryos produced in bioreactor were germinated in petriplates consisted MS agar-gelled medium + 3% sucrose + 0.1 mgl^{-1} GA_3 + 0.1 mgl^{-1} BA. Synchronized normal somatic embryos and normal embryos produced per gram of embryogenic cell mass which improved 8–20 times as a result of cultivation in bioreactor. Somatic embryos germinated into plantlets and after hardening for 2 months transferred to field.

Production of secondary metabolites: Valluri et al. [62] reported production of phenolics by two heterotropic suspension cultures (SW-1 and SW-2) of *S. album,* cultivated in a 2.5L bioreactor. Cultures of cell suspension of SW-1 produced maximum phenolic content of 32.5 mgl^{-1} as compared to 12.5 mgl^{-1} produced by SW-2. Crovadore et al.[11] carried out studies on selection and production of calli of *S. album* for induction of sequiterpenes. Green and soft callus was obtained from hypocotyl of in vitro seedling on B_5 medium with 0.1 mgl^{-1} 2,4-D and 2.0 mgl^{-1} Kn. For inducing sequiterpene synthesis, B5 medium with 2,4- D + Kn, 1 amino cyclo propane-1-carboxylic acid (ACC), 2-chloro ethyl phosphonic acid (ethaphon), polyB-(1–4)-(D)-glucosamine (chitosan), salicylic acid, methyl jasmonate, L-methionine, coconut water and 4-amino-1-B-D ribofuranosyl-1,3,5-triazin-2 (1H) azacytidine were used. Various hormone (2,4-D and Kn) combinations were tested for sequeterpene induction in the callus. GC–MS analysis revealed that selected calli were able to produce a range of terpenic molecules, including some desired terpene important in sandalwood odour profile, viz. beta-santalol, betasantalene and three more, which illustrate the capacity of in vitro callus culture to produce terpene molecules constitutive of the *S. album* oil order profile.

Mishra and Dey [25] reported shikimic acid (Tamiflu precursor) production in suspension cultures of *S. album* in airlift bioreactor. In suspension culture in shake flask and airlift bioreactor of 50 ml and 2.0 L volume, yield of shikimic acid was 0.07 and 0.8% (w/w), respectively, in 2–3 weeks period.

Rani et al. [32] carried out studies on squalene production in the cell suspension cultures of *S. album* in shake culture and airlift bioreactor. Squalene is a chemical important in nutraceutical, pharmaceutical, vaccine and cosmetic industries due to the anticancer, antioxidant, skin hydrating, immune-stimulating and emollient activities. Accumulation of squalene in the cells was dependent on type of culture system, i.e. shake flask and bioreactor. In flask, 32 mg/g dry weight was accumulated in 6 weeks, whereas in bioreactor accumulation of squalene was 5.5 mg/g dry weight in 4 weeks.

8 Genetic Transformation

Shiri and Sankara Rao [54] reported genetic transformation and regeneration of transgenic plant for the first time. This study deals with introducing and expressing foreign genes in sandalwood and the regeneration of transgenic plants from embryogenic cultures derived from transformed somatic embryos. *Agrobacterium tumefaciens* strains carrying β-glucuronidase UidA (GUS) and neomycin phosphortransferase II (NPT II) genes on binary vector PKIW1105, pBI121, PIGI121-Hm transformed torpedo and cotyledon stage embryos. About 20% of inoculated embryos induced callus and developed embryos. Transformation was confirmed by analysing in the presence of kanamycin, GUS and NPT II assy. Transgenic putative embryos were identified after two months and developed rooted plants.

Shekhawat et al. [52] reported an efficient method for the genetic transformation of *S. album* using cell suspension culture by *Agrobacterium tumefaciens* mediated genetic transformation and regeneration of transformed plants. Cell suspension cultures were established from the stem internode callus, transformed with *A. tumefaciens* carrying pCAMBIA1301 plant expression vector. Selection of transformed colonies was carried out on hygromycin (5.0 mgl^{-1}) medium. Expression of β-glucuronidase was assessed by RT-PCR and GUS assays. Plantlets from the transformed embryogenic cells were regenerated through somatic embryogenesis. Southern blotting confirmed transformation and stable insertion of T-DNA into the host genome. This is the first report of a stable and high level of foreign protein expression using cell suspension culture in *S. album*. In another study, [53] Shekhawat et al. reported transformation of cell suspension cultures of *S. album* using hepatitis B small surface antigen using *A. tumefaciens* having PD35SHER plant expression vector with hepatitis B surface antigen (HBsAg). Transformed cell suspension colonies were selected using kanamycin in the medium and subsequently using PCR analysis. RT-PCR and western blot analysis confirmed the expression of HBsAg. The expression was quantified using monoclonal antibody based on ELISA.

9 Future Perspectives

Despite extensive research and development in micropropagation and genetic transformation in *S. album*, micropropagated plants in field trials are yet to materialize (Fig. 3). Robust technologies should be transferred to commercial micropropagation units for large-scale production of clonal planting material of desirable traits (growth, heartwood and oil). There is a need to research interspecific protoplast fusion and production of novel hybrids and upscale automation for large plantlets plantlets through somatic embryogenesis in *S. album.* Cell suspension culture is required to explore the potential of sandalwood oil production by identifying genes, cell line selection, use of precursors and elicitors. Studies are required for genetic improvement of *S. album* by genetic transformation for biotic and abiotic resistance.

Fig. 3 Field trial of tissue cultured raised plants of sandalwood

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Chapter 23
Genetic Diversity Analysis of Indian Sandalwood

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Abbreviations

RAPD	Random amplified polymorphic DNA
RFLP	Restriction fragment length polymorphism
SSR	Simple sequence repeats
ISSR	Intersimple sequence repeats
PCA	Principal component analysis
DAMD	Directed amplification of minisatellite DNA
IWST	Institute of Wood Science and Technology
UPGMA	Unweighted pair group method with arithmetic mean

1 Genetic Diversity of Sandalwood

Sandalwood is a very important species in the Indian subcontinent both economically and culturally. It is valued for its fragrant heartwood as well as essential oil [1]. Till date, several studies have been carried out applying molecular tools and techniques such as isozymes, RAPD, RFLP, SSR and ISSR markers to analyse the genetic diversity in Indian sandalwood [2]. The genetic diversity studies on Indian sandalwood have been done on populations from different geographical locations across India, as shown in Fig. 1.

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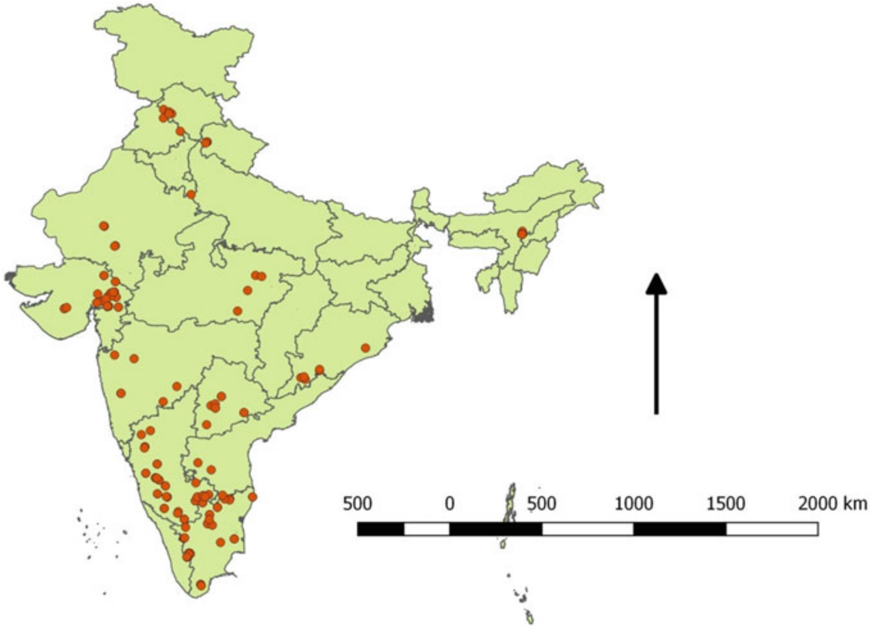

Fig. 1 Consolidated map of collection locations for studies on genetic diversity of *Santalum album* (the data were derived from the sites and GPS coordinates mentioned in the literature, and the map was constructed with QGIS 2.18.7)

Genetic diversity is important in terms of long-term stability and short-term productivity in forest ecosystems. The amount of genetic variation within a species and its distribution within and among the populations contributes to the maintenance of variation, inbreeding and gene flow, thereby maintaining evolutionary potential in a changing environment. It helps in pest resistance and protects against the negative consequences of inbreeding [3–5].

Genetic diversity analysis using isozymes: Initial studies concentrated on isozyme-based diversity analysis in Indian sandalwood. First genetic diversity study was by Brand in 1994 [6]. His studies focused on the genetic diversity analysis in 10 West Timor (Indonesia) and two Indian populations of sandalwood using 23 enzyme systems and found that Indian populations are genetically well separated from West Timor populations. The authors predicted that the Indian populations having higher genetic diversity are largely due to bigger population size and distribution range from the observations. Further, Suma and Balasundaran (2003) studied the genetic diversity within and between five Indian sandal provenances, namely Marayoor (Kerala); Bangalore, Mandagadde and Thangli (Karnataka); and Javadi (Tamil Nadu) using five metabolic enzymes peroxidase, shikimate dehydrogenase, glycophosphate isomerase, malate dehydrogenase and esterase. It was observed that the average gene flow rate between the provenances was very low. From the overall variation, 78.3% variation occurred between the provenances, whereas the remaining 21.7% occurred within provenances. Genetic relatedness among the provenances was analyzed by UPGMA. The provenances clustered based on the genetically more similar (Bangalore and Thangli) and relatively less genetic similarity (Marayoor and Mandagadde) [7]. Further, Suma and Balasundaran [6] studied diversity analysis and seed survival of eight Indian provenances and suggested that Marayoor provenance had better genetic diversity and adaptability.

A critical analysis of sandalwood populations' distribution throughout India using isozymes was developed with comprehensive distribution maps. Hotspots of genetically diverse sandalwood populations distributed over different parts of peninsular India using allozyme markers were identified. The PCA maps and the dendrogram showed separation of the sandalwood populations based on their geographical origins and observed high level of gene flow within and among the populations, within geographical area rather than across the geographical areas. Relatively high levels of heterozygosity (31%) were observed in the sandalwood populations in peninsular India. Although the sandalwood is distributed mainly in South and Central India, it was mainly concentrated in the Deccan plateau region, and higher level of heterozygosity was observed in the Deccan plateau compared with that of Western and Eastern Ghats. It was suggested that sandalwood populations at the Deccan plateau can be considered as the hotspot of genetic variability in India [8].

Genetic diversity in the leaf samples of 40 sandalwood clones assembled at IWST, Bengaluru, collected from the natural growing areas and plantations in Tamil Nadu and Karnataka was done using four enzyme systems, viz. peroxidase (POD), aspartate aminotransferase (AAT), glutamate dehydrogenase (GDH) and malate dehydrogenase (MDH). All the enzymes showed polymorphism; however, as such, no pattern of geographic distribution of isozyme variation was observed [9]. It was observed that the genetic relatedness was high among the provenances that were geographically close, while it was low in provenances which were located relatively apart [8]. The differences in genetic variability among the populations of a geographically separated species are also influenced by climatic factors such as altitude, temperature, humidity and rainfall [10]. *S. album* also occurs at varied altitudes across India which may result in different selection pressures, hence resulting in genetic diversity [6]. It is known that genetic drifts are mainly caused by geographical separation and poor gene flow. Owing to this, it was predicted that the independent evolution of the sandalwood provenances might have occurred as single discrete units and the selective inbreeding of the superior genotypes might be responsible for the higher level of observed heterozygosity [6]. Further, lack of gene flow may be attributed to the isolation and fragmentation of sandalwood populations, and low seed and pollen dispersal, which are also reported in other species of sandalwood [8].

2 Genetic Diversity Analysis Using Molecular Markers

2.1 RAPD and ISSR Studies

Genetic diversity analysis was done for *S. album* populations using RAPD markers for 51 genotypes which were collected from different geographical regions of India and three exotic lines of *S. spicatum* from Australia. Separation of the 51 Indian genotypes from the three Australian lines revealed that the Indian sandalwood germplasm constitutes a broad genetic base. The values of genetic dissimilarity ranged from 15 to 91%. A core collection of 21 selected individuals revealed the same diversity of the entire population [11]. Similarly, Azeez et al. in 2009 studied the genetic diversity of 30 accessions of *S. album* from Southern India using RAPD markers. The accessions were obtained from the germplasms maintained at IWST. The sandalwood accessions belonged to different geographical regions in the southern states of India. They used 30 RAPD primers to obtain polymorphic amplicons to reveal the genetic relatedness using the PCA plot. The sandalwood genotypes were dispersed on the PCA plot, suggesting a wider genetic base of *S. album,* and some of the genotypes overlapped with each other. The accessions from Bangalore and Hyderabad were distinct from each other, while the accessions collected from different parts of the country were interspersed and did not form distinct groups [12]. In another study, DAMD and RAPD primers were used to study the genetic variation between and within three populations of *S. album* collected from Kunigal and Kengeri in Karnataka and Kallipatti in Tamil Nadu. Sampling was done based on certain criteria such as age, phenotypic differences and distance between the successive samples. The data from RAPD and DAMD were combined and analysed using dice pairwise distance method. A neighbour joining tree dendrogram showed the genetically diverse populations of sandalwood trees. A high genetic variation among these populations was observed along with indications of clonality within the existing Indian sandalwood populations, due to habitat fragmentation, isolation and vegetative reproduction [13].

A study was conducted to integrate set of 57 different DNA markers (25 RAPD, 21 ISSR and 11 SSR markers) for diversity analysis in 20 sandalwood genotypes from Gujarat. SSR primers developed in other *Santalum* species, viz. *S. austrocaledonicum* and *S. insulare,* were exploited for the diversity analysis, and the cross-species transferability of SSRs indicates that the primer binding sites were conserved across the genera. The RAPD and ISSR primers showed results which were highly correlated and the similarity percentage among the samples ranged from 52 to 81%. The SSR primer pairs however lacked any genetic variation within the sandalwood samples. This could be due to the highly conserved loci in the genera *Santalum* [14]. Jones et al. in 2009 studied the diversity pattern of 233 sandalwood trees in 2004 from FC Kununurra, Australia collection using RFLP markers. Most of the trees were from Indian core collection, while a few samples originated from Timor. The germplasm collected from Kununurra region was highly homozygous. The level of genetic diversity was lower than previously reported figures for natural stands of *S. album* in India [15].

In a recent study, the morphological, genetic variation as well as population structure has been evaluated using different marker assays from geographically widespread sandalwood populations of India. A total of 37 primers (15 RAPD and 22 ISSR) were used to characterize the genetic diversity. Sandalwood accessions ($n = 70$) were collected from various populations across the states of Karnataka, Kerala, Tamil Nadu, Telangana, Andhra Pradesh, Assam, Maharashtra, Punjab, Madhya Pradesh, Gujarat, Rajasthan, Himachal Pradesh, Odisha and Uttarakhand. Maximum genetic variation was present within populations with less variation among populations. Also, South Indian populations showed maximum morpho-variations. The study indicated low genetic variability necessitating immediate attention towards its sustainable utilization, propagation and long-term conservation [2].

3 SSR Studies

SSR markers have also been used to study the genetic diversity analysis of sandalwood populations collected from three states, viz. Karnataka, Telangana and Kerala. It was observed 3% of the genetic variation was attributed to the differences among population while the remaining 97% was due to differences within the population. The gene flow was estimated among the populations of Kodad, IWST Karnataka, Telangana and Kerala. The exchange of genepool between Telangana populations was high and was genetically more related to Kerala than Karnataka populations. A relatively high gene flow of populations was observed in Telangana state when compared to Karnataka and Kerala [16]. Further, the PCA analysis grouped the samples into two mixed groups of Karnataka, Kerala and Telangana populations. The PCA analysis revealed that Telangana and Kerala populations were more similar than Telangana and Karnataka populations. The populations were clustered into two discrete groups. Karnataka and Kerala state formed one group and Telangana with the overlapping of few samples of Karnataka, Kerala and Telangana forming the second. The gene flow was high in natural populations compared to that of populations under plantation. The genetic distance was farthest between Telangana and Karnataka populations indicating that the populations of Telangana mostly comprised Kerala rather than Karnataka populations. The selected SSR markers showed high polymorphism and helped in identifying genetically diverse populations from southern parts of India [16].

Similar findings were observed in another study where morphological and genetic variability was analysed for 177 accessions from 14 populations collected from three different states of Southern India, viz. Karnataka, Telangana and Kerala. The genetic diversity was estimated using genetic SSR markers. A moderately high level of polymorphism was observed. Also, at population level, the Karnataka and Telangana populations expressed a high exchange of gene pools. Analysis of genetic differentiation using AMOVA revealed that major genetic variation was present among the individuals as compared to among the populations and within the individuals. The analysis revealed that most of the total variance obtained was attributed to the differentiation among the individuals rather than among the populations. The lowest genetic differentiation was found in Kerala (F_{ST} value = − 0.03), while the highest genetic difference was found in Karnataka (F_{ST} value = 0.08), followed by Telangana (F_{ST} value = 0.06). Kerala population had the lower level of gene flow compared to other sandalwood populations. In Telangana samples, the admixtures were found, and the accessions overlapped with those of Karnataka and Kerala, while major variation was observed in Karnataka and Kerala [17].

Due to limited availability of native SSRs, most of the diversity analysis studies in sandalwood were conducted independently with isozymes, RAPD, ISSR and cross-species-specific transferrable SSR markers [18–20]. Most of the early studies on sandalwood populations within and outside India mention isozymes as reliable markers in sandalwood [7, 21]. However, these biochemical markers are very less in abundance, and hence the degree of detection of polymorphism is less compared to the other genetic markers like SSRs. Isozymes are phenotypic markers and easily gets affected by environmental conditions, and they vary according to the type of tissues used for the analysis [22].

Due to environmental and anthropogenic factors, sandalwood populations have declined in India, which in turn also led to the loss of genetic diversity. Low genetic variability within populations might be due to the fragmentation, discrimination of attributions due to random genetic drift and minimum gene flow between the populations [7]. Therefore, efforts should be directed towards conserving the genetically varied sandalwood populations. Genetic diversity can be captured and stored in the form of gene bank or DNA library, which preserves genetic material for years. The conserved genetic resources can be utilized for further tree improvement using micropropagation techniques [8, 16, 23].

4 Summary

Studies till date identified genetically rich sandalwood germplasm populations in Karnataka, Telangana and Kerala which may not represent whole country distribution of sandalwood. Geographically closer populations are genetically more similar than those which are geographically distant. Thus, the genetic variability is correlated with the spatial distribution of the sandalwood population. Studies on SSRs and functional markers (EST-SSRs and SNPs) are lacking in sandalwood populations across India. Further comprehensive studies should be focused integrating high resolved molecular marker like SSRs, EST and SNP studies, ecological niche distribution and chemical variability of sandalwood populations. These could further help in developing conservation strategies.

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Chapter 24
Photosynthesis in Indian Sandalwood

A. N. Arunkumar and K. N. Nataraja

1 Introduction

Photosynthesis is an important physiological process associated with the growth and development of trees. Tree growth depends on canopy photosynthesis. In most trees, photosynthesis is a relatively inefficient process with only less than 10% of solar energy is converted to reduced sugars. Further, due to autotrophic respiration and limitation imposed by other factors, the realized conversion efficiency is estimated to be less than 2–4% of the energy of the solar energy received [8, 15]. Therefore, concerted efforts are made to increase the photosynthetic rates of plants to achieve higher energy conversion efficiency [13, 15]. Growth response to elevated CO_2 concentrations in many trees suggests that increase in photosynthesis results in enhanced growth. This supports that breeding or tree improvement towards greater photosynthetic capacity is beneficial. The usefulness of increasing photosynthetic capacity can be maximized through efficient silvicultural practices which can lead to growth maximization. Since the information on photosynthesis is limited on sandalwood, there is a need to evaluate the variation in photosynthesis among different geographical locations both within and between its natural range. However, studying the photosynthesis or related parameters like water use efficiency or transpiration efficiency of a perennial species like sandalwood requires experimentation of a long duration. There are options and opportunities to evaluate growth and basic physiological parameters like photosynthesis during the early stages of development. Physiological characterization of diverse sandalwood genotypes is essential to identify elite genotypes or plus trees and also to design sandalwood breeding strategies.

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The growth performance of superior genotypes/clones can be effectively assessed or predicted using certain physiological parameters such as photosynthesis and transpiration. Net photosynthetic rate and transpiration rates of the individual leaf and total leaf area per plant are some of the important factors that determine the biomass production efficiency and also water use efficiency of trees. To evaluate the clonal/genotypic differences, attempts have been made in the trees to study the single leaf photosynthesis, leaf stomatal conductance and transpiration [10]. Significant genotypic variation has been reported in various tree species. Attempts have also been made in sandalwood to examine the variability in photosynthesis, stomatal conductance in diverse genotypes at the seedling stage [6]. Such studies are relevant because there exists a positive correlation between photosynthesis and biomass in many species. For example, the productivity of hazelnut has been predicted to be increased through increased canopy photosynthesis which was achieved by improving the light distribution inside the canopy [5]. *Hevea brasiliensis* clones with high photosynthetic parameter, especially carboxylation, efficiency produced relatively high biomass and maintained high water use efficiency [10].

2 Variation in Photosynthesis in Sandalwood Genotypes

Studies on genotypic variation in photosynthesis and photosynthetic efficiency are limited in sandalwood. Although photosynthesis is a primary determinant of productivity, unfortunately, concerted efforts have not been made in sandalwood to examine the variation in photosynthesis. Such studies are essential to look for the elite clones with maximum energy conversion potential as sandalwood is predicted to be a C_3 plant. In many plant systems, studies have been conducted to explore the options for enhancing the conversion efficiency through genetic manipulation of Calvin cycle enzyme activity, altering the properties of primary carboxylating enzyme Ribulose-1,5-bisphosphate carboxylase oxygenase (RuBisCO), increasing the non-photochemical quenching (q_N), etc. These attempts have translated into increased photosynthesis and biomass [4]. Such attempts must be made to achieve higher photosynthesis in sandalwood. It is interesting to note that significant variation was found between different sandalwood clones ($n = 37$) for gas exchange traits such as net photosynthetic trait (Pn), stomatal conductance (gs), intercellular CO_2 concentration (Ci), transpiration rate (Tr), water use efficiency (Pn/gs) [WUE] and carboxylation efficiency (Pn/Ci). The maximum and minimum values for different gas exchange traits were Pn (6.33–12.40 μ mol m^{-2} s^{-1}; Fig. 1) Ci (244–313 $\mu l\, l^{-1}$; Fig. 2), Tr (3.51–6.16 mol m^{-2} s^{-1}; Fig. 3), gs (220–469 mmol m^{-2} s^{-1} Fig. 4), WUE (0.014–0.040 μ mol milli mol^{-1}; Fig. 5) and carboxylation efficiency (0.022–0.043 μ mol m^{-2} s^{-1} $\mu l\, l^{-1}$; Fig. 6) [6].

There is no information on photosynthesis at tree canopy level in sandalwood. Attempts have been made to examine the variation in photosynthesis at the seedling level using growth regulators, cytokinin. It is well known that cytokinin plays an essential role in plant growth and development and delays senescence. Liu et al. [7]

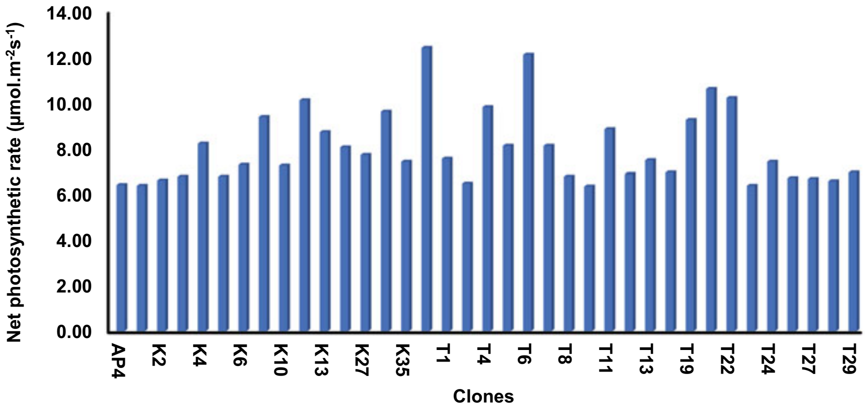

Fig. 1 Variation in sandalwood clones for net photosynthetic rate

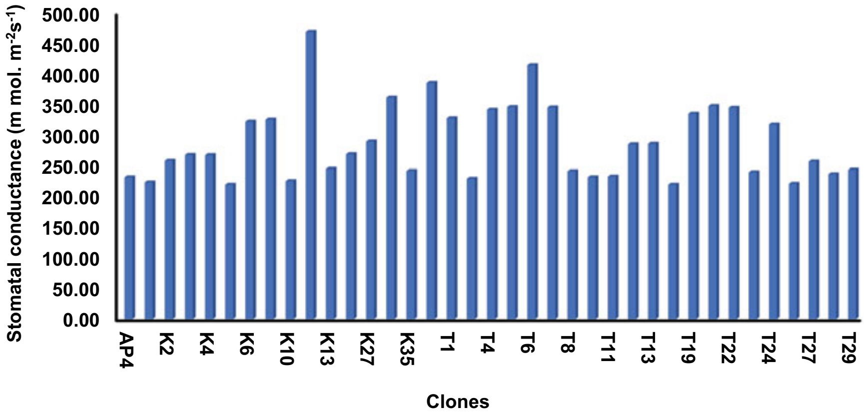

Fig. 2 Variation in sandalwood clones for stomatal conductance

demonstrated that exogenous application of benzyladenine (BA) at a concentration of 1 mg/l enhanced the Pn and WUE of Indian sandalwood seedlings. The authors also reported an increased accumulation of photosynthetic pigment under BA treatment. These studies suggest that there are ample opportunities to increase photosynthesis using growth hormones. Although it may be difficult to modulate or increase the growth of sandalwood trees using growth hormones like cytokinins, foliar application of growth regulators can be attempted to increase the photosynthetic pigments, enhance the photosynthetic rate and improve seedling quality in forest nursery [7]. There are other related hormones that have a direct role in seedling establishment and growth. It is worth initiating or trying chemical manipulation of plant growth to boost the seedling vigour and growth in the nurseries.

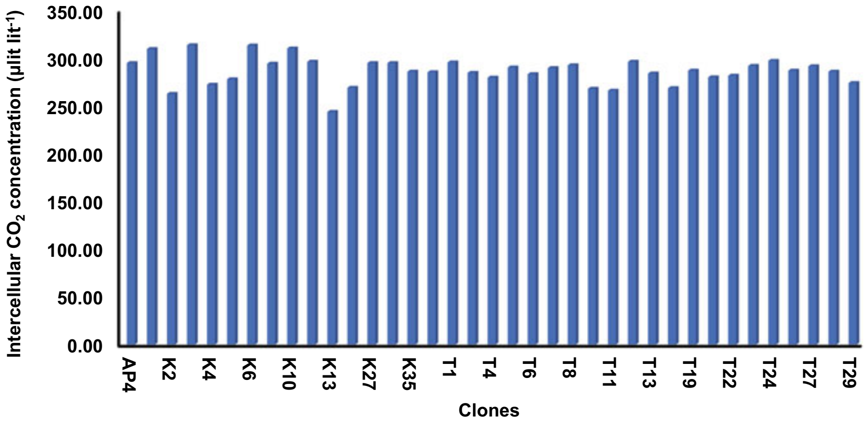

Fig. 3 Variation in sandalwood clones for intercellular CO_2 concentration

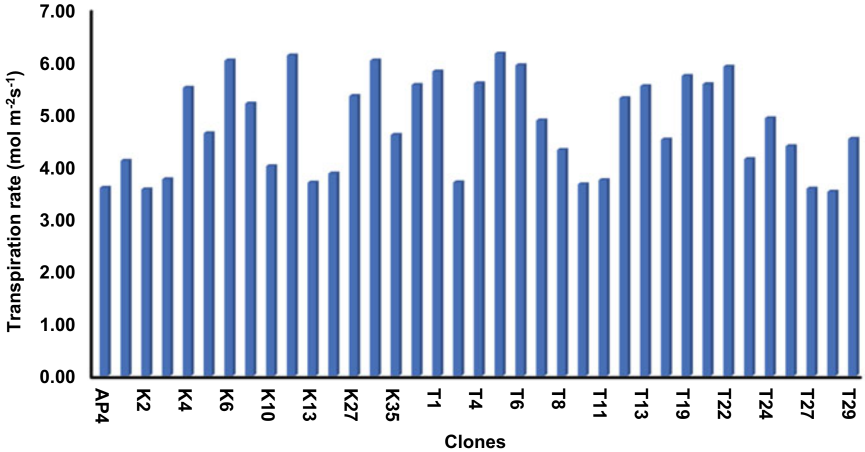

Fig. 4 Variation in sandalwood clones for transpiration rate

3 Contribution of Host Plant Photosynthesis

Santalum species are hemiparasites that partially rely on the host for their normal growth and development. Although *Santalum* has functional chloroplast to perform photosynthesis, they seem to be associated with the host through the haustorium for nutrients or other growth-promoting/nitrogenous compounds [1]. There are reports indicating that sandalwood has host preference and the host can influence plant physiological processes including photosynthesis. In a study, Lu et al. [9] examined four different host species (two nitrogenous and non-nitrogenous) and evaluated the role of the host in sandalwood photosynthesis. The authors reported no clear

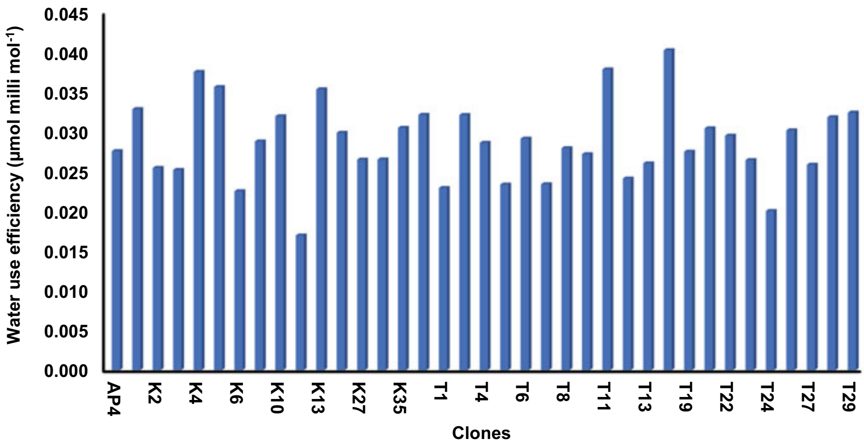

Fig. 5 Variation in sandalwood clones for water use efficiency

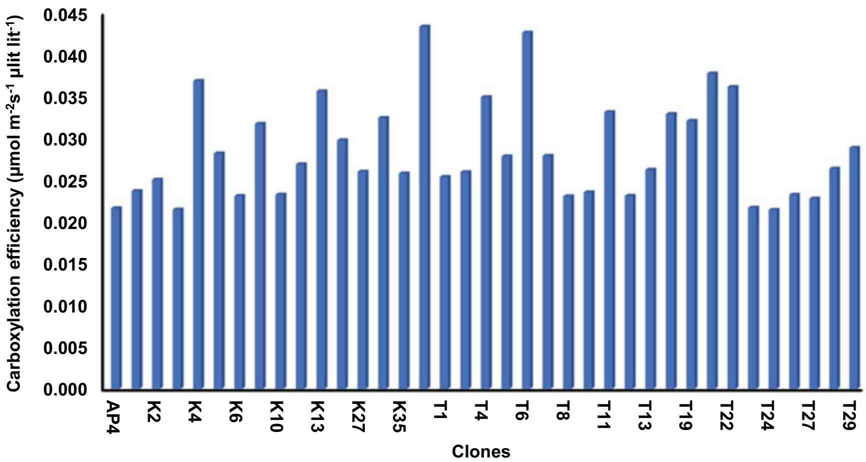

Fig. 6 Variation in sandalwood clones for carboxylation efficiency

trend between the photosynthetic rate of sandalwood and host. The transpiration rates were significantly higher in sandalwood than its associated hosts, and WUE was significantly higher in hosts than in sandalwood. Similarly, Rocha et al. [12] examined the influence of host plant on photosynthesis of field-grown sandalwood tree. Sandalwood tree growing with the host had significantly higher photosynthesis than the trees without the host plant. Even though the host governs the growth of sandalwood by increasing rates of photosynthesis, focused studies are required on elucidating the impact of diversified hosts on sandalwood photosynthesis and growth.

4 Factors Determining the Photosynthetic Rate

Photosynthetic rates are governed by several external and endogenous factors. Variability in photosynthesis reported in sandalwood could be associated with biochemical and anatomical features which directly or indirectly contribute to stomatal and mesophyll limitations of photosynthesis. There are no studies in sandalwood on biochemical factors and anatomical features contributing to the variation in photosynthesis. Some of the limitations associated with photosynthesis can be examined using response curves of photosynthesis (Pn) as a function of sub-stomatal CO_2 concentration (Ci) also known as Pn/Ci curves [10]. It has also been demonstrated that most of the observed variations in photosynthesis in diverse species were attributed to the differences of variation in photosynthetic capacity, especially carboxylation efficiency and Ribulose 1,5-bisphosphate (RUBP) regeneration [14]. In many crops, increasing RuBisCO carboxylation efficiency is considered as an alternative to improve or to sustain photosynthesis [11]. From this context, there is a need to diversify our attention on understanding or examining the factors governing the variation in sandalwood photosynthesis and use the information for targeted tree improvement programmes. There are studies suggesting that variation in photosynthesis is determined by acclimatization to a particular environmental condition. As sandalwood is a hemi-root parasite, host growth conditions and stages i have a direct influence on sandalwood photosynthesis and growth.

Stomatal and mesophyll conductance are considered key trait contributing to photosynthesis. It is interesting to study the influence of host on stomatal and mesophyll limitations on photosynthesis. Such studies would help in identifying the right combination of the host to sustain the photosynthesis under diverse climatic conditions. The stomatal movement which regulates the stomatal limitation has not been examined in sandalwood. Stomata open and close in response to changes in environmental cues such as water availability, light distribution, vapour pressure difference and also plant hydraulic capacity which in turn depends on host interaction. There was significant linear positive relationship between net photosynthetic rate and stomatal conductance ($r = 0.80$, $p < 0.001$; Fig. 7) [6] suggesting that photosynthesis is predominantly controlled by stomatal factors. Therefore, sustaining stomatal conductance is crucial for higher photosynthesis in sandalwood. As sandalwood is naturally found in harsh conditions where there is less water and high VPD is common, low photosynthesis is likely associated with high stomatal resistance under such conditions. Sandalwood being a light demander, distribution of photosynthetic active radiation (PAR) can also have a direct influence on canopy photosynthesis. Therefore, it is important to make sure that host trees should not provide shade and reduce the PAR availability which might limit photosynthesis.

Night-time stomatal conductance and associated transpiration seem to be contributing to growth and development although there are no clear emerging trends [2]. Night-time transpiration can vary depending on the season and growth condition, and the water loss during the night time is not restricted to plants that are grown under particular conditions. Losing water in significant quantities during the

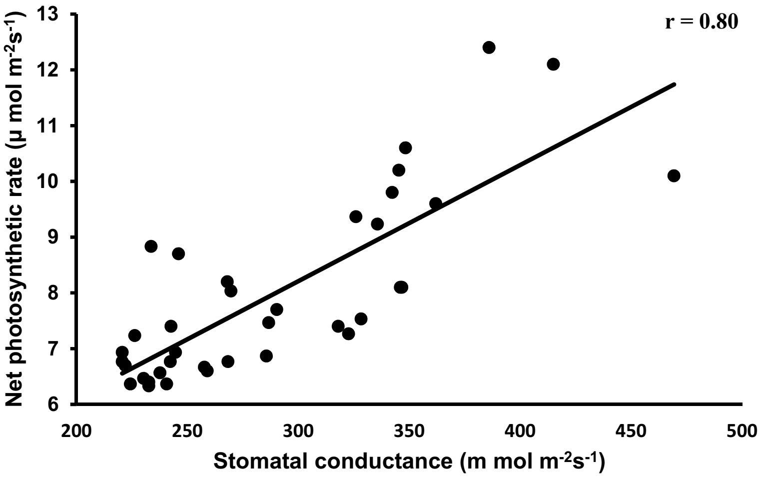

Fig. 7 Correlation matrix between net photosynthetic rate and stomatal conductance

night without associated carbon gain must have some ecological significance. Such studies are needed in sandalwood which is lacking. In *Betula papyrifera* (paper birch) high night-time transpiration was associated with a rapid growth rate [3]. Therefore, night-time transpiration can be used as an indicator for rapid growth if phenotyped critically.

5 Concluding Remarks

Despite the economic importance of sandalwood trees, information describing tree photosynthesis is limited. As a consequence, the interpretation of canopy photosynthesis and associated events relies on comparative analysis using data from other tree systems or crops. The significant diversity of the photosynthetic process of different plant species has been reported. Physiological understanding of sandalwood and host plant photosynthesis is needed, and such data would form the basis for designing strategies to increase photosynthesis for optimum productivity under a variety of soil and climatic conditions of sandalwood.

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Chapter 25
Omics in Sandalwood

H. V. Thulasiram, Rekha R. Warrier, and K. N. Nataraja

1 Introduction

The modern molecular biology techniques and tools have become essential to biological research. Rapid progress in high-throughput data generation and analysis has enabled us to perform systems biology research and to offer opportunities to advance 'omics sciences' in tree species. The processes of molecular characterization, mapping, prospecting genes and functional validation, and comprehending complex traits in tree systems have become affordable.

Genome information of tree species enables understanding complexity of the genome, genes and gene functions. This helps to speed up genetic improvement programmes and targeted trait manipulation using diverse molecular tools and techniques. The massively parallel DNA sequencing technology also known as next-generation sequencing (NGS) has created opportunities for rapid genome sequencing and gene expression analysis. The high-throughput, NGS technologies provide unique opportunities to obtain high-quality data from small amounts of tissues or cells to address a wide range of biological questions. Innovative bioinformatics tools are helping us to examine the unique genomic features of different organisms, and such data sets support the studies on evolutionary relationships, and aid in the assessment

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of genetic diversity. From this context, it is important to generate genomic information in important tress like sandal which would pave the way for targeted tree improvement, planning for sustainable use and conservation.

2 Need of Data on Omics and Relevance of Omic-Based Approaches in Trees

Genomics, transcriptomics, proteomics, metabolomics, metagenomics, epigenomics, etc., are some of the most popular 'omics' technologies available today. Genomics and transcriptomics have been applied to various aspects of research in trees. Genomics in forest trees focused on genetic mapping and DNA sequencing in the initial years. Genomics provided a new platform for the high-throughput genetic analysis of forest trees. With more of research on the applications of genomics, prediction models for breeding, defining species specific and site adaptations, detecting and characterizing variations, revealing the mechanisms of gender determination and flowering, and decoding complex regulatory networks underlying quantitative traits [60] are some of the new areas. Genomics will continue to play a major role in deciphering the mechanisms underlying trees' adaptation and evolution. The information developed will enable innovative and scientific management to preserve natural forests' adaptability and intensively managed plantations.

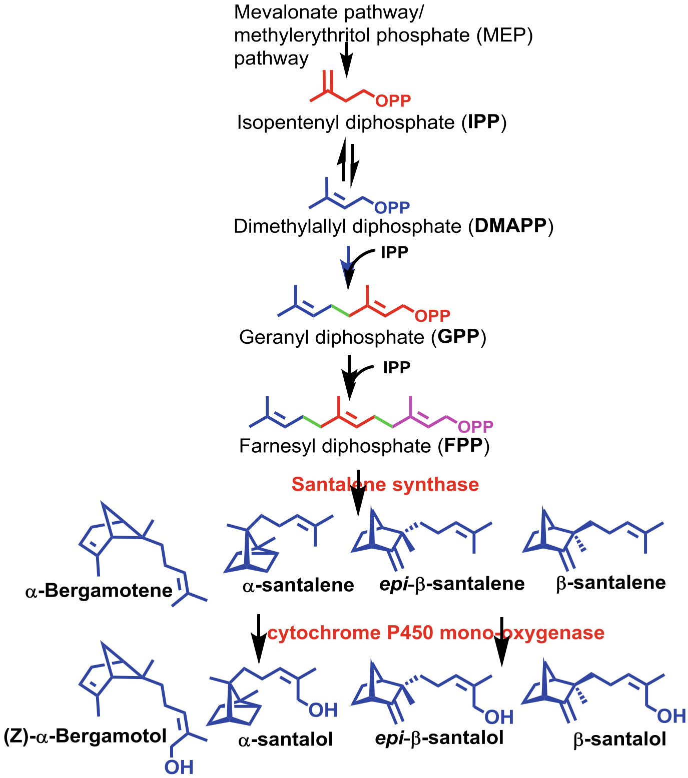
Transcriptomics provide information on various aspects of tree biology such as the regulatory network of age effects on the wood formation processes and pathways, genes controlling the wood formation, phylogenetic relationships based on multiple species and answer the functional differences between orthologous genes after species divergence in different environments [24]. Metabolomics, the understanding of end products of complex biochemical cascades link the genome, transcriptome and proteome to phenotype. Metabolomics can be used to determine relative and absolute amounts of metabolites from a wide range of tissues and diverse geoclimatic environments [37, 38]. A new concept of "trans-omics" a comprehensive analysis approach using layers of omics datasets has also evolved [66]. This data integration has created exciting opportunities and immense challenges for scientists from varied disciplines. Understanding responses to stress, the molecular basis of genetic variation and evolution of species are forestry areas where 'omics' finds direct application. Knowledge gained through the use of 'omics' technologies can help support forests adapt to the challenges they would face in the future. Tools, resources, databases and software for analysis and visualization of proteomics and metabolomics data [39] are being updated regularly.

Forest trees are underrepresented among available plant genome sequences. The major challenge is the large genome size of these species, with most ranging from 18 to 35 Gbp [34]. The first forest tree genome sequence to be published was black cottonwood *Populus trichocarpa* [59]. More than a decade now, rapidly evolving 'omics' has advanced our understanding of tree growth and development and response for environmental stresses [17]. Presently, 56 full genomes are available in the National Centre for Biological Information (NCBI) genome database. However, most of the sequence data generated are not from reference genomes. Such data is, therefore, labelled non-model. A significant portion of data is obtained from genome-based or restriction site-associated sequencing and transcriptomic approaches. Major challenges in achieving high-quality reference genomes in forest trees are high heterozygosity, ploidy, gene duplications and repetitive sequences [22]. To overcome the problem of lack of reference genomes and handling huge genomes, gene discovery based on large-scale expressed sequence tags (EST) and complimentary DNA (cDNA) sequencing has been adopted in forestry [34, 44].

3 Status of 'Omics' Research in Sandalwood

Sandalwood oil is commercially produced by steam distillation of heartwood chip with varying yield from 4 to 7% from a well-matured tree. Among the reported constituents of sandalwood oil, major components are sesquiterpene alcohols identified as (*Z*)-α-santalol, (*Z*)-β-santalol, (*Z*)-α-bergamotol, (*Z*)-*epi*-β-santalol along with minor quantities of parental hydrocarbons, α-santalene, β-santalene, α-bergamotene, *epi*-β-santalene, sesquisabinene hydrates, α-curcumene, β-curcumene, γ-curcumene, β-bisabolene, α-bisabolol, cedrene, cedrol, sesquisabinene, triterpenoids and phenylpropanoids. (*Z*)-α- and (*Z*)-β-santalols are the major constituents (~80%) of the essential oil from a well-matured tree heartwood and are responsible for most of the biological activity of the heartwood oil. Specific aroma of sandalwood oil is produced by mainly two compounds (*Z*)-α- and (*Z*)-β-santalols. Therefore, in order to maintain the quality of Sandalwood oil, ISO standards have been formulated for *S. album* heartwood oil with (*Z*)-α-santalol: 41–55%, (*Z*)-β-santalol: 16–24%. Isopentenyl diphosphate (IPP) and Dimethylallyl diphosphate (DMAPP) which are synthesized from either the melavonate (MVA) or methylerythritol phosphate (MEP) pathway condense in a head to tail fashion to generate farnesyl diphosphate (*E,E*-FPP) catalysed by farnesyl diphosphate synthase (FDS). In the next step, sesquiterpene synthases catalyse the cyclization of FPP to produce sesquiterpene hydrocarbon skeletons which will undergo hydroxylation at their *cis*-methyl position to form corresponding sesquiterpene alcohols including santalols catalysed by CYP450 systems (Scheme 1).

Genomics: Mahesh et al. [35] applied an integrated genomic, transcriptomic and proteomic approach to assemble and annotate the Indian sandalwood genome. A draft map of the entire genome of size 221 Mb was established. Annotations revealed about 40,000 protein-coding genes and about 72,000 unique peptides, confirming about 10,000 predicted genes. The integrated approach revealed fifty-three novel proteins, 34 gene-correction events, reassigning potential noncoding RNAs as bona fide protein-coding messenger RNAs. In another study, though the estimated genome



Scheme 1 Sesquiterpene biosynthesis in *S. album*

size was higher (286 Mb), the protein-coding genes identified were less (37,500). A consensus chloroplast genome of 147.25 kb size was also reconstructed [14].

Though large-scale transcriptomic data sets were generated for sandalwood [7, 18, 58, 68, 69], a whole-genome sequence was reported in 2018 only. Three draft genome sequences of Indian sandalwood are available in the NCBI database. Two of them are from India, while one is from China. The first draft genome of *S. album* [35] used as a reference genome [14] was from a single tree. Later genomes have been generated based on increased depth of sequencing and improved algorithms. There have been revisions in the genomes submitted. However, there is a need for improving data on the genomic resources in Indian sandalwood. High depth sequencing, resequencing and improved assembly, annotation and analysis would enable a more informative reference genome for the species.

Apart from the whole genome and transcriptome, *S. album* has also been studied for its chloroplast genome/plastome. The circular chloroplast genome (cpDNA) sequence of *S. album* is 0.14 Mbp in length, contains a large single-copy region (LSC) of 0.08 Mbp and a small single-copy region (SSC) of 0.01 Mbp, separated by a pair of inverted repeats (IR) regions of 0.02 Mbp. The genome contains 123 genes, including 80 protein-coding genes, 8 ribosomal RNA genes and 35 transfer RNA genes [65]. It also contains seven pseudo-genes and five deleted genes [20]. Barcodes from cpDNA, namely rbcL, matK and trnH-psbA, obtained from chloroplast genomic sequences help to distinguish wood adulterants of *S. album* [16]. Jiao et al. [25] developed four conserved DNA barcodes, trnK, trnL, matK and psbAtrnH. Of these, a combination of psbAtrnH + trnK DNA barcodes helped distinguish five different *Santalum* species.

Transcriptomics: The first transcript study in Indian sandalwood used restriction mapping and hybridization to code a PR1 gene [4]. Cloned products of Terpene synthase (TPS) genes produced a mixture of bergamotene and santalenes. The santalene and bisabolene/bisabolol synthases present in the genus suggest that these compounds played a significant role in its evolution [28, 58]. Tissue-specific expression of santalol biosynthesis genes in Indian sandalwood [49–51] utilized transcriptomics and proteomics. Suppression subtraction hybridization (SSH) using heartwood mRNA from *a* > 30-year-old and *a* < 10-year-old tree yielded unique clones in mature wood. They isolated two sesquiterpene synthases, farnesyl diphosphate synthase (SaFDS) and santalene synthase (SaSS) [28, 58]. They functionally characterized the genes through enzyme assays and tissue-specific expression in leaf (immature and mature), wood (immature sapwood, mature sapwood, mature transition zone and mature heartwood) and fruit (unripened and ripened) tissues by RT-PCR. The genes sesquisabinene synthase (SaSQS 1 and 2), bisabolene synthase (SaBS) were cloned and characterized [58]. Kinetic studies and gene expression level studies showed that exceptionally high kinetic efficiency of santalene synthase and its high expression level at the interface of heartwood and sapwood indicating the basis for high level of santalene/santalols in the heartwood [58]. These results paved way for in vivo production of sandalwood sesquiterpenes in genetically tractable heterologous systems. Misra and Dey [36] found that sesquiterpene biosynthesis and accumulation are highly polymorphic by studying the transcript levels of 1-deoxy-D-xylulose-5phosphate synthase (DXS), farnesyl diphosphate synthase, sesqui- and mono-TPS in different tissues. Diaz-Chavez et al. [18] mined the transcriptome database of *S. album* for candidate cytochrome P450 genes, and characterized cDNAs encoding a small family of ten cytochrome P450-dependent monooxygenases. Annotated as SaCYP76F37v1 &2, SaCYP76F38v1 &2, SaCYP76F39v1 & 2, SaCYP76F40 to 43, nine genes were functionally characterized using in vitro assays to encode santalene and bergamotene oxidases.

Zhang et al. [68] identified changes in gene expression and metabolic pathways associated with the development of the *S. album* haustorium through RNA sequencing (RNA-seq) analyses. They identified phytohormone-mediated regulation as a key to haustorial development. Auxin-signalling triggered haustorial initiation, while cytokinin and gibberellin biosynthesis genes effected haustorial development. Genes encoding nodulin-like proteins facilitated haustorial morphogenesis. This information provided the base for detailed exploration of molecular mechanisms in host–plant interaction in *S. album.*

The first gene discovery in sandalwood was a Terpene synthase (TPS). Primers of the gene from sandalwood leaf and wood tissues amplified two genomic fragments. From the fragments, the cDNAs—SamonoTPS1 and SasesquiTPS1—were synthesized. The translated products were a mixture of terpenoids available in trace quantities in the plant. Though not responsible for santalene biosynthesis, these genes paved the way for the discovery of TPS genes in sandalwood [26, 27]. The research groups [28, 58] further characterized a multiproduct terpene synthase, santalene synthase which catalysed the formation of six sesquiterpenes such as α-santalene, exo-α-bergamotene, epi-β-santalene, β-santalene as a major products with (*E*)-β-farnesene and exo-β-bergamotene as a minor products when incubated the recombinant protein with (*E,E*)-Farnesyl diphosphate (FPP).

A PCR-based cloning strategy was used to isolate cDNAs encoding four multi-product terpene synthases from *S. spicatum* that were functionally expressed in *E. coli*, including a santalene synthase. The functions of these enzymes explain 25 percent of the oil components and several P450 sequences have been mined as potential contributors to oil production [40]. In-depth transcriptome analysis revealed 12,537 contigs, seven different TPSs, several cytochromes P450 and allylic phosphatases. The cDNA of SspiTPS4 was identified as a multiproduct sesquisabinene B synthase [41, 42].

Though earlier studies attempted to understand the santalene and bergamotene synthesis pathways, researchers were unable to replicate the actual composition of the oil. This was because sandalwood oil contains Z isomers of the different oils, namely (Z)-α-santalol, (Z)-β-santalol, (Z)-α-exo-bergamotol and (Z)-epi-β-santalol. Celedon et al. [7] realized that sandalwood cytochromes P450 of the CYP76F subfamily hydroxylated santalenes and bergamotene; however, these enzymes produced mostly (E)-santalols and (E)-α-exo-bergamotol. They deduced through a combination of methods that a gene and subsequently its enzyme in cytochrome P450 is responsible for the fragrance defining, the final step in the biosynthesis of (Z)-santalols. Different santalene/bergamotene hydroxylases stereoselectively produce (E)- or (Z)-sesquiterpenols. The genes encoding (Z)-specific P450s contribute to sandalwood oil formation when co-expressed in the heartwood with other genes. This information, along with the identification of heartwood-specific transcriptome signature SaCYP736A167 for sesquiterpenoid biosynthesis, completed the discovery of the critical components of sandalwood fragrance. Tissue-specific RNA-seq analysis across the gradient of developing *S. album* wood tissues, including the outer sapwood (SW), the intermediate transition zone (TZ), and the inner oil-accumulating heartwood (HW) confirmed this. The complete fragrance biosynthetic pathway was later reconstructed in yeast (*Saccharomyces cerevisiae*) [8, 9, 70].

To generate information about the molecular mechanisms that underlie the cold stress response in *S. album*, to increase its area under cultivation in cold regions in China, physiological and transcriptomic changes in sandalwood seedlings exposed to 4 °C for 0–48 h were characterized [69]. Cold stress induced accumulation of malondialdehyde, proline and soluble carbohydrates, and increased the levels of antioxidants. Eight candidate genes of the terpenoid biosynthetic pathway were significantly involved in the cold stress response. Gene expression analyses using qRT-PCR showed a peak in the accumulation of SaCBF2 to 4, 50-fold more than control leaves and roots following 12 and 24 h of cold stress, respectively. The C-related Binding Factor (CBF)-dependent pathway may play a crucial role in increasing cold tolerance in sandalwood.

Following the generation of transcriptomic and genomic data, appropriate reference genes for RT-qPCR in four tissues (stem, root, leaf and callus) were identified. Thirteen candidate reference genes were selected and validated by SaSSy gene expression analysis. The results revealed that data varied depending on experimental conditions suggesting a need for further refinement [62]. The group further identified 64 SaWRKY genes, a superfamily of transcription factors (TF). Among them, SaWRKY1 was significantly upregulated by salicylic acid and methyl jasmonate, suggesting imparting salinity tolerance to *S. album* [63]. Further to the role of transcription factors, the team also identified a 1390-bp promoter sequence of the Bisabolene synthetase (SaBS) gene which carry specific environment stresses and phytohormone-activated cis-acting elements [64].

4 Proteomics and Metabolomics

One of the first reports in understanding molecular mechanisms in sandalwood was to isolate and clone a proline-rich protein (PRP) cDNA from leaves of *S. album* [3, 4]. Further several recombinant proteins were purified to homogeneity by over expression of genes in various expression systems as discussed above. Attempts were made to understand the proteome in sandalwood using mass spectrometry [35]. Over one million tandem mass spectra were generated which led to identification of 72,000 peptides which were mapped to over 10,000 predicted genes in sandalwood genome. Such analysis is needed to understand the pathways associated with diverse processes in sandalwood.

The heartwood oil of *S. album* shows a complex mixture of closely related terpenoids consisting of over 12 mono- and 90 sesquiterpenoids. Sandalwood oil is commercially produced by steam distillation of heartwood chip with varying yield from 4 to 7% from a well-matured tree. Among the reported constituents of sandalwood oil, major components are sesquiterpene alcohols, i.e. α-santalol, β-santalol, α-bergamotol, *epi*-β-santalol along with small quantities of parental hydrocarbons, α-santalene, β-santalene, α-bergamotene, *epi*-β-santalene, α-curcumene, β-curcumene, γ-curcumene, β-bisabolene, α-bisabolol, cedrene, cedrol, sesquisabinene, triterpenoids and phenylpropanoids. α- and β-santalols are the major constituents (~80%) of the essential oil from a well-matured tree (≥20 years old) and responsible for most of the biological activity. Good-quality heartwood oil extracted from a matured *S. album* tree contains (*Z*)-α-santalol (49%), (*Z*)-α-bergamotol (5%), (*Z*)-β-santalol (21%) and (*Z*)-*epi*-β-santalol (4%) with total santalol content was ≥80%.

The essential oil from stem heartwood of *S. album* has been widely investigated [2, 6, 15, 30, 55]. Sandalwood oil is an excellent base and fixative for other high-grade perfumes and, by itself, is an excellent, mild, long-lasting and sweet perfume.

The quality of sandalwood oil mainly depends on the concentration of oxygenated sesquiterpenes, *i.e.* α-santalol and β-santalol, due to which it has a pleasant characteristic aroma. Earlier reported main sesquiterpene and sesquiterpene alcohols of Indian sandalwood oil were α-santalol, β-santalol, α-bergamotol, epi-cis-β-santalol, cis-lanceol, α-bisabolol, etc. (Fig. 1a, b). The hydrocarbons sesquiterpenes such as α-santalene, β-santalene, epi-β-santalene, α-bergamotene, β-bisabolene, α-curcumene are also present in the oil which are formed through electrophilic intramolecular carbocation cyclization of farnesyl diphosphate (Fig. 1a).

5 Constituents of Oil

Several groups involved in isolation and characterization of sandalwood oil constituents by subjecting the heartwood chips for steam distillation/solvent extraction to obtain the crude mixture which was further subjected to various chromatography to isolate the pure compounds.

Over the years, many groups isolated specialized metabolites from *S. album* (Fig. 2). Demole et al. [15] carried out vacuum distillation of the 1 kg of sandalwood oil at resulting in 40.3 g of a volatile fraction which was further fractionated by using Teflon spinning band distillation column, and those fractions were subjected to column chromatography to characterize the compounds (**18–41**). The successive treatments of 3 kg of crude sandalwood oil with inorganic bases and Girard 'P' reagent and subsequent purification led to the isolation of the compounds (**42–58**) [15]. Heartwood chips of 1.53 kg were extracted with methanol. The concentrated methanol extract was suspended in 20% methanol and partitioned between hexane and ethyl acetate. Hexane extract was subjected to column chromatography [30–32]. This allowed the isolation of compounds (59–66) Fig. 4 and (94–111) Fig. 8. Ethyl acetate extract was purified over HPLC to obtain compounds (**67–77**). Christenson et al. [11] carried out steam distillation to obtain sandalwood oil which was subjected to HPLC purification to isolate compounds (**78–84**). Ochi et al. [45] carried out methanolic extract of heartwood of *S. album* and then partitioned between water and ethyl acetate. Further they carried out bioassay guided purification of ethyl acetate extract for the isolation of compounds (**85–93**). Sandalwood chips were subjected to steam distillation by Hasegawa et al. [21], and oil obtained was extracted with hexane and purified over HPLC to obtain compounds (**112–119**) (Fig. 2).

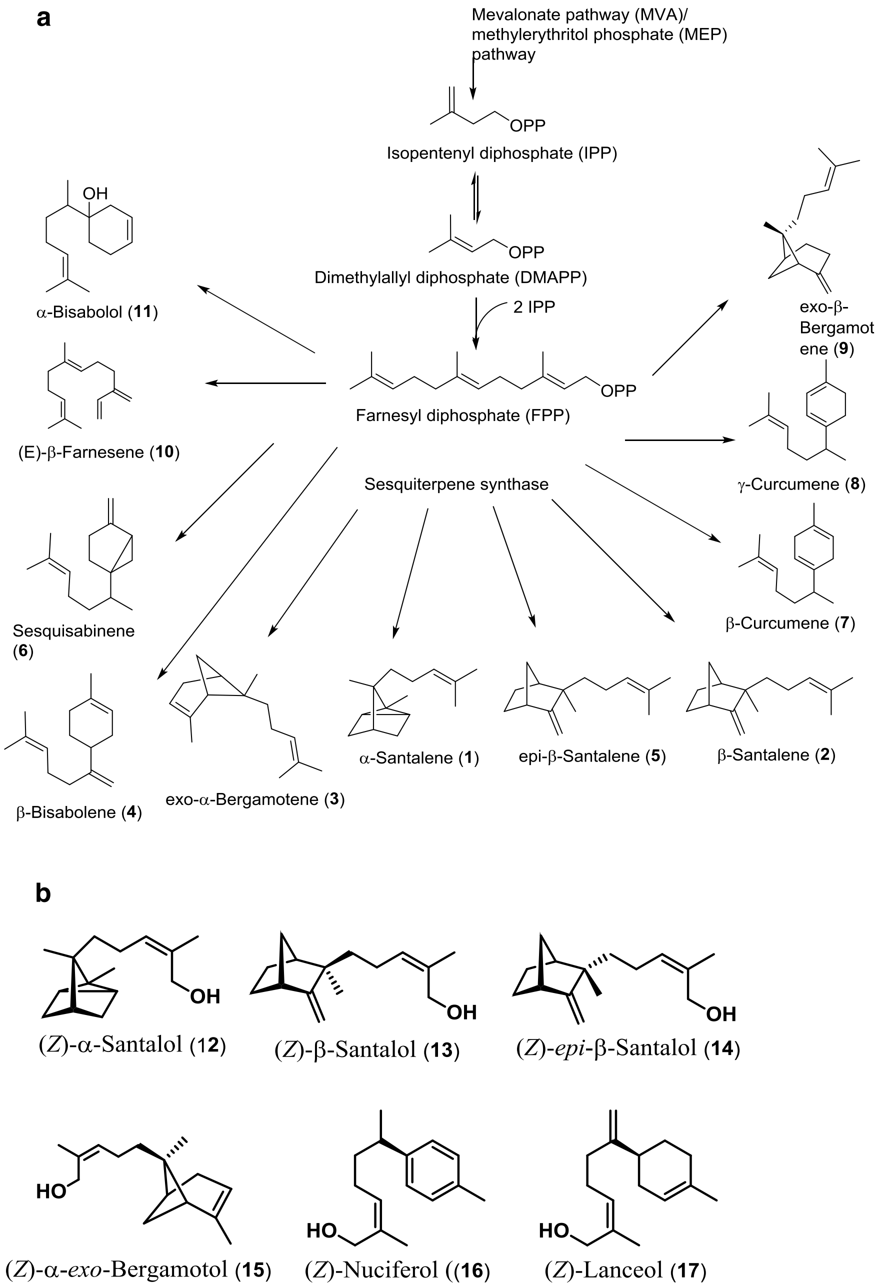


Fig. 1 **a** Sandalwood sesquiterpenes generated from cyclization of (*E*,*E*)-FPP [58]. **b** Notable sesquiterpene alcohols from sandalwood oil

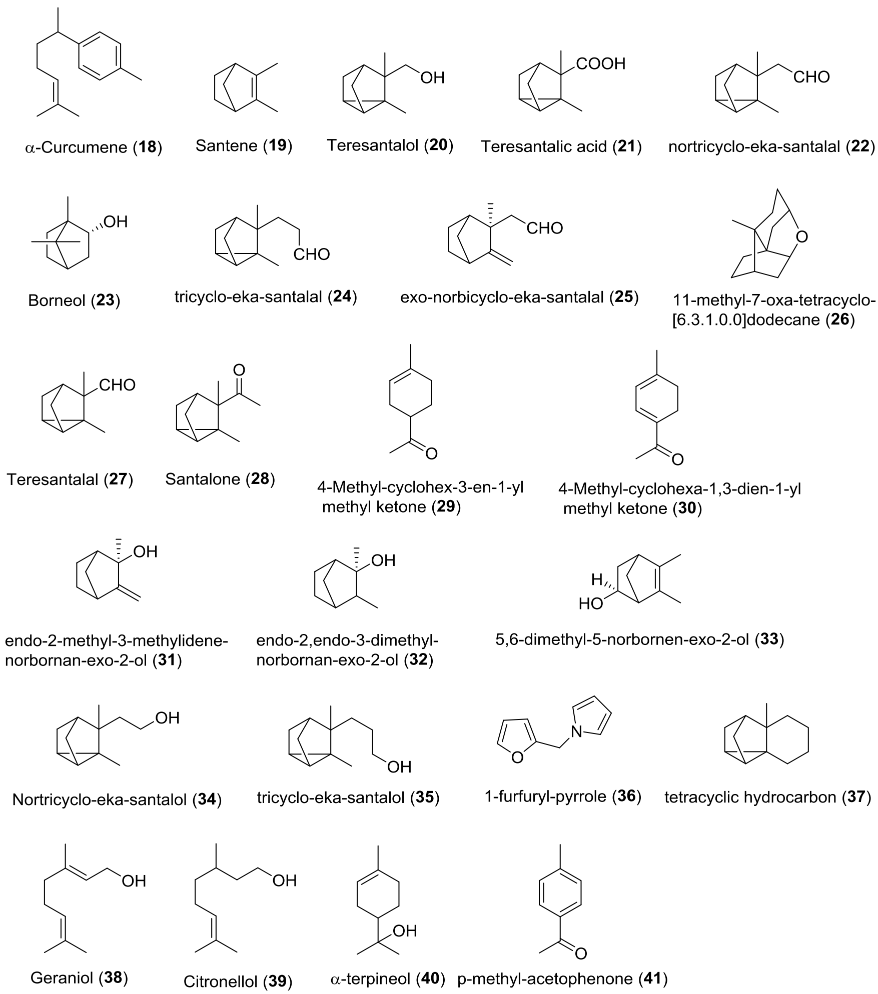
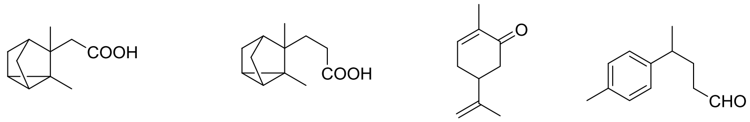
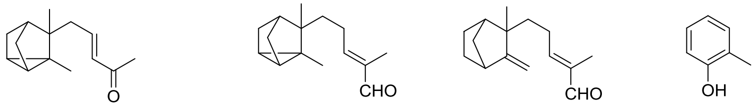


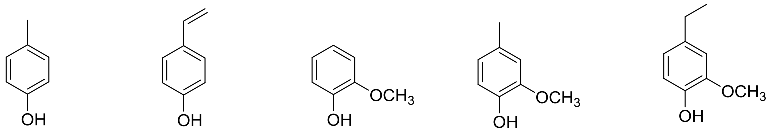
Fig. 2 Major metabolites isolated from *S. album*



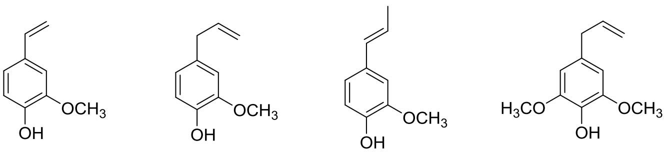
nortricyclo-eka-santalic acid (**42**) tricyclo-eka-santalic acid (**43**) Carvone (**44**) 4-(p-tolyl)-valeraldehyde (**45**)



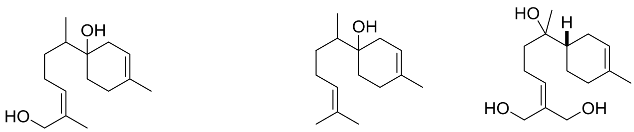
(E)-5-(2,3-dimethyl-3-nortricyclyl)-pent-3-en-2-one (**46**) (E)-α-santalal (**47**) (E)-β-santalal (**48**) ortho-cresol (**49**)



para-cresol (**50**) 4-vinylphenol (**51**) Guaiacol (**52**) 4-methylguaicol(**53**) 4-ethylguaiacol (**54**)

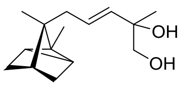


4-vinylguaiacol (**55**) Eugenol (**56**) Isoeugenol (**57**) 6-methoxyeugenol (**58**)

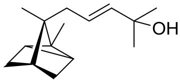


(1R,7R)-1,12-Dihydroxybisabola-3,10-diene (**59**)
(1R,7S)-1,12-Dihydroxybisabola-3,10-diene (**60**)
β–Bisabolol (6**1**)
7,12,13-Trihydroxybisabola-3,10-diene (**62**)

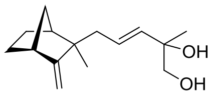
Fig. 2 (continued)



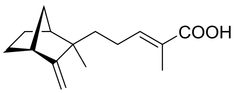
9(E)-11-Hydroxy-α-santalol (**63**)



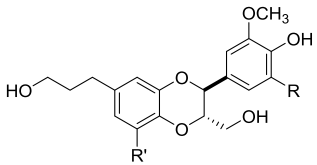
α-Photosantalol A (**64**)



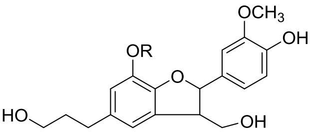
9(E)-11Hydroxy-β-santalol (**65**)



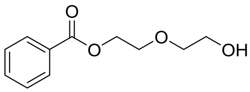
10(E)-β-Santalic acid (**66**)



R = OH,$\Delta^{7'(8')}$, R' = OCH_3
5-[(2S,3S)-2,3-dihydro-3-(hydroxymethyl)-7-[(1E)-3-hydroxy-1-propenyl]-5-methoxy-1,4-benzodioxin-2-yl]-3-methoxy-1,2-benzenediol (**67**);
R = R' = OCH_3
7S,8S-Nitidanin (**68**);
R = R' = H
(7S,8S)-3-methoxy-3',7-epoxy-8,4'-oxyneoligna-4,9,9'-triol (**69**)

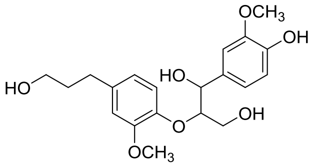


R = H
(7S,8R)-dihydro-3'-hydroxy-8-hydroxy-methyl-7-(4-hydroxy-3-methoxy-phenyl)-1'-benzofuranpropanol (**70**)
R = CH_3
(7R, 8S)dihydrodehydrodiconiferyl alcohol (**71**)

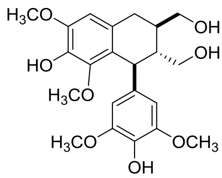


Diethylene glycol monobenzoate (**72**)

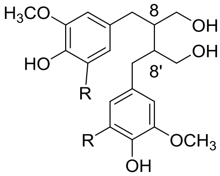
Fig. 2 (continued)



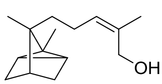
7,8-erythro-4,9,9'-trihydroxy-3,3'-dimethoxy-8.0.4'-neolignan (**73**)
7,8-threo-4,9,9'-trihydroxy-3,3'-dimethoxy-8.0.4'-neolignan (**74**)



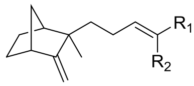
(7'S,8R,8'R)-lyoniresinol (**75**)



(8S,8'S) R = OCH_3 : 2,3-bis[(4-hydroxy-3,5-dimethoxyphenyl)-methyl]-1,4-butanediol (**76**)
(8R,8'R) R = H : (-)-secoisolariciresinol (**77**)

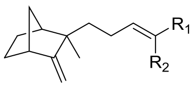


α-santalol (**78**)

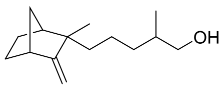


R_1 = Me, R_2 = CH_2OH
β-santalol (**79**)

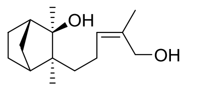
R_1 = CH_2OH, R_2 = Me
trans-β-santalol (**80**)



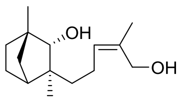
R_1 = Me, R_2 = CH_2OH
epi-cis-β-santalol (**81**);
R_1,R_2 = Me
epi-β-santalene (**82**);
R_1 = CHO, R_2 =Me
epi-trans-β-santalal (**83**)



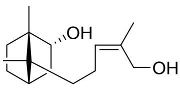
epi-dihydro-β-santalol (**84**)



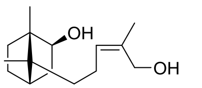
(Z)-2β-hydroxy-14-hydro-β-santalol (**85**)



(Z)-2α-hydroxyalbumol (**86**)

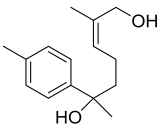


2R-(Z)-campherene-2,13-diol (**87**)

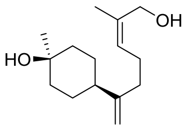


(Z)-campherene-2β,13-diol (**88**)

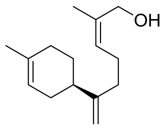
Fig. 2 (continued)



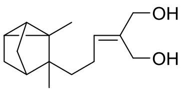
(Z)-7-hydroxynuciferol (**89**)



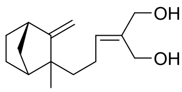
(Z)-1β-hydroxy-2-hydrolanceol (**90**)



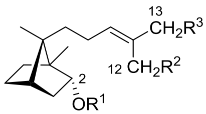
(Z)-lanceol (**91**)



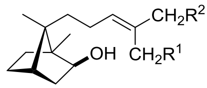
α-santaldiol (**92**)



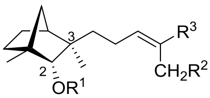
β-santaldiol (**93**)



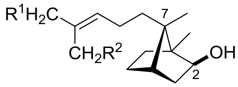
R^1 = H , R^2 = OH , R^3 = OH
(2R,7R)-2,12,13-trihydroxy-10-campherene (**94**);
R^1 = H, R^2 = OH, R^3 = H
(2R,7R)-2,12-dihydroxy-10(Z)-campherene (**95**);
R^1 =R^2 =R^3 = H
(2R,7R)-2-hydroxy-10(Z)-campherene(**96**)



R^1 = OH , R^2 = OH
(2S,7R)-2,12,13-trihydroxy-10(Z)-campherene (**97**);
R^1 = OH, R^2 = H
(2S,7R)-2,12-dihydroxy-10(Z)-campherene (**98**);
R^1 =R^2 = H
(2S,7R)-2-hydroxy-10(Z)-campherene (**99**)

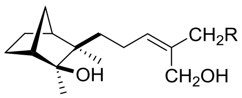


R^1 = H, R^2 = OH, R^3 = CH_2OH
(2R,3R)-13-hydroxysandalnol (**100**);
R^1 = H, R^2 = OH, R^3 = CH_3
(2R,3R)-10(Z)-sandalnol (**101**);
R^1 = H, R^2 = H, R^3 = CHO
(2R*,3R*)-10E-sandalnol-13-al (**102**)

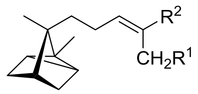


R^1 =R^2 = OH
(2S*,7S*)-2,12,13-trihydroxy-10-campherene (**103**);
R^1 = R^2 = H
(2S*,7S*)-2-hydroxy-10-campherene (**104**)

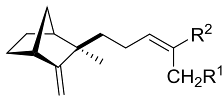
Fig. 2 (continued)



R = OH
(2S*,3R*)-13hydroxy-neosandalnol (**105**);
R = H
(2S,3R)-10(Z)-neosandalnol (**106**)

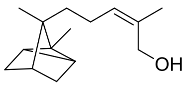


R^1 = H, R^2 = CHO
(E)- α-santalal (**107**);
R^1 = OH, R^2 = CH$_2$OH
α-santaldiol (**108**);
R^1 = H, R^2 = COOH
α-santalenoic acid (**109**)

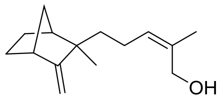


R^1 = H, R^2 = CHO

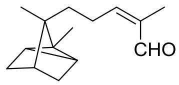
(E)- β-santalal (**110**);
R^1 = OH, R^2 =
CH$_2$OH
β-santaldiol (**111**)



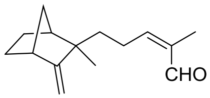
(Z)-α-santalol (**112**)



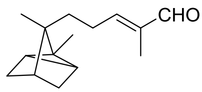
(Z)-β-santalol (**113**)



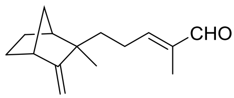
(Z)-α-santalal (**114**)



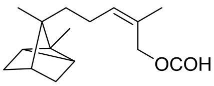
(Z)-β-santalal (**115**)



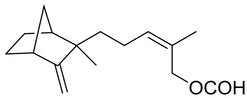
(E)-α-santalal (**116**)



(E)-β-santalal (**117**)



(Z)-α-santalyl formate (**118**)



(Z)-β-santalyl formate (**119**)

Fig. 2 (continued)

6 Artificial Synthesis of Metabolites and Their Applications

Several groups have worked on the synthesis of sesquiterpenoids specifically santalenes and santalols. β-santalene was regio and stereoselectively transformed to β-santalol by an N-oxide, sigmatropic rearrangement [61]. α-santalol was synthesized from a functionalized prenyl fragment having a tricyclene component by the cross-coupling reaction [53]. Stereospecific total synthesis of α-santalol was achieved by chain extension using 3-trimethylsilylpropargyl lithium, stereo and position-specific addition of diisobutylaluminium hydride to the lithium salt of a propargylic alcohol and by stereospecific methoxycarbonylation of a vinylic iodide by nickel carbonyl and sodium methoxide in methanol [13]. Synthesis of rec-(Z)-β-santalol was achieved in five steps. It involved catalytic coupling of santene with methyl pentadienal diacetate and (Z)-selective catalytic 1,4-hydrogenation of dienol acetate as key steps [5]. With the help of asymmetric Diels–Alder addition reaction synthesis of enantiomerically pure (-)-β-santalene was accomplished [1]. Lewis-acid promoted Diels–Alder reaction yielded (-)-β-santalene with efficient enantioselectivity [47]. Π facial cycloaddition in the evolution of asymmetric Diels—Alder reaction and Wittig reaction involved in the synthesis of (-)-β-santalene [48]. Diastereo and enantio controlled synthesis of (-)-β-santalene starting from (+)-norcamphor was achieved [52]. Synthesis involving acid catalysed rearrangement of lactone with subsequent reduction followed by Wittig reaction led to the formation of (±)-β-santalene and (±)-β-santalol [10]. Enantioselective synthesis of (-)-β-santalol was achieved, it involves copper catalysed cyclization fragmentation of an enynol as a key step [19]. Selective carbine insertion into C-H bond of α-diazo ketone played important role in the synthesis of (-)-β-santalene [57]. Stereospecific synthesis of (±)-β-santalol was achieved in four steps [54]. (±)-α-santalene was synthesized starting with (±)-campherenone [22]. Synthesis of α-santalene and α-santalol were initiated with Π-Bromotricyclene [29]. Synthesis of α-santalene was achieved in six steps starting with (+)-α-bromocamphor [12]. Oxidative degradation of norbornane-2-carboxylic acid followed by stereoselective alkylation and subsequent Wittig reaction and reduction resulted in formation of β-santalol [33]. β-santalol was synthesized from camphenesultone in seven steps [56]. Synthesis of α-santalene was achieved starting with tricyclic alcohol [43]. However, there is no efficient and economically viable synthesis for industrial production of these high-value fragrance. On the other hand, synthetic biology platforms are highly promising for the industrial production these sesquiterpenes and their mixtures.

Studies reported that topical application of (*Z*)-α-santalol (5%, w/v) showed significant chemopreventive effects on 7,12-dimethylbenzanthracene (DMBA)-initiated and 12-*O*-tetradecanoylphorbol-13-acetate (TPA)-promoted skin cancer development, and inhibited ornithine decarboxylase (ODC) activity and DNA synthesis induced by TPA in both CD-1 and SENCAR mice. Furthermore, (*Z*)-α-santalol (5%, w/v) application significantly inhibited skin tumorigenesis by

UVB-initiated and TPA-promoted, DMBA-initiated and UVB-promoted, and UVB-initiated and UVB-promoted in SKH-1 hairless mice, and also suppressed UVB-caused induction of epidermal ODC activity in SKH-1 mice. Dose–response experiment indicated that 5% of (*Z*)-α-santalol (w/v) application resulted in a relatively higher inhibition of skin tumorigenesis induced by UVB in SKH-1 mice. Both in vivo and in vitro models suggested that one of the possible mechanisms of its chemopreventive effects is related to induction of apoptosis through both extrinsic and intrinsic pathways. Zhang et al. [67] studied effects of (*Z*)-α-santalol in G2/M phase arrest and described detailed mechanisms of G2/M phase arrest by this agent. The data demonstrated that treatment with (*Z*)-α-santalol resulted in a concentration- and time-dependent inhibition of cell viability on A431 cells and UACC-62 cells as determined by MTT assay. Treatment with (*Z*)-α-santalol (50 μM) for 12 h did not significantly decrease cell viability of A431 and UACC-62 cells. However, flow cytometric analysis of cell cycle distribution revealed that (*Z*)-α-santalol (50–75 μM) from 6 to 24 h treatment led to a 49–285% and 71–306% induction of G2/M phase in A431 cells and UACC-62 cells, respectively, as compared to control cells. These findings indicated that G2/M phase cell cycle arrest induced by (*Z*)-α-santalol treatment may be one of the mechanisms which resulted in a decrease of cell viability in A431 and UACC-62 cells after (*Z*)-α-santalol treatment.

As mentioned previously, (*Z*)-α-santalol showed moderate cytotoxic activities against HL-60 cells and exhibited negligible effect on TIG-3 cell growth even at a concentration of 40 μM. Effects of (*Z*)-α- and (*Z*)-β-santalols on selected CNS parameters were studied [46]. On intraperitoneal (*i.p.*), oral and/or intracerebroventricularly (*i.c.v.*) administration to mice, (*Z*)-α-santalol showed better effects on hypothermia and reduction in spontaneous locomotor activity than (*Z*)-β-santalol, while (*Z*)-β-santalol had better analgesic activity than (*Z*)-α-santalol. Both compounds produced the same effects on hexobarbital-induced sleeping time by *i.p.* administration (50 mg/kg) that was almost the same as that of Nitrazepam at 5 mg/kg. (*Z*)-α- and (*Z*)-β-santalols reduced both Methamphetamine and Apomorphine-induced activities. However, hypnosis, muscle relaxation, reversal of reserpine-induced hypothermia and anticonvulsive effects were not produced by (*Z*)-α- and (*Z*)-β-santalols in mice.

The in vivo antihyperglycemic and antioxidant experiments were conducted in alloxan-induced diabetic and D-galactose-mediated oxidative stress-induced male Swiss albino mice models, respectively [36]. Administration (*i.p.*) of (*Z*)-α-santalol (100 mg/kg BW) and sandalwood oil (1 g/kg BW) for a week modulated parameters such as body weight, blood glucose, serum bilirubin, liver glycogen and lipid peroxides content to normoglycemic levels in the alloxan-induced diabetic mice. Similarly, administration of (*Z*)-α-santalol (100 mg/kg BW, *i.p.*) and sandalwood oil (1 g/kg BW, *i.p.*) for two weeks altered parameters such as serum aminotransferases, alkaline phosphatase, bilirubin, superoxide dismutase, catalase, free sulfhydryl, protein carbonyl, nitric oxide, liver lipid peroxide contents and antioxidant capacity in D-galactose mediated oxidative stress induced mice. It was also observed that the other terpene components of sandalwood oil had synergistic effects on the beneficial activity exhibited by (*Z*)-α-santalol, thus demonstrating an enhanced activity with the traditionally used natural resource.

The anti-influenza A/HK (H3N2) virus activity of (*Z*)-β-santalol was evaluated in MDCK cells, and the effect of (*Z*)-β-santalol on synthesis of viral mRNAs was investigated. (*Z*)-β-Santalol was investigated for its antiviral activity against influenza A/HK (H3N2) virus using a cytopathic effect (CPE) reduction method. It exhibited anti-influenza A/HK (H3N2) virus activity of 86% with no cytotoxicity at the concentration of 100 μg/mL, by reducing the formation of a visible CPE. Oseltamivir, marketed antiviral drug, also showed moderate antiviral activity of about 83% against influenza A/HK (H_3N_2) virus at the concentration of 100 μg/mL.

7 Conclusion and Perspectives

The ‘omics’ in Indian sandalwood has been studied since 1996 although there was analysis of targeted metabolites much earlier. With the ease and affordability of molecular tools, efforts are underway to decode the genome using integrative ‘omics’ approaches. Key pathways in oil production have been unravelled, making artificial synthesis easier. Proteogenomic and transcriptomic approaches have been used for predicting gene models and to identify novel protein-coding genes in sandalwood associated with oil biosynthesis. Such studies enabled the generation of large volume of genomic resources which might be useful for future ‘omics’ efforts. Knowledge of the genes controlling secondary metabolite production has enhanced the scope for artificial sandalwood oil production in *E. coli* or yeast through metabolite engineering. In many cases, a multiomics approach has been adopted. It would be prudent to adopt an integrated omics approach involving more platforms so that the species’ biological knowledge and the identification of key molecules and networks would efficiently translate the findings.

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Part VI
Utilisation

Chapter 26
Chemistry and Analysis of *Santalum album*

Dhanushka S. Hettiarachchi, Andrew Brown, and Mary C. Boyce

1 Background

Sandalwood is among the earliest perfumery and medicinal ingredients recorded in human history, playing a significant role in traditional and modern lifestyles from times of antiquity to current times. The defining factor of sandalwood is the chemistry of heartwood essential oil, which leads to reverence as the king of the woods. Sandalwood is commercially sourced from eight different species of *the Santalum* genus; *S. album* is considered as the authentic species of sandalwood which sets the benchmark for sandalwood aroma. The scope of this chapter is limited to the chemistry of *S. album* heartwood essential oil in reference to constituents, biosynthesis and analysis.

Chemistry of *Santalum album* has been researched and reported since the early twentieth century by a number of European and Indian researchers. Notable work includes identifying the major sesquiterpene composition of *S. album* essential oil, further research on essential oil composition for fragrance development and later for the synthesis of sandalwood odorants. As a result of these early studies, sandalwood chemistry has developed to the current day, playing an important role in conserving and continuing the legacy of the 'Royal Tree' for future generations enjoy its much-loved aroma.

Dedication: This chapter is dedicated in the memory of Prof. John E. D Fox, who has dedicated his life to sandalwood and inspired a generation of researchers.

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Heartwood is the only part of the sandalwood tree that contains the volatile principles which produce the characteristic aroma. Sandalwood oil is available for consumers as pure wood, powder, essential oil, absolute and hydrosol; all the product forms have different chemistry thus imparting a different aroma profile. This chapter will discuss commercially and laboratory produced essential oils and extracts obtained from tree core samples. Over 250 different chemical constituents have been reported from sandalwood in numerous scientific publications. These variations are due to a number of intrinsic and extrinsic reasons discussed later in this chapter.

It is understood that the origin, age of the tree, soil and climatic conditions affect the heartwood essential oil chemistry. Apart from these variations, factors such as fungal attack to the heartwood, sapwood content and distillation methods can influence the oil chemistry altering the trace constituents. Due to these idiosyncrasies, the reoccurrence of trace constituents across *S. album* samples are rare and subjective. Therefore, it is more appropriate to focus only on reoccurring constituents when *S. album* wood or oils are compared.

2 Major Constituents

Sandalwood essential oil is mainly constituted of sesquiterpenes and their corresponding alcohols. Unique sandalwood aroma is produced by two sesquiterpene alcohols cis-α-santalol and cis-β-santalol, first identified by Semmler (1910) and Ruzicka (1935) [41, 43]. Reoccurring major constituents of sandalwood were identified by several researchers in the past decades. Brunke and Klein (1982) have compiled the chemistry and structural elucidation of the key fragrance molecules of *S. album* essential oil [7]. The essential oil of *S. album* is comprised of 70–90% of cis-α-santalol, cis-β-santalol, cis-α-trans-bergamotol and epi-cis-β-santalol. Trans isomers of the above sesquiterpenes are reported from *S. album* but in minor concentrations. Other key sesquiterpene alcohols are α-bisabolol, β-bisabolol, cis-lanceol, cis-nuciferol, β and γ-curcumen-12-ol [1, 4, 5, 8]. These sesquiterpenes and their alcohols are reported to occur typically in *S. album* heartwood independent of the source or process. The presence and reoccurrence of these constituents are observed in the biosynthesis of sandalwood essential oil [17, 19]. *Santalum album* shows little or no variation in the composition of major components between populations, age, individual trees and morphological parts of the tree. Table 1 lists the major constituents reported with their mass spectroscopic and retention indices. Figure 1 illustrates the chemical structure of these molecules as reported. Some of these constituents are found only in Santalaceae family tree heartwood, making them unique marker compounds to identify sandalwood even in minor quantities (Fig. 2; Table 2).

Table 1 Major constituents identified in *Santalum album* with corresponding mass fragmentation ratio with relative abundance , molecular weight (MW), retention indices Chemical Abstract Service (CAS) number and the corresponding original citation

Compound name	m/z (relative abundance %)	MW	CAS#	Retention index*	Reference
α-santalene	94 (100), 93 (85), 41 (60), 95 (48), 69 (41), 121(39), 107(35), 79 (31), 91(30), 55 (26)	204	512-61-8	1410/1412	[18]
β-santalene	94(100), 122 (35), 41 (22),79(20), 93(20),55 (15), 67 (10), 107(10)	204	511-59-1	1456	[18]
β-bisabolene	69 (100), 93 (71), 41 (70), 94(28), 67(26), 109 (24)	204	495-61-4	1509	[18]
β-curcumene	119(100) 93 (42), 105 (34) 41(34) 91 (30) 121 (24) 77 (22)	204	28976-67-2	1507	[5]
γ-curcumene	119(100), 121 (79)m 93 (51), 105(40), 204(36), 91(32), 41 (29)	204	451-55-8	1473	[5]
epi-β-santalene	94(100), 122 (40), 41 (30),79(25), 93(25), 67 (15), 55 (10) 107(10), 161 (5), 119(5)	204	37876-51-0	1444	[18]
cis-α-bergamotene	119(100), 93 (95), 41 (60), 69(45), 91 (40), 80 (35), 79(35), 107(35), 55 (25), 133(10), 16 (10)	204	18252-46-5	1415	[5]
cis-α-santalol	93(100), 94 (79), 121(61), 91(40), 107(32), 122(28), 79(28), 77(26)	220	115-71-9	1672/1669	[1]
epi-*cis*-β-santalol	94(100), 122(39), 93(30), 79(29), 91(20), 67 (15)	220	79081-90-6	1699/1709	[2]

(continued)

Table 1 (continued)

Compound name	m/z (relative abundance %)	MW	CAS#	Retention index*	Reference
cis-β-santalol	93(100), 121(69), 94(63), 55(34), 18(34) 79(33), 91(27)	220	77-42-9	1694	[1]
cis-α-*trans*-bergamotol	93(100), 43(66), 119(64), 41(63), 91(52), 55(41), 79(40), 77(39)	220	88034-74-6	1686/1700	[2]
cis-β-curcumen-12-ol	119(100) 132(61) 93 (53) 92(38) 105 (37) 77(24) 121 (77), 145(22)	220	698365-10-5	1746/1761	Pers. Comms. Ashely Dowell
cis-γ-curcumen-12-ol	119(100) 132(50) 93 (46) 121 (43) 105(42), 91 (42) 92 (34), 79 (30), 41 (28)	220	151513-85-8	1741/1733	Pers. Comms. Ashely Dowell
cis-lanceol	93(100), 79(74), 119(68), 43(63), 67(62), 134(59), 94(50), 107 (49), 91(47) 105(45)	220	10067-28-4	1752/1739	[2]
cis-nuciferol	119(100) 132(47), 41 (32), 43 (30), 105(25), 120(17) 91(14) 117 (12)	218	78339-53-4	1721/1734	[2]
β-bisabolol	82(100) 93(60) 111(44) 69(43) 41 (41) 121(40)83(32) 67(32) 119(32) 55(31)	222	15352-77-9	1653	[2]
α-bisabolol	43(100), 41 (89) 69 (80) 109(50) 119(40) 93 (39) 55(35) 67 (28) 95 (28)	222	515-69-5	1684/1683	[2]

*Kovat's retention indices were calculated for 5% phenyl/95% methyl siloxane column

3 Minor Constituents

Sandalwood heartwood contains a number of minor components that are intrinsic and identified to reoccur with major components. These endogenous compounds follow the same biosynthetic pathway as the major constituents, but a change in isomerism

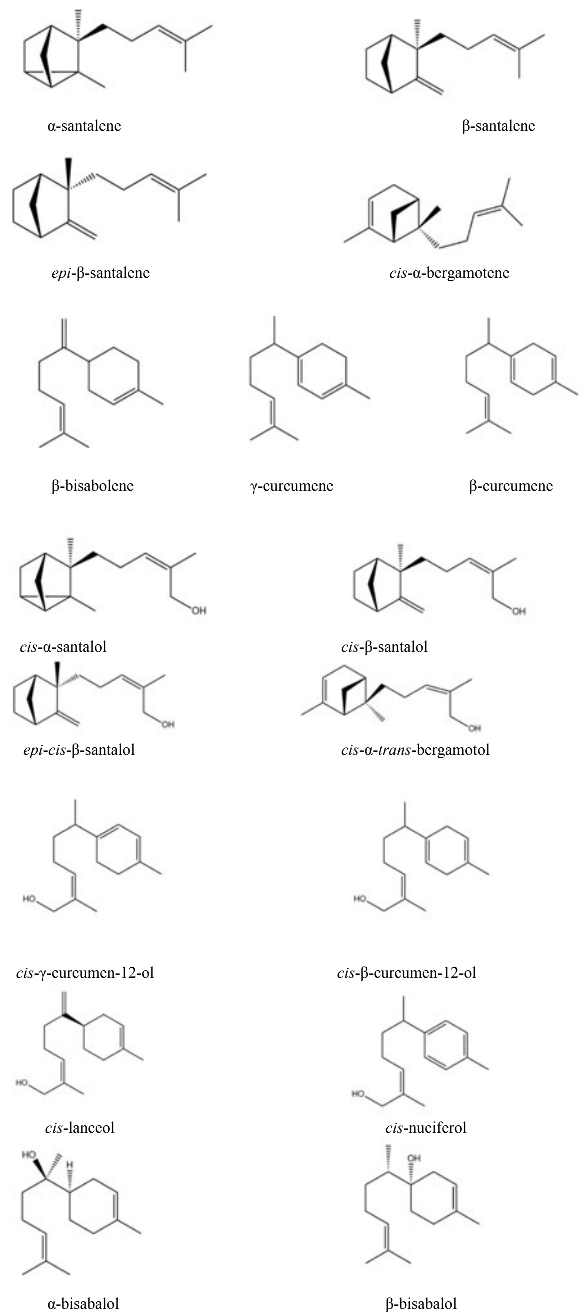

Fig. 1 Chemical structures of major constituents of *Santalum album* [1, 2]

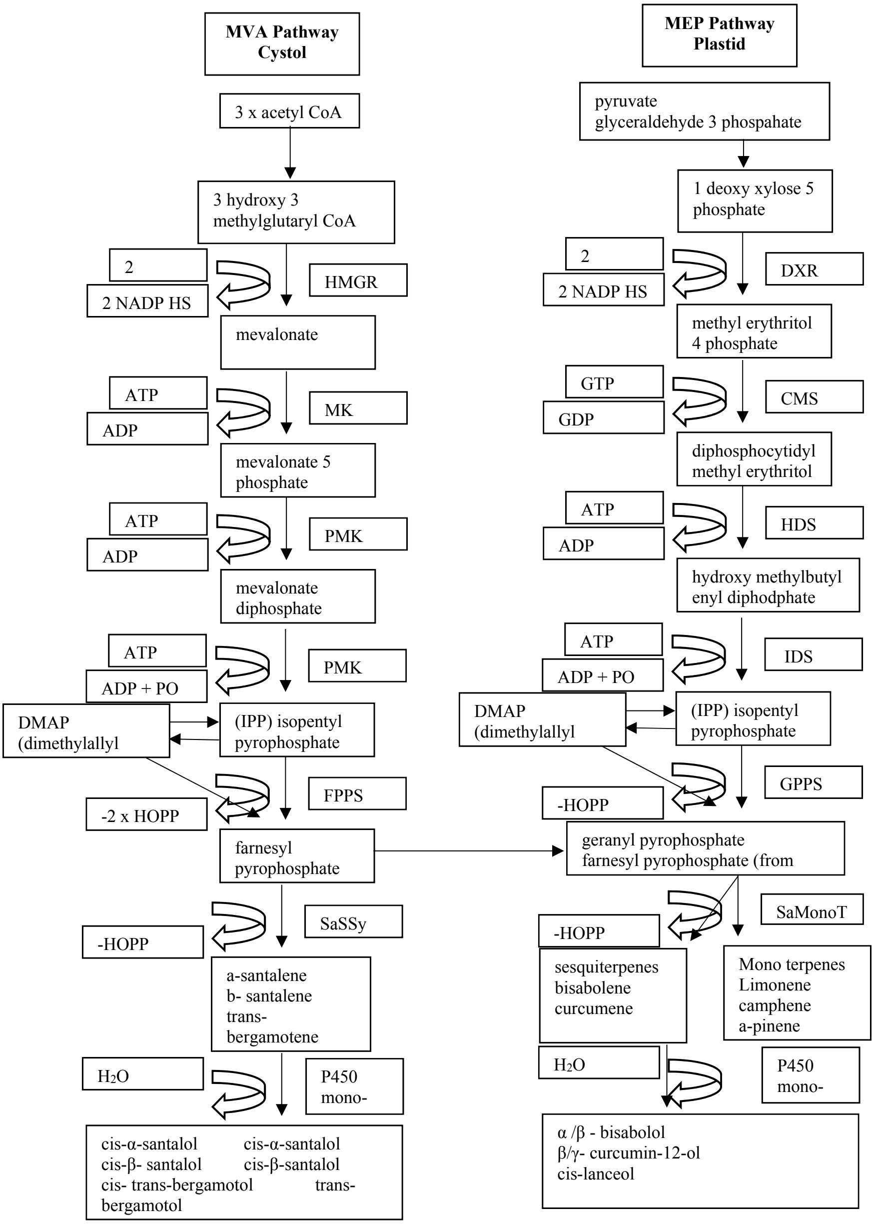

Fig. 2 Summary of the mevalonic acid (MVA) pathway and the methylerythritol 4-phosphate(MEP) pathway for the production of sesquiterpenols in sandalwood. Note that sesquiterpene synthases are multisubstrate and farnesyl pyrophosphate finds its way into the plastid to be converted into various isomers of curcumene and bisabolene [17, 18, 20]

Table 2 Minor constituents' classes and compounds identified in *Santalum album* with corresponding Chemical Abstract Service (CAS) number and the original citation

Compound class	Compound name	CAS number	Reference
Hydrocarbon	Santene	529-16-8	[2]
	α-cedrene	469-61-4	[5]
	trans-α-bergamotene	13474-59-4	[2]
	trans-β-bergamotene	18252-46-5	[5]
	trans-β-farnesene	15438-94-5	[5]
	cis-γ-bisabolene	13062-00-5	[5]
	trans-γ-bisabolene	53585-13-0	[5]
	α-curcumene	644-30-4	[5]
Alcohols	geraniol	106-24-1	[11]
	linalool	78-70-6	[5]
	α-terpineol	98-55-5	[11]
	borneol	507-70-0	[2]
	α-santenol	90694-60-3	[11]
	β-santenol	59432-92-7	[11]
	5,6,dimethyl-5-norbornen-*exo*-2-ol	59300-41-3	[11]
	tetrasantalol	29550-55-8	[2]
	nortricycloekasantalol	5523-84-2	[11]
	tricycloekasantalol	16933-12-3	[11]
	trans-nerolidol	40716-66-3	[2]
	Iso-β-bisabolol	496868-48-5	[6]
	trans- α-santalol	14490-17-6	[2]
	trans-β-santalol	37172-32-0	[2]
	12,13-dihydro-α-santalol	126209-93-6	[2]
	12,13-dihydro-β-santalol	34289-89-9	[2]
	cis-α-photosantalol	276885-92-8	[33]
	cis-β-photosantalol	61825-56-7	[33]
	epi-*cis*-β-photosantalol	61754-02-7	[33]
Diols and triols	*cis*-campherene-2,13-α-diol	859501-97-6	[34]
	10-*cis*-neosandalnol	905564-33-2	[34]
	10-*cis*-sandalnol	905564-30-9	[34]
	9-*trans*-11-hydroxy-α-santalol	872880-59-6	[21]
	9-*trans*-11-hydroxy-β-santalol	872880-60-9	[34]
	α-santaldiol	173615-76-4	[2]
	β-santaldiol	173615-77-5	[2]
	13-hydroxyneosandalnol	905564-29-6	[22]

(continued)

Table 2 (continued)

Compound class	Compound name	CAS number	Reference
	13-hydroxysandalnol	905564-32-1	[22]
	6,13-dihydroxybisabolola-2,10-diene	872880-55-2	[34]
Aldehydes and ketones	furfural	98-01-1	[11]
	α-tetrasantal	59300-39-9	[11]
	β-tetrasantal	71252-53-4	[11]
	eka-nortricyclosantalal	59300-38-8	[2]
	exo-eka-norbicyclosantalal	37720-84-6	[2]
	eka-tricyclosantalal	16933-18-9	[24]
	exo-eka-nortricyclosantalal	131232-80-9	[33]
	cis-α-santalal	152186-23-7	[22]
	trans-α-santalal	19903-70-9	[11]
	trans-β-santalal	59331-82-7	[11]
	trans-epi-β–santalal	13827-98-0	[11]
	cis-β-santalal	887491-74-9	[2]
	cis-lanceal	92729-33-4	[2]
	cyclosantalal	168099-27-2	[2]
	epi-cyclosantalal	168252-33-3	[2]
	santalone	59300-51-5	[11]
	nor-α-Santalenone	63569-01-7	[33]
	epi-nor-β-Santalenone	176689-46-6	[11]
	nor-β-Santalenone	176777-63-2	[33]
Acid	β-Teresantalic acid	78247-54-8	[2]
	epi-β-Tetrasantalic acid	78220-46-9	[2]
	β-Ekatrasantalic acid	1132-84-9	[2]
	epi-β-Ekatrasantalic acid	78247-52-6	[2]
	α-Teresantalic acid	562-663-3	[2]

and spatial arrangement or due to further oxidation. Their occurrence depends upon multiple factors such as tree genetics, nutrition and stress levels of the tree. *S. album* is found to contain monoterpenes originated from a different biosynthetic pathway to major components. These constituents such as pinene and geraniol play a significant role in light fractions of sandalwood oil [11]. Extrinsic minor components are generated as a result of fungal attack, wood processing and distillation methods. Distillation generates artefacts unique to the process; high temperature and moisture in combination with usually long distillation times result in breakdown and oxidized products. These minor constituents are not found in the natural heartwood of sandalwood. Many of the earlier studies on *S. album* were conducted on commercially distilled authentic sandalwood oils from India. As the major constituents of *S.*

album show very less variation corresponding to the source, it is important to develop an understanding of the reoccurring trace constituents for source and product variation and authenticity. Minor constituents are important in production and quality assurance point of view to retain or rectify the organoleptic properties of high olfactory threshold molecules. Rearranged variants of santalols such are spirosantalol and photosantalol are found in distilled oils [33]. Oxidative breakdown products such as santalols and santalic acids as well as their cleaved hydrocarbon tail variants nor (C14), eka (C13) and tere (C13) products have specific aroma profile. Breakdown santalene hydrocarbon compounds such as albene and santene are seen commonly in distilled essential oil. Both distillation time and temperature have an effect on wood components of sandalwood; polyphenols can produce breakdown products such as eugenol and vanillin, and sapwood components can breakdown and condensate to produce furfural pyrrol [2, 11]. Minor constituents of sandalwood can be chemically classified into hydrocarbons, alcohols, diols/triols, aldehyde, ketones and acid [2].

4 Sandalwood Oil Biosynthesis

Sandalwood oil biosynthesis is a metabolically expensive proposition for the tree that results in the generation of some important molecules, so it is worth understanding what is known about this process. Fortunately, there has been some excellent research by a number of researchers and as a result, a reasonable understanding of the process is available [12, 17, 18, 20].

Sitting at the start of the process are the Malvonic Acid (MVA) and the Methylerythiritol phosphate (MEP) pathways. These two pathways are common to all plants that produce terpenes. Both pathways essentially reduce sugars with electrons supplied from the TCA cycle and result in the production of the two monomers isoprene pyrophosphate (IPP) and dimethyl allyl pyrophosphate (DMAPP). These monomers are then converted into either geranyl pyrophosphate (GPP) in the case of the MEP pathway or farnesyl pyrophosphate (FPP) in the MVA pathway. GPP is then rearranged by enzymes to mono (C10) and di (C20) terpenes while FPP is destined for sesquiterpenes (C15) and triterpenes (C30) terpenes. Figure 1 shows a generalized view of these pathways.

While the MVA pathway is of most interest to the sandalwood chemist as it results in the formation of the santalols. The MEP pathway should also be understood as it contributes molecules to the essential oil derived from sandalwood. The now accepted hypothesis that a single enzyme is responsible for the rearrangement of FPP to the various santalenes was first proposed in 2006 by Jones et al. with the observation of quantitative co-occurrence of z-α-santalene, z-β-santalene, trans-α-santalene and epi-β-santalene [17]. A second enzyme was proposed for the second group of constituents as there was co-occurrence between these constituents but not between the groups, constituents being isomers of curcumene and isomers of bisabolene. The cyclase enzymes were identified and isolated in 2011. *Santalum album* sesquiterpene synthase (SaSSY) and *Santalum album* monoterpene synthase

(SaMonoTPS), in which the former is responsible for the cyclization of FPP to the santalenes and the latter for the cyclization of FPP to the bisabolenes and curcumenes [18]. The final step in the biosynthesis of sandalwood oil was elucidated in 2013 with the identification of a family of cytochrome P450-dependent monooxygenases [12]. These enzymes result in the preferential oxidation of the hydrocarbon tail to alcohol in the cis position.

The current understanding of the biosynthetic pathways involved is good, but there remains a good body of research to be done to better understand the complete picture of all biosynthetic pathways within the tree that produce sandalwood oil. With sandalwood oil, the importance of minor constituents and their contribution to the unique character of sandalwood oil cannot be underestimated. As a result, questions remain to be answered as to the origins of molecules including the C15 sesquiterpene alcohols such as isomers of eudesmol, rearranged variants of santalols such as spirosantalol and photosantalol, oxidative breakdown products such as santalols and santalic acids as well as their cleaved hydrocarbon tail variants, breakdown hydrocarbons such as albene, and santene and wood breakdown products such as furfural pyrrole, eugenol and vanillin.

5 Chemical Analysis of Sandalwood

5.1 Samples Extraction and Distillation

The essential oil can be extracted from the heartwood using a number of approaches, including distillation, solvent extraction or supercritical fluid extraction. The method of steam distillation, where steam is passed through a stationary bed of woodchips, is the approach adopted for the commercial production of *S. album* essential oils. There are variations in the method of steam distillation: the wet steam method is where water is included in the distillation unit, and woodchips are positioned above the water level on a perforated basket or separator, allowing the low pressure steam generated to pass through the wood chips. An alternative and more efficient method are to boil water in a separate container, and the generated steam is passed through the woodchips placed in a distillation unit.

In both cases, the steam carrying the oil passes through condensers that facilitate a high volume of steam. The separated oil is dehydrated by physical means prior to storage.

The most common distillation method for analytical purposes is hydro-distillation, where wood powder or chips are boiled for 8 h or more using a Dean–Stark or Clevenger's apparatus to collect the oil [14]. Analytical distillations are commonly used to determine the yield and quality of raw materials used for commercial oil distillation. The application of microwave technology to assist the distillation process has been adopted for the extraction of many essential oils. This 'greener' technology has led to savings in energy and time as well as improved yields [9]. Kusuma and Mahfud

[28, 29] reported similar benefits when they investigated microwave assisted hydrodistillation for extraction of *S. album* oils. The potential impact of the composition of essential oil composition has yet to be investigated.

Solvent extraction is a common and alternative approach used to isolate the essential oils from heartwood. As the oil consists mainly of sesquiterpenoids and oxygenated sesquiterpene alcohols, the oil components are soluble in solvents that range in polarity from n-hexane to ethanol. Several factors influence the efficiency and reproducibility of solvent extraction and they include solvent choice, sample/solvent ratio, particle size and shape, use of agitation, extraction time and temperature. Solvent extraction methods reported for sandalwood vary widely from maceration in ethanol for up to two weeks to a 30 min extraction in hexane aided by sonication [13, 32, 35]. The use of an internal standard in the extracting solvent is necessary to correct for the loss of sample during extraction. Despite the variation in solvent extraction methods reported, the chemical composition of sandalwood is relatively consistent [35].

Extraction using CO_2 in the supercritical state is widely used to extract essential oils from plant material [47]. The technique has the advantage of producing very pure *Santalum album* oils, as the low temperature and minimal water content conditions employed reduce thermal degradation and hydrolytic processes, respectively [30]. Furthermore, the extraction efficiency and specificity can be manipulated somewhat by varying the temperature and pressure of the CO_2. The percentage yield is also higher for supercritical fluid extractions [39]. The main disadvantage is that the technique is not routinely available and requires specialized hardware.

Irrespective of the extraction method, the particle size of sandalwood material is an important parameter in method optimization. Smaller particle sizes have a large surface area allowing increase partition co-efficiency for extraction or vaporization. However, decreased particle size has the disadvantage of particle aggregation, eventually leading to poor extraction capacity [14].

5.2 Chromatographic Analysis

Gas chromatography in tandem with flame ionization detection (FID) or mass spectrometry (MS) is the analytical method of choice for the separation and subsequent detection of the volatile components in essential oils. Several GC methods have been reported for the separation of sandalwood oils, and they usually involve either a non-polar column having a stationary phase of 95% methylsiloxane and 5% phenylsiloxane or a polar column with a polyethylene glycol or wax stationary phase [30, 32]. While the polar column provides better separation of the sesquiterpenes, the more robust non-polar column, with less column bleed, is routinely used. The analysis time is usually quite lengthy, typically 60 min to aid separation of the closely related sesquiterpenes present in the oil. The major compounds can be easily detected and quantified using gas chromatography; the international standards organization has specified the limits for sandalwood oil with prototype chromatograms of polar

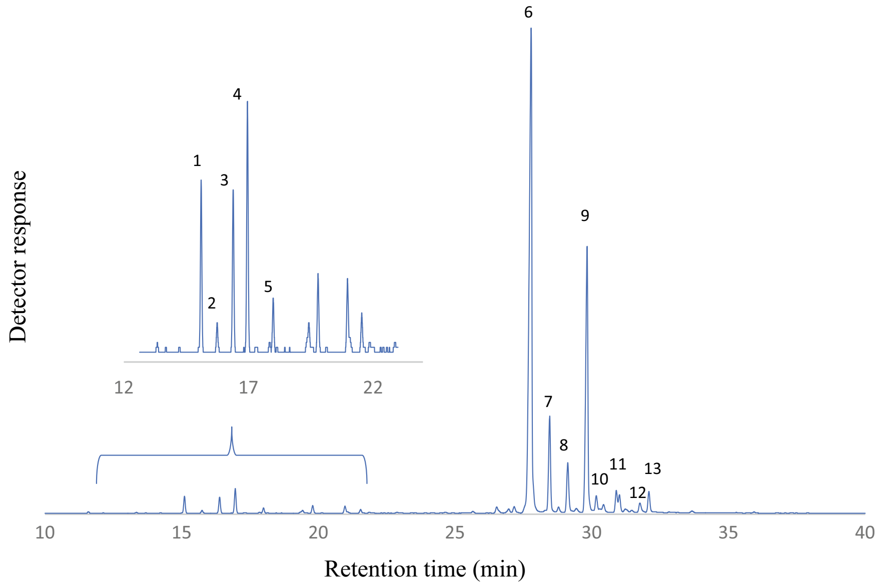

Fig. 3 Gas chromatogram of *Santalum album* essential oil on 5% phenyl/95% methyl siloxane column 30m × 0.25mm × 0.25u. Compound identification given in Table 3

and non-polar column separations. Verghese et al. have studied different grades and origins of *S. album* in India by capillary gas chromatography, which is the first report to suggest α-santalol and β-santalol as the key markers of quality, subsequently adopted by the international standard [16, 45]. Howes et al. have suggested a change in the current ISO method and limits, suggesting the actual percentage compositions quoted for the santalols need to be lowered [15]. A typical chromatogram for *S. album* obtained in our laboratory with composition range is given in Fig. 3 and Table 3.

Flame ionization is the detector commonly used for routine analysis of sandalwood oils as it is widely available and highly sensitive to hydrocarbons. The elution order and Kovat's retention indices (KI) for the key analytes separated on both polar and non-polar columns are well documented. The KI is where the retention time of a molecule is indexed in relation to the carbon chain length of an alkane, typically between C12 and C20 for sandalwood. Quantitative analysis is typically by internal normalization also referred to as percentage area composition. When applying the method of internal normalization the detector response, or response factor, RF, for all the analytes should be the same to ensure correct proportions are reported [3, 10]. However, the RF of an FID is not only dependant on analyte concentration but is also influenced by the chemical structure of the analyte, and for a complex mixture such as sandalwood oil, the analytes will have a range of RFs. To determine and normalize for the varying RFs, it is necessary to prepare calibration standards for each analyte, which in the case of sandalwood oils is not possible as most of the analytes are not

Table 3 Composition of major constituents as observed (internal reports) and given in ISO3518:2002

Reference*	Compound	Observed range (% Area)	ISO 3518:2002 (% Area)
1	α-santalene	3.0–0.0	–
2	*trans*-α-bergamotene	0.5–0.0	–
3	epi-β-santalene	3.0–0.0	–
4	β-santalene	4.0–0.0	–
5	α-curcumene	1.5–0.0	–
6	cis-α-santalol	51.0–33.0	41.0–5.0
7	trans-α-bergamotol	7.0–2.0	–
8	epi-β-santalol	5.5–3.0	–
9	β-santalol	25.0–12.0	16–24
10	cis-nuciferol	3.0–1.0	–
11	γ-curcumen-12-ol	2.0–0.0	–
12	β-curcumen-12-ol	1.0–0.0	–
13	cis-lanceol	3.0–0.0	–

*Refer to the peak numbers given on Fig. 3

readily available as pure standards. A more feasible approach is to determine the response factor for classes of compounds [3]. By using FID, peak identification is limited to comparing the analyte retention times with standards or using KI. When identification of sandalwood analytes is required, for example, to identify the minor constituents that may be characteristic of an extraction regime or growing conditions, mass spectrometry is preferred, as it provides structural information to aid in the identification of the analyte (Table 4).

Mass Spectrometry is universally used in essential oil analysis. Research reports on sandalwood chemistry and standards emphasize its use for characterization and identification purposes [16]. In the most common operating mode, electron impact, each analyte leaving the separation column is bombarded by high energy electrons causing fragmentation of the analyte. The fragment ions generated are characteristic of the chemical structure of the analyte and provide a reproducible fingerprint or

Table 4 Physiochemical parameters of *Santalum album* essential oil as given on ISO3518:2002

Physical characteristics
• Density:0.968 to 0.983 @ 20 °C • Refractive index @ 20 °C: 1.503 to 1.508 • Optical rotation@ 20 °C: − 15 to − 21° • Solubility in 70% ethanol (v/v) @ 20 °C: less than 5 volumes of 70% ethanol for 1 volume of oil
Chemical characteristics
• Ester number: max 10 • Total alcohol content, calculated as santalol: 90% minimum

profile for that analyte. There are libraries (generated in-house or commercially available, such as NIST) detailing the fragmentation of compounds. The basic mass selective detector employs a single quadrupole or ion filter to separate the fragment ions which are then directed to the detector for quantitation. The resolution is typically one atomic mass unit. High-resolution instruments such as time of flight or orbitrap MS instruments are capable of recording mass to three decimal places, which is useful for identification purposes. While MS is a powerful tool for structure elucidation and identification purposes, it alone is not sufficient to determine the structure. The analyte of interest must be isolated or chemically synthesized and undergo nuclear magnetic resonance studies to determine/confirm the full structure [2].

Essential oils, including sandalwood oil, have many compounds with identical masses, similar structures and so similar fragmentation patterns (e.g. β- and γ-curcumen-12-ol), so if they coelute and enter the MS together they are not distinguishable by MS. In these instances, separation is required prior to MS. In two-dimensional GC (GC x GC), two columns of different polarities are coupled to enhance separation. Two-dimensional GC studies conducted on sandalwood oil reported better separation of sesquiterpene alcohols, and successful quantification of minor constituents of sandalwood was achieved by this method [23, 40, 42].

While MS is essential for identification/qualitative purposes, FID has been shown to be more reproducible and accurate when compared to MS for internal normalization [2, 3]. When a comprehensive analysis of sandalwood oil is required, that is both quantitative and qualitative, then splitting of the sample after separation so that the sample is directed to both FID and MS is advantageous.

For studies seeking to better understand the sandalwood biosynthesis, investigate trace contaminants or monitor change in essential oil profile as a result of changes in extraction protocols or environmental plantation conditions, GC–MS is the technique of choice. However, there is a role for rapid and less expensive techniques that require less operator expertise. Such techniques can be used for routine purposes such as screening for α-santalol content or checking the authenticity of a sample or the presence of adulterants. These methods can also be complementary to any GC analysis. Some promising techniques are described here.

Ofori et al. [36, 37] demonstrated the potential of high-performance thin-layer chromatography, HPTLC, to profile and authenticate sandalwood oils. They analysed some common sandalwood species: *S. album*, *S, spicatum*, *S. austrocaledonicum* and *S. paniculatum* and identified bands unique to each species (Fig. 4). Furthermore, the researchers compared the α-santalol content reported by GC with the intensity of the α-santalol in the HPLTC band and got good agreement indicating that HPTLC may be useful to screen for oils of high α-santalol content. Misra and Dey [31] used HPLTC to quantitatively determine α-santalol content in sandalwood oil samples. HPTLC offers several advantages over GC. Up to 20 samples can be analysed in parallel and in a relatively short period of time, less than 1 h. It is less expensive and can be operated safely with minimal training. A very attractive advantage, especially when used for screening purposes, is that the technique can tolerate crude extracts, unlike most column chromatography techniques.

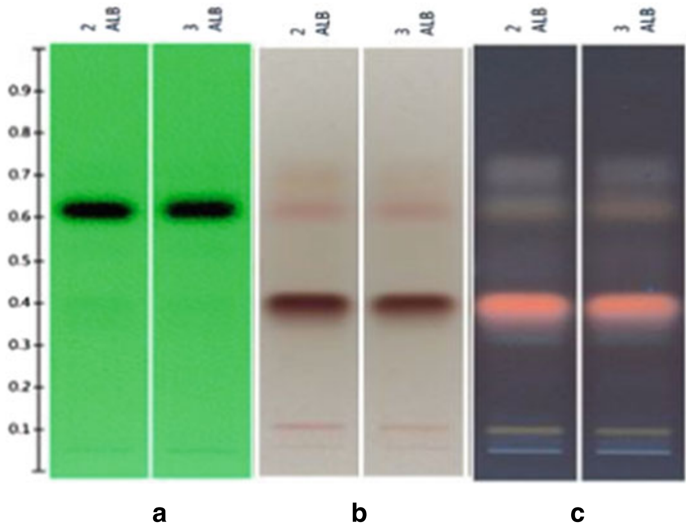

Fig. 4 HPTLC fingerprinting of two samples of *S. album* essential oil at 254 nm (**a**), white light after derivatization (**b**) and 366 nm after derivatization (**c**) [36, 37]

While its role in discriminating between species has been explored, studies to determine its application to detect adulterated or blended oils have yet to be reported. Another potential application of HPTLC is the characterization of non-volatile components of the heartwood and sapwood tissue, which could be used for wood authentication and plantation assessment.

Kuriakose and Joe demonstrated near-infrared spectroscopy (NIR) in combination with chemometric techniques to be an excellent tool for assessing sandalwood oil quality [25–27]. In one study, they spiked *S. album* oils with increasing amounts of a common adulterant (castor oil) and using NIR in combination with principal component regression and partial least squares regression, they were able to detect additions of castor oil as low as 1% [27]. In another study, the same research group investigated the adulteration of premium *S album* oil with *S. spicatum* oil, and again they were able to determine sample authenticity by examining the wavelength range 1850–1800 nm where biomarkers of adulterants were observed [25]. In yet another study, Kuriakose and Joe demonstrated the ability of NIR in combination with principal component analysis and hierarchical cluster analysis to discriminate *Santalum album* oil samples based on geographical origin within India [26]. A recent publication also confirmed the potential role of IR in discriminating *S. album* from other sandalwood species [46]. NIR is ideal for the sandalwood industry as it is rapid, requires less investment than GC–MS, is non-destructive and requires minimal or no sample preparation.

Another technique, solid-phase microextraction (SPME) in combination with gas chromatography has great potential to provide a rapid assessment of oil quality so as to inform the selection of plantation trees for harvesting. Using SPME-GC milled heartwood is sampled directly for essential oil content removing the solvent extraction or steam distillation step completely. Using this approach, the woodchip (typically less than 1 g) is transferred to a sealed vial and heated (typically 30–40 °C). The headspace is then sampled and concentrated onto a polymeric material which is coated onto a thin fibre. The fibre with the polymeric material is then inserted into the heated GC injector where the analytes are desorbed and separated using traditional GC. Unpublished work from our laboratory has demonstrated the ability of SPME-GC to screen *S. spicatum* trees for farnesol content (Boyce, personal communication). The technique can be optimized to quantify for santalol content helping inform plantations as to when to harvest trees.

These complementary or alternative techniques to GC–MS have been explored and adopted for other essential oil industries. In the next decade, more research needs to be completed for these techniques to be adopted by the sandalwood industry. These techniques have the potential to provide rapid on-site analysis and can revolutionize harvesting regimes, current wood grading and processing operations to facilitate a more consistent high-quality raw material for oil distillation.

5.3 Physiochemical Analysis

Despite the availability of advanced analytical methods, physicochemical parameters of sandalwood essential oil are widely accepted by industry to determine the quality. The combination of these methods helps in the identification of any adulteration or product oxidation. Low cost, rapid analysis and universal applicability are the main reasons for the popularity of these methods.

Santalol content is determined by acetylation reaction to determine total alcohol content, which is calculated to be a minimum of 90%. Ester value is an important parameter to determine adulteration by fatty oils. The solubility of sandalwood oil in 70% ethanol is measured to detect adulteration and to determine oxidative products. Apart from the above titrimetric methods, physical methods such as refractive index, optical rotation and density are measured to detect adulteration. Especially in the case of *S. album* essential oil these physical methods can approximately measure blending with oils from other sandalwood species until further analysis by GC [16].

6 Conclusion

Chemistry is an integral part of sandalwood research, starting from agroforestry to final application as a cosmetic or medicine. The chemical analysis helps to determine the quality of natural populations of sandalwood which helps in propagation for reforestation and seed sourcing for plantation establishment [38, 44]. Regular chemical analysis of heartwood tissue is also vital in plantation management in establishing heartwood development and harvest planning. Once harvested, processing and distillation of heartwood depend very much upon chemical assessment, especially as the trade of sandalwood is governed by the quality assurance established on the chemistry of the heartwood essential oil.

Another important industrial application of chemistry is identifying adulteration by other essential oils or non-volatile substances. In conclusion, the chemical understanding of the characteristics and analysis of sandalwood is the most important industrial aspect of the sandalwood industry. Although the chemistry of sandalwood has been studied for over a century, there is more space for further research in supporting the ever-expanding plantation industry. Novel methods for source authentication and traceability, rapid analysis for agroforestry, identification of minor components with olfactory characteristics, identification of genetic markers and sample analysis from clinical studies are the future applications of the chemistry of sandalwood. Chemists have played an important role in bringing *S. album* from the brink of extinction to a thriving industry in the past few decades. This will continue with the development of a sustainable sandalwood industry globally.

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Chapter 27
Cancer-Preventive and Antitumour Effects of Sandalwood Oil and Alpha-Santalol

Kaitlyn Blankenhorn, Abigayle Keating, James Oschal, Daniel Maldonado, and Ajay Bommareddy

Abbreviations

Cdc25B	Cell division cycle 25B
CDKs	Cyclin-dependent kinases
COX-2	Cyclooxygenase-2
DMBA	7,12-Dimethylbenz(a)anthracene
EGFR	Epidermal growth factor receptor
ER	Estrogen receptor
EISO	East Indian Sandalwood Oil
HNSCC	Head and neck squamous cell carcinoma
HUVECs	Human umbilical vein endothelial cells
IAP	Inhibitor of apoptosis
ODC	Ornithine decarboxylase
PARP	Poly ADP-ribose polymerase
PDE	Phosphodiesterase
PCNA	Proliferating cell nuclear antigen
SWO	Sandalwood oil
TPA	12-O-tetradecanoyl-phorbol-13-acetate
VEGFR2	VEGF receptor 2

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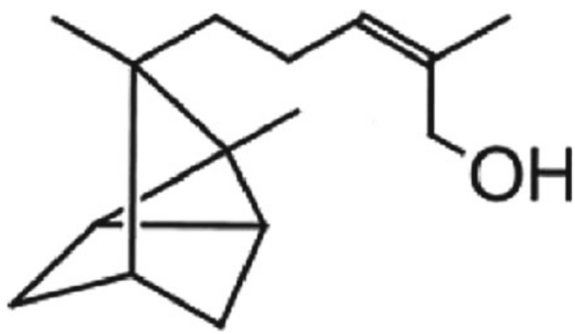
1 Introduction

Cancer is currently the second leading cause of death in the USA. Global incidences of cancer continue to increase yearly, responsible for an estimated 9.6 million deaths in 2018, indicating that 1 in 6 global deaths are due to cancer [8]. Furthermore, it is expected that the number of cancer deaths would reach over 13 million worldwide by 2030. In 2020, about 1.8 million new cancer cases and over 600,000 cancer deaths are estimated to occur in the USA [27], and the cancer mortality rate has exceeded many diseases, including chronic lower respiratory diseases, stroke, Alzheimer's, and diabetes. The most common forms of cancer treatment include surgery, radiotherapy, immunotherapy, and chemotherapy. Chemotherapy is one of the major therapeutic approaches in the treatment of various cancers. However, side effects associated with its usage include pain, cardio-, hepato- and renal toxicity, along with an increased risk of recurrence and metastasis [28]. In addition to the associated side effects, patient's mental state, emotional state, and overall quality of life can also be significantly impacted by chemotherapy. Thus, in efforts to enhance patient health outcomes, it is imperative that new and effective treatment forms capable of avoiding these detrimental side effects be discovered.

The quest for agents that can prevent or treat chronic disease and limit the occurrence of adverse effects has led to the use of plant-derived compounds and essential oils for their anti-inflammatory, antiproliferative and antioxidant effects. Sandalwood oil (SWO), an essential oil extracted from the heartwood of *the S. album*, consists of several structurally related compounds. Alpha-santalol (Fig. 1), present in the highest levels, has gained momentum in the scientific community. Traditionally, SWO has been used in different cultures for its medicinal value [19]. Literature from in vitro and in vivo studies report the cancer-preventive and antitumour properties of SWO and alpha-santalol. The unique characteristics of these natural agents are their ability to target malignant cells and have little to no toxicity towards normal cells. The antitumour properties of sandalwood against various cancer models were recently reviewed [24]. Studies, including those from our group, have shown the cancer-preventive and growth-suppressive properties of SWO and alpha-santalol against a wide range of

Fig. 1 Structure of alpha-santalol



human tumour cell lines. It is well documented that alpha-santalol exhibits cytotoxic effects against tumour growth by inhibiting angiogenesis and induction of cell cycle arrest and apoptosis. A detailed summary of the cancer-preventive and antitumour properties of SWO and alpha-santalol is presented in Table 1. Despite the evidence pertinent to these natural agents' medicinal value, our knowledge regarding the full spectrum of their pharmacological activities is limited. Additional studies, including relevant clinical trials, are warranted to establish their therapeutic potential and clinical utility against different diseases. The current chapter updates our previous review on the medicinal properties of alpha-santalol [2] and summarizes the latest findings of studies on the cancer-preventive and antitumour properties of SWO and alpha-santalol.

2 Skin Cancer

Skin cancer is the most prevalent form of cancer in the USA [17], causing an estimate of 11,480 deaths in the USA in 2020 [27]. Some common treatment options for skin cancer include excision surgery, radiation therapy and treatment with targeted immunotherapies that could result in many adverse effects. Based on the skin-protective benefits of sandalwood preparations, exploring their potential benefits against prevention of various skin ailments, including non-melanoma skin cancer, was logical. Treatment of skin cancer with the use of alpha-santalol and SWO has proven to be very promising. In early studies investigating the chemopreventive effects of SWO with a CD1 mice model for skin carcinogenesis, topical application of SWO (5% w/v in acetone) reduced papilloma incidence by 67% and tumour multiplicity by 96% [12]. In a follow-up study, pretreating mice with SWO reduced papilloma incidence and multiplicity in a concentration and time-dependent manner [16]. Subsequent studies focused on investigating the cancer-preventive and antitumour properties of alpha-santalol, extracted from SWO employing in vivo and in vitro models. Treatment with alpha-santalol significantly prevented papilloma development during the promotion phase of DMBA and TPA carcinogenesis protocol in both CD-1 and SENCAR mice [13, 14]. These studies provided compelling evidence of alpha-santalol's inhibitory effects on skin cancer development.

Alpha-santalol's ability to inhibit chemically induced skin carcinogenesis led to further studies employing other carcinogenesis models. For example, alpha-santalol was shown to exhibit chemopreventive effects against UVB-induced skin tumourigenesis in SKH-1 hairless mice under three different protocols (DMBA-initiated, UVB-promoted; UVB-initiated and TPA-promoted, UVB initiated and UVB-promoted). The treatment was most effective in UVB-induced complete tumourigenesis, with a 72% reduction in tumour multiplicity [4, 15, 25]. Systemic absorption into the skin was suggested as the mechanism of action [15].

Tumour incidence and multiplicity were significantly reduced when the same experimental animal model was further exposed to alpha-santalol an hour prior

Table 1 Cancer-preventive and antitumour effects of alpha-santalol and sandalwood oil

Lead author	Year	Specimen (in vivo/in vitro model)	Cancer specific	Carcinogen	Treatment	Results
Dwivedi	1997	CD-1	Skin cancer	7,12-dimethylbenz(a)anthracene (DMBA) and 12-O-tetradecanoyl-phorbol-13-acetate (TPA) carcinogenesis	SWO (5% w/v) acetone	Decreased papilloma incidence by 67%, multiplicity by 96%, and TPA-induced ornithine decarboxylase (ODC) activity by 70%
Dwivedi	1999	CD-1	Skin cancer	DMBA-initiated and TPA-promoted carcinogenesis	SWO (1.25, 2.5, 3.75, 5% w/v) in acetone	SWO pretreatment decreased the papilloma incidence and multiplicity in a concentration and time-dependent manner
Dwivedi	2003	CD-1, SENCAR mice	Skin cancer	DMBA-initiated and TPA-promoted carcinogenesis	Alpha-santalol (5% w/v) acetone	Prevented papilloma development in both CD-1 and SENCAR mice, possibly by inhibiting TPA-induced ODC activity and DNA synthesis
Dwivedi	2005	CD-1 mice	Skin cancer	DMBA and TPA carcinogenesis	Alpha-santalol (1.25 and 2.5%) in acetone	No significant difference in the effects of 1.25% and 2.5% alpha-santalol on tumour incidence, multiplicity, epidermal TPA-induced ODC activity, or DNA synthesis

(continued)

Table 1 (continued)

Lead author	Year	Specimen (in vivo/in vitro model)	Cancer specific	Carcinogen	Treatment	Results
Dwivedi	2006	SKH-1 mice	Skin cancer	UVB radiation	100 µl of α-santalol (5%, w/v, in acetone,)	Topical application of alpha-santalol inhibited UVB-initiated and promoted skin tumour development
Bommareddy	2007	SKH-1 mice	Skin cancer	UVB radiation	2.5% and 5% alpha-santalol in acetone	Inhibited UVB-induced skin tumour development; higher concentration proved more effective
Arasada	2008	SKH-1 mice	Skin cancer	UVB radiation	Alpha-santalol 1 h prior to UVB exposure	Increased p53, caspase-3, and caspase-8 levels; reduced tumour incidence and multiplicity
Matsuo	2012	HL-60 human promyelocytic leukemia cells		N/A	Seven alpha-santalol derivatives from the heartwood	Exhibited tumour-selective cytotoxicity
Bommareddy	2012	PC-3 and LNCaP cells	Prostate cancer	N/A	0–75 µM concentrations of alpha-santalol in DMSO	Induced apoptosis with activation of caspase-3 activity and PARP cleavage

(continued)

Table 1 (continued)

Lead author	Year	Specimen (in vivo/in vitro model)	Cancer specific	Carcinogen	Treatment	Results
Chilampalli	2013	SKH-1 mice	Skin cancer	UVB radiation	Topical administration of alpha-santalol (5 mg in 200 μL acetone); honokiol (30 μg in 200 μL acetone); alpha-santalol (5 mg in 100 μL acetone) and honokiol (30 μg in 100 μL acetone)	Induced apoptosis
Santha	2013	SKH-1 mice	Skin cancer	UVB radiation	Topical administration of alpha-santalol (10%, w/v in acetone)	Decreased expression of cyclins (A, B1, D1, D2) and Cdk1 (Cdc2), Cdk2, Cdk4 and Cdk6, up-regulated expression of Cip1/p21, elevated levels of cleaved caspase-3 and PARP
Santha	2013	MCF-7 and MDA-MB-231 cells	Breast cancer	N/A	10–100 μM concentrations of alpha-santalol in DMSO	Inhibited cancer cell viability and proliferation by inducing G2/M cell cycle arrest and apoptosis; less toxic effect on normal breast epithelial cells

(continued)

Table 1 (continued)

Lead author	Year	Specimen (in vivo/in vitro model)	Cancer specific	Carcinogen	Treatment	Results
Saraswati	2013	Swiss Albino Mice (male nude) PC-3 or LNCaP cell s.c. xenograft	Prostate cancer	N/A	5–40 µM concentrations of alpha-santalol in DMSO	Reduced volume and weight of solid tumours, reduced the cell viability, and induced apoptosis
Dickinson	2014	HaCa T Keratinocytes	Skin	N/A	Different concentrations of EISO	EISO-treatment of HaCaT keratinocytes results in a blockade of cell cycle progression as well as a concentration-dependent Inhibition of UV-induced AP-1 activity, two major cellular effects known to drive skin carcinogenesis
Pallaty	2014	Humans	Head and neck cancer	N/A	Cream containing sandalwood oil and turmeric	Beneficial effects in preventing radiodermatitis in patients with head and neck cancer
Bommareddy	2015	MCF-7 and MDA-MB-231 cells	Breast cancer	N/A	20 µM and 40 µM concentrations of alpha-santalol	Suppression of survivin levels not regulated through the PI3K–AKT pathway

(continued)

Table 1 (continued)

Lead author	Year	Specimen (in vivo/in vitro model)	Cancer specific	Carcinogen	Treatment	Results
Lee	2015	Female athymic mice (xenograft), Head and neck squamous carcinoma cells	Oral cancer	N/A	Daily topical administration 50% EISO in DMSO: 5μL days 0–2, 10μL days 3–4, 20μL days 7–11 and 14–18	Caused formation of multipolar mitotic spindles and disturbed microtubule polymerization, stopping the HNSCC in G2/M phases
Ortiz	2016	Human Breast Cell Lines MCF-7 and MCF-10A	Breast cancer	N/A	2, 4, 6, and 8 μg/mL SWO	Reduction of class 1 comets, induction of single and double stranded DNA breaks in cancerous cells
Dave	2017	Female Sprague–Dawley rats	Breast cancer	DMBA	Cream formulation of α-santalol (10% v/v in Dermabase ® cream) or 10%, 25% v/v of alpha-santalol phospholipid microemulsions	Transdermal/Transpapillary delivery of α-santalol reduced tumour incidence and multiplicity in rat chemical carcinogenesis model of breast cancer
Rao	2017	Humans	Skin	Ionizing radiation	Cream formulation of turmeric extract 16% *w/w*, Sandalwood Oil 0.5% *w/w* in a non-greasy base	Reduced radiation dermatitis in women receiving radiation therapy for breast cancer treatment
Bommareddy	2018	MCF-7 and MDA-MB-231 cells	Breast cancer	N/A	20 μM and 40 μM concentrations of alpha-santalol	Reduced migratory potential and wound healing ability of breast cancer cells. Affected the localization of β-catenin from cytosol to nucleus in MDA-MB 231 cells

(continued)

Table 1 (continued)

Lead author	Year	Specimen (in vivo/in vitro model)	Cancer specific	Carcinogen	Treatment	Results
Bommareddy	2020	PC-3 and LNCaP cell	Prostate cancer	N/A	20 µM and 40 µM concentrations of alpha-santalol	Apoptotic cell death induced by alpha-santalol is mediated through inhibition of PI3K/AKT-survivn pathway

to UVB exposure. Molecular changes included enhanced expression of tumour suppressor protein, p53 and apoptotic proteins (Caspase-3 and 8) [1].

The properties of alpha-santalol in preventing cancer due to UVB-induced photocarcinogenesis were identified as inflammation inhibition, proliferation of epidermal cells, arresting cell cycle and apoptosis induction. There was significant inhibition of epidermal hyperplasia and epidermis thickness. The levels of proliferating cell nuclear antigen (PCNA), Ki-67 and cyclooxygenase-2 (COX-2) used as proliferation and inflammation markers also reduced [25].

Cell cycle arrest detected by a decrease in expression of cyclins and cyclin-dependent kinases (CDK)s with an up-regulated expression of CDK inhibitor Cip1/p21 and apoptosis induction caused by the increased level of cleaved caspase-3 and cleaved PARP [25] were observed.

Follow-up studies from the same group employing non-melanoma and melanoma skin cancer cells demonstrated G2/M phase cell cycle arrest upon alpha-santalol treatment in p53-mutated A431 human epidermoid carcinoma cells and p53 wild-type UACC-62 human melanoma cells. Knockdown of p21 in A431 cells or knockdown of both p21 and p53 in UACC-62 cells did not change G2/M phase arrest caused by alpha-santalol treatment [29]. Studies performed using combination regimens with honokiol and magnolol demonstrated the chemopreventive potential of alpha-santalol against skin tumour development in SKH-1 mice when used together as opposed to the individual compounds. Pretreatment of SKH-1 mice prior to UVB exposure with combinations of alpha-santalol, honokiol and magnolol significantly decreased tumour multiplicity up to 75% compared to control, alpha-santalol, honokiol and magnolol alone treated groups [9]. Most recently, it was shown that East India Sandalwood oil (EISO) which constitutes 45–50% of alpha-santalol induces autophagy and promotes cell death in proliferating HaCa T keratinocytes, irradiated by UVB radiation [11]. These results provide convincing evidence that EISO and its components would be effective in the treatment of precancerous events such as actinic keratosis .

3 Breast Cancer

Based on the successful demonstration of the chemopreventive effects in skin cancer, alpha-santalol was also investigated for its effectiveness against breast cancer development. The first study [23] employing breast cancer cells, p53 wild-type MCF-7 cells as a model for estrogen receptor (ER)-positive and p53 mutated MDA-MB-231 cells as a model for ER-negative provided evidence on the antitumour effects of alpha-santalol. In both cell lines, alpha-santalol hindered cell viability and proliferation regardless of their ER and/or p53 standing in a concentration and time-dependent manner. Consistent with previous observations, there was less toxicity exhibited by alpha-santalol towards the normal breast epithelial cell line, MCF-10A [23]. Alpha-santalol treatment in breast cancer cells caused G2/M cell cycle arrest and apoptosis. Changes in the protein levels of BRCA1, Chk1, G2/M regulatory cyclins, CDKs, cell division cycle 25B (Cdc25B), Cdc25C and Ser-216 phosphorylation of Cdc25C were associated with cell cycle arrest. MDA-MB-231 cells treated with alpha-santalol also experienced a reduced expression of mutated p53 and an up-regulated expression of p21. In the case of MCF-7 cells, the expression of wild-type p53 and p21 was not increased. Further, alpha-santalol also triggered the executioner caspase-6, 7 in MCF-7 cells and caspase-3, 6 in MDA-MB-231 cells along with PARP cleavage in both cell lines. Also, activation of caspase-8, 9 resulted in inducing extrinsic and intrinsic pathways of apoptosis [23].

It was, therefore, evident from recent studies that down-regulation of total survivin levels irrespective of estrogen receptor (ER) and/or p53 status [3] occurs in alpha-santalol treatment inducing apoptosis.

Survivin overexpression correlates with tumour recurrence and therapeutic resistance. Studies have shown that inhibition of the PI3K–AKT pathway leads to decreased survivin levels that correlate to decreased tumour burden. The study showed that alpha-santalol-mediated antitumour effects in breast cancer cells might be regulated in part through suppression of survivin levels, occurring via a pathway other than the PI3K–AKT circuit [3]. Furthermore, it was revealed in a follow-up study that alpha-santalol-mediated growth suppression in breast cancer cells may be regulated through the Wnt//β-catenin pathway [5]. In this study, alpha-santalol treatment of MDA-MB 231 human breast cancer cells inhibited the migratory potential of the cells when compared to the DMSO—treated control group. It also impeded the translocation of β-catenin to the nucleus and reduced the expression of phospho-β-catenin levels in breast cancer cells [5]. A different study examined the cytotoxic and genotoxic effects of SWO in MCF-7 breast adenocarcinoma cells and non-tumour breast epithelial cells, MCF-10A [20]. After treatment of both cell lines with different concentrations of SWO (2, 4, 6 and 8 μg/mL), the IC50 was found to be 8.03 μg/mL for MCF-7 cells, while for the MCF-10A cell line, it was 12.3 μg/mL. Additionally, increasing concentrations of SWO showed a reduction of class 1 comets, a genotoxic agent that can cause cellular mutation to breast cancer, to almost 10%. The results indicate that SWO has selective genotoxic effects in MCF-7 cells compared with MCF-10A cells and can induce single and double stranded DNA breaks in MCF-7 Cells.

In vivo significance of alpha-santalol was established in a study that examined the role of a microemulsion formulation of alpha-santalol in a rat model of chemical carcinogenesis for breast cancer [10]. Transdermal/transpapillary delivery of alpha-santalol significantly reduced the tumour incidence and multiplicity. A more recent clinical study investigated turmeric and SWO-based cream's effectiveness, which contained turmeric extract 16%w/w, Sandalwood Oil 0.5%w/w in a non-greasy base, against radiation-induced dermatitis in women undergoing treatment for breast cancer. The study concluded that the protective effects of curcumin and SWO are due to their anti-inflammatory and antioxidant ability in modulating cytokines [22].

4 Prostate Cancer

Consistent with previously published studies pertinent to other cancer models, treatment of prostate cancer cells with alpha-santalol resulted in induction of apoptosis as verified by DNA fragmentation and nuclear staining of apoptotic cells by DAPI [7]. The growth inhibitory effects and induction of apoptosis by alpha-santalol were evident in both PC-3 and LNCaP cells irrespective of their androgen or p53 status, and results were concentration and time-dependent. The alpha-santalol-induced apoptotic cell death and activation of caspase-3 significantly diminished in the presence of pharmacological inhibitors of caspase-8, 9 [7]. A study from our group recently identified that alpha-santalol-induced apoptotic cell death in prostate cancer cells might be regulated by targeting PI3K/AKT/Survivin pathway [6]. In the study, we showed that alpha-santalol-induced apoptosis was enhanced in the presence of a known pharmacological inhibitor of the PI3K/Akt pathway. We also showed that alpha-santalol suppressed total survivin levels, an important downstream regulator of Akt, whose overexpression often confers treatment resistance and inhibition of cell death by apoptotic agents. Because PI3K/Akt pathway plays a major role in cellular signalling and is linked to cell survival and inhibition of apoptosis, agents that target this pathway are highly sought after and a known Akt inhibitor is yet to be approved for clinical utility. An earlier study [26] that investigated the in vivo efficacy of alpha-santalol against prostate cancer development by employing a xenograft mouse model for prostate cancer demonstrated its antitumour properties and inhibition of angiogenesis. Human umbilical vein endothelial cells (HUVECs) and prostate cancer cells (PC-3 or LNCaP) were used to demonstrate anti-angiogenic effects of alpha-santalol. Alpha-santalol suppressed the invasion of HUVECs and capillary tube formation and inhibited the migration of endothelial cells in a dose-dependent manner. Alpha-santalol reduced tumour growth through inhibiting angiogenesis by targeting the VEGFR2-regulated AKT/mTOR/P70S6K signalling pathway. The potential of alpha-santalol in treating prostate cancer was demonstrated by an increase in lifespan and fewer adverse effects in tumour-bearing mice. Significant reduction in weight and volume of solid tumours in the prostate xenograft mouse model was also observed following treatment with alpha-santalol [26].

This study further provides evidence that the PI3k/Akt pathway can be a viable target of alpha-santalol in inhibiting prostate cancer growth and cell proliferation.

5 Oral, Head and Neck Cancers

The earlier stages of oral cancers are most often treated with surgery, sometimes in combination with radiotherapy. However, this treatment frequently results in severe toxic side effects such as an increased exertion in speaking and/or swallowing. As the disease progresses, treatment of oral cancers includes chemotherapy, which presents undesired side effects that may reduce the quality of life. Unfortunately, disease diagnosis and management advancements have not been substantial in HPV-negative head and neck squamous cell carcinoma (HNSCC) tumours in the past 30 years. Therefore, there is a need for the development of better treatments for HNSCC. A pilot study [21] on 50 patients (with head and neck cancer requiring curative radiation and/or chemotherapy) on the efficacy of sandalwood containing creams on the neck and head cancer discovered that the sandalwood cream had significantly better treatment than the comparison (Johnson's baby oil). Participants showed a significant decrease in dermatitis and reduction at the time of follow-up (2 weeks) that was unlike the oil group [21]. Similarly, according to the National Cancer Institute, a mouth rinse containing 0.25% ESIO, may exhibit chemokines and pro-inflammatory cytokine inhibitory effects that may be attributed to the effects of alpha- and beta-santalol. The mechanism of action is theoretically contributed to the inhibition of COX enzymes to lessen the inflammatory response of the mucosal membranes. Overall, the likeliness of oral mucositis through chemotherapy may be prevented by administration of SWO mouth rinse.

In a different study employing HNSCC cells, alpha-santalol treatment resulted in G2/M cell cycle arrest and cell growth suppression [18]. Additionally, it was found that treatment with alpha-santalol caused the formation of multipolar mitotic spindles analogous to those observed upon treatment of cells with compounds that disturb microtubule polymerization. Modelling studies propose that santalols can weakly bind to the colchicine site on tubulin and can inhibit the polymerization of microtubules, similar to anticancer activity observed with established chemotherapeutic agents. However, alpha-santalol exhibits reduced toxicity as compared to other compounds having the property to interact directly with tubulin. Based on the results demonstrated, it is reasonable to conclude that sandalwood and its components may serve as therapeutic agents that can be used in the treatment of oral cancers.

6 Conclusion

This chapter's focus is to compile information pertinent to the antitumour and cancer-preventive properties of SWO and alpha-santalol and summarize the in vitro and in vivo findings, including the results of available and/or completed human studies. Based on the results from preclinical studies, it is reasonable to conclude that the administration of SWO and alpha-santalol may have protective effects against the development of various cancers. Studies suggest that SWO and its components are safe and promising therapeutic agents against cancer development with their potential to target multiple pathways and modulate the expression of markers involved in carcinogenesis. Based on available data from studies involving cancer prevention and treatment with SWO and alpha-santalol, the antitumour and cancer-preventive properties are attributed to their pro-apoptotic, antiproliferative, anti-angiogenic, antioxidant and anti-inflammatory activities. Uniquely, these agents minimize undesirable side-effects and could improve patient compliance/quality of life.

In conclusion, alpha-santalol and SWO have shown promise against the development of deadly malignancies. However, there are certain limitations, such as bioavailability and the concentrations of SWO and alpha-santalol required to exert these beneficial effects. Therefore, studies are warranted to confirm their exact role when used alone or in combination with other agents in disease prevention and treatment.

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Chapter 28
Chandana (*Santalum album* L.) in Ayurveda

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1 Introduction

Candana has been the most valuable tree for its cultural, religious and medicinal uses since time immemorial. *Candana* is a *pittaśamaka* (pacifying *pitta*) drug having *tikta rasa* (bitter taste) and *śītavīrya* (cold in potency). On an analysis of the available Ayurveda classical texts and *nighaṇṭus,* it was found that *Candana* is known by almost 35 different names. Most of the synonyms are related to the habit, habitat and organoleptic characters of the plant. Lexicons differ in their opinion regarding the varieties of *Candana*, the number being three, five and seven in various *nighaṇṭus* and *sāligrāmanighaṇṭu* describes two varieties on the basis of how it is cut and dried. Therapeutically, it is beneficial in *raktapitta* (bleeding disorder), *tṛṣṇā* (excessive thirst), *dāha* (burning sensation), *viṣa* (poison), *śoṣa* (emaciation) and *klama* (fatigue). Most of the formulations containing *Candana* are indicated for *raktaprasādana* (blood purification) and also in diseases involving higher mental functions like *unmāda* (insanity) and *apasmāra* (convulsion disorders). Owing to its *varṇya* (improving complexion) and *viṣahara* (anti toxic) property, *Candana* is a main ingredient in medicinal preparations for skin diseases.

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2 Historical Background

Candana, botanically identified as *Santalum album* of Santalaceae family, is a well-known medicinal plant even from the vedic times. '*Rig Veda*', one of the oldest available literatures written around 2000 B.C., mentions the use of Sandalwood (*Santalum album*), not only in religious ceremonies but also in medicinal preparations. During the age of '*Yajur Veda*', sandalwood was used in sacrificial fire [4]. *Candana* is mentioned in the *Nirukta* of *Yakṣa* which is one of the oldest Vedic commentaries. It is also mentioned in the ancient Hindu epic poems *Rāmāyana* and *Mahābhārata.*

3 Mythological Origin

Brahma vaivarta purāna considers the importance of Indian sandalwood and narrates that *Brahma* created it through meditative contemplation. In *Brahma vaivarta purāna*, it is mentioned that 'Goddess Lakshmi' (Goddess of wealth) resides in sandalwood, thus Indian sandalwood tree is believed to be auspicious and provider of wealth [21].

4 *Candana* in Ayurveda Classics and Lexicons

There is a comprehensive description of *Candana* in ancient ayurvedic literature. The white sandalwood was held in high esteem because of the aromatic smell of its heartwood. Nighaṇṭus give the derivation of the term *Candana* as '*Candanatiāhlādayati iti'* (pleasure giving). Acharya Caraka included *Candana* in *dāha praśamana* (pacifying burning sensation), *aṅgamarda praśamana* (bringing down the pain in various parts of the body), *tṛṣṇā nigrahaṇa* (overcoming thirst), *varṇya* (improving complexion), *kaṇdughna* (curing pruritis) and *viṣaghna mahakaṣāya vargā* (group of drugs that bring down toxicity) [10]. *Candana* is included among the drugs of *tiktaskandha* (a group of bitter drugs) by Caraka. Suśruta mentioned *Candana* in *Patolādi*, *Guluchyādi*, *Sālasarādi*, *Śarivādi*, *Priyānguvādi* [29] and *Pittasamśamanavarga.* Kaśyapa has included *Candana* in *Jīvanīyagaṇa* (a group of herbs which invigorates/ nourishes the body) [28]. *Candana* is included among *Karpūrādivarga* in Bhāvaprakāśa Nighaṇṭu [6]. Dhanvantari Nighaṇṭu [1] and Rājanighaṇṭu [20] included it among *Candanādivarga.*

5 Synonyms

A lot of synonyms are introduced to drugs during the Nighaṇṭu period. On an analysis of the available nighaṇṭus, it was found that *Candana* is known by almost 35 different names. Most of the synonyms are related to the habit, habitat and organoleptic characters of the plant. The synonyms *Malaya*, *Malayotbhava and Malayaja* indicate its place of origin Malaya desha probably the regions of Western Ghats. Synonyms like *Gandharāja*, *Gandhasāra*, *Sugandha*, *Gandhādya* refer to the aromatic smell of its heart wood. Synonyms *Sarpavāsa and Sarpapriya* denote the affinity of snakes to the tree due to its extreme fragrance making the tree or nearby its place of living. *Tilaparṇa and Tilaparṇaka* denote the shape of its leaves similar to that of the leaves of *Tila* (*Sesamum indicum*). Synonyms of *Candana* from various available nighaṇṭus are furnished in Table 1.

6 Varieties

Three varieties of *Candana* are described in Kaiyādevanighaṇṭu, *rakta* (red variety), *pīta* (yellow variety) *and pāṇḍura* (white variety). Among the three, *Raktavarṇa Candana* is considered as *uttama* (best). *Raktasāra Candana* is *guru* (difficult to digest), *madhura* (sweet), *tikta* (bitter), *śīta* (cold), *Cakṣuṣya* (promoting eye health) and *śukrala* (Enhancing the quality of reproductive elements). It is indicated in *jvara* (fever), *chardi* (vomiting), *tṛṣṇā* (excessive thirst) and *raktapitta* (bleeding disorders). Seven varieties of *Candana* are mentioned in Rājanighaṇṭu. *Śrikhanda*, *Śabara*, *Pīta*, *Patrānga*, *Raktacandana*, *Barbara and Harigandha* are the seven varieties. Another classification as *Vetta Candana* (freshly cut and dried) and *Sukkadi Candana* (dried naturally) is seen in *Śāligrāmanighaṇṭu.* Nighaṇṭuratnākara mentions that the *Candana* grown in *Vettaparvata* near Malayadri is *Vetta Candana* [8].

7 Wood Characters Described in Ayurveda Classics

Lexicons give descriptions regarding the characteristics of wood of *Candana.* According to Bhāvamiśra, superior quality *Candana* is *tikta* (bitter) in taste, gives yellow colour on rubbing, reddish inside and white outside and possesses knots and ridges. Same characters are mentioned for superior quality *Candana* in Rājanighaṇṭu also. According to Kaiyādeva, *Ārdrachinna Candana* (freshly cut) is *pittahara* (pacifies *pitta* - one of the biohumours), *śuṣkachinna* (cut and dry) is *vātahara* (pacifies *vāta*), and *Ārdraśuṣkachinna Candana* is *śleṣmahara* (pacifies *kapha*).

Table 1 Synonyms of *candana* in ayurveda lexicons

Synonyms	BPN	DN	RN	PN	KN	MN	NiSe	SN	PaRa	SGN	SaCa	HDN	AM
Bhadrasrī	*	*	*		*	*	*		*	*	*	*	
Bhōgīvallabha			*										
Candanam	*		*		*	*	*	*		*	*	*	
Chandradyuti	*												
Gandhādya			*										
Gandharājam			*										
Gandhasāram	*	*	*	*	*	*	*	*	*	*	*		
Gōśirṣam		*	*			*	*						
Himam					*				*	*	*	*	
Indukāntham													*
Mahārgham		*	*		*	*	*			*			
Malayaja	*	*	*	*	*	*	*		*	*	*		
Mālayam					*								
Malayōdbhavam			*										
Mangalyam			*										
Nṛpabhōgam													*
Pāvana			*										
Phalaki							*						
Rajayogya								*	*				
Rohanodbhavam							*						
Śaragandham											*		
Sarpapriya								*		*			
Sarpavāsa			*										
Śirṣa Candanam					*								
Śiśiram					*							*	
Śīta gandha			*										
Śītalam			*										
Śītam													
Śrīkhandam	*	*	*	*			*			*			
Śrīpriya								*					
Śubhra											*		
Sugandha			*	*									
Surabhi							*						
Surōttara											*		
Suśreekam													*
Śveta candanam			*		*			*					
Śveta śreṣtam					*								

(continued)

Table 1 (continued)

Synonyms	BPN	DN	RN	PN	KN	MN	NiSe	SN	PaRa	SGN	SaCa	HDN	AM
Tila parṇika	*	*	*		*	*	*			*			

BPN Bhāvaprakāśa Nighaṇṭu, *DN* Dhanvantari Nighaṇṭu, *RN* Rājanighaṇṭu, *KN* Kaiyādeva Nighaṇṭu [15], *MN* Madanapāla Nighaṇṭu [19], *PN* Priyanighaṇṭu [23], *NiSe* Nighaṇṭuśeṣa [13], *SGN* Śāligrāma Nighaṇṭu [2], *SN* Śodhāla Nighaṇṭu [25], *PaRa* Paryāyaratnamāla [14], *HDN* Hṛdayadīpika Nighaṇṭu [12], *SaCa* Sabdacandrika [16], *AM* Abhidhānamanjari [11]

8 Attributes and Pharmacological Actions

Many attributes and pharmacological actions of these drugs are described in different ayurvedic texts. In Ayurveda, *Rasapanchaka* is the tool to explain the pharmacological action of drugs. Acharya Caraka included *Candana* among *Tiktaskandha. Candana* possesses *tiktarasa* (bitter taste), *laghu* (easily digestable), *rūkṣa guṇa* (dryness), *śītavirya* (cold in potency) and *katuvipāka* (turns pungent on metabolism). It is *raktapittahara* (mitigates *rakta* and *pitta*), *viṣaghna* (antitoxic), *tṛṣṇahara* (thirst relieving), *dāhahara* (relieves burning sensation), *śoṣahara*, *āhlādana* (nourishing the body and mind), *klamahara* (removes tiredness), *hṛdya* (cardioprotective) and *varṇya* (improving complexion). *Rasapanchaka* and *Karma* of *Candana* from various *nighaṇṭus* are shown below (Table 2).

9 Therapeutic Uses

Candana is used in the treatment of many diseases, and ayurvedic texts considerably vary in the description of its therapeutic utility. Caraka included *Candana* in *dāhapraśamana*, *aṅgamardapraśamana*, *tṛṣṇānigrahaṇa*, *varṇya*, *kaṇdughna and viṣaghnamahākaṣāya vargās*. *Candana* is mainly indicated in *raktapitta* (bleeding disorders), jvara (fever), *chardi* (vomiting), *vātarakta* (arthritis), *prameha* (diabetes), *śītapitta* (urticaria), etc. It is one of the most useful drugs in *raktavahasrotavikārās* (vascular diseases). It is also an important ingredient in the formulations used to treat *unmāda* (insanity) and *apasmāra* (convulsion disorders).

10 Important Single-Drug Usages of *Candana*

- *Candana* mixed with sugar, honey and taken along with kanji (water of rice gruel) cures *dāha* (burning sensation), *tṛṣṇā* (thirst), *prameha* (diabetes) and *raktasrāva* (bleeding disorder) (A.H.Ci., 9.92) [26].
- *Candana* along with *Āmalaki* (*Emblica officinalis*) *svarasa* (juice) checks vomiting (C.S.Ci., 20.32)

Table 2 Rasapanchaka (five properties) and karma (pharmacological activity) of *candana*

Nighaṇṭu	Rasa	Guṇa	Vīrya	Vipāka	Karma
DN	Svadutikta	Guru rūkṣa	Śīta		*Raktaprasādana*, *Vṛṣya* (aphrodisiac), *Antardāhahara*, *Raktapittahara*, *Kṛmighna* (destroys worms), *Viṣaghna*, *Tṛṣṇahara*
KN	Tikta	Laghurūkṣa	Śīta		*Raktapittahara*, *Viṣaghna*, *Tṛṣṇahara*, *Dāhahara*, *Śoṣahara*, *Āhladana*, *Klamahara*, *Hṛdya*, *Varṇya*
MN	Tikta	Rūkṣa	Śīta		*Raktapittahara*, *Dāhahara*, *Śoṣahara*, *Āhladana*, *Hṛdya*
BPN	Tikta	Laghurūkṣa	Śīta		*Raktapittahara*, *Viṣaghna*, *Tṛṣṇahara*, *Dāhahara*, *Śoṣahara*, *Ahladana*, *Śramahara*
RN	Kaṭutiktamadhurakaṣāya		Śīta	Kaṭu	*Vriya*, *Kṛmighna*, *Tṛṣṇahara*, *Tanumardavakara* (softens body), *Jvarahara*, *Chardihara*, *Vaktrarujāpaha* (pacifies pain in mouth)
SGN	Tikta	Rūkṣa	Śīta		*Raktapittahara*, *Viṣaghna*, *Tṛṣṇahara*, *Dāhahara*, *Klamahara*
PN	Tikta	Laghu	Śīta		*Raktapittahara*, *Viṣaghna*, *Tṛṣṇahara*, *Dāhahara*, *Śoṣahara*, *Āhlādana*, *Śramahara* (pacifies exhaustion)

- *Lepana* (external application) with *Candana* on chest region is indicated in poisoning(S.S.Ka., 1.36)
- In *śītapitta* (Urticaria) paste of *Candana* and *Guḍūci* (*Tinospora cordifolia*) should be taken (V.D.,11.22)
- Suśṛuta prescribes the decoction of *Arjuna* (*Terminalia arjuna*) and *Candana* in *śukrameha* (a type of diabetes) (S.S.Ci., 11.9)
- Similarly in *manjiṣtameha* (a type of diabetes), decoction of *Manjiṣta* (*Rubia cordifolia*) and *Candana* is useful
- In *majjātulyārtava* (menstrual disorder with foetid and purulent blood), use of *Candana kvātha* is beneficial. *Candana* may be used along with milk, sugar, ghee and honey (S.S.Sa., 2.14)
- In *nābhipāka* (inflammation of umbilicus), the naval should be dusted with powder of *Candana* (B.P.Ci., 71.180) [7, 24]
- *Candanādi kvātha* is prescribed in *pitta jvara* (pyrexia variant) (S. S Ci. 5.8)
- *Candana* rasa along with *Śuṇṭhi* (*Zingiber officinale*) is beneficial in *Raktārśas* (bleeding piles) (C.S.Ci., 14.185)
- Snuffing the powder of *Candana* checks epistaxis (*nāsagataraktapitta*)
- *Nasya* of *Candana cūrṇa* with breast milk (*stanya*) is indicated in *hikkā* (hiccough) (C.S.Ci., 17.131). *Candana* is a *śītavīrya* drug and has predominant *pittaśamaka* property. Owing to its *varṇya* and *viṣahara* property, *Candana* is a main ingredient in medicinal preparations for skin diseases. External application of *Candana* is soothing and acts on *bhrājaka pitta.* Being *śīta* it is very useful in burning sensation. *Tikta rasa* which is *medhya* and *śītavīrya* of the drug make it beneficial even in diseases involving higher mental functions. The drug mainly acts on *rasa*, *raktavahāsrotas* and very much useful in *raktapitta, raktārśas* and *pradara* (bleeding). It also acts on *mūtrāvahāsrotas* and is very much useful in *paittika mūtrakṛchra.* Major formulations containing Candana are given in Table 3.

(A.H.Ci.—*Aṣṭāṅgahṛdaya cikitsāsthāna*, C.S.Ci.—*Carakasaṃhita cikitsāsthāna*, S.S.Ci.—*Suśṛutasaṃhita cikitsāsthāna*, S.S.Sa.—*Suśṛutasaṃhita śarīrasthāna*, B.P.Ci.—*Bhāvaprakāśasaṃhita Cikitsa*).

11 Conclusion

In short, *Candana* has been the most valuable tree for its cultural, religious and medicinal uses since time immemorial. The significance of *Candana* as medicine is greatly reflected in the available Ayurveda classics, compendia and lexicons. Due to overexploitation and illicit felling, Sandalwood is enlisted in Vulnerable category of IUCN Red List. Considering its traditional and medicinal value, it is high time to conserve the species.

Table 3 Formulations containing *candana* in Ayurveda texts

SN	Formulation	Indication	Kalpana	References
1.	*Abhayāmalaki rasāyana*	*rasāyana*	Avaleha	B.B.R, Vol. 1: 143
2.	*Ajeya ghṛta*	*viṣaghnam*	Ghṛta	B.B.R., Vol. 1: 160
3.	*Ajeya ghṛta*	*viṣaghna* (antitoxic)	Ghṛta	S.S.Ci. 2/48
4.	*Āmalakya rasāyanam*	*rasāyana*	Avaleha	B.B.R., Vol. 1: 416
5.	*Amṛta ghṛta*	*viṣaghnam*	Ghṛta	B.B.R., Vol. 1: 161
6.	*Amṛtabhallātaka ghṛta*	*amṛta samam* (equivalent to ambrosia), *guṇadāyi* (rejuvenative)	Ghṛta	B.B.R., Vol. 1: 147
7.	*Amṛtabhallātakyāvaleha*	*visarpa*, *kaṇḍu* (pruritis)	Avaleha	B.B.R., Vol. 1:146
8.	*Amṛtādi taila*	*apasmāra* (convulsion disorders), *unmāda* (insanity), *arti* (restlessness)	Taila	C.S.Ci. 28/158–164
9.	*Amṛtādi taila*	*dhātukṣinta* (emaciation), *mandāgnī* (poor digestion), *nirbalta* (weakness), *chittavibhrama* (disturbed mental status), *unmāda*, *vyākulata* (depression), *apasmāra*, *vāta vyādhi*	Taila	B.B.R., Vol. 1:182
10.	*Amṛtādi taila* (4)	Useful in *vātarakta*, *kṣinta* (under nourished), *alpavīrya* (with diminished potency), *kampana* (tremor), *vātaroga*, *yoni doṣa* (gynaecological disorder), *apasmāra*, *unmāda*, *viṣamajvara*		B.B.R., Vol. 1: 185
11.	*Amṛtādya ghṛta*	*yakṣma* (malnourishment), *raktapitta*	Ghṛta	B.B.R.,Vol. 1: 8849
12.	*Amṛtaprāśa avaleha*	*mūtrakṛchra* (dysuria), *jvara*	Avaleha	B.B.R.,Vol. 1: 144
13.	*Amṛtaprāśa cūrṇa*	*aṅgadāham* (burning sensation), *raktapitta*	Cūrṇa	B.B.R., Vol. 1: 68 [22]
14.	*Amṛtāṣtaka cūrṇa*	*arocaka*, *chardi*	Cūrṇa	B.B.R., Vol. 1: 71
15.	*Amṛtāṣtakam*	*pitta sleṣma jvara* (fever due to vitiated *pitta* and *kapha*)	Kaṣāya	S.S. M.K. 2/25
16.	*Aṅgamarda praśamana kaṣāya*	*aṅgamarda* (generalized body ache)	Kaṣāya	B.B.R., Vol. 1:591

(continued)

Table 3 (continued)

SN	Formulation	Indication	Kalpana	References
17.	*Aṅgamekhala modaka gulika*	*balavardhaka*, *buddhivardhaka* (improving mental faculties), *kāmaśaktivardhaka* (aphrodisiac), *vīryastambhaka* (aphrodisiac in nature), *agnisandīpaka* (carminative), useful in *pāṇḍu* (anaemia), *śvāsa* (dyspnoea), *śūla* (pain), *bhrama* (giddiness)	Gutika	B.B.R., Vol. 1: 107
18.	*Aśokāriṣṭam*	useful in *jvara*, *raktapitta*, *mandāgnī*, *aruci*, *prameha*	Ariṣta	B.B.R., Vol. 1: 197
19.	*Aśvagandha pāka* 1	*kāntivardhaka* (improving complexion), *śukravardhaka* (aphrodisiac), *puṣtivardhaka* (nourishing), *agnisandīpana*, useful in *prameha* (antidiabetic), *jīrṇajvara*, *śoṣa* (malnutrition), *gulma*, *vāyu pitta* roga (diseases due to the vitiation of *vāta* and *pitta*)		B.B.R., Vol. 1: 152
20.	*Aśvagandha pāka 2*	*agnisandīpana*, *śaktivardhaka*, *vīryavardhaka*, *kāmavardhaka*; useful in *vāta rakta*, *medoroga* (diseases connected with *medo dathu*), *ṣūla* (pain), *gulma* (tumour/growth in intestine), *vayuroga*, *kapha*roga,		B.B.R., Vol. 1: 153
21.	*Aśvagandhādi taila*	*sarva jvara naśaka* (antipyretic), *sarva dhātu vardhaka* (rejuvanative/ nourishing), *kṣayaroganāśaka* (preventing emaciation)	Taila	B.B.R., Vol. 1; 189
22.	*Aśvagandhāriṣta*	Useful in *mūrcchā* (helpful in loss of consciousness), *apasmāra*, *śoṣa*, *unmāda*, *kārśyam* (emaciation), *mandāgnī* (poor digestive power), *vātaroga*	Ariṣta	B.B.R., Vol. 1; 198
23.	*Avakpuṣpyādi ghṛta*	*arśa* (haemorrhoid/piles), *atīsāra* (diarrhoea), *mūtrāvarodha* (urinary obstruction), *mandāgnī* (poor digestion), *aruci* (anorexia), *balavardhaka*, *varṇavardhaka* (improving complexion), *agnivardhaka*	Ghṛta	B.B.R., Vol. 1; 170
24.	*Balā taila*	*vātahara* (pacifying *vāta* vitiation)	Taila	A.H.Ci. 21/75
25.	*Balā taila*	*śirovibhrama* (vertigo), *paresis* (weakness), *paralysis*, *unmāda*, *apasmāra*, *vātaroga*, *śiraṣūla*	Taila	K.S.Ci. Dhatricikitsa

(continued)

Table 3 (continued)

SN	Formulation	Indication	Kalpana	References
26.	*Balādi taila*	*vātaroga*	Taila	A.H.Sa. 2/48
27.	*Bilvādi* cūrṇa	*mastiṣkaroga* (diseases of brain)	Cūrṇa	B.R. Mastiṣkaroga [18]
28.	*Brāhma rasāyanam*	*rasāyana* (rejuvenative)		C.S.Ci., 1/1/47
29.	*Candana bala taila*	*Sapta dhātu vardhaka* (rejuvenative), *raktapitta*, *dāha*, *aṅgadāha* (burning sensation), *śiroroga*, *vāta roga nāśaka* (curing *vāta* disorders)	Taila	B.N.R., IV, Jvara Cikitsa
30.	*Candana balālākṣādi tailam*	*sapta dhātu vardhaka* (rejuvenating/ nourishing), useful for children, old and weak persons, used in *pitta kapha roga*, *dāha*, *jvara*, *śiroroga*, *netra dāha* (burning eyes)	Taila	B.B.R., Vol. 1;1789
31.	*Candana cūrṇa*	*antargataraktapitta* (internal bleeding disorder)	Cūrṇa (as nasya)	V.M., 2/7 [17]
32.	*Candana cūrṇa*	*śiśonābhipāka* (inflammation of umbilicus)	Cūrṇa	V.S
33.	*Candana* cūrṇa with *stanya*	*hikkā* (hiccups)	As nasya	C. S.Ci., 17/131
34.	*Candana cūrṇa yoga*	*chardi*	Cūrṇa	B.B.R., Vol. 1;1694
35.	*Candana kaṣāya*	*pradara* (menorrhagia)	Kaṣāya	S.S.Sa., 2/14
36.	*Candana kirātatiktādi kaṣāya*	*raktārśas* (bleeding piles/ haemorrhoids)	Kaṣāya	C. S.Ci., 14/186
37.	*Candana pralepa*	*durgandha* (unpleasant odour), *dāha* (burning sensation)	Lepa	C.S.S., S25/40
38.	*Candana siddha kṣīra*	*raktātīsāra* (dysentery)	Kṣīra	K.S., Khilasthāna 10
39.	*Candana svarasa* with *Śuṇṭhi*	*raktārśas* (bleeding piles/ haemorrhoid)		C.S.Ci., 14/185
40.	*Candana* with *āmalaka svarasa*	*chardi* (vomiting)		C.S.Ci., 20/32
41.	*Candana* with *āmalaka svarasa* and *honey*	*chardi*		V.M., 15/6

(continued)

Table 3 (continued)

SN	Formulation	Indication	Kalpana	References
42.	*Candana* with *guḍūci*	*śītapitta* (urticaria)		V.M., 11/22
43.	*Candana* with *tandulambu*	*uṣṇavāta* (cystitis/ urthritis)		B.P. Mūtrāghāta Cikitsa
44.	*Candana* with *tandulambu, madhu and śīta*	*raktātīsāra* (diarrhoea with bleeding)		B.P. Atīsāra cikitsa
45.	*Candana*, *śīta*, *madhu* with *tandulambu*	*dāha*, *tṛṣṇā* (excessive thirst), *prameha*		C.S.Ci., 19/86, A.H.Ci., 9/92
46.	*Candanādi avaleha*	*apasmāra*	Avaleha	B.N.R., Apasmāra
47.	*Candanādi avaleha*	*apasmāra*, *unmāda, raktapitta nāśaka*, *mastakaroga*, *pittātīsāra*, *raktātīsāra*, *śotha* (inflammatory swelling), *dāha*	Avaleha	B.N.R.V., Apasmarkarma Vipāk
48.	*Candanādi cūrṇa*	*dāharoga* (burning sensation)	Cūrṇa	Y.R., Dāharoga
49.	*Candanādi cūrṇa*	*raktapitta*	Cūrṇa	B.N.R., Raktapitta
50.	*Candanādi cūrṇa*	*pitta vyādhi*	Cūrṇa	B.B.R., Vol. 1;1697
51.	*Candanādi cūrṇa*	*atīsāra*, *raktapitta nāśaka* (curing bleeding disorders)	Cūrṇa	B.N.R.V., Raktapittakarma Vipāk
52.	*Candanādi cūrṇa* (2)	*raktapitta nāśaka*, *aṅgadāha*, *mastakadāha* (burning sensation of forehead), *śirovibhrama*, *pittajvara*	Cūrṇa	B.N.R.V., Dāhakarmavipāk
53.	*Candanādi cūrṇāñjan*	*śukrarma* (effective in pterygium)	Añjana	B.B.R., Vol. 2: 1848
54.	*Candanādi ghṛta*	*jvara*	Ghṛta	V.S. [27]
55.	*Candanādi ghṛta*	*pitta visarpa*	Ghṛta	B.H.S.Ci. 21
56.	*Candanādi kalka*	*pitta visarpa*	Kalka	B.H.S.Ci. 21
57.	*Candanādi kaṣāya hima*	*santatādijvara* (various kinds of intermittent fever)	Hikakaṣāya	A.S. 1/60

(continued)

Table 3 (continued)

SN	Formulation	Indication	Kalpana	References
58.	*Candanādi kṣīra kaṣāya*	*raktapradara* (menorrhagia)	Kśīrakaṣāya	S.D.N
59.	*Candanādi kvātha*	*vātarakta* (inflammatory arthritis)	Kaṣāya	S.S.Ci., 5/8
60.	*Candanādi kvātha*	*dāha*	Kaṣāya	B.N.R., Dāhakarma
61.	*Candanādi kwatha*	*dāha*	Kaṣāya	B.N.R.V., Dāhakarmavipāk
6.2..	*Candanādi lepa*	*bhagna* (fracture)	Lepa	S.S
63.	*Candanādi lepa*	*śiroroga* (diseases of head)	Lepa	C.D. [9]
64.	*Candanādi lepa*	*visarpa pitta*	Lepa	A.S., 20/8
65.	*Candanādi lepa*	*śiraśūla*	Lepa	C.D., Śirorog Cikitsa, 11
66.	*Candanādi mantham*	*jvaram*	Mantham	Y.R. Jvara Cikitsa
67.	*Candanādi nasya*	*śiraśūla* (headache)		B.P. Śiroroga
68.	*Candanādi nasya*	*śvāsa hidhma* (diseases connected with respiratory tract and hiccups)		A.S., 6/57
69.	*Candanādi* pana	*chardi*		B.N.R.V, Chardikarma
70.	*Candanādi ropana tailam*	*vraṇaropana* (wound healing)	Taila	B.B.R., Vol. 2: 1797
71.	*Candanādi taila*	*vraṇa* (wound)	Taila	S.S
72.	*Candanādi taila*		Taila	S.S.M.K., 10/191
73.	*Candanādi taila*	*jīrṇajvara* (subsiding fever)	Taila	B.N.R., Jvara
74.	*Candanādi taila*	*sarvajvara* (fever)	Taila	B.N.R., Jvara
75.	*Candanādi taila*	*jīrṇajvara*	Taila	B.N.R., IV, Jīrṇajvara Cikitsa
76.	*Candanādi taila* (2)	*apasmāra, unmāda, dāha, jīrṇajvara, kṣaya*	Taila	B.N.R., IV, Jīrṇajvara Cikitsa

(continued)

Table 3 (continued)

SN	Formulation	Indication	Kalpana	References
77.	*Candanādi tailam*	*raktapitta*, *kṣaya*, *jvara*	Tailam	B.B.R., Vol. 1: 1790
78.	*Candanādi tailam* (2)	*rasāyana*, *saundarya*, *vṛddhi*, *kāntivardhaka*, *puṣṭivardhaka* (nourishing), *lāvaṇyavardhaka* (enhancing beauty), useful in *vātarakta*, *marmāghāta* (injury to marma/vital points), *dāha*, *jvara*, *apasmāra*	Tailam	B.B.R., Vol. II: 1791
79.	*Candanādi tailam* (3)	*balavardhaka*, *varṇa sanskaraka* (improving complexion), *ojavardhaka* (immuno modulatory), *medhavardhaka* (improving mental faculties), *āyuvardhaka* (improving lifespan), *pragya vardhaka* (enhancing mental faculties), *saundarya vardhaka*, useful in *apasmāra*	Taila	B.B.R., Vol. II: 1792
80.	*Candanādi tailam* (4)	Useful in *jvara*	Taila	B.B.R., Vol. II: 1793
81.	*Candanādya ghṛta*	*grahaṇī* (sprue)	Ghṛta	C. S.Ci.,15/ 125–128
82.	*Candanādya ghṛta*	*viṣamajvara* (intermittent fever)	Ghṛta	B.N.R., Jvara [3]
83.	*Candanādya ghṛta*	*unmāda*, *viṣam*, *jvara*, *śvāsa*,	Gnrita	B.N.R., IV, Jvara Cikitsa
84.	*Candanādya taila*	*jvarapraśamana*, *dāha*	Taila	C.S.Ci., 3/258
85.	*Candanādyam tailam* 2	*balavardhaka*, *varṇa sanskaraka*, *agnivardhaka*, useful in *kāntihita* (enhancing complexion), *viṣa*, *rāja yakṣma*, *kuṣṭha*	Taila	B.B.R., Vol. II: 1799
86.	*Candanādyam tailam* 1	Useful in *unmāda*, *apasmāra*, *raktapitta*, *balavardhaka*, *varṇa sanskaraka*, *puṣṭivardhaka*, *āyuvardhaka*	Taila	B.B.R., Vol. II: 1798
87.	*Candanādyam tailam* 3	*apacī* (tumour)	Taila	B.B.R., Vol. II: 1800
88.	*Candanādyam tailam* 4	*dāhajvara*	Taila	B.B.R., Vol. II: 1801
89.	*Candanāsava*	*śukradoṣam* (correcting urinary functions), *rajodoṣam mūtrādoṣam* (corrects Genito-urinary functions)	Asava	B.B.R., Vol. II: 1812
90.	*Candanāsava* 2	*aruci, śukradoṣa*, *rajodoṣa*, *prameha*, *agnimāndya* (loss of appetite)	Asava	B.B.R., Vol. II: 1812
91.	*Candanasiddha ghṛta*	*kuṣṭha* (skin diseases)	Ghṛta	S.S

(continued)

Table 3 (continued)

SN	Formulation	Indication	Kalpana	References
92.	*Candanāvaleha*	*unmāda*		B.B.R., Vol. V
93.	*Candanośirādi kaṣāyam*	*raktapitta*	Kaṣāya	A.H.Ci., 2/31
94.	*Candrodaya agada*	*viṣaghnam*		B.B.R., Vol. 1:1705
95.	*Candanalepa*	*viṣaghna*	Lepa	S.S.Ka.,1/36
96.	*Caitasa ghṛta*	*sarva chetavikāra* (diseases connected with mind)	Ghṛta	B.B.R., Vol. 1: 1783
97.	*Campakādi* cūrṇa	*pāṇḍu* (anaemia), *prameha*, *raktapitta*	Cūrṇa	B.B.R., Vol. 1:1706
98.	*Candanādi varti*	*śirotpāta* (disease of the white of the eyes)	Varti	B.B.R., Vol. 2: 1849
99.	*Cyavanaprāsa*	*rasāyana* (rejuvenative/ anti-ageing)		C.S.Ci., 1/1/58
100.	*Cyavanaprāsa avaleha*	*rasāyana* (rejuvenating)	Avaleha	S.S.M.K., 8/12
101.	*Dhātryādi ghṛta*	*plīha* (diseases of spleen), *halīmaka* (jaundice)	Ghṛta	K.S.Ci. 5
102.	*Drākṣādi kaṣāyam*	*jvaram*	Kaṣāyam	A.H.Ci., 1/56
103.	*Elādi* cūrṇa	*chardi*	Cūrṇa	B.B.R., Vol. 1: 556
104.	*Elādi tailayogam*	*vātaroga*	Taila	B.B.R., Vol. 1: 582
105.	*Elādyāriṣṭam*	Indicated in *visarpa*, *masūrikā* (skin eruptions), *śītapitta*, *viṣamajvara*, *duṣṭavraṇa* (chronic ulcer), *dāruna* (skin lesion), *śvāsa* (dyspnoea), *prameha*	Ariṣṭa	B.B.R., Vol. 1: 583
106.	*Eleyaka tailam*	*dāham*, *kampam* (tremor)	Tailam	B.B.R., Vol. 1: 588
107.	*Eleyasarpi ghṛta*	*pittavikāra* (disease caused by vitiated *pitta*), *vāta pitta roga*, *śirobhrama* (giddiness/vertigo), *kampana*	Ghṛta	B.B.R., Vol. 1: 587
108.	*Gairikādi sneha*	Vruddhi (growth/tumour)	Sneha	S.S.Ci.,19
109.	*Guḍūcyādi nirūha basti*	*jvara praśamana* (antipyretic), *balavardhaka* (improving strength), *śvetakāraka* (inducing perspiration)		C.S.Ci., 1–3/247249
110.	*Hṛbera candanādi*	*pipāsa* (excessive thirst)	Śritaśītajalam	C.S.Ci., 4/31

(continued)

Table 3 (continued)

SN	Formulation	Indication	Kalpana	References
111.	*Hṛberādi ghṛta*	*visarpa* (erysipelas)	Ghṛta	S.S
112.	*Ikṣuvālikādi kṣīra kaṣāyam*	*kṣatam* (trauma)	Kṣīrakaṣāyam	C.S.Ci., 11/18
113.	*Jalajalaja kaṣāya*	*jvaram*	Kaṣāya	Y.R. Jvara Cikitsa [5]
114.	*Kakubhacandana kaṣāya*	*śukrameha* (a kind of metabolic disorder)	Kaṣāya	S.S.Ci., 11/8
115.	*Kalyāna ghṛta*	*jvara*	Ghṛta	V.S
116.	*Kalyānaka ghṛta*	*kaṇdu* (itching), *pāṇdu*, *viṣa*	Ghṛta	B.B.R., Vol. 1: 826
117.	*Kalyānaka ghṛta*	*graha* (conversion disorders), *apasmāra*	Ghṛta	S.S.Ka., 6/12
118.	*Kalyānaka ghṛta*	*apasmāra*, *unmāda*	Ghṛta	C.S.Ci. 9/36–41
119.	*Kāmeśvara cūrṇa*	*valī palita* (wrinkles and grey hair)	Cūrṇa	B.B.R., Vol. 1: 9494
120.	*Kaśmaryādi kvātha*	*pittavikāra*	Kaṣāya	B.B.R., Vol. 1: 641
121.	*Kaṭphalādi kvātha*	*pittajvara* (fever due to vitiated *pitta*)	Kaṣāya	S.S. M.K. 2/43
122.	*Kaṭphalādi pānīyajalam*	*dāha*, *tṛṣṇā*	Pāna kalpana	B.B.R., Vol. 1: 604
123.	*Kavalagrahayogam*	*arocaka* (anorexia)		C.D., Arocakacikitsa/5–7
124.	*Khuddakapadmaka tailam*	*dāha*, *vātarakta*	Tailam	C.S.Ci., 29/114
125.	*Kirātādi kvātha*	*jvara*	Kaṣāya	B.B.R., Vol. 1: 649
126.	*Kirātatiktādi* cūrṇa	*rakta pitta* (bleeding disorder)	Cūrṇa	C.Ci.4/76
127.	*Kuṅkumādi taila*	*piḍakā* (erysipelas), *vyanga* (melasma)	Taila	B.B.R., Vol. 1: 871
128.	*Mahākalyānaka ghṛta*	*gulma*, *kāsa*, *apasmāra*	Ghṛta	B.B.R., Vol. 4: 5226

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Table 3 (continued)

SN	Formulation	Indication	Kalpana	References
129.	*Mahāpadmaka taila*	*viṣamajvara*	Taila	B.H.S.Ci., 2
130.	*Mahāsugandhi Laxmivilas taila*	*buddhivardhak*, *medhavardhak*	Taila	C.D
131.	*Mahātikta ghṛta*	*kuṣṭharoga*	Ghṛta	A.S., 21/5
132.	*Mahātiktaka ghṛta 1*	*kuṣṭha*, *raktapitta* (skin and bleeding disorders)	Ghṛta	B.B.R., Vol. 4;5235
133.	*Mahātiktaka ghṛtam* (2)	*raktapitta*, *raktārśa* (bleeding piles), *vātarakta*	Ghṛta	B.B.R., Vol. IV 5236
134.	*Mahāvāsādya ghṛta*	*raktapitta*	Ghṛta	B.B.R., Vol. IV 5248
135.	*Manjiṣta candana kaṣāya*	*manjiṣtameha* (a kind of metabolic disorder)	Kaṣāya	S.S.Ci., 11/9
136.	*Manjiṣtādi ghṛta*	*visarpa*	Ghṛta	B.H.S.Ci., 15
137.	*Mṛtasanjīvani sura*	*smṛtivardhaka* (enhancing memory power)		B.B.R., Vol. IV
138.	*Natotpala candanādi pradeha*	*śiroruja* (headache)	Lepa	C.S.S. S3/23
139.	*Natotpalādi pradeha*	*śiroruja* (headache)	Lepa	B.R., Śiroroga/19

(continued)

Table 3 (continued)

SN	Formulation	Indication	Kalpana	References
140.	*Nimba taila*	*ślīpada* (filariasis)	Taila	S.S.Ci., 20
141.	*Panīyakalyanaka ghṛta*	*unmāda*, *apasmāra*	Ghṛta	C.D
142.	*Paṭolādi kaṣāyam*	*kāmalā* (jaundice)	Kaṣāya	A.H.S.S., 15/15
143.	*Patrambulodhrādi pradeha*	*śarīradaurgandhya* (unpleasant body odour)	Lepa	C.S.S., S3/29
144.	*Pippalimustādi ghṛta*	*jīrṇajvaram* (subsiding stage of fever)	Ghṛta	C.S.Ci., 3/2223
145.	*Prapaundarīkādi tailam*	*vraṇaropana* (wound healing)	Tailam	C.S.Ci., 25/92
146.	*Rudra taila*	Useful in *śiroroga*, *netra roga*, *kaphaja roga*	Taila	BR, Śiro Rogādhikār, 122 128
147.	*Ṣadaṅga panīya*	*jvara* (pyrexia/fever)	Pana kalpana	C. S.Ci.3/145
148.	*Ṣadaṅga toyam*	*jvaraharam*	Toya kalpana	A.H.Ci.1/15
149.	*Sahacara taila*	*unmāda*		B.B.R., Vol. V
150.	*Samaṅgādi kalka*	*vraṇaropana*	Kalka	S.S.S., 36/25
151.	*Śatapuṣpādi lepanam*	*śirapārśvaśūla* (hemicrania/unilateral headache)	Lepa	C. S.Ci., 8/77
152.	*Śatāvari ghṛta*	*grahaṇī*	Ghṛta	V.S
153.	*Śatāvari taila*	*smṛtivardhaka*	Taila	B.B.R., Vol. IV

(continued)

Table 3 (continued)

SN	Formulation	Indication	Kalpana	References
154.	*Śiva ghṛta*	*balya*, *vṛṣya* (aphrodisiac), *hṛdya* (cardioprotective), *putra prada for vandhyastrī* (nourishing the reproductive process in infertility), useful in *vātaroga*, *apasmāra*, *śoṣa*, *pīnasa* (common cold/ sinusitis)	Ghṛta	B.R., Unmāda Rogādhikār, 81–92
155.	*Śiva taila*	Useful in *unmāda*, *vāta vikāra*, *apasmāra*, *jvara*, *kāsa*, *hanustambha* (locked jaw),	Taila	B.R., Unmāda Rogādhikār, 93–100
156.	*Śrīparṇicandanādi kaṣāya*	*paittikajvaram* (fever due to *pitta* vitiation)	Kaṣāya	S.S.U., 39/175
157.	*Sudarśana* cūrṇa	*jvara*	Cūrṇa	S.S.M.K., 6/28
158.	*Śvetacandana kalkam*	*masūrikā* (skin eruptions)	Kalka	V.S
159.	*Taptraj taila* (1)	Useful in *kaphaja roga*, *kāsaroga*, *śotha* (Inflammatory swelling), *ṣūlaroga* (colichy pain), *śiraṣūla*, *netraṣūla*, *śotha*, *jvara*	Taila	B.R., Śiro Rogādhikār, 129, 138
160.	*Taptraj taila* (1)	Useful in *sannipāta*, *dāruṇa śiroroga* (chronic headache due to *tridoṣa* vitiation), *śiraṣūla*, *netraroga*, *jvara*	Taila	B.R., Śiro rogādhikār 139, 146
161.	*Tṛvṛta taila*	*sūtikā vyādhi* (postpartum health issues)	Taila	K.S.Ci. 3
162.	*Uśira candanādi*	*raktapitta*	Kaṣāya	Y.R. Raktapitta
163.	*Uśirādi cūrṇa*	*raktavanti* (haematemesis)	Cūrṇa	B.B.R., Vol. 1: 489
164.	*Uśirādi cūrṇa*	*kṣaya*, *raktapitta*, *pādadāha* (burning feet), *raktapradara*, *Mūtrāghāta* (diseases connected with urinary system), *raktasrāva*, *vātaja roga*, *prameha*	Cūrṇa	B.B.R.,Vol. 1: 112
165.	*Uśiradi kaṣāya*	*paittikameha* (kind of metabolic disease)	Kaṣāya	B.B.R., Vol. 1: 81
166.	*Vacāditaila vasti*	*vātaroga* (diseases due to *vāta* vitiation)	Taila	S.S.Ci. 37/12

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Table 3 (continued)

SN	Formulation	Indication	Kalpana	References
167.	*Vangeśwarādi vaṭī*	*medhavardhaka* (enhancing intellect)	Varti	B.B.R., Vol. IV
168.	*Vāyuchyayasurendra taila*	*apasmāra*, *unmāda*	Taila	D.H.N
169.	*Viṣaghna lepa*	*viṣahara* (antitoxic)	Lepa	A.H.S. S7/20

Appendix A: Glossary of Sanskrit Terms

agnimāndya	loss of appetite
agni sandīpana, agni sandīpaka, agni vardhaka	kindles digestive fire
āhlādana	Nourishing the body and mind
alpavīrya	with diminished potency
amṛta samam	equivalent to ambrosia
aṅgadāha, aṅgadāham	burning sensation
aṅgamarda	generalized body ache
aṅgamarda praśamana	bringing down the pain in various parts of the body
antargata raktapitta	internal bleeding disorder
apacī	tumour
apasmāra	convulsion disorders
arocaka	anorexia
arśa	haemorrhoid/piles
arti	restlessness
aruci	anorexia
atīsāra	diarrhoea
āyuvardhaka	improving lifespan
balavardhaka, balya	improving strength
bhagna	fracture
bhrama	giddiness
buddhivardhaka	improving mental faculties
chardi	vomiting
chittavibhrama	disturbed mental status
dāha	burning sensation
dāha jvara	fever with burning sensation
dāhapraśamana	pacifying burning sensation
dāharoga	burning sensation
dāruṇa	skin lesion
dāruna śiroroga	chronic headache due to *tridoṣa* vitiation
dhātukṣinta	emaciation
durgandha	unpleasant odour
duṣta vraṇa	chronic ulcer
graha	conversion disorders
grahaṇī	sprue, malabsorption syndrome
gulma	tumour/growth in intestine
guṇadayi	rejuvenative

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agnimāndya	loss of appetite
guru	difficult to digest
halīmaka	jaundice
hanustambha	locked jaw
hikkā	hiccups
hṛdya	cardioprotective
jīrṇajvaram, jīrṇajvara	subsiding fever
jvara	pyrexia/fever
jvaraharam, jvarapraśamana	antipyretic
kāmalā	jaundice
kāmaśaktivardhaka, kāmavardhaka	aphrodisiac
kampa, kampana	tremor
kaṇdu	pruritis, itching
kaṇdughna	curing pruritis
kāntihita	enhancing complexion
kāntivardhaka	improving complexion
kaphaja roga	diseases caused by *kapha* vitiation
kārśyam	underweight
kāsa, kāsaroga	cough
klama	fatigue
kṣatam	trauma
kṣayaroganāśaka	preventing emaciation
kṣinta	under nourished
kuṣṭha	skin diseases
lāvaṇya vardhaka	enhancing beauty
lepana	external application
madhura	sweet
majjātulya ārtava	menstrual disorder
mandāgnī	poor digestion
manjiṣtameha	a kind of metabolic disorder
marmāghāta	injury to marma/vital points
mastaka dāha	burning sensation of forehead
mastiṣka roga	diseases of brain
masūrikā	skin eruptions
medha vardhaka	improving mental faculties
medoroga	diseases connected with *medo dathu*
mūrcchā	helpful in loss of consciousness
mūtrāghāta	diseases connected with urinary system

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agnimāndya	loss of appetite
mūtrakṛchra	dysuria
mūtrāvarodha	urinary obstruction
nābhipāka	inflammation of umbilicus
netradāha	burning eyes
netraroga	eye diseases
netraṣūla	pain in eye
nirbalata	weakness
ojavardhaka	immuno modulatory
pādadāha	burning feet
paittika jvaram	fever due to pitta vitiation
paittika meha	kind of metabolic disease
pāṇdu	anaemia
piḍakā	erysipelas
pīnasa	sinusitis
pipāsā	excessive thirst
pitta jvara	fever due to vitiated *pitta*
pitta rōga	diseases due to the vitiation of *vāta* and *pitta*
pitta śleṣma jvara	fever due to vitiated *pitta* and *kapha*
pitta vikāra	disease caused by vitiated *pitta*
pitta visarpa	a skin disease caused by *pitta* vitiation
pitta vyādhi	diseases caused by *pitta* vitiation
pittaśamaka	pacifying *pitta*
pittātīsāra	diarrhoea caused by *pitta* vitiation
plīha	diseases of spleen
pradara	menorrhagia
pragyā vardhaka	enhancing mental faculties
prameha	diabetes
puṣtivardhaka	nourishing
Putra prada for vandhyastrī	nourishing the reproductive process in infertility
rāja yakṣma	tuberculosis
rajōdōṣa	menstrual disorder
rajōdōṣam mūtradoṣam	corrects genito-urinary functions
raktapitta	bleeding disorders
raktapitta nāśaka	curing the bleeding disorders
raktapradara	menorrhagia
raktaprasādana	blood purification

(continued)

(continued)

agnimāndya	loss of appetite
raktārśa	bleeding piles
raktārśas	bleeding piles/haemorrhoids
raktasrāva	bleeding disorder
raktātīsāra	dysentery
raktavahāsrotavikāra	vascular diseases
raktavanti	haematemesis
rasāyana	rejuvenative/anti-ageing
śakti vardhaka	enhancing muscle power
santatādijvara	various kinds of intermittent fever
sapta dhātu vardhaka	rejuvenating/nourishing
śarīradaurgandhya	unpleasant body odour
sarva chetavikāra	diseases connected with mind
sarva dhātu vardhaka	rejuvenative/nourishing
sarva jvara	fever
sarva jvara nāśaka	antipyretic
saundarya	beauty
saundarya vardhaka	enhancing beauty/complexion
śirapārśvaśūla	hemicrania/unilateral headache
śiraśūla	headache
śirobhrama	giddiness/vertigo
śiroroga	diseases of head
śiroruja	headache
śirotpāta	disease of the white of the eyes
śirovibhrama	giddiness
śiśonābhipāka	inflammation of umbilicus
śīta	cold
śītapitta	urticaria
śītavīrya	cold in potency
sleṣmahara	pacifies kapha
ślīpada	filariasis
smṛti vardhaka	memory enhancer
śoṣa	cachexia
śotha	inflammatory swelling
śukradoṣa	diseases connected to reproductive elements
śukrameha	a kind of metabolic disorder
śukrarma	pterygium
śukravardhaka	aphrodisiac

(continued)

(continued)

agnimāndya	loss of appetite
śūla	pain
śūlaroga	colichy pain
sūtikā vyādhi	postpartum health issues
svarasa	juice
śvāsa	dyspnoea
śvāsahidhma	diseases connected with respiratory tract and hiccups
śvetakāraka	inducing perspiration
tikta	bitter
tikta rasa	bitter taste
tiktaskandha	a group of bitter drugs
tṛṣṇā	excessive thirst
tṛṣṇā nigrahana	overcoming thirst
unmāda	insanity
uṣṇavāta	cystitis
valī palita	wrinkles and grey hair
varṇa sanskaraka	improving complexion
varṇa vardhaka	improving complexion
varṇya	improving complexion
vāta, pitta, kapha	basic functional units of the body according to ayurveda
vātahara	pacifying *vāta* vitiation
vātaja	associated with *vāta doṣa*
vātapittaroga	diseases caused by *vāta* and *pitta* vitiation
vātarakta	inflammatory arthritis
vātaroga	diseases due to *vāta* vitiation
vātaroga nāśaka	curing *vāta* disorders
vātavikāra	conditions caused by *vāta* vitiation
vātavyādhi	diseases caused by *vāta* vitiation
vāyu	synonym for *vāta doṣa*
vāyuroga	diseases caused by *vāta* vitiation
vīrya stambhaka	aphrodisiac in nature
vīrya vardhaka	aphrodisiac
viṣa	poison
viṣaghna, viṣahara	antitoxic
viṣama jvara	intermittent fever
visarpa	erysipelas
visarpa pitta	a skin disorder caused by *pitta* vitiation

(continued)

(continued)

agnimāndya	loss of appetite
vraṇa	wound
vraṇaropana	wound healing
vṛddhi	hydrocele
vṛṣya	aphrodisiac
vyākulata	depression
vyanga	melasma
yakṣmā	malnourishment
yonidoṣa	gynaecological disorder

Appendix B: Transliteration key

अ	a	आ	ā	इ	i	ई	ī	उ	u
ऊ	ū	ए	e	ऐ	ai	ओ	o	औ	aū
अं	aṃ	अः	ḥ	क	ka	ख	kha	ग	ga
घ	gha	ङ	ṅa	च	ca	छ	cha	ज	ja
झ	jha	ञ	ña	ट	ṭa	ठ	ṭha	ड	ḍa
ढ	ḍ ha	ण	ṇa	त	ta	थ	tha	द	da
ध	dha	न	na	प	pa	फ	pha	ब	ba
भ	bha	म	ma	य	ya	र	ra	ल	la
व	va	श	śa	ष	ṣa	स	sa	ह	ha
क्ष	kṣa	ळ	ḷa	℘	l̲a	ॠ/ॄ	ṛ	∩	r̲a
ॅ	ŭ								

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Chapter 29
Sandalwood—Perfumery

Andrew Brown, Alexandra Mettetal, and Dhanushka Hettiarachchi

1 Introduction

The distinctive and unique character of the aromatic heartwood of Indian sandalwood is one of the first recorded fragrance materials and remains today the backbone of many perfume compositions. The unique fragrance qualities of this essential oil are attributable to some very sophisticated chemical synthesis the tree *Santalum album*. By understanding how and why Indian sandalwood is employed in perfumery and how the various constituents work in combination to give this fragrance material, its unique character is fundamental to getting the most out of the oil. Indian sandalwood is one of the oldest documented fragrant materials. In perfumery, Indian sandalwood oil is considered as the second most expensive wood oil after oud, a powerful wood fragrance extracted from the agarwood tree (*Aquilaria* sp.) which has been infected with a fungal pathogen.

2 Traditional Perfumery

With its first use recorded in *Yasaka Nirukta* (seventh century BCE), reference to sandalwood as a perfume and its aroma are made extensively in subsequent Hindu literature including the great epics Ramayana and Mahabharata. Early Buddhist and Jain texts (300 BCE) make constant reference to sandalwood [11]. Sandalwood paste and scented water are the main applications mentioned in these texts; bathing and perfuming rituals of king Yudhishthira in Mahabharata and Bhodisattva Mahaushadhi in Jataka Stories have detailed the use of sandalwood in numerous applications. Arthashastra by Kautilya (300 BCE), which is considered the first detailed treatise

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on economics and taxation, included sandalwood as a taxable good. The given identification criteria for tax collectors were that good sandalwood oil had the texture of clarified butter, a hardwood with a soft appearance and tenacious sweet woody aroma [14]. Since then, sandalwood has found its way into many cultures because of its fragrant appeal and its medicinal qualities. Its medicinal qualities have seen it become part of the China Pharmacopeia and Ayurveda Pharmacopeia, and the distilled oil was monographed in the British Pharmacopeia in 1932 and was reintroduced in 2020.

Sandalwood is considered as one of the eight key aroma ingredients (Ashtagandha) in ancient India [9]. The great compendium of materialistic life, the Brihatsamhita by Varahamihira (500 BCE), has introduced a blending chart for 16 key aroma ingredients to make up to 43,680 perfume formulas [3]. The classical period of Northern India had many perfumery texts, the formularies written during this time, with Haramekala and Gandhayukta the first to mention sandalwood as a base ingredient. *Gandhavada* (Theory of Perfumery), written during the same period, has explained the principles of applications and compatible blends, with sandalwood and agarwood always considered the best base perfume ingredients, and the combination was called *Chandanagaru* [11].

Later texts *Manasollasa, Ghandavada* and *Nagarasaravasa* were written by connoisseurs of perfumery for consumers on use for day-to-day and special occasions, such as the significance of perfumes in business or intimate meetings or for a royal audience. Ancient Indian perfumers categorized aroma as per the emotion rather than the physiochemical nature; sandalwood is classified as an aroma to evoke clarity and pureness, thus used in official or religious meetings to elevate one's character [11].

It is worth noting that major Indian texts on perfumery were written during the late classical period of India (Rashtrakuta and Pala dynasties) in the ninth–tenth century where the capital of the empire was Kannauj, which is still considered as the epicentre of perfumery ingredients. Until this period, sandalwood was used only as a fine powder, paste or scented water—it is uncertain whether distillation of sandalwood or the use of essential oil was practised before the Islamic rule in the northern part of India. Traditional distillation from the Deg Bhapka system was not mentioned in any of the perfumery literature discussed above despite the detailed accounts of collection and preparation of aromatic ingredients recorded.

Prevalence of Islamic rule has revolutionized perfumery in South Asia, like what was observed for music and architecture. Since eleventh–twelfth century, sandalwood essential oil became the foundation of perfumery, as a fixative and the base note. An important discovery from this time is the Attar, the most significant perfumery product from the middle ages until now. Attars are sandalwood oils infused with floral and other aromatics; sandalwood oil is loaded to the collector (Bhapka), and floral or other light aromatics are distilled in the pot (Deg) until the required aroma is concentrated to the sandalwood oil; usually, multiple distillations and different co-distillates are collected to a single sandalwood oil collector. Attar manufacture is a distillation technique rather than oil blending. Some of the well-known pure Attars are Gulab Attar (*Rosa damascena*), Motia Attar (*Jasminum sambac*), Henna Attar (Henna flowers) and Mitti/Gill Attar (distillate of dry clay in sandalwood oil) containing geosmin, producing a fresh earth aroma. A wide range of Attars are made by co-distillation of florals with spices and herbs, and on rare occasions, sandalwood is co-distilled with other woody aromas like agarwood or vetiver. The principle of Attar is to distil or extract but never to blend finished products. Unlike Western-style perfumes, Attar compositions are more than fragrance and customers purchase them for other uses such as health benefits, raw material in other products as well as for use as a fragrance; a good example of this is the Attar Shamama. Attar compositions are generic for key ingredients, but the minor additions, proportions and process vary between perfume houses to give a unique identity; perfume houses in Kannauj have a continuous tradition and lineage dating back to tenth century CE [12, 17]

Attar is not limited to perfume use; it is used in medicine and for flavour purposes. A wide application of attars is in mouth fresheners, which are considered an essential part of perfumery in Indian and Arabic cultures. An Arabic perfumery innovation is the art of blending; merchants purchase the pure oils or Attars from primary perfumers and then blend by a perfumer as per own or clients' palate; these blends are known as Mukhallat and are widely used the Middle East and North Africa. Sandalwood plays an important role in Mukhallat blending as the base and fixative [16].

The economic wealth of the Arabian Gulf region has encouraged a wave of traditional perfume appreciation. Traditional perfumers from South Asia have revolutionized the traditional perfumes by introducing modern perfumery technology. Attar- and Mukhallat-type blends containing sandalwood oil are dissolved in alcohol in a similar manner to Eau de Parfum (Ali, 2018 Pers.Comms).

3 Western Perfumery

Cleopatra, who's beauty was legendary, used sandalwood as part of her beauty regime. Queen Elisabeth I of England was purported to have had her bed sheets scented with sandalwood; however, it was not until the extraction of the essential oil undertaken commercially from the 1870s that sandalwood oil became widely used in European fragrances. Many of the most prestigious and time-honoured perfumes are constructed around Indian sandalwood oil including iconic brands like Chanel, Guerlain, Dior, Lanvin, Jean Patou.

Founded in 1828, Guerlain is one of the most famous fragrance houses with nearly 200 years expertise in fragrance compositions. Indian sandalwood oil can be found in the impressionist perfume *Jicky* created by Aimé Guerlain in 1889. 100 years later and Guerlain launched the milestone fragrance *Samsara* (1989), a warm woody oriental fragrance which relies heavily on Indian sandalwood, considered a bold move by Jean-Paul Guerlain at the time. A more recent addition by Guerlain is *Santal Noir* which involved establishing a partnership with Indian foresters to ensure that only high-quality and ethically sourced Indian sandalwood oil obtained from the Mysore region was used.

In 1921, fashion designer Gabrielle (Coco) Chanel worked in collaboration with perfumer Ernest Beaux to create and launch the timeless and world-renown *N0 5*.

A floral aldehydic composition is a good example of what Indian sandalwood can bring to a perfume composition. The early success of its first perfume saw Chanel launch *Bois des Iles* (1925), a woody oriental women's fragrance inspired by *N°5* which relies on Indian sandalwood oil. Jacques Polge was inspired by *Bois des Iles* to compose masculine fragrances such as Pour Monsieur Concentree (1987) a strong and audacious woody perfume where sandalwood is combined with a fresh mandarin lavender top note, rose, a balmy touch of vanilla and musk; *Egoïste* (1990), a more commercial version, warm spicy cinnamon-like, ambery and tobacco-like; and *Egoïste Platinum* (1998), a modernized and fresher version of *Egoïste*, without the leathery tobacco and rose notes but floral geranium, jasmine and neroli, with a fresh green aromatic top and a woody long-lasting scent.

Following the floral aldehydic trend created by Chanel *No 5* (1921), Lanvin launched *Arpège* in 1927, a floral aldehyde, wrapped by a blooming floral bouquet and a warm sandalwood milky vetiver and vanilla, considered as an inescapable standard for perfume lovers. This trend was followed 40 years later by Hermès with *Calèche*, a floral aldehyde with more depth containing Indian sandalwood, vetiver, cedarwood, moss, amber and musk.

The luxury perfume brand Jean Patou also valued sandalwood in its compositions, as its two major successes. *Joy* by Henri Almeras, renowned as the most expensive perfume in the world, an elegant and sophisticated floral bouquet, was launched in 1930 at the beginning of the great depression, and *1000,* a floral woody chypre perfume linked to violet and jasmine, was launched in 1972.

With *Diorissimo* (1956) by Dior, Edmond Roudnitska, one of the world's most esteemed perfumers, composed one of the great scents considered as a reference in terms of lily of the valley. A scent evokes '*picking flowers on a fresh spring morning'* where sandalwood gives all its softness and long-lastingness.

There remains a lot of interest from perfumers and brand owners in Indian sandalwood for perfume launches in recent times; however, due to availability, price and many reputable brand owners looking to distance themselves from black market operators, brands have been turning to synthetic sandalwood scents and other sandalwoods in their perfume compositions. With commercial quantities of quality Indian sandalwood oil becoming available from Australian plantations, it is hoped this trend can be reversed.

The last 40 years has seen the increasing popularity of niche perfumes which have now become established in the marketplace. The goal of these niche brands is to propose sophisticated and audacious perfumes to a discerning audience. In this case, fragrance development does not depend on the marketing, trends and consumer testing but highlights the work of perfume creation. Niche brand owners provide an opportunity for perfumers to show creativity, which is often constrained by cost, a result of price pressure. With niche brands, perfumers are able to express themselves and create original impactive fragrances. In this way, they can promote rare and precious ingredients in perfumes such as sandalwood, oud, orris, rose, the beauty of their rich scent fascinating customers. It is a strategy that supports a luxurious image via exclusive distribution channels or their own boutiques. This market has seduced big brands such as Lancôme, Hermès and Armani, who have launched their own private perfume collection based on the same concept to target their high-end customers.

Some important niche and private brand release perfumes are underpinned by sandalwood and are often iconic fragrances. L'Artisan Parfumeur, pioneer of niche perfumery since 1976, launched *Santal* (1978), first to honour the mystique and sensual tree. This was followed by an intriguing perfume *Bois Farine* (2003) inspired by Ruizia cordata, an atmosphere transcribed by sandalwood, cedarwood and gaïacwood.

Serge Lutens, a very avant-garde brand in their fragrance development, has several perfume references giving different olfactive interpretations of sandalwood by Christopher Sheldrake, from milky spicy and balmy to luminous floral and musky or to warmer oriental spicy ones: *Santal de Mysore* (1991), *Santal Blanc* (2001), *Santal Majuscule* (2012) and the iconic *Féminité du Bois* (2009), a woody oriental fragrance that is considered a benchmark in woody feminine fragrances. Comme des Garçons, a niche brand that knows how to take risks with their fragrances, launched *Blue Santal* (2013) combining Australian sandalwood and a fresh and aromatic effect from juniper berries, and *Concrete* (2017) in which Nicolas Beaulieu used *Santalum album* from Australia to structure this surprising and abstract scent.

Niche brands can also be best sellers such as *Tam Dao* (2003) by Diptyque, named after a national park in Vietnam, that reveals a more aromatic side of sandalwood combined, with cypress and cedarwood; *Santal 33* (2011) by Le Labo, a long-lasting and voluminous wake (sillage) with its green violet top notes that become more and more wrapping, milky and leathery; or *Milky Musc* (2017) from Parle Moi de Parfum, a very diffusive fragrance where the milkiness of fig tree and sandalwood is elusively wrapped into dry woods and musks.

Niche brands have influenced the market with a luxurious, timeless and innovant fragrances. Big brands follow these trends and have expand their private collections with these concepts. Hermès with *Santal Massoia* (2011) a sweet intense and additive wood with lactonic and dry fruits facets; Guerlain with *Santal Royal (2015)* a middle-east oriental work around oud, rose and leather; more recently Dior with *Santal Noir* (2018), an authentic celebration of sandalwood highlight by Turkish rose with the deepness of musks and ambrette.

4 How Sandalwood Works in Perfumery

Sandalwood is considered as a base note on the fragrance evolution pyramid (top-heart-bottom notes). Bottom notes are the most long-lasting scents in a fragrance. It is often the case that woods can act as hinge notes in perfumery, and in this way, sandalwood acts as a backbone to a composition, a basic structure to which other notes will be attached to. Sandalwood oil makes the fragrance more substantive on the skin or on any application material, and fixes and diffuses the top and heart note with the base note which can last for several days.

Perfumers use sandalwood oil in their compositions over other woods for its harmony, exotic sensuality, warmth, opulence and spirituality attributes. It is also valued for its substantivity and fixative qualities due to its high vapour pressure, primarily due to hydrogen bonding as a result of the high proportion of sesquiterpene alcohols present. A small quantity of sandalwood oil is enough to have a notifiable impact on a fragrance depending on the desired effect—between 1 and 3% of the total fragrance is typical, a little for just its fixative qualities or more to contribute the unique odour quality.

In perfumery, sandalwood is considered as a noble wood, one of the most precious that perfumers have in their raw material pallet. The most known and used species of sandalwood in fragrance composition is *Santalum album* renowned for its mild warm, milky and woody scent attributed to the complex blend of molecules produced by the tree rather than one single molecule. *Santalum album* is considered native to South-East India, Sri Lanka, Timor, Indonesian islands of Célèbes, Sumbawa and Northern Australia.

Today, there are alternatives to Indian sandalwood oil-driven primarily by the supply shortage at the end of the twentieth century. Alternatives can be broken down into three groups: single-molecule synthetics; these include products such as Givaudan's *Ebanol* or IFF's *Bacdanol*; other species of sandalwood such as *Santalum austrocaledonicum* from New Caledonia and *S. spicatum* from South West of Australia (very different from *S. album* with a greener and more terpenic version); and more recently, a genetically modified version of sandalwood oil launched by Firmenich, *Dreamwood*. None of these alternatives offers a direct substitute to Indian sandalwood oil with its unique warm, lactonic woody scent, and as a result, brands often use alternatives in combination with Indian sandalwood oil to maintain the unique multifaceted character of the woody notes that this scent brings to the composition.

The reference description in terms of odour quality expectations can be defined as woody, warm, animalic, exotic, powdery, lactonic/milky, nutty, terpenic freshness, velvety, substantive and amber scents. This unique combination of scents can make Indian sandalwood oil the most desirable option for a woody base note in a perfume composition. To anyone using sandalwood, it is important to understand why the oil produces these scents and how the oil is influenced by many factors including the wood processing methods employed, extraction methods used, part of tree extracted, age of the tree and even the length of time in storage. All have the ability to highlight different facets of the oil, some good and other contributing to undesirable notes in the oil. It is necessary to delve into the molecules present, how they are produced and their effect on the olfactory qualities of Indian sandalwood oil.

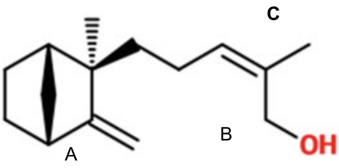
5 The Chemistry Behind the Odour

The unique olfactory properties of Indian sandalwood oil are not due to a single constituent or the main constituents but due to a combined effect of major and minor constituents possibly having a synergistic effect to produce the intense persistent soft, warm, woody, lactonic, animalic and terpenic notes for which sandalwood oil is renowned for. This is likely the reason why synthetic sandalwood oil odorants which can have similar notes do not have the complexity and character of sandalwood essential oil. It is also the likely reason why oils from other sandalwood species are different from each other.

6 Sesquiterpene Alcohols

Anyone that has had any exposure to the sandalwood industry is aware that the main constituent in Indian sandalwood oil is z-α-santalol [2]. It is generally accepted that while this molecule has the greatest contribution by weight it does not contribute greatly to the odour, having a week woody odour reminiscent of cedarwood, and as such is likely the contributor to the slight nutty cedar characteristic of Indian sandalwood oil. The literature generally refers to z-β-santalol (1) as the source of the intense warm, woody, lactonic notes for which Indian sandalwood oil is renowned [6].

The molecular structure characteristics of sandalwood odour causing molecules have been proposed [16, 17] with the key relationships demonstrated on z-β-santalol (1). Firstly, the presence of a bulky electron-rich moiety such as a double bond, in the case of z-β-santalol, (A) or a cyclopropane ring in the case of z-α-santalol needs to be in the cis position to a hydroxyl containing carbon (B) at a distance of 6.3–6.4 Å. Another key feature of sandalwood odour causing molecules is the presence of a branched flexible hydrocarbon chain linking the hydroxyl group to the bulky moiety with the branched methyl group on the carbon β to the hydroxyl (C). This conformation has been used to synthesize many synthetic sandalwood odorants Elbanol for example.



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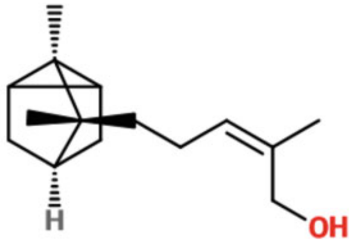

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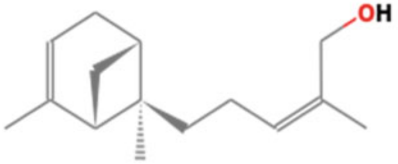
The importance of the cis (z) orientation of the hydroxyl-containing carbon at B is determined by the observation that the trans or (E) orientation renders the molecule odourless [7]. The trans isomers are found in small quantities in Indian sandalwood oil, and typically, they contribute about 2% of the mass of Indian sandalwood oil.

There are 2 further major sesquiterpene alcohols that are present trans-a-z-bergamotol (3) and epi-b-santalol (4).



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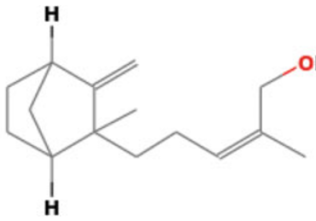

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These four molecules make up about 80% of the mass of Indian sandalwood oil, but an isolate of these four molecules, while having a clear, woody lactonic odour, does not have the character of a good Indian sandalwood oil, and it lacks the intensity and complexity for which Indian sandalwood oil is renowned.

The importance of minor constituents in the olfactory qualities of Indian sandalwood oil cannot be underestimated. The origin of these minor constituents can be put down to three broad categories: precursor molecules, which are molecules that have not been fully synthesized by the tree, santalenes for example; molecules that are produced from other biosynthetic pathways, bisabolol via monoterpene synthases for example; and breakdown products aldehydes and ketones, for example.

7 Sesquiterpene Hydrocarbons

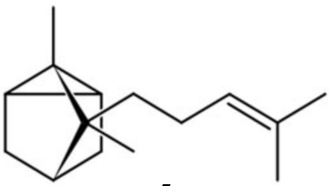
The olefinic constituents of Indian sandalwood oil are an important contributor to the sandalwood oil odour, constituting about 6% of the total mass of the oil and contributing a woody, green terpenic note to sandalwood, the major olefin being α-santalene (5). All the olefin equivalents to the alcohols can be found in the oil. The contribution of these molecules to the sandalwood odour can best be described by what happens if these molecules are removed by fractionation. The resulting oil lacks intensity and loses the slight green terpenic notes that are typical of sandalwood. Some of the terpenes are normally removed from the oils during distillation by the removal of foreruns during the distillation process. However, it is worth pointing out that the importance in removal of foreruns is not so much in the removal of the olefinic sesquiterpenes, but in the removal of more volatile high odour molecules that can contribute to notes not typical of Indian sandalwood oil.

8 Other Sesquiterpene Alcohols

There is not a lot of information available on the effect of other sesquiterpene alcohols and their impact on the odour of Indian sandalwood oil. These molecules are produced by enzymatic systems other than santalene synthases, of which at least one has been elucidated monoterpene synthase action of farnesene pyrophosphate. These molecules consist of a number of isomers of bisabolol and lanceol as well as other molecules such as nerolidol, farnesol and isomers of eudesmol and curcumen-12-ol. These molecules are typically approximately 4.5% to 6.0% of the mass of Indian sandalwood oil, z-lanceol (8) being the largest contribution at about 35% of the mass of this group; z-lanceol is considered to have a week woody odour [5] and as such not considered to contribute much effect to the odour.

9 Aldehydes and Ketones

Oxidation of sesquiterpenes to the corresponding aldehyde or ketone produces some important intense odour molecules that contribute to the lactonic milky woody notes of sandalwood [13]. The effect on sandalwood oil odour of these molecules can be ascertained by isolation with Girard reagent. The resulting isolate is intensely woody. Most of the sesquiterpenes have their corresponding aldehyde or ketone present. The most significant in terms of odour contribution is considered to be E-β-santalal (6), E-α-santalal (7) and E-epi b-santalia (8).



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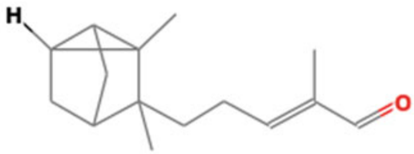

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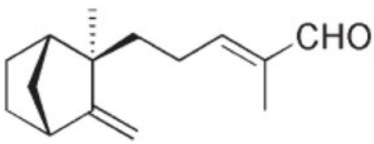

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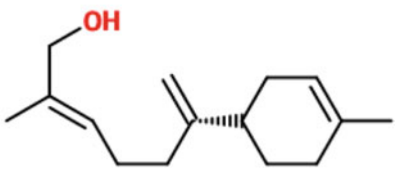

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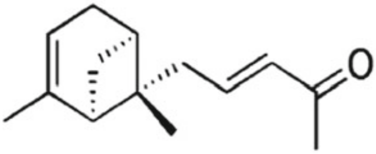
Breakdown and rearrangement products of are also seen in this group of molecules. While the alcohols have a cis (z) configuration, it appears that the aldehydes and ketones are produced in the trans (E) configuration [5]. The hydrocarbon chain is also observed to cleave with the presence of nor-trans-α-bergamotone (9), nor-α-santalone and nor-β-santalone, both C14 molecules and the presence of santalone (10), being a molecule with a powerful woody odour. These constituents typically form about 3–5% of sandalwood oil by weight, and their formation may be part of the reason why it is generally considered that the odour of the oil improves with age and that oil distilled from old heartwood is considered superior to oil distilled from the heartwood of young trees.



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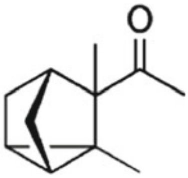

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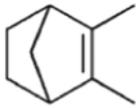
10 Carboxylic Acids

This group of molecules does not contribute wood notes to sandalwood oil. Isolation of these constituents from sandalwood oil yields a sweaty, overripe fruit odour and thus is a likely contributor to the animalic and sweet notes of sandalwood oil. The formation process of these carboxylic acids involves cleavage of the hydrocarbon chain [5] and the subsequent formation of the nor (C14), eka (C13) or tere (C12) santalic acids. It has been reported that these acids are esterified [4]. However, the presence of esters is not widely observed and the presence of carboxylic acids is. The most common is santalic acid (isomer not identified), β-teresantalic acid (5) and α-tricycloekasantalic acid (6).

Organic acids account for just under 1% of the oils mass. It is not clear if this group of constituents is produced by the tree, in the tree after harvest or by oxidative action on the oil. It has been reported that bioconversion of santalols to the acid can occur. *Aspergillus niger* has been identified to produce teresantalic acid, teresantalols and photosantalols from a-santalene [10].

11 Hydrocarbons

Smaller hydrocarbons can be found in Indian sandalwood oil. These can broadly be divided into two groups. One is derived from degradation pathways via a mechanism that has not been determined at this stage; these are santene (11), albene and dihydroalbene. Santene in particular is important as it has a very powerful leather odour and is readily found in Indian sandalwood. It can be isolated by fractional distillation of the oil or foreruns under vacuum. At the right concentrations, this constituent adds a small amount of sweetness to sandalwood oil.



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Also present are monoterpenes such as α-pinene, limonene, ρ-cymene and ρ-cymenen. These constituents are thought to be produced by monoterpene synthases in response to mechanical damage to the woody parts of the tree. These molecules have powerful odours and contribute to undesirable odours in Indian sandalwood oil.

12 Wood Breakdown Products

During the extraction process of Indian sandalwood oil, a number of constituents can be formed which if allowed to accumulate in the oil can lead to undesirable odours [5]. These constituents can be classified into three broad groups. Phenols from the breakdown of lignin these are highly odoured and contribute harsh and smoky characteristics to the oil. Constituents include p-cresols (12), guaiacol (13), eugenol (14) and vanillic and syringic acid. Furfurals can also be produced from cellulose. These can then undergo mallard-type reactions with hydroxy proline found in the aromatic heartwood to produce furfural pyrrole (15) [5], a constituent which has a vegetal odour not considered as favourable for Indian sandalwood oil.

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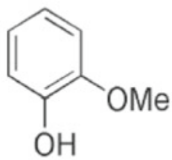

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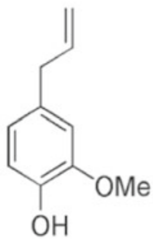

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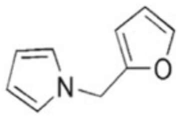

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13 The Future of Indian Sandalwood Oil in Perfumes

Indian sandalwood oil has stood the test of time in providing the frame upon which many classic and contemporary fragrances are constructed, and there is an expectation that this utility will continue. There are, however, some additional features that tomorrow's consumers will see as benefits.

The tree *Santalum album* has been assigned a vulnerable rating by the ICUN red list [1]. Sophisticated consumers are interested in the impact that their purchasing decisions have on the environment as well as the ethical and social implications. This provides opportunity for a sustainable plantation industry that grows its sandalwood in an ethical and sustainable manner to fill in the gaps in supply caused by the dwindling supply of wild sandalwood. Providing a chain of custody can allow this information to be used to demonstrate the ethical purchasing decisions made by brand owners.

Multifunctional ingredients in perfumes are something that has not been widely explored with aroma chemicals. Indian sandalwood oil has been identified to cause physiological changes in heart rate as well as an increase in self-rated levels of attentiveness, mental calmness and reduced anxiety [8]. Skin care benefits are also possible with Indian sandalwood oil as it has been identified as an anti-inflammatory and antioxidant [15]. This functionality could be used to provide skin anti-ageing claims such as reducing redness, evening our skin tone, skin de-stressing or wrinkle reduction to perfume compositions.

To ensure the continued widespread use of Indian sandalwood oil in perfume compositions will rely on the sustainable plantation industry producing a quality product that meets the expectations of consumers and the industry working with perfumers and brand owners to provide information and product features that consumers will see as a benefit.

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Chapter 30
Santalum album Oil as a Pharmaceutical Agent

Corey Levenson

1 Introduction

East Indian sandalwood (*Santalum album*) has a long history of use in traditional systems of medicine, in particular in Asia [48]. Several parts of the plant have been found to have compounds with interesting biological activities, including leaves, bark and the seeds, which are a source of the acetylenic compound, ximenynic acid [14]. Although medically intriguing molecules have been isolated from sandalwood by solvent extraction [61], this chapter will focus on the oil produced by the traditional method of steam distillation from the heartwood of the *S. album* tree. This essential oil has played the most prominent role with respect to pharmaceutical development.

For many years, the oil was listed as a medicine in both the British and United States Pharmacopeias (BP and USP), often by its Latin name, *Oleum Santali.* The BP and USP monographs for sandalwood oil listed it for oral administration to treat, among other things, urinary tract and upper respiratory tract infections. The use of the oil fell into disfavour in the early twentieth century with the advent of sulfa drugs, penicillins and other 'modern' antibiotics. It is encouraging that a proposed monograph for East Indian sandalwood oil was recently introduced into the US Pharmacopeia's Herbal Medicine Compendium [77] confirming a rekindling of interest in the oil as a medicinal botanical substance.

East Indian sandalwood oil is a complex mixture comprised of small, structurally-diverse compounds [1]. Because sandalwood oil is produced by steam distillation, its constituent compounds are volatile (low molecular weight) and only sparingly water-soluble. Although many of the compounds are based on a sesquiterpene skeleton of fifteen carbon atoms, there is great structural diversity represented by the individual components in the mixture. From a pharmacology perspective, such structural diversity, high lipid solubility and low molecular- weight offer the promise of multiple

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biochemical targets and mechanisms of action for sandalwood oil as a pharmaceutical agent.

2 Pharmacology/Biochemistry of Sandalwood Oil

There has been a resurgence in interest in the antimicrobial properties of sandalwood and other essential oils in recent years due, at least in part, to their activity against many strains of bacteria that have become resistant to many common antibiotics [78]. As sandalwood oil becomes increasingly considered for its potential as a botanical drug, its biochemical and pharmacologic properties are being studied in a variety of model systems.

The broad antibacterial activity, especially against gram-positive organisms, is well recognized [15, 16, 45, 50, 57, 62]. Antifungal [24, 35, 36, 40, 41, 60, 66] and anti-viral properties [4, 47, 65] of sandalwood oil have also been widely documented. Sandalwood oil has also been studied as an inhibitor of key enzymes in the pathogens *Mycobacterium tuberculosis* and *Plasmodium falciparum* [67].

The oil has been found to be anti-inflammatory via multiple mechanisms including suppression of upregulation of proinflammatory chemokines and cytokines [72] and inhibition of phosphodiesterase-4 (PDE4) which is believed to play a role in many inflammatory conditions [74]. The oil has antioxidant activity [46, 51] and inhibits 5-lipoxygenase [3] as well as phosphodiesterase-4 [73]. Its antioxidant activity has been reported to potentially mitigate the cardiotoxicity associated with the cancer chemotherapeutic, doxorubicin [83]. It also inhibits tyrosinase [52, 53] and the production of cortisol by 11β-HSD-1 [44]. Sandalwood oil has been reported to modulate hepatic glutathione S-transferase activity in mice [2]. Neuroprotective effects of sandalwood oil in *Candida elegans* models have also been recently reported through its ability to reduce oxidative stress-induced damage [54–56].

Sandalwood oil has also been shown to induce cell death via autophagy [23], disrupt microtubule dynamics causing cell-cycle arrest at G_2/M [49], suppress expression of proliferation markers [25] and inhibit angiogenesis [70, 71]. The many effects of sandalwood oil related to cancer [69] are too numerous to list here and are the focus of another chapter in this volume [8].

Sandalwood oil appears to work via multiple mechanisms of action, which are not surprising given the complexity of the oil's composition. The broad range of biochemical activity, combined with a relatively benign safety profile [13], makes sandalwood oil a potentially promising candidate for a number of pharmaceutical applications [7, 59, 75].

3 Safety of Sandalwood Oil

Because of the long historical use of sandalwood oil and its current use in many personal care products as a fragrance material (perfumes, soaps, etc.), *S. album* oil has been extensively studied from a safety perspective. In rats, the dermal LD_{50} is greater than 5 gm/kg of body weight [63]. Among the general population, 0.1–2.4% of subjects have been found to be allergic to topically applied *Santalum album* oil [21, 22]. The oil contains no known carcinogens and was found to not be genotoxic in the *B. subtilis* rec-assay [42]. The safety profile of East Indian sandalwood oil has been reviewed by Burdock in 2008 [13] and by Tisserand and Young in 2014 [76]. Overall, *Santalum album* oil has a safety profile that suggests it would be well-tolerated as a pharmaceutical.

3.1 Regulation of Botanical Drugs

Botanical, or herbal, drugs such as sandalwood oil are treated as a special class of drugs in many countries. In Germany, there is a system of herbal medicine based on a series of monographs known as Commission E [20]. The monographs describe various materials of plant origin that have purported medicinal properties and describes the characterization of the herbal drugs and their uses. In Australia, many plant -derived substances are allowed as ingredients in the class of drugs known as ‘Listed Medicines’. *S. album* oil is allowed as an active ingredient as well as an excipient. Listed medicines are considered safe but the indications claimed are not verified by the Australian Therapeutic Goods Administration (TGA).

As of March 2020, the FDA revised its review process for introducing new over-the-counter (OTC) drug monographs to allow the sale of drugs without a prescription [31]. The new process for requesting an FDA OTC monograph for a compound considered Generally Recognized As Safe and Effective (GRASE) involves the submission of an OTC monograph order request (OMOR).

Although the OTC route for sandalwood oil has not yet been pursued commercially and should be considered by sponsors seeking the right to sell and market sandalwood oil as a drug in the USA, this chapter will focus on the development of *Santalum album* oil as a potential prescription (non-aromatherapy) pharmaceutical agent in the USA. The benefits of prescription botanicals (and proprietary formulations) include assurance of quality/potency, less pricing constraint than OTC drugs as well as the potential for insurance coverage for the cost of the drug.

The US Food and Drug Administration (FDA) oversees and regulates the development and approval for sales and marketing of pharmaceuticals in the USA. The FDA recognizes botanical drugs as a special category of pharmaceuticals and has issued guidelines for those seeking to obtain marketing approval for botanical drugs in the USA [26]. The path to marketing approval is substantially the same as that for single-agent drugs. An Investigational New Drug (IND) application must be filed prior to initiation of human clinical trials [29]. Preclinical and clinical development, if successful, eventually leads to the creation and submission of a New Drug Application (NDA) to the FDA which is subject to review and approval prior to sales and marketing approval being granted. The FDA has an internal Botanical Review Team (BRT) with deep expertise in botanical drugs. The BRT plays an integral role in the review and evaluation of regulatory oversight of this class of drugs [27].

The contents of botanical drug applications (IND and NDA) mirror the structure of applications for conventional single-agent drugs. There must be extensive documentation regarding the methods of production of the drug substance (the 'active ingredient') as well as the proposed drug product (the final dosage formulation for the botanical drug).

The US FDA maintains an excellent website [33] that allows those interested in pursuing the development of botanical drugs, such as sandalwood oil, to access extensive guidance and other regulatory documents. Early communication with the FDA via pre-IND meetings and other interactions is essential. One must identify which of the various FDA drug divisions will be responsible for reviewing the IND [30]. This depends on the intended use for the drug, not the drug itself. For any drug development programme to succeed, there must be consensus between the developer and the regulatory agency regarding the studies and data required to support an NDA.

Although there is no filing fee associated with submitting a commercial IND to the FDA, when one considers the scope of the document (which can run to 500–1000 pages or more) and the amount of work required to prepare the IND, the cost of submission for the developer is significant. A full discussion of the drug review and approval process is beyond the scope of this chapter but suffice to say that compiling an IND will require the input of those with expertise in the areas of medical writing, drug manufacturing, regulatory affairs, animal toxicology, biostatistics, analytical method development/validation, pharmacokinetics, formulation, etc. Clinical trial materials (drug product and placebo, if necessary) will need to be manufactured, tested, packaged, labelled, put on stability testing, randomized and delivered to clinical trial sites.

Physicians will need to be involved in the drafting of clinical trial protocols to include the objectives of the trial, the study population, inclusion/exclusion criteria for participation in the trial, primary and secondary endpoints for determination of efficacy and safety/tolerability, etc. Clinical trials sites and principal investigators will need to be identified, forms generated (informed consent forms, clinical response forms, etc.) and site personnel trained. An investigator brochure will need to be drafted to inform site personnel of the known properties of the study drug.

Once the IND is prepared and submitted to the FDA, the agency will send a letter to the drug's sponsor to acknowledge receipt of the application. The FDA has thirty days from receipt of the IND to raise any concerns or ask any questions that need to be resolved before human clinical trials may begin. If the agency has no objections to the initiation of the trial, the sponsor may initiate studies pending approval of an appropriate Institutional Review Board (IRB) which serves to protect the rights and welfare of human clinical trial subjects.

Although the contents of INDs are not publicly available, those interested in the approval process for botanical drugs might be interested in reviewing the contents of the FDA's Drug Approval Packages for Veregen™ and Fulyzaq (now known as Mytesi™), the two drugs which have been approved thus far under the FDA's botanical drug development guidelines [28, 32]. A thorough reading of the various FDA reviews for these drugs, approved in 2006 and 2012, respectively, will provide a good overview of the extent of the data that must be generated to successfully support the submission of an NDA.

Like all other drugs approved for sale in the USA, botanical drugs must be shown to be safe and effective for their intended use. From a regulatory standpoint, a unique aspect of botanical drugs is that they may be developed not as single, highly purified compounds, but as complex, well-characterized mixtures. The requirement for rigorous physiochemical and biological characterization remains as well as the requirement for production of the drug product under all applicable good practices (agricultural, harvesting and manufacturing). There must be minimal batch-to-batch variation in the composition of the botanical drug mixture. Being able to comply with the botanical drug development guidelines requires the development and validation of suitable analytical methods for the major components in the mixture. For sandalwood oil, this generally means gas and liquid chromatography coupled with mass spectral analysis.

Patient safety is paramount, and even though sandalwood oil is considered to be relatively safe, sponsors should expect to be required to conduct a thorough investigation into the toxicology of the drug based on the formulation and proposed dosing regimen. In general, acute and chronic toxicity/safety studies will be required in both rodent and non-rodent species prior to initiating human clinical studies.

Given the complexity of the sandalwood oil mixture and the challenges associated with tightly controlling the chemical composition of the oil from batch to batch, it is desirable to have a bioassay that can evaluate the biological activity of the oil in a simple model system that is relevant to the intended therapeutic use of the oil. For example, if the oil is being developed to treat an inflammatory skin condition, it would be useful to have a model system that can serve as the basis for assaying suppression of inflammation in intact skin or cultures of various types of skin cells. This would allow the bioactivity of each lot of oil to be quickly assessed.

Sandalwood oil has been, and continues to be, extensively used in fragrances, personal care products and foods. As a result of its extensive commercial use, an international standard for East Indian sandalwood oil (ISO 3518:2002) was created that specifies the minimum concentrations of the oil's two primary isomeric components, alpha- and beta-santalol, as well as basic physiochemical properties of the oil such as density, colour, refractive index, optical rotation, solubility in alcohol and chromatographic profile [43]. At a minimum, any preparation of sandalwood oil intended for use as a botanical drug substance must be compliant with the ISO standard. Additional testing will be required to look for heavy metals, residual pesticides, solvents, adventitious toxins and other possible contaminants.

Development of sandalwood oil as a botanical drug includes a requirement that the oil be produced from cultivated trees only. Preferably, such trees should be sustainably grown in plantations. Wild-grown trees are considered ‘threatened’, and it is not possible to know the entire history of a tree that is not been grown from a seedling. The trees must be grown, and wood is collected using good agricultural and collecting practices [79]. The oil must be produced using good manufacturing practices with all the appropriate quality assurance and quality control measures in place.

4 Challenges of Developing Sandalwood Oil as a Drug

Sandalwood oil is predominantly produced in the heartwood of the mature tree (typically 4–6% by weight). It takes many years for trees to produce oil, even when the trees are cultivated under favourable conditions [9]. This means that anyone wishing to produce their own supply of sandalwood oil by starting a plantation will not have significant quantities of oil for a number of years. Given that there are few sandalwood plantations globally, the issue of oil supply can be a daunting challenge for those contemplating the development of sandalwood oil as a pharmaceutical in the USA.

If the potential botanical drug is widely available commercially and broadly used with minimal safety issues (as is the case with sandalwood oil), according the FDA botanical drug development guidance, it may be possible to enter human clinical trials without the full range of animal safety and toxicity studies [80]. If the proposed botanical drug substance is produced using traditional methods (so that its composition is consistent with traditionally produced samples) and its intended use is consistent with traditional uses (i.e. applied topically, ingested or inhaled), the risk of new side effects or toxicities is minimized. With *S. album* oil, the FDA has allowed Phase 2 human efficacy clinical trials to be conducted without requiring the traditional Phase 1 safety and dose-range finding studies. This is a potential opportunity for the developer of the drug to save time and money in early stages. Of course, any clinical development plan envisioned must be discussed with the FDA prior to initiation of studies.

There are properties of sandalwood oil that can make clinical development difficult. The oil’s characteristic fragrance/odour can make the conduct of double-blinded, placebo-controlled clinical trials a challenge because the placebo must be indistinguishable from the sandalwood oil-containing product based on scent. This requires the addition of a compound to the placebo that mimics the sandalwood scent. Of course, the sandalwood odorant must not have any biological properties that would skew the clinical data.

Pharmacokinetic studies are typically required as part of advanced human clinical trials. Since there is no requirement under the FDA botanical drug development guidelines to identify active compounds in the plant mixture, it begs the question: which compound (s) should one monitor during the clinical investigation? Often, the consensus is to follow the absorption, distribution, metabolism and excretion (ADME) of the most prevalent compound (s). In the case of sandalwood oil, those compounds would be alpha-santalol and beta-santalol which are typically present in the oil at 41–55% and 16–24%, respectively. Even though there are well over one hundred identified components in East Indian sandalwood oil, these two isomeric compounds typically comprise approximately 70% of the oil by weight. It is probable that many of the compounds present in the oil at lower levels may have biological activity, but it is impractical to develop and validate analytical methods for every component in the oil, especially since the vast majority of them are not commercially available in pure form to be used as reference standards.

Very little has been published about the metabolism and excretion of sandalwood oil components in humans. Work done in canines suggests that oxidative metabolism to more water-soluble carboxylic acid derivatives of sandalwood oil compounds occurs [86]. Because of the complexity of the composition of sandalwood oil, there will be challenges related to elucidating the metabolic fate of the many components of sandalwood oil in humans. Such studies will likely require the synthesis of radiolabeled sandalwood oil components.

In order to determine the alpha- and beta-santalols in pharmacokinetic studies, one needs validated analytical methods. In order to develop such methods, it is necessary to prepare highly purified samples of each compound that can be used as reference standards. With validated assays available, one can detect the santalols in plasma and other biological samples. Although the synthesis of both alpha- and beta-santalol have been reported in the literature [5], it is often more cost-effective to isolate and purify these reference materials by preparative chromatography from sandalwood oil than to produce them by de novo organic synthesis.

Because sandalwood oil is produced over many years within individual trees, the composition of the oil is not as subject to seasonal variations in sunlight, water, temperature, etc., as botanical raw materials that are produced in a single growing season (like green tea extracts, for example). Individual batches of sandalwood oil may have slight variations in composition which may be addressed, if necessary, by blending to achieve target concentrations of key components.

The development of complex botanical mixtures such as sandalwood oil requires suitable analytical methods. Traditional separation methods such as gas, liquid and thin-layer chromatographic methods have been supplemented by novel approaches more appropriate for complex mixtures such as Fourier transform infrared spectroscopy (FTIR) and principal component analysis (PCA) methods [39, 82]. These analytical methods are needed not only to verify identity and purity of pharmaceutical-grade sandalwood oil but also to detect adulteration in samples of commercially available sandalwood oil [6].

Sandalwood oil is suited to the production of topical formulations. The oil is only sparingly soluble in aqueous solutions, but its high lipophilicity makes the production of ointments, cream emulsions and non-aqueous serums practical. Since the oil is produced by steam distillation, it is not surprising that sandalwood oil has reasonable thermal stability and resistance to hydrolysis. The main route of degradation, like many oils, seems to be oxidation which results in the conversion of alcohols to aldehydes and carboxylic acids over time [12]. The sensitivity to oxidation must be kept in mind when preparing formulations of sandalwood oil.

Protection of intellectual property is always important in the development of novel pharmaceuticals. Sandalwood oil is a natural product, and it is not possible to obtain a composition-of-matter patent protection for the oil itself. However, one can seek patents that cover new methods of use of sandalwood oil. This is a challenging approach because the oil has been used for so many medical applications over centuries of recorded use. Generally speaking, method-of-use patents are not as desirable as composition-of-matter patents. Another possible strategy is to seek composition-of-matter patent protection for novel formulations of sandalwood oil or novel combinations of sandalwood oil with other agents.

5 Clinical Trials of *Santalum album* Oil

Some of the earliest formal clinical studies of sandalwood oil in the USA were conducted under investigator-sponsored INDs and examined the activity of the oil in paediatric populations against common skin warts caused by human papillomavirus (HPV) and *Molluscum contagiosum.* These two small studies both showed promising therapeutic activity with a good safety profile [37, 38].

A clinical study was conducted to study the ability of Vicco® Ayurvedic cream which contains sandalwood oil and turmeric to reduce the incidence of radiation-induced dermatitis in breast cancer patients [64, 68]. Although the treatment seemed to be helpful, it is hard to draw conclusions about the effect of sandalwood oil since there were multiple potentially bioactive ingredients in the cream studied.

More recently, a number of clinical trials were conducted in the USA under several botanical drug INDs. Conditions studied included *Verruca vulgaris* (common warts), *Condylomata acuminata* (genital warts), plaque psoriasis, ectopic dermatitis/eczema, *Molluscum contagiosum* and radiation-induced oral mucositis.

A search of clinicaltrials.gov using the phrase ‘East Indian Sandalwood Oil’ returned the results shown in Table 1 [19]. The trials shown were all Phase 2 efficacy and safety trials, some of which were randomized, placebo-controlled studies. For the most part, these small trials showed that various formulations of East Indian sandalwood oil showed moderate efficacy and good tolerability. Additional, larger studies are needed to confirm safety, efficacy and statistically significant benefit versus placebos.

Sandalwood oil in an ointment formulation (10, 20 and 30% strengths) was studied in subjects with common warts (*Verruca vulgaris*) in a four-arm, placebo-controlled, randomized double-blind dose-range finding trial. Primary endpoints included efficacy, safety and tolerability. All treatment arms were found to be safe and well-tolerated. No serious adverse events related to the study medication were reported. There were only four adverse events (three in the 30% arm and one in the 10% arm) which were deemed to be related to the study medication. All were mild, reversible irritation at the site of application. The three treatment arms all showed greater rates of wart clearance and reduction in wart area than the placebo arm [18].

Table 1 Clinicaltrials.gov listing of East Indian sandalwood oil clinical trials

Indication	Drug formulation	Treatment duration	Patients	Subject age	Status
Verruca vulgaris (common warts)	10, 20 and 30% oil in an ointment versus placebo	12 weeks	183	18 years or older	Completed
Molluscum contagiosum	10% oil in a cream versus placebo	90 days, twice a day	27	2–17 years	Terminated
Atopic Dermatitis/Eczema	5 and 10% oil in a cream versus placebo	28 days, twice a day	71	Over 18 years	Completed
Mild to Moderate Plaque Psoriasis	10% oil in a cream	42 days	69	Over 18 years	Completed
Oral Mucositis	0.25% oil in a mouth rinse	During treatment, three times a day	7	Over 18 years	Completed
Condylomata acuminata (genital warts)	10% oil in a cream	Up to 60 days	–	Over 18 years	Terminated

For the three-arm randomized, placebo-controlled trial in atopic dermatitis, results were posted on the clinicaltrials.gov site [17]. The treatment was well tolerated and moderate efficacy was seen in both treatment arms, although not much difference in efficacy was seen between the two treatment arms and the placebo arm. This trial, like the other Phase 2 trials listed on the site, was relatively small, and results would need to be verified in larger, confirmatory trials.

A non-dermatology Phase 2 clinical trial of sandalwood oil looked at the ability of a 0.25% sandalwood oil mouth rinse to prevent or reduce the incidence of oral mucositis in head and neck cancer patients undergoing chemo- and/or radiotherapy for their disease. Subjects were asked to rinse, gargle and spit the formulation three times a day throughout their treatment period. Incidence of oral mucositis was measured and compared to historical rates of incidence in similar patients.

Tolerability and safety were also studied. Although some subjects discontinued use of the drug product due to its flavour and consistency, there were no serious adverse events related to the drug. There were several adverse events that were deemed possibly or probably related to the drug, but they were mild and resolved the same day or after discontinuation of the drug.

The data from the small study (eight subjects), when compared to historical results from other institutions, were suggestive of benefit and the investigators felt that sufficient signal was present to warrant further development of sandalwood oil as a potential alleviator of mucositis once a more tolerable preparation is prepared [34].

Several small clinical studies were also conducted wherein sandalwood oil was added as an 'inactive' ingredient to over-the-counter monograph drugs for acne, atopic dermatitis and common warts.

A single-centre, open-label pilot study of a blend of 0.5% salicylic acid and up to 2% sandalwood oil was conducted in adolescent and adult subjects with mild to moderate facial acne. During the eight-week treatment period, the treatment was well-tolerated and 89.4% of participants saw improvement in their acne compared with baseline [58].

A paediatric population with atopic dermatitis/eczema was also studied using a regimen containing 0.1% colloidal oatmeal in combination with sandalwood oil in a single-centre, open-label study. Twenty-two patients were treated for eight weeks. The treatment regimen was safe and well-tolerated, and there was good improvement in the disease severity ratings with 86% of evaluable patients having 'improved', 'much improved' or 'very much improved' eczema at Day 60 [11, 73].

For the treatment of common warts, a blend of 17% salicylic acid and sandalwood oil in a gel formulation was used in two open-label studies in children and adolescents. For the two studies, 44% (11/25) and 30% (10/33) of patients who completed treatment and follow-up met the primary endpoint of having greater than 50% reduction in total wart surface area. In addition, a total of 4/25 (16%) and 7/33 (21%) of patients experienced complete resolution of treated warts. Overall, treatment was well tolerated with mild to moderate itching, burning, dryness and stinging being the most common adverse events [10].

6 Future Development of Sandalwood Oil as a Pharmaceutical

Availability of adequate quantities of pharmaceutical-grade sandalwood oil from cultivated trees is likely to be an ongoing issue for those wishing to develop the oil as a prescription drug. There are few plantations that are well-established and large enough to be able to provide the *Santalum album* wood required for large-scale manufacturing and commercialization of sandalwood oil-containing prescription pharmaceuticals. However, this scarcity can be a benefit: if one can secure a reliable and exclusive source of oil, it can act as a barrier to market entry for others wishing to develop sandalwood oil-based prescription drugs.

Even though natural products such as sandalwood oil are not patentable as novel compositions of matter, it is important to note that for New Chemical Entities (NCEs) that have not previously been approved (such as sandalwood oil), any FDA approval to sell and market the botanical drug would be protected by a five-year period of exclusivity.

Expanded use of sandalwood as an herbal medicine (as is being done in Germany) is likely to occur in the light of the increasing volume of supportive biochemical data being generated worldwide. The reinstatement of monographs for *Santalum* *album* oil in pharmacopeias such as the USP and BP would provide methods and criteria for assuring identity and purity of the botanical material. Use of oil that is compliant with pharmacopeial standards would significantly reduce risks due to impurities or adulteration. The herbal medicine approach addresses safety concerns and removes the lengthy and costly preclinical and clinical studies that are required for the marketing approval of prescription drugs. The downside to this approach from a commercial standpoint is that herbal medicines cannot command the premium pricing that is typically realized by prescription pharmaceuticals and the cost of herbal medicines is typically not reimbursed by insurance companies.

Much attention has been focused in recent years on the enzymes responsible for the biosynthesis of some of the key components produced by *Santalum album* trees. Genetic engineering of yeast cells has led to the production of santalols in culture [84, 85]. It has been shown that alpha- and beta-santalol both have biological properties that make them attractive as active pharmaceutical ingredients [7]. Large-scale production of biologically active components such as alpha- and beta-santalol by expression in cell culture may eventually lead to lower cost of goods and an alternative path for the development of sandalwood -derived components, not as botanical drugs, but as conventional high-purity active pharmaceutical ingredients (APIs).

A thorough and very informative article was published in 2020 by Dr. Wu and members of the US FDA Botanical Review Team summarizing the botanical drug development experience from a regulatory perspective [81]. Since the US FDA's development guidelines were created, there have been more than 800 botanical drug IND applications filed with the FDA between 1984 and 2018. Approximately, one-third of those INDs were filed by commercial drug developers and less than 5% of those drug products progressed into Phase 3 clinical development. As of the writing of the Wu article, only two botanical drugs have been approved under the FDA's botanical drug development guidelines: sinecatechins (Veregen®), a green tea extract for treatment of genital warts was approved in 2006 and crofelemer (Mytesi™, previously known as Fulyzac), a bark extract from a *Croton* tree for treatment of non-infectious diarrhoea was approved in 2012. This relatively low success rate is testament to the challenges of developing this class of drugs.

The FDA botanical drug development guidelines afford some benefits to those wishing to take traditional botanical drugs into human clinical trials. However, the overriding requirement to demonstrate safety and efficacy also imposes challenges that sponsors developing single-agent drugs do not face. Although it may be less burdensome/expensive to take botanical drugs into early clinical trials compared to novel single-agent drugs, the requirements to enter advanced Phase 3 trials are nearly as rigorous for botanical drugs as for single-agent drugs. Chemistry, Manufacturing and Controls (CMC) requirements, including development and validation of analytical methods, the conduct of stability studies and ADME studies are all more difficult with complex mixtures such as sandalwood oil than they are with single-agent drug substances and products.

FDA realises this and has taken a 'Totality-of-the-Evidence' approach that may allow development and eventual marketing approval based on aggregate properties of the botanical drug, as verified in bioassays confirming the activity of the mixture. Also, pivotal clinical trials can be conducted with botanical drug products manufactured for multiple batches of sandalwood oil, the botanical raw material (BRM), to demonstrate therapeutic consistency.

In summary, the FDA encourages the development of botanical drugs and has created specific guidelines for those wishing to pursue marketing approval for this class of drugs. The Agency's Botanical Review Team (BRT) is familiar with sandalwood oil as traditional medicine and is well-qualified to provide feedback and guidance regarding proposed drug development plans. Limited Phase-2 efficacy and safety studies have been conducted, and the promising results seen need to be confirmed in larger, well-controlled Phase 3 trials.

Santalum album oil eventually reaching the market in the USA as an approved prescription drug would depend on many factors including the availability of high-quality oil from sustainable sources, the successful outcome of pivotal clinical trials, close interactions with appropriate regulatory agencies and the ability of the botanical drug to address a therapeutic need in the competitive pharmaceuticals market profitably.

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Chapter 31
Indian Sandalwood Market Trend

H. S. Ananthapadmanabha

1 Introduction

Sandalwood trade in India started as early as seventeenth century. Realizing the value of sandalwood, Tipu Sultan, King of Mysore, declared it a Royal Tree in 1792. Indian sandalwood is one of the most precious commodities for export, earning an excellent foreign exchange. It is also being imported in small quantities in the form of a value-added product. The wood was mainly exported to China during the first half of the eighteenth century; a small quantity was also exported to countries like France, England, Germany and the Middle East. With time, the wood trade with China was stopped and arrangements were made with the USA and European countries to extract oil. The understanding of exporting well-dressed sandalwood logs, roots and billets for distillation of oil continued with Germany and USA until the First World War, as the technology was not available with India. Since Germany was a major partner in the First World War, it severed connections with all the world trades. There was a disturbance in the sea route transport systems, as many countries were also involved in the war; consequently, India had no alternate but to establish its own distillation unit.

2 Sandalwood Early Trade and Export

The earliest sandalwood trade available was during 1866–1867. The Mysore Government had sandalwood stock worth INR 156,321 and selling realized revenue of INR 74,598. During 1885–1886, Government of India exported sandalwood stock worth INR 444,241 and imported value-added product worth INR 16,404. During 1889–1890, the export wood increased to INR 1,009,152, out of which stock worth INR

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Table 1 Harvest value of sandalwood during late 1800s and early 1900s [3]

Year	Export value (INR)
1885–1886	444,241
1889–1890	1,009,152
1907–1908	1,000,000

770,791 was ported through Madras and the rest from Bombay. The selling price for wood at Bombay was INR 120–180 per 21 Mounds (10 Pounds). The price for sandalwood oil was INR 8.5 for a pound [3].

During the beginning of the nineteenth century, (1907–1908), 85,000 pounds of wood was exported to different countries worth INR 1,000,000. After World War II, the export of wood was restricted to 2500 tonnes; 52% was sent to Germany, 18% to USA and the remaining to England and other countries (Table 1).

3 Sandalwood Harvest

Sandalwood harvest information was not systematically maintained before 1950. Forests of Karnataka and Tamil Nadu states contributed 90% to the country's production; other states like Kerala, Andhra Pradesh, Madhya Pradesh and Orissa contributed a small quantity.

The production in India solely depended on the trends in Karnataka and Tamil Nadu. In 1952–1953, production was 2459 tonnes, which increased to more than 4000 tonnes during 1956 and 1957. During 1957–1961, the production was more or less stable. The second quinquennium, i.e. 1965–1966 to 1969–1970, started with an increase in 3867 tonnes in 1965–1966. However, it dipped in 1966–1967, but maintained an upward trend during 1967–1968, 1968–1969 and 1969–1970 (Fig. 1). During this quinquennium, the average production was 3922 tonnes, which was higher by 23.5% than the previous quinquennium. The average production during 1970–1971 to 1974–1975 was 3842 tonnes, which was lower by about 2% to the previous quinquennium. The data regarding production are patchy and lack authenticity, as the statistics was not maintained properly. The average production in the third quinquennium presented a gloomy picture as the production achievement was at 2517 tonnes.

The average yearly production of sandalwood from 1981 to 1985 was 3,209.80 tonnes. The increase in production is due to the major contribution from Karnataka State. During 1980–1983, poaching activities were rampant in the sandalwood growing areas in Shimoga and Chandrakala forest ranges, where a very good sandalwood population with good girth class existed. The extensive illegal harvest resulted in removal of only the stem portion leaving behind the root portion as it was difficult to extract. The Forest Department initiated the removal of such leftover roots and sent to forest depot for storing and further disposal. This was the reason for the increased sandalwood production. The lowest production was noticed in 1990 (1648 tonnes).

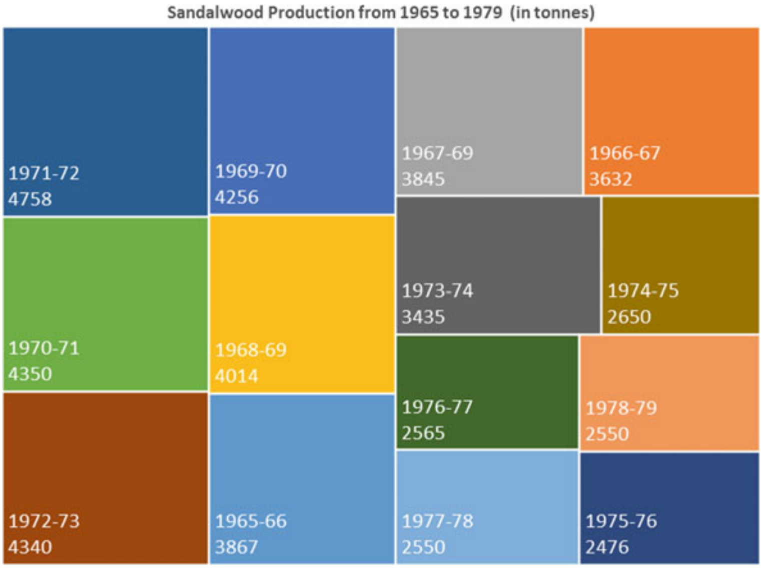

Fig. 1 Tree map of Sandalwood production in India from 1970 to 1980 [3]

The decreased production observed in the later years is because of extensive illegal harvest and the establishment of a number of illegal distilleries that realize the high value of sandalwood in the international market. The share in the contribution towards sandalwood production from Karnataka was reduced due to overexploitation. On an average, yearly production during 1987–1990 was only 2805 tonnes which was less than 18% production from the previous years. The average production from 1991 to 2000 further reduced to 1630 tonnes due to shortage of mature sandalwood trees in the natural habitat. During these years, the bigger girth class of heartwood reaching sandalwood depot also considerably reduced (Fig. 2).

The production further declined from 2000 to 2004, and the main contribution was from Tamil Nadu (over 80%); Karnataka contributed only 15%. The annual average production of sandalwood during this period was 1370 tonnes. This quantity could be achieved because the Tamil Nadu Forest Department extracted all the available dried and dead trees from the natural forest as a precautionary measure against the illegal harvest. The leftover trees in the natural forest were predominantly of small girth class (<30 cm).

Subsequently, the average annual production of sandalwood further declined to 834 tonnes in 2007, while in 2019, it dropped to a meagre 300 tonnes (Fig. 3). Tamil Nadu Forest Department did not auction the wood since 2009, and the major contribution was from Kerala Forest Department. The drastic reduction in production was due to inadequate steps to regenerate and conserve natural resources effectively.

During earlier years, heartwood of ten trees weighed more than a tonne; later 100 trees were needed to make a tonne. Presently more than 200 trees are required to produce one tonne of heartwood. There is a progressive decrease in the size of

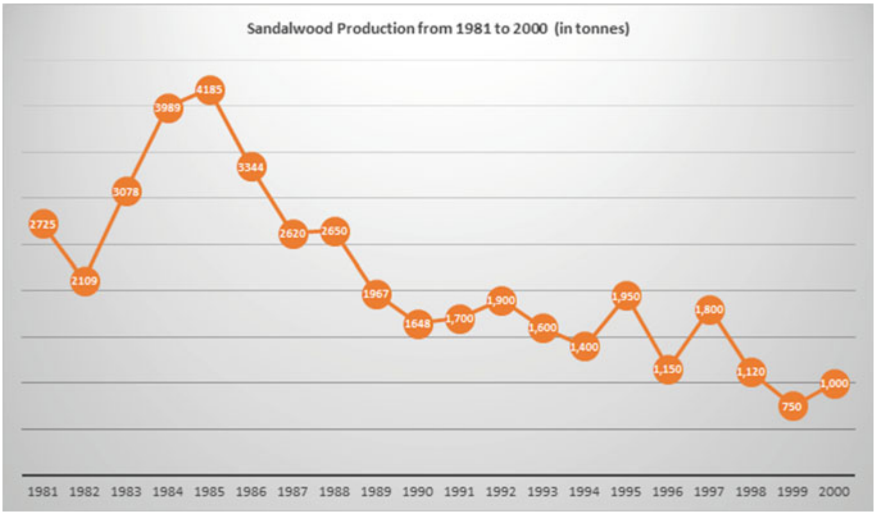

Fig. 2 Sandalwood production during 1991–2000 [3]

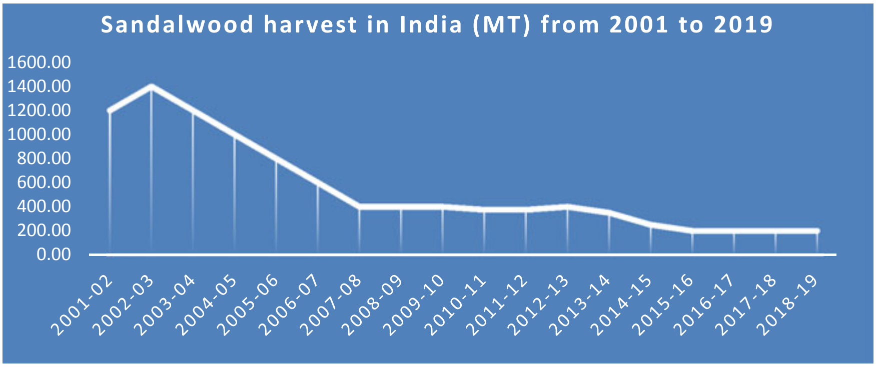

Fig. 3 Sandalwood harvest in India (MT) from 2001 to 2019 [4]

extractable trees. During current sandalwood auctions, some of the bigger category class were eliminated since they do not exist in the natural populations. From 2025, the only source would likely to be from farmer's private field.

4 Sandalwood Market

Sandalwood and its products are in great demand in the domestic and international market.

About 20% of the wood produced is used in the handicraft industry. Attractive carvings and art pieces from the wood are exported to different countries, earning good foreign exchange. This industry has suffered heavily due to a sharp decline in production and the removal of subsidized wood price to artisans, which they were getting till 1995. The prohibitive increase in sandalwood price is also one of the reasons for the short supply of wood handicraft industry. In India, religious institutions use about 2–5% of wood towards making a paste, which is used on idols and distributed among devotees.

5 Import of Sandalwood

Sandalwood was never imported to India until 1995. Merchants were not prepared to accept any alternates to Indian sandalwood. This was because the sandalwood was readily available to merchants both from legal and illegal sources. The price was also moderate and not fluctuating in the domestic market. During 1999, Australian sandalwood *Santalum spicatum* was introduced to Indian merchants. Though there were initial inhibitions for the exotic sandalwood, later it was accepted as it was less expensive.

At the same time, merchants explored the possibility of getting other scented wood as alternates, because of the inconsistent supply from Western Australia. African (Tanzanian wood) sandalwood, which belongs to the genus *Osyris*, was imported in large quantities for various value-added products. The wood was comparatively cheaper and captured a wide domestic market. Indian merchants have imported about 2000 tonnes of wood annually since 2001. Though this wood has been imported in large quantities, the need and the demand for Indian sandalwood has not decreased. Since 2010, the Government of India has restricted the import of logs. The Tanzanian Government to conserve *Osyris* species imposed export restrictions during 2004. It amended the export rules, mentioning that only value-added products from *Osyris* wood can be exported. The Indian merchants, due to high demand for African sandalwood oil in the domestic market, established sandalwood distilleries in Africa.

6 Sandalwood Prices

Sandalwood is perhaps the only wood in the world sold by weight and not by volume. During the past one hundred years, the prices of sandalwood have seen many variations. During 1882–1883 to 1887–1888 in the erstwhile Mysore State (Present Karnataka State), sandalwood was sold at the rates mentioned in Table 2.

The above prices illustrate that there was not much variation in the price. During the early 19 century, sandalwood fetched a little over INR 400 per tonne, which in the next few years steeped to INR 500. In 1913, the prices shot up to INR1000 per tonne, which increased to INR 2000 during the year 1914. The price of wood has

Table 2 Sale of sandalwood during 1800s [5]

Years	Price (INR per tonne)
1882–1883	328
1883–1884	300
1884–1885	307
1885–1886	329
1886–1887	337
1887–1888	302

increased to INR 5000 a tonne prior to World War II and remained almost stable till 1957–1958. Sandalwood is sold in the open auction by classifying into different grades based on the wood's weight and soundness. The oil content in the wood varies in a tree from the roots to the stem and to the major branches. Consequently, the price for the different categories also varies.

There was a constant rise in the price structure from the beginning, as the demand increased, and the price also kept pace with it. There was a gradual increase in price from 1962 to 1966 (INR 6874), and during 1967–1970, the price hiked to INR 10,910. The price increase was almost double compared to the previous five years to INR 20,371 and 33,776 during 1971–1976 and 1976–1980, respectively. In India, only Tamil Nadu Forest Department was publicly auctioning sandalwood, and the sale price conferred by the state forest department was always taken as the national sandalwood sale price of sandalwood for the year. Karnataka State Forest Department was transferring the wood to the state-owned distillery to extract sandalwood oil. The price of sandalwood was never consistent; it was purely based on oil demand and the Indian government policy on the export. The price from 1991 to 1995 was unimaginable—INR 220,000 (Table 3).

The price of wood per tonne from 1995 to 2000 increased in arithmetic progression reaching its peak INR 646,000 in just 6 years, indicating the high demand and short supply. The annual premium increase is more than 50%.

Realizing merchants' eagerness towards the purchase of sandalwood, Tamil Nadu government introduced a different system for fixing the basic price for different categories of wood to earn more revenue. The government fixed 10% higher bid

Table 3 Average market price (pooled) realized by auction sale during the twentieth century, Tamil Nadu Forest Department [1, 6]

Year	INR
1962–1965	6874
1966–1970	10,910
1971–1975	20,371
1976–1980	49,732
1991–1995	220,000
1995–2000	646,000

Plus taxes (Central tax 5% + FDT 12%) to the basic price

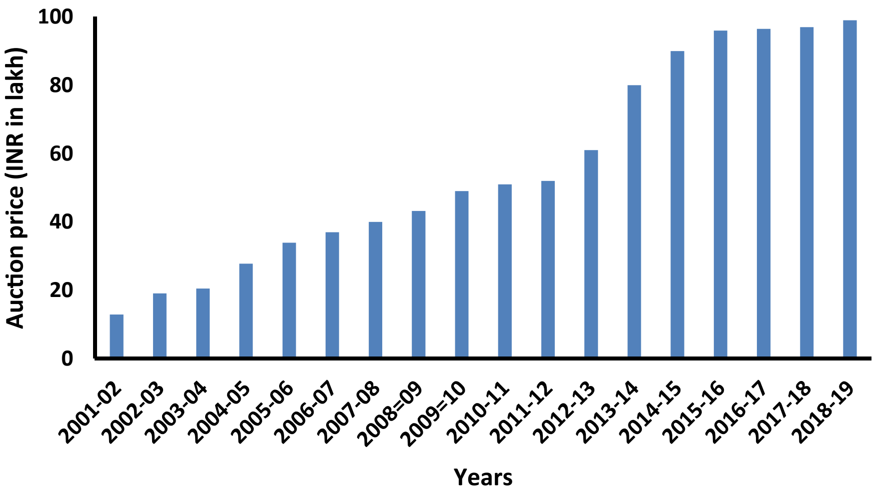

Fig. 4 Average market price (pooled) realized by auction sale during the twenty-first century [4]

price than the previous auction as the basic bidding price for all categories. There used to be four auctions in a year, and consequently, the annual price increment used to be more than 40%. Merchants protested to this, and on several occasions, the auction was cancelled. However, prior commitments forced them to buy at a premium price (Fig. 4).

Due to short supply and high demand, sandalwood's price was too high, and there were only few buyers who wanted to make value-added products, since there was a ban on export of wood. The wood price from 2014 to 2019 reached about nine million INR, because of very short supply.

7 Sandalwood Oil Trade

7.1 Trade During First World War

Sandalwood oil used to be exported to different countries by various means of transportation. In medieval days, it used to be exported to Egypt, Greece and Rome. In those days, the oil was used for perfumery, and only the affluent like kings, landlords were able to afford its use.

For the first time in 1400, a crude form of sandalwood oil was extracted by Europe, and Germany refined the extraction procedure, which was later accepted as British pharmacopoeia grade. Due to war and restrictions in trade routes, the Mysore Government, under the farsightedness of the Maharaja of Mysore and Sir M. Visweshawaraiah the minister of Mysore, established the first sandalwood oil distillery in

Table 4 Early production of sandalwood oil in India [1, 2]

Year	Production in Pounds
1917–1920	24,000
1921	55,641
1922	121,602
1923	149,464

the year 1916–1917 and named it Mysore sandalwood oil factory. Dr. Watson and Dr. Sudburough of Indian Institute of Science provided scientific support for sandalwood oil distillation. They produced British Pharmacopoeia grade sandalwood oil acceptable to the European market.

Initially, sandalwood oil factory was distilling 2000 pounds of oil per month which gradually increased to 55,641 pounds during 1921. By then, it had begun exporting oil to different countries. The production increased in the next two years – in 1922, the production was 121,602 pounds, while during 1923, it was 149,464 pounds, and similarly, the export increased proportionately earning huge foreign exchange (Table 4).

The distillation of sandalwood oil on a large scale continued successfully year after year. The Government of Karnataka started a second factory at Shimoga. The estimated production during 1916–1925 was 579 tonnes which increased gradually to 1026 tonnes from 1966 to 1975. Apart from these, there were many private distillation units established in Salem and Mettur (Tamil Nadu), Kuppam and Hyderabad (Andhra Pradesh), Bombay (Maharashtra), Kanpur and Kannauj (Uttar Pradesh) and Sultan Batteri (Kerala). However, 75% of sandalwood oil production was produced from the two government oil factories.

Due to its high value and increase demand in the internal and external market, sandalwood prices skyrocketed. The price increase was partially due to a decrease in supply from 1930 to 1950s. In 1950, 120 tonnes of oil was produced; an increase in demand was attributed to the popularity of aromatherapy and cosmetic industry trends towards natural products.

7.2 Production of Sandalwood Oil After 1960

The relatable data on the actual production of oil of sandalwood in India are not available.

Official statistics shows far less production than its use in various industries. Private distillers illegally produced sandalwood oil and sold to both domestic and international market for their needs.

From 1963 to 1981, the bulk of the contribution (about 75%) was from Karnataka and the rest from different states. During a span of fifty years from 1916–75, the production increased by about 500 tonnes. However, there has been a declining

Table 5 Estimated sandalwood oil production from 1916–2010 [2]

Year	Production in tonnes	Year	Production in tonnes
1916–1925	579.45	1976–1978	180.22
1926–1935	783.38	1980–1985	265.95
1946–1955	651.62	1996–2000	400.00
1956–1965	849.26	2004	140.00
1966–1975	1026.15	2005–2010	500.00

trend since then (Table 5). The oil demand increased in both domestic and international markets, and the price also increased substantially. This encouraged the private distillers to procure illegal wood. During 1960, there were only 15 private distillation factories in the country, with a distilling capacity of about 45 tonnes. Later, during 1965, the number of private distillers increased to 30 distilling more than 85 tonnes of oil.

The estimated production decreased further due to non-supply of sandalwood to the government-owned distillers at subsidized price by the forest department. In later years, the major supply of oil to both domestic and international market was from private distillers.

The official production of sandalwood oil figures from 1981 to the present date is around 100 tonnes, but based on the different industries requirements, the annual production quantity should be over 150 tonnes. Legislation by India government to protect the sandalwood tree has been inconsistent as sandalwood trade represents a significant export potential to the USA, European and Middle East markets.

8 Export of Indian Sandalwood Oil

India exports sandalwood oil to more than 40 countries of the world. Earlier to 1960, India met the world's requirements up to 70–80%. The total Indian production was of the order of 125–200 tonnes. The production came down to about 40 tonnes in 1981 of which 64% is still exported to different countries of the world (Table 6).

The export was high during 1960–1973 and later fell down sharply; this is due to the government's ban on export policy. Later, a quota system was introduced. The private and government institutions' export quantity was fixed based on the quantity of wood purchased during the auctions.

Sandalwood oil's market trend is exciting, and the price fluctuates based on the demand (Table 7). A kilogram of oil which was costing a mere 5 USD in 1941 fetched 1400 USD in 2005. There is an acute short supply of the raw material coming from the natural forest, since the regeneration efforts are not adequate. The value of wood and oil is increasing every year, hence, numbers of corporate bodies in the world and farmers have come forward to grow sandalwood in agricultural land, and industry may remain for several centuries.

Table 6 Export of sandalwood oil for the years 1960–1961 to 1980–1981 [2]

Year	Quantity (in tonnes)	Value in (000'Rs)	Year	Quantity (in tonnes)	Value in (000'Rs)
1960–1961	98.0	17,408	1970–1971	103.8	24,540
1961–1962	97.1	19,321	1971–1972	117.9	26,099
1962–1963	72.2	12,854	1972–1973	119.9	27,820
1963–1964	81.1	12,290	1973–1974	92.7	35,116
1964–1965	97.1	14,514	1974–1975	71.4	70,869
1965–1966	89.4	13,466	1975–1976	22.7	13,994
1966–1967	90.5	20,426	1977–1978	22.6	28,572
1967–1968	99.0	23,610	1978–1979	25.3	24,040
1968–1969	123.0	31,488	1979–1980	43.0	33,348
1969–1970	108.1	24,540	1980–1981	37.1	28,839

Table 7 Export prices of oil [2]

Year	Rate per kg in USD	Year	Rate per kg in USD
Pre-war	3.5–4.00	1980	135
1941	5.00	1985	166
1944–1948	13.00	1990	200
1955	12.00	1995	385
1960	16.00	2000	580
1965	35.45	2003	700
1970	32.00	2004	1046
1975	84.30	2005	1400

9 Conclusion

Sandalwood has been overexploited due to high demand. The price increase for the last two decades was exceptional. This incremental increase in price for Indian sandalwood may not happen in future, as many countries have started growing sandalwood. But, the demand for sandalwood and oil would not come down as many sandalwood-based industries have come up in different parts of the world.

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Part VII
Perspectives

Chapter 32
Modeled Distribution of and Threats to Sandalwood in a Changing Environment

Riina Jalonen, Hannes Gaisberger, Rekha R. Warrier, Vivi Yuskianti, and Smitha Krishnan

1 Introduction

Species distribution modelling and other spatial approaches can help identify conservation priorities for threatened tree species and their genetic resources. They do not replace field studies but can importantly complement those by helping target field efforts. This is especially valuable in tropical and subtropical regions, where the diversity of tree species is high and resources for studying and conserving individual species are often limited.

The number of studies involving species distribution modelling has increased rapidly in the past years. Among other objectives, these studies have been used to.

1. Identify centres of species diversity to optimise conservation efforts, as in Castañeda-Álvarez et al. [1] who modeled the distributions of over a thousand crop wild relatives and compared those with geographic and ecological diversity indicators to identify priorities for germplasm collection,

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2. Assess how well the current protected areas cover the priority areas for conservation, as in Vinceti et al. [2] who identified target populations for filling the gaps in the existing protected area network for the medicinal tree *Prunus africana*,
3. Identify areas where species' populations may be most threatened by climate change, as in Gaisberger et al. [3] who analysed the combined impacts of climate change and short-term threats on important food tree species in Burkina Faso and
4. Plan studies on genetic diversity and provenance trials that are representative of the species' range and the variation in environmental conditions, as in Gaisberger et al. [4] who compared the predicted distribution of Common Walnut (*Juglans regia*) with genetic diversity and distinctiveness to recommend conservation and management options for the species.

Here, we present the results of a spatial analysis of the distribution of and threats to Sandalwood (*Santalum album* L.) in India and Indonesia. Sandalwood (*S. album* L.) is one of the most valuable tree species globally, cherished for the essential oil found in its heartwood. Sandalwood is used in religious ceremonies, funeral rites, incense sticks and wood carving, the cosmetic industry and medicinal purposes. It is also used as an agroforestry species to provide wind break, green manure and edible fruits. The exact origin of Sandalwood is somewhat unclear. It is assumed to be native to the Lesser Sunda Islands' islands in Indonesia's East Nusa Tenggara province and Timor-Leste [5, 6], where it grows in deciduous forests and has been cultivated in private traditional plantation for centuries [7]. The island of Sumba, in particular, is historically known as 'Sandalwood Island', reflecting its long history and significance as a source of Sandalwood. The species is rare on the Lesser Sunda Islands today, and there are concerns about the viability and genetic diversity of the remaining natural populations [8]. According to some sources, Sandalwood is also native to India [9], where it was cited in ancient medical texts like *Charaka Samhita* dating back more than 2000 years [10], and has also been widely cultivated.

Our analysis covers the species potential distribution under current climate and climate predictions for 2050, the impacts of land use change on the species and the extent of currently protected area networks. We also used global ecoregions [11] as a proxy of the genetic diversity in the species to help identify areas with potentially adapted and distinct populations and assess their conservation status. We conclude with suggestions for conservation actions for India and Indonesia's species, based on the results of the spatial analyses and expert knowledge. To our knowledge, the distribution of Sandalwood has not previously been modeled across its range. Rajan [12] predicted the species distribution in Tamil Nadu, India, and concluded that the species is threatened by anthropogenic impacts across most of its distribution in the state. Elsewhere, Gillieson et al. [13] modeled the distribution of the congeneric *Santalum austrocaledonicum* in Vanuatu in order to identify conservation priorities and opportunities for establishing plantations.

This study was conducted in the context of a regional initiative, 'APFORGIS—Establishing an information system for native Asian tree species and their genetic resources'. The initiative was implemented in South and Southeast Asian countries

Table 1 Occurrence records of Sandalwood used in habitat suitability modelling

Country	Records
Australia	14
India	122
Indonesia	1
Timor-Leste	2
Total	139

from 2017 to 2019, collaborating with over 40 partner organisations and experts. It was coordinated by Bioversity International and funded by Germany's Government through the Federal Ministry of Food and Agriculture. For more information on the project, visit www.apforgen.org/activities/apforgis.

2 Materials and Method

2.1 Occurrence Data

Species occurrence data were collected in 2018 from literature, global databases and through the network of the Asia Pacific Forest Genetic Resources Programme (APFORGEN, www.apforgen.org). The data set underwent a three-step cleaning process to ensure quality control. Firstly, all records having both longitude and latitude coordinates with less than two decimal places, corresponding to a precision of ca. 1.1 km at the equator were removed. Secondly, records indicated to be from planted populations such as parks and botanical gardens were removed. Lastly, the coordinates' accuracy was assessed using the tool GEOQUAL [14], and records from areas unsuitable for plant growth and records where location name did not match the coordinates were removed. The final data set used for spatial analysis consisted of 139 occurrence points across four countries, as shown in Table 1.

2.2 Habitat Suitability Modelling

A correlation matrix of 34 environmental input variables across the study area was calculated, and highly intercorrelated variables were removed [15]. A subset of 16 remaining predictor variables, including variables on temperature, precipitation and their seasonality, soil and elevation variables, was used as input for species distribution modelling using the maximum entropy (Maxent 3.4.1) algorithm [16]. Negative effects of spatial sampling bias were further reduced by applying the target group method [17]. Potential distribution models were considered for further analysis only when there were at least 10 occurrence records for the species after spatial thinning [18] and when the Maxent model complied with validation criteria [19].

The resulting maps, at a spatial resolution of 2.5 arc minutes (ca. 4.5 km at the equator), were validated through a regional workshop and an online consultation in 2019 and a review of the literature and existing species databases. As part of this process, occurrence points not confirmed as being from natural populations and states not confirmed as part of the natural distribution of the species (e.g. due to barriers to dispersal, such as mountain ranges) were identified and excluded from maps depicting natural distribution, to focus on identifying conservation priorities for the genetic resources of the species. The actual natural distribution of Sandalwood is unclear due to its long history of cultivation. In Indonesia, we limited the analysis to Nusa Tenggara, Maluku, Sulawesi and eastern and central Java [6, 9, 20, 21] and in India to the states of Kerala, Karnataka, Tamil Nadu, Andhra Pradesh, Maharashtra and Telangana [6, 9, 21, 22].

2.3 Threat Assessment

Threat from climate change was assessed by projecting suitable habitat of Sandalwood to downscaled future climate conditions for 2050 (2040–2059 period), as predicted by five Global Circulation Models (GCMs) with maximized dissimilarity under two different representative concentration pathways (RCP 4.5 and 8.5). The five selected GCMs—ACCESS1-0, CSIRO-Mk3-6-0, GFDL-CM3, IPSL-CM5A-MR and MPI-ESM-LR—were accessed through the CCAFS downscaled climate data portal (http://www.ccafs-climate.org/).

The Maxent logistic output layers were restricted to the states of expert validated distribution, and a binary raster of suitable versus unsuitable habitat was created for the current and the future climate scenarios applying a commonly used threshold ('maximum training sensitivity plus specificity'), based on the ROC curve [23]. We combined all binary raster in one single map to visualize the predicted change of suitable habitat from present to 2050. We classified areas as 'No change' (habitat remains suitable), 'Loss' (habitat becomes unsuitable) and 'Gain' (habitat becomes suitable) when at least six out of ten future GCMs predictions coincided. To assess land conversion threat, we used the ESA land cover map for 2015 [24] and resampled it to the same resolution as the modeled distribution raster (ca. 4.5 km at the equator). Land cover classes corresponding to 'cropland', 'mosaic cropland (>50%)' and 'urban area' were combined to one category to represent converted land areas. Furthermore, we selected designated terrestrial and coastal protected areas from UNEP-WCMC [25], updated with India's additional protected areas (G. Ravikanth, pers.comm.) and converted them into a raster file with the same resolution.

Finally, we overlaid the potential distribution map, the converted land areas map and the protected area map of Sandalwood and calculated the portion of the distribution that falls within the boundaries of areas converted to cropland or urban areas and protected areas. Similarly, we calculated the portion of the distribution in each ecoregion within the species' natural distribution and converted areas within each ecoregion, using the global ecoregions map [11].

3 Results and Discussion

3.1 Potential Distribution

The distribution model predicted continuous suitable habitat for Sandalwood under the current climate in Australia, India, Indonesia, Philippines, Sri Lanka, Timor-Leste and Vietnam (Fig. 1). The modeled range for annual rainfall (95th percentile value) was 565–2203 mm, which is in line with the species' observed range at 600–2000 mm [6]. The modeled range for altitude (95th percentile value) was 96–878 m a.sl. Previous studies suggest that Sandalwood populations within the elevational range of 600–900 m produce the best heartwood [6]. Sandalwood has been observed to grow naturally at elevations of up to 1200 m a.s.l. [26].

Gradients of predicted habitat suitability within the species natural range in each country are shown in Figs. 2 and 3, excluding states or provinces where the species is known to be introduced. Most of the states within the species natural distribution in India are predicted to be highly suitable. In Indonesia, highly suitable habitats are mainly restricted to the East Nusa Tenggara province, in line with previous studies showing the species to be primarily found on the province's three main islands of Timor, Flores and Sumba [5]. Land suitability analysis shows that the islands'

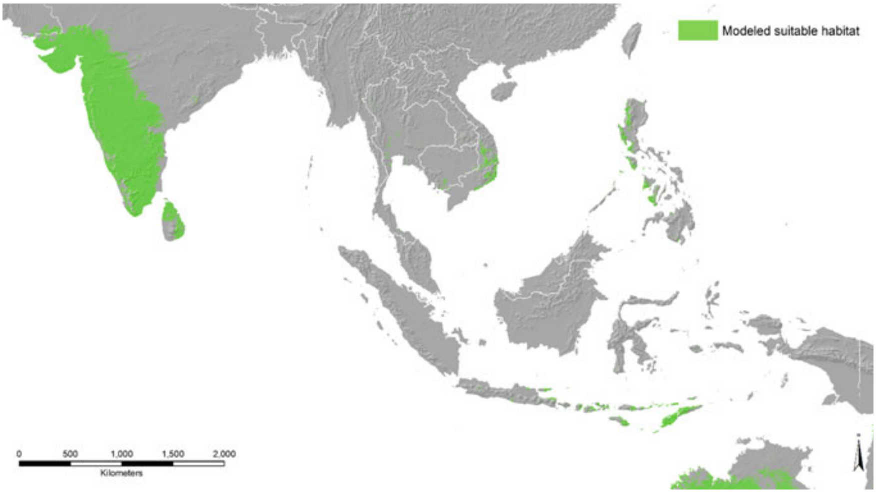

Fig. 1 Modeled suitable habitat of Sandalwood (*S. album*) in the Indomalayan biogeographic realm under current climatic conditions

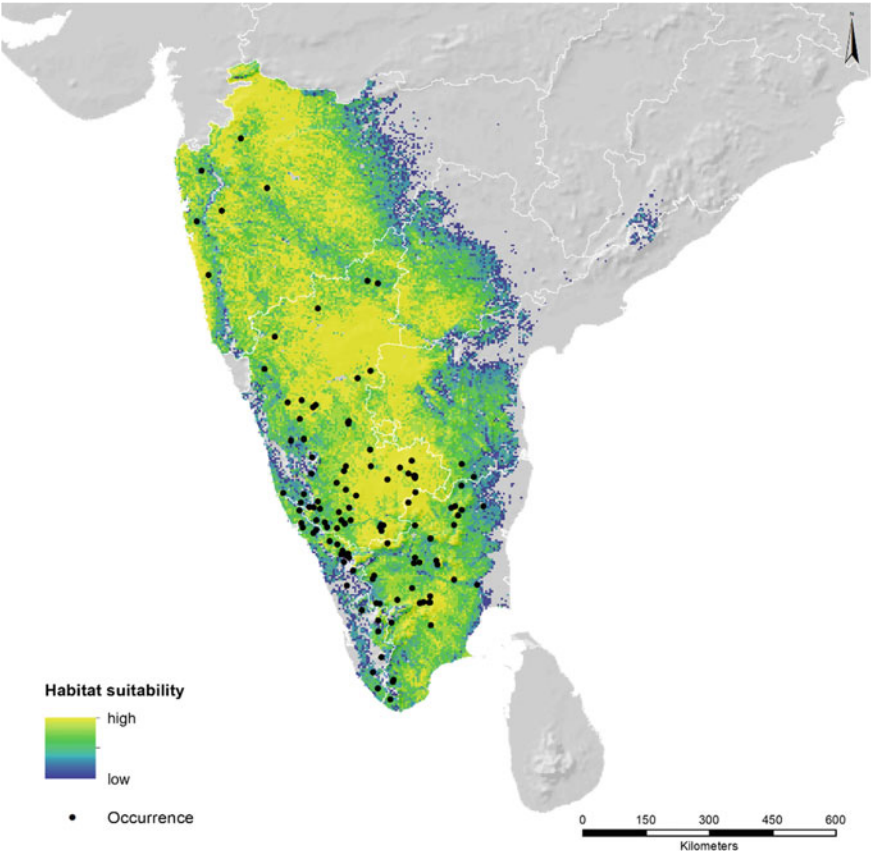

Fig. 2 Modeled suitable habitat of Sandalwood within its natural range in India

ecological conditions are highly suitable for Sandalwood growth, with nearly 90% of the assessed area on Sumba island falling in the highest suitability class [27].

Suitable habitat does not necessarily indicate species occurrence, which is often more limited due to barriers to species distribution, biotic factors such as species competition and human impacts. Based on field studies, Sandalwood forests in India are estimated to be concentrated in Karnataka, covering an area of approximately 5245 km^2, and in Tamil Nadu, of approximately 3045 km^2. The rest of the states within the species natural range, including Kerala, Andhra Pradesh and Maharastra, account for less than 300 km^2 of Sandalwood forests [26]. As a hemi-root parasite, Sandalwood relies on host plants for water and nutrients, especially nitrogenous compounds [28], and host associations may play an important role in determining the species distribution. Initially, a primary host with a life span of 1–2 years is preferable. Secondary host associations are much more successful with certain species and incline towards nitrogen-fixing species [29], although Sandalwood has been recorded to parasitize over 300 plant species [30].

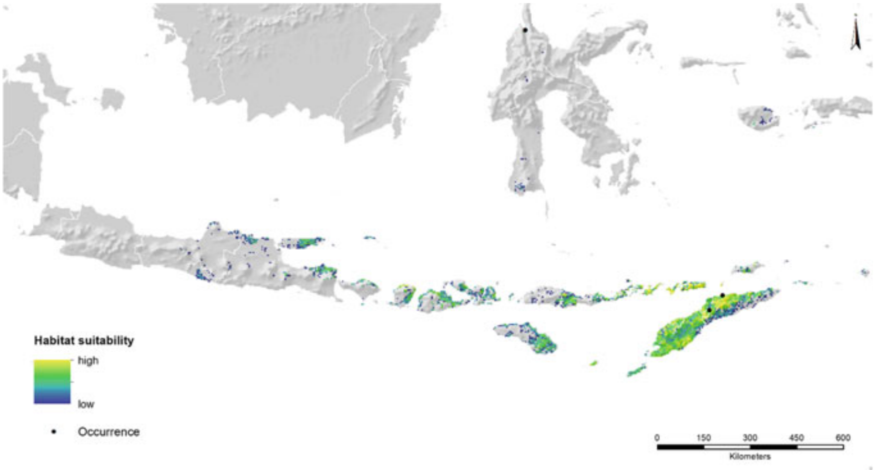

Fig. 3 Modeled suitable habitat of Sandalwood within its natural range in Indonesia and Timor-Leste

Cultivation may extend this socio-economically important species well beyond the suitable habitats predicted based on natural populations only. In India, legal barriers restricted the cultivation of Sandalwood until 2001 [31–33], but after the regulations were lifted, the species is now cultivated across the country. The state of Gujarat, which is not considered part of the species natural distribution, is predicted to be suitable habitat for Sandalwood, and large plantations exist there [31]. Sandalwood has also been planted in the Northern and North-eastern states that are not part of the species natural distribution [30].

In Indonesia, past sandalwood management policies in East Nusa Tenggara, from the Dutch colonization era until the reform era after 1998, decreed that the authorities controlled all Sandalwood trees both in the forest and on community land. People who were caught damaging the trees were harshly punished, severely discouraged by local people from planting Sandalwood [34, 35]. Awareness of the sharp decline in sandalwood's potential prompted the issuance of Governor's Instruction no. 2 of 1997 which prohibited the logging of Sandalwood. Starting from the year 2000, the official management of sandalwood became the district government's responsibility [34], and since then, many regulations and strategies have been implemented to encourage community participation in planting and managing Sandalwood in the region. Sandalwood has also been planted in other provinces of Indonesia. For example, the species was introduced in the Yogyakarta Special Region in Java as part of the rehabilitation of degraded lands since the 1970s. The area is known as the Wanagama Educational Forest and is managed by Gadjah Mada University. Ex situ conservation plots have also been developed in a nearby designated Forest Area for Specific Purposes (Kawasan Hutan Dengan Tujuan Khusus, KHDTK) in Gunung Kidul Regency since 2005. Sandalwood has shown to be able to adapt and reproduce on these plots, and some are now even known as a land race, 'Karangmojo'.

3.2 Impacts of Land Use Change

According to the modelling results, land use change has severely affected the potential distribution area of Sandalwood in India and Indonesia. More than half of the suitable habitats within the species natural range have been converted to croplands in both countries, and only a little over 2% of the remaining suitable natural habitats are found in protected areas (Table 2; Figs. 4 and 5).

Land use change has been recognized as a key threat to India's remaining natural Sandalwood populations [30, 36, 37]—but it is by far not the only one. Other identified threats to the species include fire, grazing pressures, diseases [30], invasive species, illegal harvesting [36], unsustainable extraction, fragmentation and habitat loss [37], which can accelerate the impacts of land use change on the species populations. Although lifting of the policies that restricted commercial plantations of Sandalwood until 2001 has facilitated the cultivation of the species, illegal harvesting and exploitation of natural populations has not completely ceased. Therefore, the remaining natural populations' conservation status is likely more severe than indicated by land use change only. Genetic studies showed that despite multiple threats, Sandalwood populations' observed heterozygosity in Peninsular India remained relatively high, averaging at 31%. However, it correlated positively with population density [37], indicating a risk of genetic erosion with population decline.

In Indonesia, too, the presence of Sandalwood within its natural distribution in East Nusa Tenggara has been rapidly decreasing. A recent study found the species' natural habitat in East Nusa Tenggara to be sporadically distributed in nine districts, i.e. Kupang, Timor Tengah Selatan, Timor Tengah Utara, Belu, West Sumba, East Sumba, Manggarai, Alor and Solor [27]. Sandalwood populations in Timor Tengah Utara had decreased by 99% from 1997 to 2006 and 79% in Timor Tengah Selatan district from 1997 to 2010 [7]. Purwiastuti et al. [8] detected declining genetic diversity in a seed production area within the species' natural range (He = 0.1329–0.1800). In

Table 2 Suitable habitat of Sandalwood across land use types within its natural distribution area in India, Indonesia and Timor-Leste

Suitable habitat	India km^2 (%)	Indonesia km^2 (%)	Timor-Leste km^2 (%)	Total km^2 (%)
Area converted to croplands	502,667 (79.4)	19,316 (59.5)	5057 (55.6)	527,041 (78.1)
Area remaining as natural habitats (not converted), outside of protected areas	116,958 (18.5)	12,402 (38.2)	3770 (41.4)	133,130 (19.7)
Area remaining as natural habitats, within protected areas	13,446 (2.1)	732 (2.3)	273 (3.0)	14,452 (2.1)
Total distribution area	633,071 *(93.8)	32,450 *(4.8)	9101 *(1.3)	674,622

The area calculations are estimates based on modeled natural distribution at a spatial resolution of 2.5 arc minutes (ca. 4.5 km at the equator) across land use types

* (% of total distribution area)

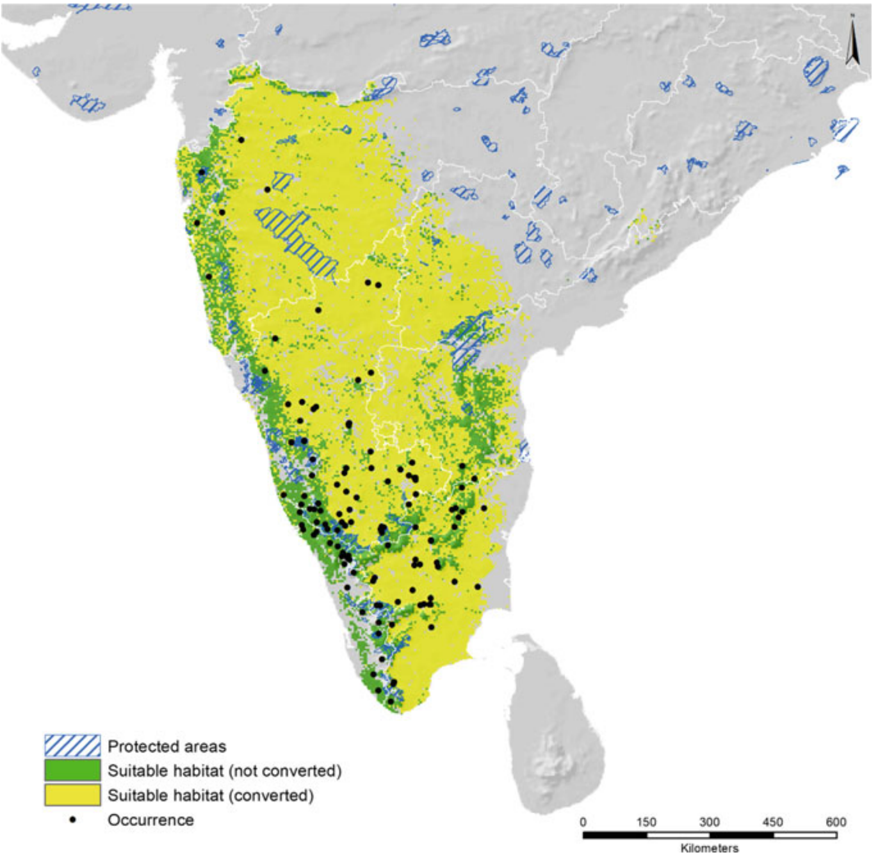

Fig. 4 Land cover change within the natural distribution of Sandalwood in India

addition to land use change, the main causes of Sandalwood decline in Indonesia are overharvesting, degradation of secondary forests as the species' natural habitats and forest and land fires [7]. Overharvesting includes digging up Sandalwood stumps and roots. This hinders natural regeneration which often happens through root suckers. The previous government policies in East Nusa Tenggara also contributed to the decline of Sandalwood populations over the years, as they limited the participation of local people in sustaining and cultivating the species [38]. A recent study in a seed production area in East Nusa Tenggara showed declining genetic diversity [8].

Although Sandalwood has been widely planted in India and to a lesser extent in Indonesia, the genetic diversity of planted populations does not necessarily represent natural populations' diversity. Conversion rates, therefore, imply a loss of diversity and the urgency of surveying and conserving remaining natural populations of the species in ecoregions that have been largely converted to non-forest lands. Given the small size and fragmented nature of remaining suitable natural habitats in East Nusa Tenggara, Sandalwood's genetic diversity is of particular concern. Clonal production

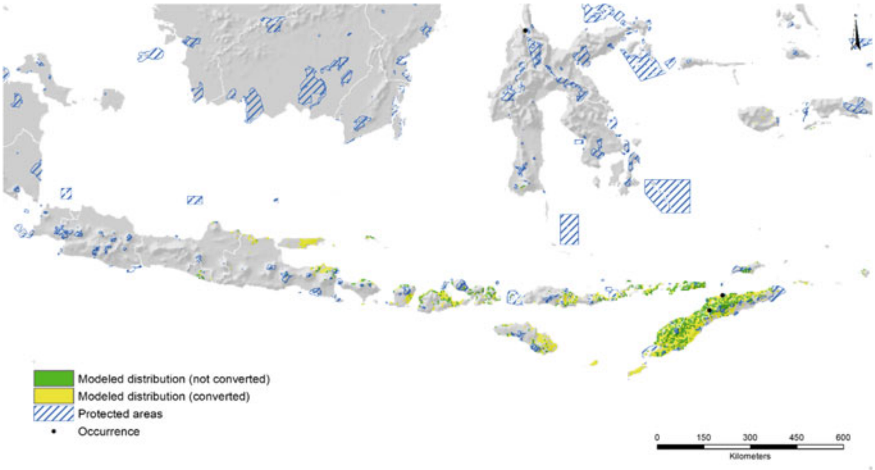

Fig. 5 Land cover change within the natural distribution of Sandalwood in Indonesia and Timor-Leste

through root suckers has been shown to prevail in fragmented or isolated habitats, resulting in inbreeding depression and sexual reproductive failure [39].

3.3 Climate Change

The distribution models indicate that Sandalwood would not be adversely affected by climate change in the coming decades (Figs. 6 and 7). More than 99% of the species' current potential distribution in the studied countries was also predicted to remain suitable in 2050. With the changing climate, new areas are also predicted to become suitable habitats for the species by 2050, especially in Andhra Pradesh, Maharashtra, Madhya Pradesh and Rajasthan in India (Fig. 6) and in Java in Indonesia (Fig. 7). Nevertheless, climate change could indirectly still affect Sandalwood, for example, through its impacts on pests, pathogens or fire frequency. Potential negative impacts of climate change on preferred host species could also increase Sandalwood's vulnerability. Priority areas for Sandalwood conservation should be identified by considering areas that are suitable for a range of preferred hosts under both current and future climate conditions. Further studies applying distribution modelling for both Sandalwood and its preferred hosts can support conservation planning and require additional information on host preferences across ecosystem types within Sandalwood's current distribution range and host traits associated with climate vulnerability.

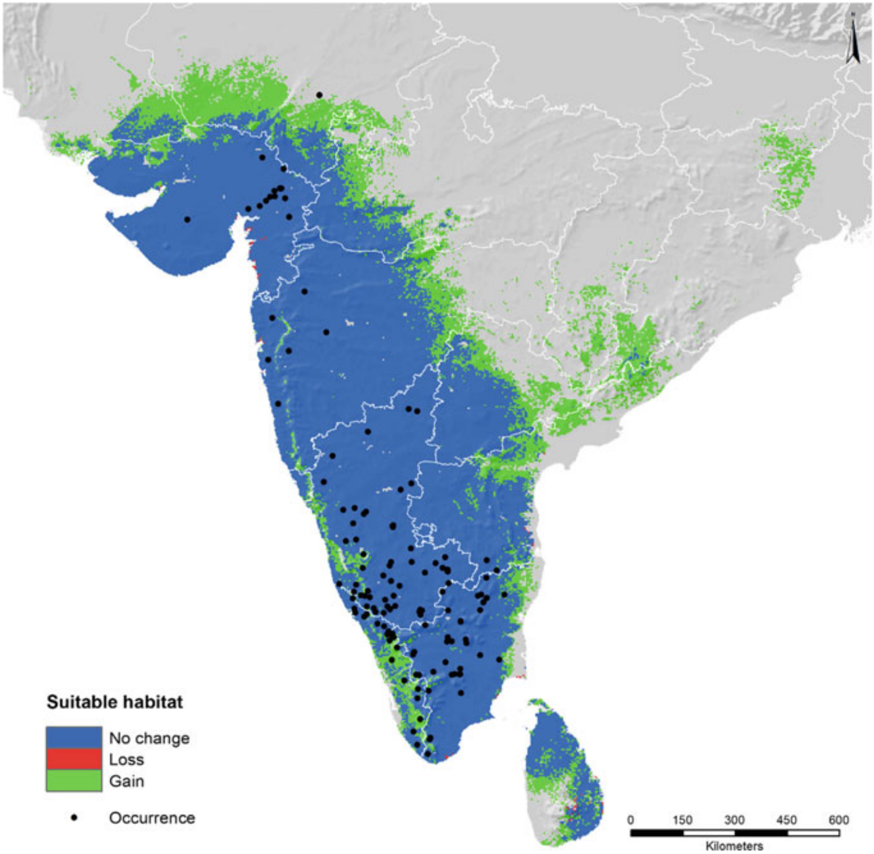

Fig. 6 Impact of climate change on the potential distribution of Sandalwood in India by 2050 (including areas both within and outside of the species natural distribution in the country)

3.4 Conservation Status by Ecoregion

Sandalwood is predicted to occur in 11 ecoregions across India's natural range (Fig. 8a) and in nine ecoregions in Indonesia. However, in Indonesia, the predicted distribution is minimal in most ecoregions (Fig. 9a). Land conversion impacts on suitable habitats vary widely between ecoregions, with less than 10% of suitable habitats remaining in some ecoregions (Table 3, Figs. 8b and 9b). Analysis by ecoregion demonstrates how conservation status considered only at species level may not accurately reflect the species genetic resources conservation status that ultimately determines the species' capacity to adapt, survive and thrive.

In India, East Deccan dry-evergreen forests in Andhra Pradesh and Tamil Nadu and South Deccan dry deciduous forests in Tamil Nadu were identified as a high priority for the conservation of Sandalwood due to the lack of protected areas and the few

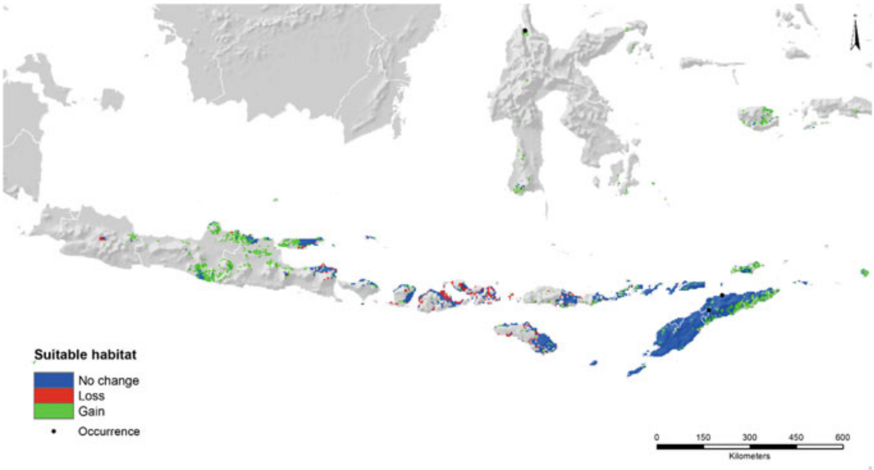

Fig. 7 Impact of climate change on the potential distribution of Sandalwood in Indonesia and Timor-Leste by 2050 (including areas both within and outside of the species natural distribution)

remaining natural habitats for the species (Table 3). Previous studies have identified East Deccan populations to have lower observed heterozygosity than populations in Central Deccan Plateau and the Western Ghats and be more genetically distinct [37], underlining their conservation value. South Deccan Plateau dry deciduous forests have been identified as diversity hotspots in previous studies [40, 41] and suggested as targets for in situ conservation of Sandalwood genetic resources. In Indonesia, the remaining natural populations of Sandalwood are mainly restricted to a minimal area in Lesser Sundas deciduous forests and Timor and Wetar deciduous forests ecoregions in East Nusa Tenggara province, where they are severely threatened by land use change and other threats, as previously discussed.

3.5 *The way forward: recommendations for conservation and sustainable management*

3.5.1 India

Potential conservation sites for Sandalwood in the most threatened ecoregion of East Deccan dry evergreen forests include the Forest Circle of Guntur in Andhra Pradesh and the Forest Circle of Trichy in Tamil Nadu, where some of the ecoregion's last natural habitats of the species are predicted to occur. Sandalwood populations were also predicted in Medicinal Plant Conservation Areas (MPCA) in both the East Deccan and the second priority ecoregion of South Deccan dry deciduous forests in Tamil Nadu. MPCAs are under the protection and management of State Forest Departments, and many have been extensively studied. These forest areas

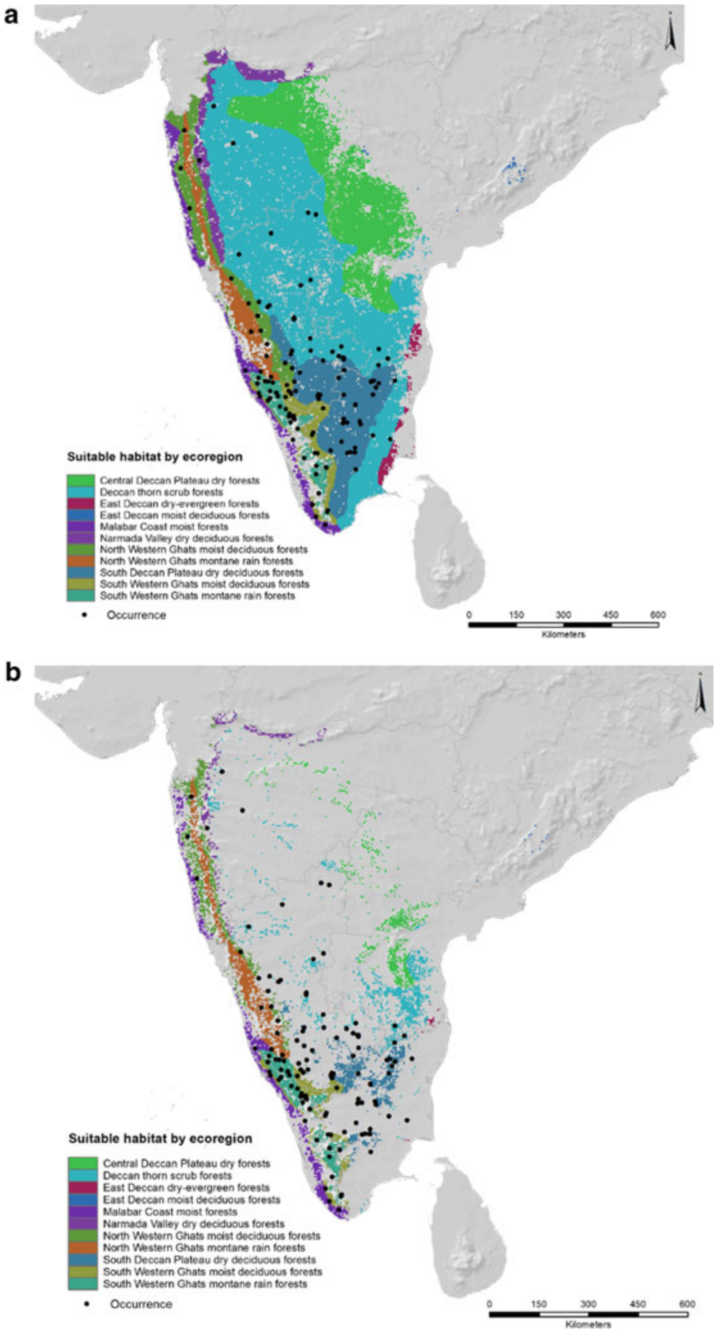

Fig. 8 Impact of land cover change on the potential distribution of Sandalwood within its natural range in India. **a** Potential distribution by ecoregion and **b** remaining natural habitat by ecoregion

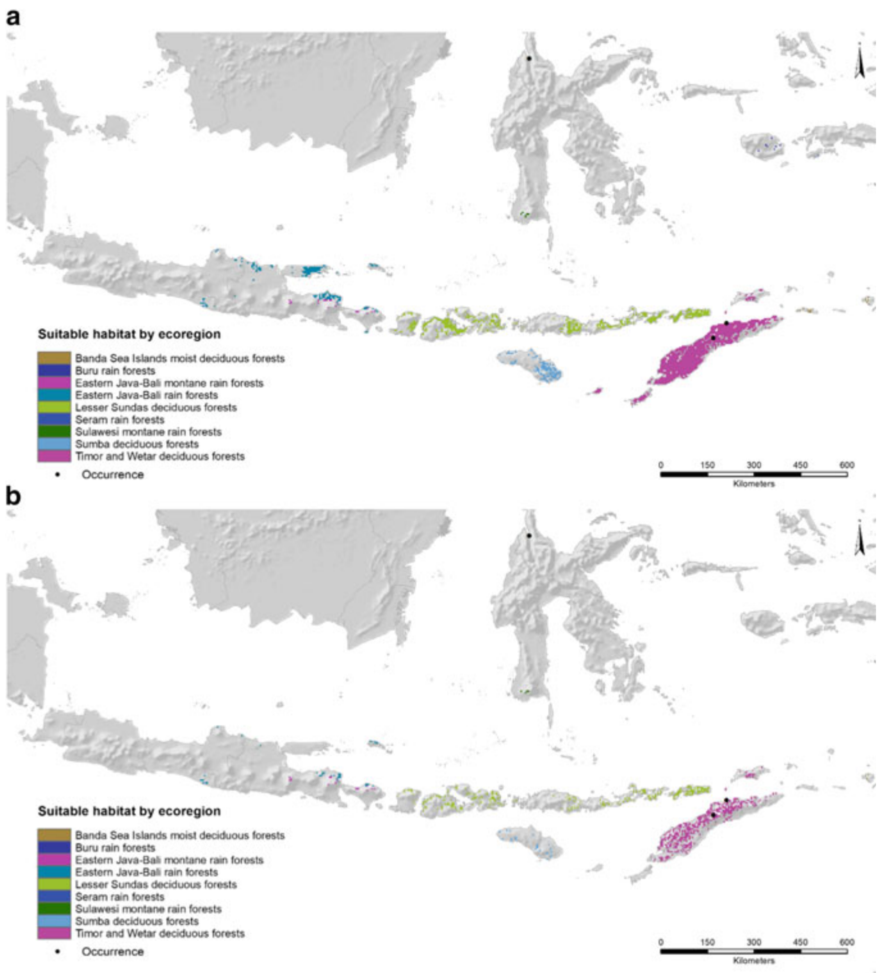

Fig. 9 Impact of land cover change on the potential distribution of Sandalwood within its natural range in Indonesia and Timor-Leste. **a** Potential distribution by ecoregion and **b** remaining natural habitat by ecoregion

should be surveyed for identifying remaining natural populations of Sandalwood and subsequently conserved.

Coordinated genetic diversity studies should be carried out in the remaining natural populations to identify priority sites for genetic conservation. Such studies will also help assess the extent of genetic erosion and the need for enhancing diversity in declining populations, for example, through fostering natural regeneration or enrichment planting. Reserves harbouring high or unique genetic diversity could be formally declared as genetic conservation units for the species. Forests with a good stocking of Sandalwood are already notified as ‘Sandal Reserves’ by State

Table 3 Impacts of land conversion and climate change on the distribution of Sandalwood in selected ecoregions

Country	Ecoregion name	Area remaining as natural habitat km^2 (%)	Area remaining as natural habitat also in 2050 km^2 (%)	Area protected km^2 (%)
India	Central Deccan Plateau dry deciduous forests	13,163 (11.3)	13,163 (11.3)	4931 (4.2)
India	Deccan thorn scrub forests	22,846 (7.7)	22,824 (7.7)	11,420 (3.8)
India	East Deccan dry-evergreen forests	441 (6.8)	441 (6.8)	4 (0.1)
India	Malabar Coast moist forests	14,235 (74.6)	14,235 (74.6)	268 (1.4)
India	Narmada Valley dry deciduous forests	5605 (25.8)	5605 (25.8)	370 (1.7)
India	North Western Ghats moist deciduous forests	15,765 (46.2)	15,765 (46.2)	755 (2.2)
India	North Western Ghats montane rain forests	18,176 (77.2)	18,176 (77.2)	2804 (11.9)
India	South Deccan Plateau dry deciduous forests	15,184 (19.3)	15,184 (19.3)	1186 (1.5)
India	South Western Ghats moist deciduous forests	10,872 (56.4)	10,872 (56.4)	3735 (19.4)
India	South Western Ghats montane rain forests	13,845 (91.7)	13,845 (91.7)	1902 (12.6)
Indonesia	Lesser Sundas deciduous forests	5,645 (50.8)	4,268 (38.4)	578 (5.2)
Indonesia	Timor and Wetar deciduous forests	5722 (41.4)	5706 (41.3)	291 (2.1)
Timor-Leste	Timor and Wetar deciduous forests	4033 (44.4)	4033 (44.4)	612 (6.7)

The area calculations are estimates based on modeled natural distribution at a spatial resolution of 2.5 arc minutes (ca. 4.5 km at the equator) across land use types

Forest Departments. One example of such reserves is the Marayoor Sandal Reserve in Kerala, which is considered genetically superior for the high oil content of the trees [42]. Profuse natural regeneration in most of the reserves has improved the density of stocks [26].

Landscape connectivity and local livelihood options are important considerations in establishing new protected areas, as in situ conservation involve restrictions to access and use of forest resources and may increase human–wildlife conflicts. Context-specific management approaches need to be identified in each area in consultation with other land users and stakeholders. One approach for conserving the species in MPCAs in the target ecoregions could be to designate the areas as Community Reserves or Conservation Reserves which offer opportunities for integrating conservation and livelihood activities.

Ex situ conservation can importantly complement *in situ* conservation of Sandalwood in India, especially given the pressures on the species from land use change. The main constraints for *ex situ* conservation are the lack of suitable land outside natural habitats, lack of funding, limited capacities and facilities. Both the conservation of natural seed sources and ex situ conservation can also support planting efforts and associated livelihood benefits from the species, which in turn can reduce pressure on the remaining natural populations. The liberalization of rules on Sandalwood cultivation in 2001 and 2002 has facilitated plantation establishment, but the long life cycle of the species and the high establishment costs continue to pose a hurdle for popularizing the domestication of the species [36].

3.5.2 Indonesia

The viability and genetic diversity of the shrinking natural populations of Sandalwood in East Nusa Tenggara are of serious concern, and a combination of strategies is needed to save the species from local extinction. A comprehensive population and genetic inventory of the remaining Sandalwood populations is needed within its natural distribution, especially on the four main islands of Timor, Sumba, Alor and Flores, as a basis for species management and conservation plans [5, 27]. Routine surveys already conducted by the East Nusa Tenggara Provincial Forestry Service provide valuable information on the number of Sandalwood trees. In addition, a previous project on Sandalwood resources management in East Nusa Tenggara (2009–2012), funded by the International Tropical Timber Organization, generated information on the remaining populations and the local management capacities [43]. The project's findings can be revisited as a basis for updated species management plans within and outside of protected areas.

Overharvesting is expected to have significantly reduced the genetic diversity of the remaining natural populations [8]. Genetic diversity of Sandalwood in ex situ conservation plots outside East Nusa Tenggara showed high expected heterozygosity as an indication of genetic diversity in KHDTK Gunung Kidul (He = 0.391) [44] and in natural regeneration in the Wanagama Forest (He = 0.333) [45]. The results indicate that when genetic material was collected for establishing these plots, the genetic diversity of natural populations was still high and that the collections were carried out using the good practice to maximize diversity. To restore the genetic diversity of natural Sandalwood populations, genetic material from the populations in Java should be returned to East Nusa Tenggara [39]. In addition, the ex situ plots confirmed to harbour high genetic diversity could be formally declared as genetic conservation units for the species, and be used as seed sources for establishing new, genetically diverse populations.

Many regulations and strategies have been implemented to encourage community participation in managing and planting Sandalwood in East Nusa Tenggara since the early 2000s, and they are yielding results. Studies show that local people are supportive of regulations regarding Sandalwood [46]. A study of community participation on Sumba island found that 30% of respondents involved in the management of community forests, family forests or home gardens had independently conserved Sandalwood [47]. Sandalwood conservation programmes targeting families and students (Gerakan Cendana Keluarga and Gerakan Cendana Pelajar) which aim at enhancing Sandalwood resources through the establishment of planted, community-managed forests have increased public awareness, to the extent that it is relatively easy to again find Sandalwood trees in East Nusa Tenggara [35].

The analysis of land suitability classes for Sandalwood [27] should be expanded to the islands of Timor, Alor and Flores, to support more effective and efficient Sandalwood development in the region. Seran et al. [48] recommended structural modelling of Sandalwood regeneration to help guide Sandalwood development in forestry and plantation management. However, wider planting of the species continues to be also constrained by socio-economic issues such as the lack of land, risk of illegal harvesting, and, above all, limited species trade, which is beyond the control of the Regional Government of the East Nusa Tenggara Province. Collaboration between regional and national governments and public and private sectors is needed to help restore East Nusa Tenggara as a Sandalwood province by 2030, as envisioned in the regional Master Plan of Sandalwood development and conservation [49].

4 Conclusions

The remaining natural populations of Sandalwood continue to be threatened by land conversion, habitat fragmentation and genetic erosion. Conservation and sustainable management of the species in the different countries within its natural distribution would benefit from the enhanced exchange of information about the species population dynamics and genetic diversity, species ecology, the impacts of conservation and management strategies on the species and propagation techniques, among others. Moreover, exchanging genetic material and establishing multicountry provenance trials to identify suitable planting material for diverse environmental contexts would also be useful. Both India and Indonesia are working on conservation of the species (Table 4). They are members of the Asia Pacific Forest Genetic Resources Programme

Table 4 Topics of Sandalwood research and development and examples of involved organizations in India and Indonesia

Research area	Involved organizations in India	Involved organizations in Indonesia
• Microbiology • Molecular genetics • Reproduction biology • Diversity mapping • Population structure analysis • Vegetative propagation including tissue culture • Factors affecting heartwood formation • Chemistry (oil content test) • Silviculture • Pest and disease management • Establishment and evaluation of Seedling Seed Orchards • Development of ex situ conservation plots • Social economy	• Indian Council of Forestry Research and Education • Kerala Forest Research Institute • Centre for Plant Molecular Biology • National Botanical Research Institute	• Forest Research and Development Center • Center for Forest Biotechnology and Tree Improvement • Kupang Forest Research Institute • Other research institutes under the Ministry of Environment and Forestry • Gadjah Mada University • Brawijaya University • Timor University • Cendana University • Private sector and non-governmental Organizations

(APFORGEN) which offers collaboration opportunities in terms of studying the species' genetic diversity and identifying conservation priorities and synergies.

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Chapter 33
Need for Geographical Information System Enabled Conversational Assistant Driven by Artificial Intelligence for Sandalwood Cultivation Support to Indian Farmer

G. S. Pujar, S. P. Reddy, and T. Ravisankar

1 Introduction

Indian farmers, looking forward to grow Sandalwood as a reliable venture after the policy revisions, need to be provided best information support, so that sustainable livelihoods are realized. Sandalwood being such a valuable species fetching high value certainly has potential for doubling farm income. New era of farm policies, as part of 'Atmanirbhar Abhiyaan', revamping support to production and marketing in truly transparent manner, enables both the producer and consumer, in turn attracting investments in high-value farming. Sandalwood being a suitable tree crop for substantial geographic regimes, especially in the arid and semi-arid zones, would certainly stand out as preferred choice as alternate land use.

The current discussion is about need and scope to develop an interactive virtual communication assistant, as a customized artificial intelligence (AI) application for communicating with the farmer, as a natural language interface in the long run and conveying the right prescription for taking up Sandalwood cultivation as well as offering assistance to him through the seedling to marketing stages, with adapted hand-holding process. The assistant may be optionally termed as 'Chandan Mitra' or Friend (Mitra) of Sandalwood (Chandan), serving the purpose of helping farmer all along.

At each critical juncture of crop growth, apt information needs to be conveyed for the best benefit of the cultivator. The farmer can communicate to a handheld digital

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assistant to learn and understand about the potential of taking up the cultivation with respect to the capability of the farm, interventions required and expected benefits at that given context. It will achieve substantial resource saving for the farmer as well as for the promoting institutions, in terms of initiating the farmer into this activity. Spatial information-based decision envelopes suitably incorporated would help to point priority areas beforehand, to provide a tentative prioritization of different regions. Specific queries can be addressed either online or offline, depending upon the complexity of the information sought. While this tool can act as an aggregator of information on the willingness and site suitability, it can scale up into handholding and step-by-step advisory mechanism to support the new incumbent through the microlevel details essential.

2 Sandalwood Cultivation Information Structure

Generally, a farmer's workflow to pick an alternate cultivation practice may choose to address major actions when he starts interacting with an information source and learning about the newer alternative. Arrangement of finance follows this learning, to develop into a cultivation practice, finally leading to the harvest of the produce (Fig. 1). At the end of the cycle, the farmer would have developed skills essential to replicating the practice in space and time, till enough confidence is gained to impart skill to others. Tradeoff for a farmer to choose from a new practice or to continue with the conventional, easy-to-manage practices can be very intriguing at small or marginal farmer level given the thin resources at his disposal. The stages presented above can be convincing for a farmer if the best possible advisory on the innovative farming alternatives is rendered to him. The information system proposed needs to consider this kind of uncertainty in the information level and the present hand-holding process intended in the proposed tool.

A detailed approach for the cultivation of a tree crop would go through the design of information support for the cultivator's decision-making, supported by expertise built using diverse sources of information available. Sensitization of the farmer to the precise need of the cultivation practice would serve the interested individual seeking the information well. A small questionnaire, either as natural language interaction or feedback format, with optimized alternatives, would help build a brief dossier about the individual requirement and develop the right insights into the need assessment. Such an initial survey would help to find the true pockets of interest in the region. Followed by this, a requirement framework needs to be furnished, which will cover the aspects such as finance available or required, crop feasibility in a given geography, site quality, and regional traits that facilitate long-term sandalwood cultivation. Detailing the trends that may coincide with the crop's maturity to price boom and bust cycle should also be advised.

Establishment of the crop phase needs to address advisory on-site preparation, quality, availability of the host plant, planting process per se, protecting the site against impending threats by animals and naturally calamitous events such as gale,

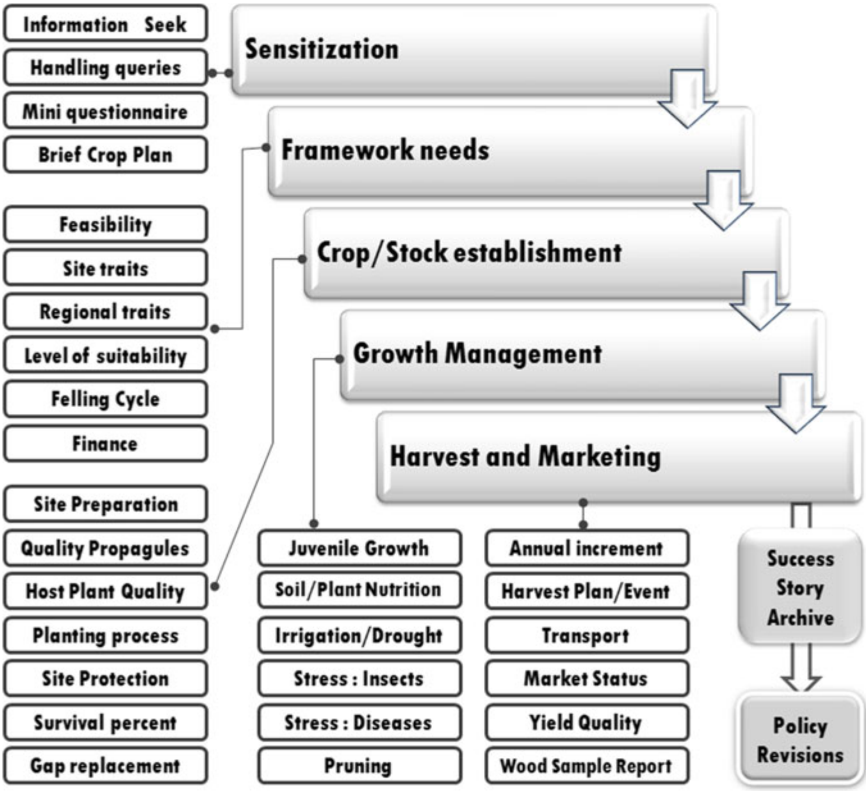

Fig. 1 Process intended for sandalwood conversation assistant design: possible components

drought, flood, fire, insect swarms, etc. Survival percent forms a critical outcome of the planting event, determining the gaps that may occur and compensating for them through replanting effort. The sandalwood seedling's genetic stock has to be advised with a high degree of precision, advising in a meaningful manner about the propagules' types and their sensitivity to site and silvicultural practices. Managing the growth of the establishing crop in terms of irrigation requirements, juvenile growth, vulnerability for insects and pests, and drought need to be served to the initiated cultivator in time. Specificities of the cultivation given the site and climate conditions in light of rainfall variability, soil nutrition levels need to be customized to the farmer requirement. Spatial datasets regarding land cover, land use and soil quality followed by the inclusion of long-term climate datasets measured and modelled are required to arrive at decision support. Apart from this, pruning advisory also has to be furnished from time to time. Harvesting and marketing of the grown produce is a critical part in consummating the valuable efforts placed in terms of gestation period and inputs invested.

Monitoring the proper timber volume or biomass of the crop that has reached maturity after 12–15 years of growth is a key criterion to determine the harvest. The quality of the yield accrued from the entire period of growth determines the market value and profitability. Grading the stock before being harvested using key indicators of the growth, such as diameter and height or related traits, including the wood sample assessment reports, is essential. The harvest is transported to the destination, and the safety until it reaches the storage is to be carefully tracked. The market status as influenced by price fluctuations needs to be continuously monitored for achieving the best price for the producer. Though sandalwood is likely to have the least collapse of the prices, minor fluctuations may impact small and medium-sized farmers' prospects.

For each action, the Artificial Intelligence (AI) application needs to analyse the prevalent situation, access the datasets and provide the appropriate answer(s). Towards this, datasets can either be rule based or oriented to machine learning. Rule-sets can stem from regression trees having bifurcation events for many dichotomous decisions, finally leading to a most suitable alternative. Alternatively, neural network-based nonparametric rules may be prepared considering many combinations of rules, with either forward or backward virtual neurons training. Rule-based decisions may rely on a few sets of rules involving weighted multilayered composites of spatial or non-spatial information.

3 Geoinformation and Promotion of Sandalwood Production

3.1 Spatial Spread

The spread of a biological resource and likely places where it can prevail has been dealt with using diverse approaches using remote sensing and GIS. The detection can be based on distinguishing spectral signatures, provided such response of the species exists or can be based on the species' association properties or composition in question. Spectral responses have variability temporal and spatially [3] and may provide distinction within a defined period. Phenological characterization of vegetation systems using high temporal remote sensing sensors such AWIFS or MODIS provides insights into temporal dynamics of habitat or a forest composition, though they may not distinguish the species per se itself due to the coarse spatial resolution. The status of habitat determines the level of productivity of the site. However, the advent of high-resolution sensors such as Cartosat –2S/3S or every day with 3.0 m resolution multispectral sensors from dove satellites of Planetlab can offer site specific high temporal high spatial context for assessing the forest cover/composition at far better details than earlier, at least for site-specific purposes. Apart from this, very high spatial resolution sensors (about 25 cm spatial colour resolution) also provide a fair level of background imagery to pinpoint the great structural detail of the habitats being explored. Detection of individual species may not be possible in such images unless the individual trees are in bloom or have characteristic leaf chemistry, making them stand out distinctly.

The advent of unmanned aerial systems (UAS) comprising of autonomous to semi-autonomous aerial vehicles has a high degree of relevance for mapping a valuable crop of this nature. UAS comprising compact Light detection and Ranging (LIDAR) sensors can be used in tandem with satellite data for planning the observation for precision structural parameterization of the crop in various stages of growth [8]. Laser scanning of the crop can be accomplished to derive the fine scale structure of the canopy. The biophysical status of the crop assessed through multispectral data integrated with high-resolution digital surface model (submeter to the centimetre) derived from photogrammetric steps or laser returns will help understand the enterprise's success. Site-level variations for medium- to large-sized plantations need to be observed, measured and understood to take up mid-course corrections for the silviculture practices adopted if required.

Using geospatial information for assessing the spread of a species is accomplished by way of sampling, using a certain level of available a priori content, implemented through field surveys. Such an approach requires substantial investment in field inventories using experts to start with since positioning technologies require enough training and caution to collect an error-free geolocation, considering the availability of GPS satellite signals in a forested region. The advent of mobile application-based inventories has brought a new edge in inventorying tree resources growing either in the forest or cultivated landscape. Currently available national datasets on species specific resources generally indicate sampled spread of species.

Prediction of species habitat using rulesets involving geographic information and satellite-derived information on land cover reflectance, meteorological parameters and the terrain is another approach to understanding the spread of species. Ruleset predictions using Genetic algorithms (GARP), ensemble models and machine learning have evolved to express the degree of relation between the realized niche and fundamental niche of the species in question. It essentially involves building statistical or advanced nonparametric relations between measured locations of species prevalence to biophysical parameterization using reflectance in the multispectral domain, known meteorological context and the terrain-induced variations at a local or regional scale. Such relations expressed as probabilities will indicate species habitats' contours for exploring species propagation expansion, hence, setting up management priorities in a long-term perspective. Web-based information systems on biological diversity such as the Indian Bioresource Information System (IBIN) also serve datasets based on intense field taxonomic inventory, which can understand regional patterns.

In the context of Sandalwood, it is important to use a combination of these approaches to understand the actual and potential habitat to prioritize the efforts of promotion. Unless a habitat is bioclimatically suitable for producing the species inclusive of its derivative, be it wood or alkaloid, it may not be worthy of investment. Sandalwood may perform weakly in producing the heartwood with enough oil quantity and quality, across various geographies, in possible similarity to sister species, it is important to convey to the enterprising stakeholders regarding this uncertainty in higher clarity.

3.2 Assessment of Planted and Natural Stock

Sandalwood cultivation post 2001 policy revision has been witnessing enhanced stock as part of the farming scenario. On the other hand, the edge of dry deciduous forest tracts, especially the thorn forests and the Eastern fringe systems of Western Ghats, is the original habitat of Sandalwood. An appropriate combination of remote sensing and mobile application can be set up to assess sandalwood's stock in forests and cultivated landscapes. Using state-of-the-art remote sensing imagery of suitable resolution and costing (preferably PAN-sharpened LISS-IV multispectral or Sentinel open-source data sets as alone or in combination) can be employed to stratify the area for forest composition strata. Existing forest delineation can be employed to reduce the search area for approximate spectral envelope corresponding to dry forests. Mapping carried out with the best possible accuracy can be field verified in samples to produce the desirable database. This can be sampled appropriately and inventoried using the mobile app.

In any wood-based enterprise, it is critical to realize the boom and bust cycle of pricing and adopt the policy of staggering stock development so that farmers will not face the uncertainty of glut. Similar cases in the pulpwood market related to species such as subabul, casuarina, eucalyptus and plywood species of Poplar have repeatedly illustrated the need for regional level stock modelling with proper consideration. A multiscale model is essential to simulate sandalwood cultivation's productivity dynamics and wild land growth needs to be thought of for bringing out the hotspots of yield. Given the varied sensors and datasets that can enable such modelling using a machine learning approach, it is apt to initiate such a process and gradually link dynamic and distributed bioeconomy intelligence collection mechanisms such as the conversational assistant tool discussed here.

Sandalwood with its weakened genetic stocks in wild areas due to unplanned exploitation yesteryears, the threat of illegal extraction, the vulnerability of critical growth stages to pests and diseases such as Spike disease, as well as lack of empathetic regulatory mechanism for cultivators [12, 16, 22]. Sandalwood cultivation faces a special risk of being a very sensitive enterprise. However, a range of stakeholders' surging interest provides sufficient scope to devise measures to mitigate risks using either technology or social moderation. The latest practices of RFID-based precision farming [20] witnessed sporadically is a distinct example of high valuation it has received.

3.3 Site Suitability

Envelopes of suitability at regional level are required for understanding the likely places of promotion of a tree crop, due to its specifics of site requirements along with the climatic envelopes. Geographic Information System (GIS) provides wide scope in eliminating geographic envelopes that may be already under more productive use or may never sustain a targeted land use [9] such as growing Sandalwood. Though bringing in site suitability is similar to species prediction at certain level, it differs at employing only statistical relations with existing a priori information for suggesting new areas of manifestation. Typical GIS based approach would be focusing on different layers of decision-making that will enable multithematic characterization of a landscape to delineate desirable areas. Decision layers such as land use and land cover, soil types, drainage, elevation range, slope, aspect, erosion status/degradation, climate gradients, ground water prospects, geomorphology, can be integrated using a GIS tool to execute a ruleset that suits the cultivation of Sandalwood. Proximity to prevailing sandalwood plantations or any other similar forestry or even woody horticulture ventures can be a good factor in suggesting the potential of new ventures. However, a clear ruleset for silvicultural practices and requirements needs to be brainstormed before deciding the GIS-based prioritization as alternate prescriptions may emerge depending upon the newer information that will flow from latest research and field feedbacks. Site suitability of East Indian sandalwood was conducted [21] involving soil chemistry and biophysical parameterization as per FAO procedure (1976). The analysis showed varied site suitability extents for development of sandalwood in various districts of in Timor island which ranged between 89 (Kupang City) and 2788 (Selatan) sq. km, which has high compatibility to spatial modelling.

3.4 Legacy Plantation Datasets

Under natural resource assessment initiatives, remote sensing datasets have been prepared especially through programmes of Land Use Land Cover NR Census at 1:50,000 Scale in three periods till date (2005–06, 2010–11, 2015–16), Coordinated Horticulture Assessment and MAnagement using geoiNformatics (CHAMAN), or national land cover base at 1:10,000 scale prepared under Space-Based Information System for Decentralized Planning (SIS-DP) programme are made available on ISRO Bhuvan portal for open visualization. These datasets can be accessed as part of Government collaboration initiatives for deriving key input for an information system being proposed here through a mobile application, having server computing infrastructure in the background. Land use land cover datasets are derived using multiseasonal remote sensing datasets for the target year to address the seasonality issues of crop cycles and the water surface dynamics. Delineation of horticultural crops is carried out using high resolution IRS Cartosat sharpened multispectral LISS

VI (5.6 m) images to account for non-spectral, structural features of different horticultural crops concerning their canopy nature, spacing, etc. Semi-automated object-based image analysis is adopted as a precursor delineation approach followed by intense quality evaluation before ascertaining the horticulture crop cover classification's identity. Datasets are furnished on Bhuvan portal for major crops such as Mango, Banana, Citrus, etc. Plantation component mapped under SIS-DP initiative also provides fairly strong content to understand the plantation spread across India at a scale relevant for village-level planning.

Apart from this, recent crop management-related interface refers to bioenergy potential for a given site, considering the overall bioenergy yield from a given proximity envelope. The approach involves satellite-derived parameterization of the crop spread. Such efforts would provide tools to optimize the fetch of resources to a point. These three levels of examples indicate the increasing ability of online GIS processing required for basic handling of the plant resource with the land cover situation and the analytics tools available.

3.5 Web GIS Data Sets

A wide variety of Governance initiatives are being monitored and recorded using Bhuvan employing a combination of smart phone applications and web-enabled GIS tools to render regular visualization and monitoring. Programmes such as Integrated Watershed Management programme (IWMP, currently renamed as Watershed Development Component: Pradhan Mantri Kisan Sinchayee Yojana), GIS implementation of MGNREGA (Geo-MGNREGA), Rashtriya Krishi Vikas Yojana (RKVY), Per Drop More Crop (PDMC) and related to Green development initiatives are few major national level programmes under the requests of Ministry of rural development, Agriculture and Farmer's Welfare, etc. These initiatives have built huge geotagging datasets comprising location information on various activities for developing villages, watersheds, microirrigation and agriculture infrastructure, eventually containing location details on planting efforts by rural stakeholders. Such content rendered as spatial analytics through gridded products can provide spatial intelligence on potential areas that may correspond to communities interested in cultivating plantations.

4 Artificial Intelligence (AI) Framework for Sandalwood Conversational Assistant

A conversational assistant is a computer program or an artificial intelligence tool capable of handling conversation via auditory or textual methods: https://en.wikipedia.org/wiki/Virtual_assistant that would replace the need for repetitive assistance tasks by personnel. Conversational assistants or virtual assistants are gradually adding value to personal space or economic activity domain by carrying out information provision or executing routine and repetitive tasks either by employing simple locally based ruleset on the device or exploiting online AI framework. Artificial intelligence framework in case of Sandalwood cultivation assistance arises from the following sequential premises, similar to insurance markets [6]

1. Availability of huge and diverse data on Sandalwood as well as related plantation practices
2. Need for personalized service for the interested farmer
3. Demand for genuine and authentic information to rely upon for cultivation
4. Quicker processing of existing data and information for query handling
5. A necessity for streamlined handholding/assistance to interested practitioners
6. Cost optimization by appropriate and timely information sharing, especially on markets, risks and crop management.

The ability to transform an economic enterprise by employing a conversational assistant is growing, making a fair case for applying Sandalwood farming. Farmers face the difficulty of choice due to the diversity of soil and climate conditions and geographical characteristics since they lack a single source that can provide them multithematic advice as a single window tool, which in turn necessitates a conversational assistant using natural language processing tool [18].

Artificial Intelligence (AI), Cloud Machine Learning, Satellite Imagery and advanced analytics are capable of empowering farmers to increase their income through higher crop yield and greater price control (Fig. 2). Advanced satellite imagery, extensive historical and real-time data about land composition, along with detailed weather and climate forecasts help farmers and businesses track, monitor and evaluate every identified aspect of cultivation. For instance, to calculate the crop-sowing period, historical climate data coupled with moisture indicators from space or field source such as weather stations determine the decision-making. Weather forecasting models for the area may be employed towards model building and down-scaling to build predictability so as to guide farmers to pick the ideal sowing time. Mature chatbots like Alexa, Cortana and Siri are available, which can be harnessed for providing live interaction between the farmers and the system. Further, there are open-source chatbots like Rasa, Botpress and Ana, which can be utilized to provide seamless interactivity with the system, models and domain experts.

Information cycle encompassing the service throughput of the assistant envisaged should consist of optimized capability for interacting with the farmer or related stakeholders seeking to learn or initiate the cultivation process, followed by an algorithm to convey the information through text or natural language process to the information system enabled by artificial intelligence operating on thematic content. Thematic content is the pool of comprehensive information drawn from formal sources covering conventional tree biology and economic research as well as geospatial content defining the silvicultural and resource exploration aspects of Sandalwood. AI process, which consists of collation of the data, cleaning up the data, training and testing model followed by iterative improvement of the learning done employs the

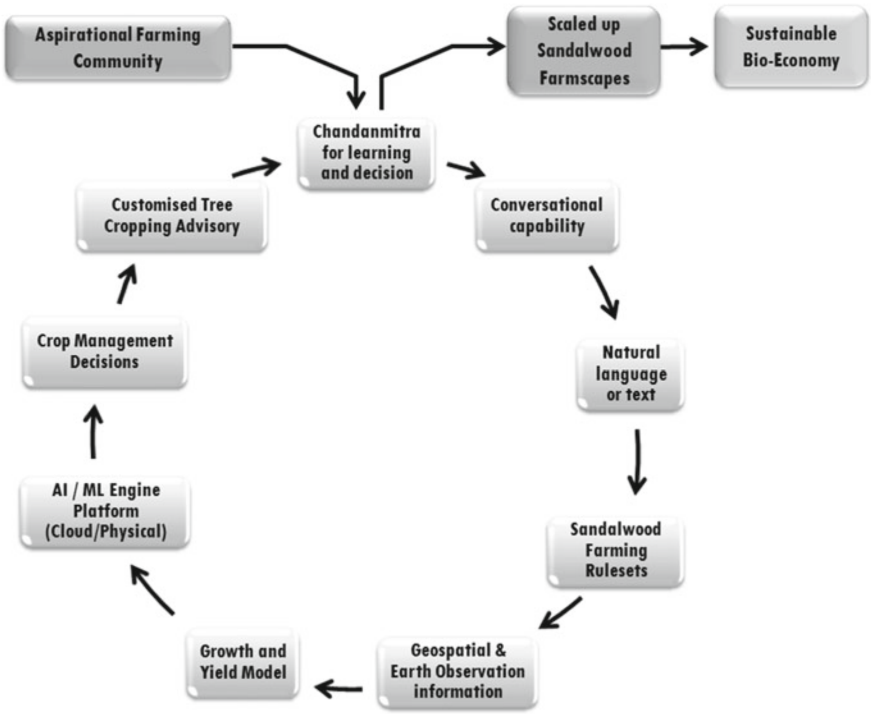

Fig. 2 Basic information cycle of virtual assistant process for sandalwood cultivation

content *vis-à-vis* queries from farmers, delivers the advisory in a customized manner. Components of establishing a framework are detailed in respect to the essentials of architecture, storage, computational needs, deliverance as well as the role of the cloud in establishing the system.

4.1 Architecture of the System

The base architecture for the intended system can be built over Spatial Database Infrastructure (SDI), or Software-Defined Data Centre (SDDC) as this approach enables to provide the most efficient and scalable cloud solutions. Such an approach should consider separating applications from their underlying infrastructure. It is generally achieved by virtualizing components of computation, networking and storage facility, followed by automating their management so as to deliver the right applications. Applications need to be delivered using the right Service-Level Agreements (SLA's) (), flexibly, safely, securely and using open standards.

Lay users and farmers should be able to interact with the chatbot or text-based interface, which would, in turn, trigger the appropriate modules running on the computer systems over the cloud. Earth Observation (EO) users should be able to discover, select and download data eventually combined with some processing services to do spatial or radiometric modifications along with collaboration. The initiative is to provide near-real-time access to data derived from EO sources or field and laboratory studies, encompassing archives, field data and derived information.

Computing resources shall be 'on-call', which is always available for processing in case of an event or demand. The most important initiative would be making the infrastructure virtual and elastic to provide capabilities of orchestration. As a beginning, the infrastructure could be a couple of servers and small storage on premises called the ground segment, which could grow over time. A ground segment should be able to seamlessly federate with the cloud infrastructure on demand in that case.

4.2 Features and Capabilities of the System Proposed.

Pilot study towards achieving this tool can be taken up addressing a limited geographic extent, having lesser complexity in terms of weather patterns and site variability. By addressing a moderately sized farming community, it may be possible to understand the needs and responses of the stakeholders. Essentially, the pilot execution of the idea can help in gauging the relevance of experiences across the globe for arriving at local advisory optimally.

Information system proposed would execute several of the processes based on the queries generated at the user end, whereas the entire gamut of data streaming into the set-up needs to be ingested into the components of AI mechanism as listed below:

- Process in-coming data in near-real-time (NRT).
- Run AI/ML models at scale.
- Run a science integration and software development cloud platform.
- Maintain shared code libraries.
- Provide access to complete data archives (based on access controls).
- Better methods for search and retrieval of archived data.
- System to register all the data sets and provide a time series.
- Provide access to services furnishing remote sensing related/geospatial data sets.
- Hosting a set of predefined processing work flows which user can deploy with appropriate data selected and submit for processing.
- Allow the users to build their own processing flow by selecting from the processing functions library for any submodule to be incorporated.

When a physical configuration is implemented (Fig. 3), it involves a cloud part and a ground segment part, which are linked through cataloguing services and a data exchange gateway. The cloud part will encompass storage in terms of a cluster as well as intermediate fashion that provision to Computing cluster functioning in tandem with the service cluster. Service cluster enables the furnishing of contents computed already. The ground segment is centred around a high-performance computing cluster, drawing strength of Graphic processing unit strength through highly scalable

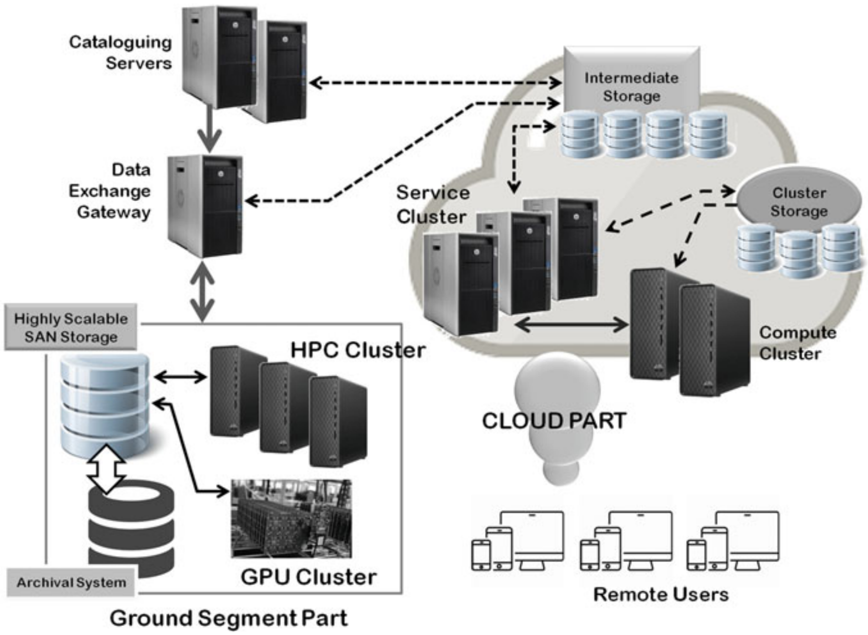

Fig. 3 Physical model of the architecture that may be optionally set up to facilitate the machine learning process of the conversational assistant planned. Remote users are the input/output interface end for the dataflow intended, which may be a desktop or handheld

SAN storage supported by Archival store. Physical provisioning has the advantages of in-house control of entire architecture design as well as a higher security component.

5 Machine Learning

AI, sometimes called machine learning, is a computer technology that simulates human intelligence through learning processes [1]. AI is a promising alternative to statistical modelling because it can efficiently handle the problems of nonlinearity and complexity. Since the performance of a tree crop or herbaceous crop is a biological process, not confirming to linear models, AI can bring in alternate solutions as a suitable prediction approach, considering the iterative learning and prediction. AI domain incorporated approaches comprising machine learning models, such as the (a) random forest (RF), (b) support vector machine (SVM) and (c) neural network models. Neural networks, in turn, ramify into an artificial neural network (ANN), convolutional neural network (CNN) and deep neural network (DNN). Artificial Neural Networks form the majority of machine learning, wherein every link (each link between the entities in the diagram below) is associated with a particular weight. Artificial Neural Networks are self-learning models that update their learning when weights for the values are updated. Upon substantial learning, a neural network will predict the result with sufficient accuracy. The multiplicity of weights and result paths are illustrated (Fig. 5), showing the prevalence of hidden layers between input and output layers. Bias and weights for each layer also determine the final output, and hidden layer units accrue weights (along with the links) along with bias (unforeseen/non-observable factor) attached to each node. Deep learning neural network is an advanced technique that facilitates the integration of advantages of traditional neural networks and machine learning models, involving a relatively higher number of layers. DNN overcomes issues related to local minima and over fitting found in ANN. CNN, one of the most popular, uses a variation of multi-layer perceptron and contains one or more convolution layers that can be either entirely connected or pooled. These layers create feature maps that record a region of image/data tile, which is ultimately broken into rectangles and sent out for nonlinear processing. Recurrent neural networks (RNN), being more complex, aim to save the output of processing nodes and feed the result back into the model (do not pass the information only in one direction) to achieve learning. Each node in the RNN model acts as a memory cell, continuing the computation and implementation of operations. If the network's prediction is incorrect, then the system self-learns and continues working towards the correct prediction during back propagation.

RF algorithm named so because of the vast number of individual decision trees it furnishes after first-level mining. Decision trees with slightly different characteristics through repetitive random sampling of the training data are the essence. The formation of trees is followed by a bootstrap that determines the suitability of the sampling distribution. Re-sampling is performed in bootstrap as needed. Bagging (taking B of bootstrap and AGG-ING of aggregating) step aggregates the results of trees derived from bootstrapping, are incorporated in the RF for ensemble modelling [4], wherein multiple rules are combined. Support Vector Machine (SVM) conducts an optimal grouping of data using maximum margin hyperplanes (MMHs) with nonlinear kernel functions and then builds a statistical model appropriate for each group [24]. It is akin to placing a mathematical plane across the point cloud at an optimal place as a hull (a curved three-dimensional surface, say a ship hull like) and segregating the clusters, which are otherwise not separable.

Remote sensing-based characterization of forests, plantations and crops [19] has been witnessing increasingly sophisticated and data-intensive approaches to delineate plantations as well as smallholder woodlots. By employing a participatory approach, Tanzanian woodlots and plantations were mapped using Google Earth Engine, employing Landsat 8 (2013–2015), Sentinel-2 (2015–2016), Sentinel-1 (2015), and SRTM-derived elevation and slope data layers into a 30 m resolution database, with an accuracy of 85%. Very high-resolution Google Earth images and Open Foris Collect Earth tools (FAO) were employed to collect samples of woodlots and analysed using decision trees [11]. Expansion of industrial Oil Palm plantations was monitored using a novel approach involving Fully CNN's to solve semantic segmentation problem for Landsat images [2]. Citrus and other crop trees from UAV images were detected as individual crowns using a combination of simple CNN algorithm, followed by refinement using superpixels derived from a Simple Linear

Iterative Clustering (SLIC) algorithm, with an overall accuracy of 96% [7]. Forest-type mapping, biomass estimation, change detection remain key issues in spite of the considerable effort to monitor tropical forests, while the land cover change to forest plantations, especially in forest edge landscapes, do rely on multispectral datasets due to the availability over the long term. Homogenous cover of forest plantation adds to the ease of discrimination. Productivity and stand age mapping are apparently under-studied properties of forest plantations [23]. Geographic information system-based studies have been carried out to indicate the likely areas of sandalwood promotion using niche modelling involving Predictive Species Habitat Distribution Model [14]. The study reported having 90% accuracy in predicting the potential area involving multisource data such as soils, slope, apart from land cover information. Further, the vulnerability of sandalwood habitats was analysed using factors related to anthropogenic sources such as settlements, roads and due to climatic reasons [15] wherein about 17.5% were found to be climatically vulnerable areas. These studies involved the use of very high volume of spatial data and have high degree of scope to use machine learning for further analysis.

5.1 Machine Learning Process

Consumer hardware may not be able to do extensive computations very quickly as a model may require to calculate and update millions of parameters in run-time for a single iterative model like deep neural networks. It is thus required to have specialized hardware to perform extensive calculations. Before the establishment of hardware is embarked upon, it is imperative to understand machine learning flow as elucidated below:

1. Preprocessing input data
2. Training the deep learning model
3. Storing product of trained deep learning model
4. Deployment of the model.

Among all these, training the machine learning model is the most computationally intensive task made up of various matrix multiplications. This can be accomplished by performing all the operations at the same time instead of taking them one after the other, also known as parallel processing. This is where the GPU comes into the picture, with several thousand cores designed for highly parallel operations. There are alternatives to the GPUs such as Field Programmable Gate Array, high-end processing VLSIs (FPGA) and Application-Specific Integrated Circuit (ASIC) which are more efficient in terms of power requirements.

6 Upscaling of Computational Infrastructure

Beyond a pilot level, infrastructure to address high-end computing and digital processing would require an upscaled framework. It would aim to comprehend the total gamut of processes for Sandalwood biology and economics spread across the subcontinent and at times in non-Asian countries as well. It can draw principles from structure detailed hereafter incorporating the machine learning process suggested.

6.1 Storage

The storage system should be least dependent on the storage hardware and should be able to deliver performance with millions of IOPS of sustained throughput (e.g. 100 Gbps) so as to cater to a large number of users. The emphasis, having eliminated movement of data, would be delivering extreme performance, highly available, highly scalable and virtualized. The use of centralized SAN storage eliminates movements of intermediate data products while also providing data—accessibility, protection, availability and scalability (up to petabytes of storage). The storage system should be able to scale to a large number of nodes. All these can be achieved by the use of parallel file systems on top of commodity storage hardware.

6.2 Computational Ability

At the current level of evolution of computing, an inexpensive supercomputer can be realized even employing only four high-end graphics cards that can deliver the same performance as a supercomputer cluster of hundreds of PCs. The proper harnessing of such computing power requires an approach of redesigning and executing existing algorithms and approaches to be rethought and rewritten [27], which will bring enormous benefits. Even moderate use of GPUs deployed properly can give performance improvements between 10 and 100 times over that of the CPU. Provided the database and analysis required for a sandalwood information system is scaled up from a pilot level, it may be required to have an (high-performance computing (HPC) cloud consisting of a cluster of physical servers, virtualized and a set of GPU clusters that can be on demand allocated, scheduled and re-allocated based on the varying demands in time. In summary, the idea would be to have a highly scalable, high throughput storage system tightly coupled with a virtualized high-performance computer that is dynamically configurable. Any process requiring higher compute can be allocated the required resources on demand, providing elasticity.

6.3 Cloud-Based Computing

Data repositories consuming content from various information paths would grow. Demand may increase for the assistance delivered to the farmer using spatial and biology-based inputs. Hence, the tools for sharing and delivering this information would require improvement. It may not be sufficient to just catalogue data but must have ease and effectiveness in searching through large holdings to find the right data. Such searches cannot be expected to be confined to just a local data store either. Cataloguing and searching must be improved, making it easier to discover and consume datasets available from multiple sources. For delivering the services, a framework for the system has to be designed as illustrated (Fig. 3). Infrastructure may rest on a virtual machine(s) or may have physical infrastructure optionally. Open-source cloud platforms rely on open-source hypervisors (KVM and Xen), but some of them also can be used along with commercial/closed hypervisors with exposed interfaces. Cloud platforms combine various tools of the underlying OS and virtualization layer with their own components in a more or less seamless cloud interface. On the other hand, important commercial cloud platforms, namely VMware's (ESXi hypervisor), Microsoft's (Hyper-V hypervisor) and Citrix's (Xen-Server hypervisor, a modified version of the open-source product Xen) offer proven and popular virtualization products for this purpose.

By incorporating these principles, an extended or upscaled framework (Fig. 4) can be designed in a layered fashion to provide separation and security at each level. The infrastructure management layer is achieved with bare metal provisioning (meaning physical hardware facility at a site/campus) and virtual machine provisioning (on web) services of the hypervisor. Enterprise management is responsible for provisioning hardware resources to the infrastructure management layer. The next top-level layers provide service-level control over the entire virtualized infrastructure. Based on the requirement, different types of services like HPC, Remote workstations,

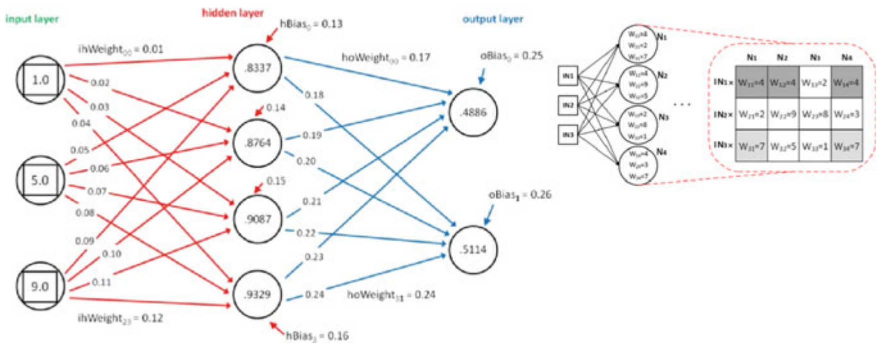

Fig. 4 Illustration of an artificial neural network (ANN). Left-side image [1] shows a typical content of a neural net having input/output and hidden layers. Right-side image illustrates the way matrix operations result in to cumulative weightages for the nodes [27]. Linkages (arrows) are weighted for a phenomenon, from which learning takes place. Biases account for uncertainty in rulesets

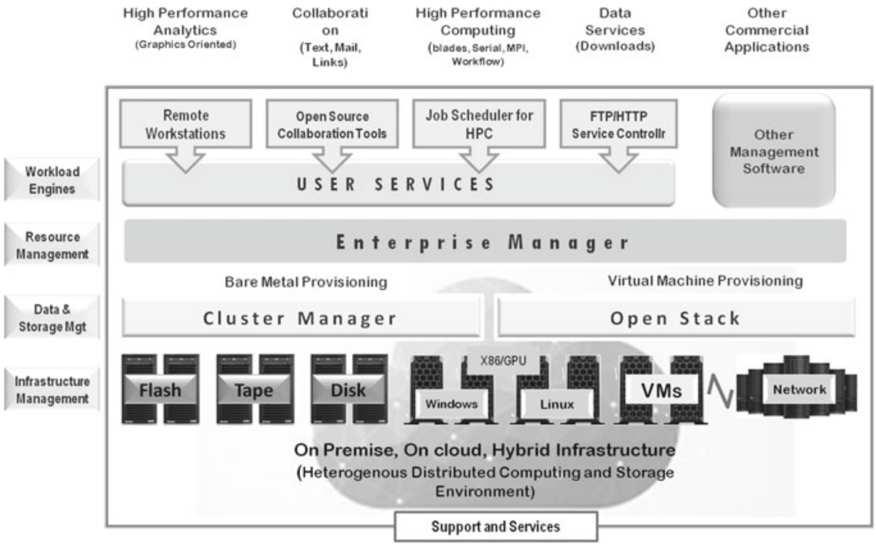

Fig. 5 Framework of the cloud system (software-defined infrastructure)

collaboration service, etc., can be created and provisioned on demand. Further, users will be able to create use and release resources on demand. In summary, the design provides a platform for software defined infrastructure. With the availability of software defined networks, in the coming years, the framework would be able to directly harness the benefits of end-to-end software-defined infrastructure.

7 Suggested Chatbot Design

Chatbots are being increasingly employed in various fields of operations such as business, medicine [10], commerce [5] and agriculture [25]. Chatbots as a personal, interactive and transaction channel generate high revenues but also reduce costs: The potential annual salary savings created by chatbots is estimated to 12 billion US Dollars in the insurance sector and 15 billion in the financial sector in 2017 [28]. Given the potential of the chatbots to bring in more interaction with customers as well as the satisfaction of learning, this tool needs serious attention in assisting the currently considered valuable business of sandalwood cultivation and management. Essentially chatbot needs to understand the user's language and intent, convert the unstructured human language to structured data that computers can interpret. When a user sends a message to the chatbot, it has to deploy algorithms to get meaning and context from every sentence so as to harvest data from those inputs. This process is called natural language understanding (NLU), and it is a subset of natural language processing. It consists of interpreting the user's message by extracting important and relevant details from it. The chatbot basically needs to recognize the entities and intents of the user's messages. In order to do that, we need to build an NLP model for every entity for intent. The NLP process is a core part of the chatbot architecture and process since it is the foundation for translating the natural human language to structured data.

There are two types of possible responses of chatbot, viz. (a) either generate a response from unstructured content as per machine learning model learning or (b) use suitable heuristics to select an appropriate response from the existing library of predefined responses. Retrieval-based models are more in use at the moment. Nearly 25% of all user-assistant exchanges were reported to be initiated from implicit conversational cues rather than from plain questions, in a scenario for chatbots [26]. Recent innovations are focusing on bringing human computation in strengthening the performance of conversational assistant or chatbots through a crowd-sourced answering pool, ably compiled by a process called collaborative reasoning system lets workers select reasonable responses from a number of crowd-produced suggestions. This allows the best responses to be forwarded on to the user and filters out undesirable content [13]. On the other hand, attempts are being made to develop Web-based Embodied Conversational Agents (ECAs), which are a humanoid representation of the bot with animated movements and hence allow interaction at a much finer grain than text or speech-based conversation [17].

Several frameworks, algorithms and APIs are readily available for developers to build chatbots on this architectural model. Botkit, Botman, Bot Maker, Rasa Stack, etc., are a few open-source frameworks for building chatbots. A bot considers the message and context of the conversation to deliver the best response from a predefined list of messages. For forestry/agricultural yield purposes, it is important that the data about field conditions, such as air and soil temperature, air relative humidity, soil moisture, rainfall, wind speed, remote sensing data and other relevant variables, be available to the AI engine rapidly for decision-making processes. The systems architectures discussed in the previous sections are aimed at providing the speed and scale for this rapid decision-making process.

In practical terms, Chatbots make it conversational and simplify the way the information [13] is communicated by steering away from multiple screens, graphics and heavy data. Further, with the integration of social media platforms with the Chatbot engines to derive additional data, the responses can be made more relevant and accurate.

The conceptual system design of the chatbot for the application is presented in this paper (Fig. 6). The AI/ML platform forms the core of the system that receives data from various sources, run models to churn results that are stored as an information knowledge base. Data can be received from various sources like sensors, RS data, field data collected manually, or feeds from social media. Since these sources of data are delivered to the AI/ML platform with different technologies like HTTP, MQTT, zigbee, Bluetooth, etc., these are shown as separate boxes in the figure. Chatbot channels and platforms are built on existing instant messaging platforms like Messenger, Slack, Telegram, Line, etc. These typically run on smartphones, terminals or simple computer systems. The Chatbot engine is the most important

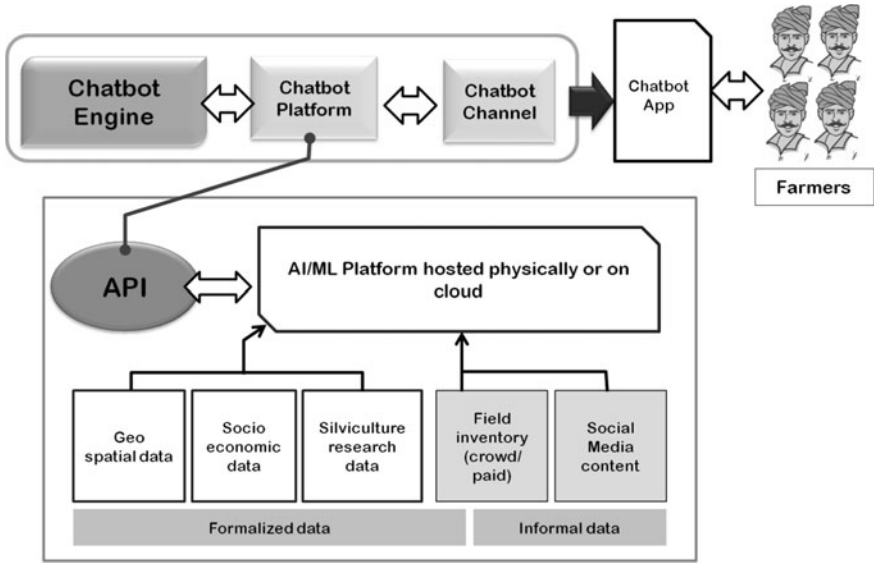

Fig. 6 Conceptual design for formulation of proposed chatbot

piece of building block which is responsible for translating the natural language into machine understandable action. Finally, the Chatbot app provides the user interface with which the user interacts. This could be running on the user's smartphone, tablet or any computer system with interfaces for audio input and output.

Experience with a chat assistant called Farmchat as an experimental product integrating transcription and translation of Google, a customized wizard, Watson Conversation service with Python Flask [25] has highlighted seven critical traits that determine quality information assistance, viz. (i) need for precise and localized answers, (ii) degree of trust, (iii) possible over-expectation, (iv) anthropomorphism, (v) quality of speech input, (vi) response speech time and (vii) order of interaction with the bot. Farm chat provided precise answers and stakeholders exhibited trust in the answers given while validating them with their local knowledge. At times assistant was expected to perform beyond its capacity; hence, a sense of overexpectation prevailed, though it could not answer only 21 of 238 queries raised. Farmers perceived bot to be a human being and dealt it with gratitude. The response timing (9.2 ± 2.8 s) was satisfactory for each input received with Hindi as the input language. Due to the literacy levels of farmers, the order of interaction was at times overlapped and tended to elicit no response from the bot.

The proposed chatbot for Sandalwood cultivation assistance can either interact with the farmer on the fixed or semi-flexible or fully flexible mode of interaction depending on the depth of the conversation. To begin with, it can ask some standard queries and to draw the person into the detailed discussion. Conversation can be initiated with basic data gathering about minimum details about the person, affiliation, motivation and land characteristics through an NLP interface. Further questions either can be allowed to be asked by him, leading to a combination of fixed or semi-flexible approach. Open conversation mode or flexible mode would enable free flowing discussion by the farmer with chat and leave the farmer with wider know-how than the initial point of interaction. Details of the queries regarding silviculture, tree protection, harvest, soil nourishment and related aspects can be designed to be collected as per the conceptualization of the life cycle of sandalwood cultivation (Fig. 2). Principles of formulating a chatbot with its language system, its acceptance, level of empathy as well as the risk of rejection and other key traits are elucidated comprehensively [28], which in turn helps to set the basic framework of the development of such a front-end mechanism. Alternatively, crowd-sourced logic [13] can also be brainstormed, since the current level of answering to be built by a machine intelligence may have possible gaps with respect to very specific habitat traits of the species, highly degraded part of large land holdings, rare pests and diseases, intricate policy implications for harvest and transport not yet inferred in policy documents, etc.

8 Conclusion

The harnessing high bioresource potential of Sandalwood needs to be complemented with the latest tools of information and communication technology coupled with a space-based observation from indigenous or other open-source satellite datasets. A vast amount of know-how built across the globe regarding tree biology and management since the end of the nineteenth century needs to be meaningfully synthesized into a farmer friendly content, available as customized information exchange and handholding tool. Artificial intelligence ably supporting such an effort can handle a diverse and large amount of information ingested from conventional silvicultural and tree improvement research as well as geospatial datasets comprising information on habitat quality and their prioritization. Chatbots or conversational assistant suitably designed based on the principles of ease of conversation as well as optimized result delivery at appropriate rate and format will keep aspirational farm-level stakeholders initiated and connected. Regular interaction with interested farmers or farmer groups can enable a true scaling up of sandalwood cultivation drives across the entire regions of sandalwood suitability. International experiences in handling such key species would also add to the approach to be established for comprehending the needs of farmers as well as standards developed to achieve the best productivity in the long run. Rapidly evolving geospatial datasets in terms of spatial and temporal resolutions and thematic content will go a long way in virtualizing the process under consideration to realize a bioeconomy so that a strong rural development alternative is established.

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Chapter 34
Future Directions for Indian Sandalwood

A. N. Arunkumar, Geeta Joshi, Rekha R. Warrier, and K. N. Nataraja

Indian Sandalwood (*Santalum album* L.) is perhaps one of those few species having a combined intricate association with culture, history and commercial significance among all the three major religions of the Asia Pacific countries. It has been recognized as 'Vulnerable' (by the International Union for Conservation of Nature) due to obvious reasons. Extensive research work on various aspects is being carried out in several countries, including India, Australia, Sri Lanka, Indonesia, China, Japan, and the USA. This chapter, more of an epilogue, attempts to consolidate all the authors' views and present a perspective of the path ahead for sandalwood. The issues seeking attention are broadly classified as scientific, social and economic. The directions addressing various gaps and need would help in conservation of Sandalwood and its sustained utilization.

The venerated Rishis and mystics of India with deep knowledge about nature of reality have widely advocated the use of Sandalwood as a model to depict wisdom thoughts. Sandalwood is the backbone of traditional Indian perfumery and India's ancient fragrance heritage and mentions India as synonymous with Sandalwood (Iyengar, Chap. 3). There are debates on Sandalwood being native to India; this issue has to be addressed through a multidisciplinary approach—historical evidences from ancient and modern texts, fossil evidences if any supported by phylogeography/phylogenetic studies (Sanjappa and Sringeshwara, Chap. 11). This would lead to a better understanding of its trade history and related aspects across the world and

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Asian countries in particular. Its global heartwood of history, environmental roots and its needs are yet to be understood. Therefore, various steps/strategies towards conserving the species to ensure its everlasting future must be the course of action (Cottrell, Chap. 1). Sandalwood has been a traded commodity since the nineteenth century in Australia (Pronk, Chap. 4). Unfortunately, in India overexploitation and endangerment of existing stocks along with mismanagement have resulted in the natural population loss. It is emphasized that if prudent and tough policy measures are practiced along with public support, the future of Sandalwood can be revived (Rashkow, Chap. 2).

The status of Sandalwood in India (Arunkumar and Sarmah, Chap. 5, Sekar, Chap. 6), Sri Lanka (Subasinghe, Chap. 8), Indonesia and neighbouring countries (Yuskianti and Warrier, Chap. 9) mention that dwindling Sandalwood population is a cause of concern. All of them conclude that the role of the Government is crucial in its extensive cultivation and conservation. In Australia, private plantation companies have taken interest in Sandalwood cultivation which perhaps provides better opportunities for Sandalwood research, trade and economy and are presently at the forefront in Sandalwood global market (Pronk, Chap. 10). This might be because it is an exotic in these regions, and hence treated as a traded commodity. Marayoor Sandalwood Reserve in Kerala state, India, perhaps the largest global repository of natural Sandalwood trees (~58,000) has to be conserved for posterity. (Arunkumar et al. Chap. 7).This can be declared as a Species Management Area (ICUN Category IV) to ensure maintenance, conservation and restoration of the species and its habitat—possibly through traditional means and awareness creation.

In the biology section, the taxonomic history of *Santalum* in general and *Santalum album*, in particular, has been discussed (Sanjappa and Sringeswara, Chap. 11). The authors emphasize the need for global taxonomic revision of the genus *Santalum*. Anatomical studies on Sandalwood have been carried out extensively, however, Sinha and Vijendra Rao (Chap. 12) while differentiating the anatomical features of the stem and root wood, report for the first time, the presence of distinct oil cells with oil globules in the bark encouraging more studies on this aspect. Pollination biology reveals contradictions concerning pollination behaviour. Information on fruit set under similar or different conditions observed by different workers vary greatly. Information on pollination biology like anthesis, pollen viability, foraging behaviour of the pollinators, pollen removal efficiency index is lacking (Hareesha et al. Chap. 13). Seed biology involving seed-handling protocol and germination has been studied extensively. Seeds are the major source of propagation in Sandalwood and issues related to storage and germination persist. Therefore, insights into these aspects would assist large-scale production and germplasm conservation (Joshi et al. Chap. 14). Further, sandalwood is a hemi-root parasite requiring a host throughout its life. A variety of host species support various growth stages. Identification of appropriate hosts for successful parasitization at different growth stages, host parasite relationship on growth, heartwood and oil formation needs investigation (Rocha and Santhoshkumar, Chap. 15).

Due to the increased interest in Sandalwood cultivation, there is a huge demand for quality planting material in terms of propagules from superior genotypes with good nursery practises. Seed certification and certified nurseries are two essential components which require immediate attention while addressing quality planting material in Sandalwood (Rathore et al. Chap. 16). While raising seedlings or in established trees, Sandalwood has been susceptible to insect pests and diseases during the cultivation process. Most of the work on insect-related aspects pertain to insects' role in spike disease transmission. There are mentions of defoliators, sap feeders and wood borers in nurseries and plantations. However, information lacking is the extent of area under infestation, periodicity of incidence, and intensity of the attack by key pest species. As Sandalwood is extensively cultivated in different agroclimatic zones with varied host species and divergent management practices, the possibility of the emergence of new insects should be critically viewed (Jacob, Chap. 17). The dreaded disease—Sandalwood spike, caused by an insect-transmitted phytoplasma has been extensively researched since 1903. Though the use of antibiotics along with vector control is considered a plausible solution, early detection and effective management needs a focussed study (Ashwini et al. Chap. 18). A thorough countrywide survey of Sandalwood spike is needed as this disease has also been reported in Marayoor Sandalwood Reserve. Future studies on Sandalwood spike should be to understand the complex interactions of vector-phytoplasma and vector–plant relationships, especially at the molecular level. Studies are also needed on epidemiology and the factors associated with it. The cascading ill effects of spike disease can directly impact Sandalwood cultivation prospects in India though spike disease has not yet been reported in other countries.

With relaxed government policy measures, Sandalwood is being commercially cultivated in India. An ideal agroforestry species, some of the immediate research interventions related to its cultivation are the availability of quality planting material, liberalization of policies, especially for harvest, transport, marketing and protection measures (Viswanath and Chakraborty, Chap. 19).

Tree improvement and advanced research have also been carried out in Sandalwood. Sandalwood has substantial morphological and genetic variation. But there is a dearth of information on variability in heartwood and oil. The process of heartwood formation is yet to be understood. It is essential to understand the interaction between genotype and environment and its impact on heartwood and oil formation. Various field trials are to be established for understanding this aspect. Considering the dwindled natural population in India, the tree improvement programme in Sandalwood has to be reinitiated. In traditional tree improvement programme generally for identifying superior genotypes the source is the natural populations, however, in this case the source material would primarily be the extensive plantations that are being cultivated across India (Arunkumar and Seetharam, Chap. 20). Physiological understanding of sandalwood growth, development along with host interaction in terms of photosynthetic activities are to be critically understood in Sandalwood. This would not only help in selection of superior genotypes, suitable hosts and also provide information for better management practices so as to obtain optimum productivity (Arunkumar and Nataraja, Chap. 24). For developing better conservation strategies, documenting genetic diversity is important, and studies reveal considerable genetic variability in Sandalwood. For augmenting tree improvement strategies, future studies should focus on integrating high resolved molecular markers like Single-Sequence Repeats, Expressed Sequence Tags and Single-Nucleotide Polymorphism, ecological niche distribution and chemical variability of sandalwood populations (Joshi et al. Chap. 23).

As one of the biotechnological tools, micropropagation in Sandalwood has been extensively carried out. However, micropropagated plants in field trials are yet to materialize and should be the research priority. Production of novel hybrids through interspecific protoplast fusion and somatic embryogenesis has to be seriously considered (Rathore et al. Chap. 22). The mystery behind fragrant santalol production in heartwood has been unravelled through advanced applications of 'omics'. It would be appropriate to evolve a comprehensive strategy using multiomics approach that enhances knowledge and aid in identification of key metabolites and networks linked to growth and oil production (Thulasiram et al. Chap. 25).

Sandalwood oil finds use in diversified fields such as medicinal, pharmaceutical and perfumes. The chemistry of the oil plays a significant role in in identifying superior genotypes that form the basis for tree improvement. Regular quality assessment of oil is important for a plantation manager, which facilitates harvest planning. Identification of adulterants is crucial, considering the high commercial value. Some of the areas that need to be strengthened are novel methods for source authentication and traceability, rapid analysis oil in the field, identification of minor components with olfactory characteristics, identification of genetic markers and sample analysis from clinical studies (Hettiarachchi et al. Chap. 26).

One of the key components of Sandalwood oil, alpha-santalol, is known for therapeutic uses in anticancer treatment. The pro-apoptotic, antiproliferative, anti-angiogenic, anti-oxidant and anti-inflammatory activities enhance its antitumour and cancer-preventive properties. Extensive research is being carried out as Sandalwood oil targets multiple pathways and modulates the expression of markers involved in carcinogenesis and has great potential in treating the development of deadly malignancies. Further studies are needed to assess the exact role when used alone or in combination with other agents. Also, the limitation in its bioavailability and concentrations essential to utilize sandalwood oil's inherent benefits needs in-depth study (Blankenhorn et al. Chap. 27). Sandalwood has been extensively used in '*Ayurveda'* the Indian traditional system of medicine. Medicinal use of sandalwood use has been indicated in one of the oldest available literatures '*Rig Veda*', written around 2000 B.C. Sandalwood's availability is now a concern, and the authors urge that conservation of Indian Sandalwood is vital from ecology and human health perspective (Kumar et al. Chap. 28). Sandalwood oil and perfume are inseparable entities, and its rich association dates back to seventh century BCE. It is expected that the framework of classic and contemporary fragrances built around Sandalwood oil will continue in the years to come. Globally sophisticated consumers opt for certification and organic cultivation. Therefore, there is a greater opportunity for growing Sandalwood ethically and sustainably. It would also bring in confidence for brand owners and consumers for ethical purchasing decisions (Brown et al. Chap. 29). With botanical drugs gaining importance globally, Indian Sandalwood oil has also found its way into the United State Food and Drug Administration as a pharmaceutical agent. Due to its inherent attributes such as structural diversity, high lipid solubility and low molecular weight. It has already in use in various phase 2 clinical trials with encouraging results. There is a need for more trials supported by numerous factors for its approval as a prescription drug in the USA. Ultimately, availability of sufficient quantities of acceptable pharmaceutical grade Sandalwood oil would be a major concern and that can happen only when extensive plantations are raised with sufficient authenticity of its cultivation attributes. But the scope is wide and economically lucrative (Levenson, Chap. 30). The price for Sandalwood and oil is at a premium because of reduced availability and huge demand. The present trend of exorbitant price may gradually become stable as there is extensive cultivation in India and across various southeast Asian countries along with Australia (Ananthapadmanabha, Chap. 31). Once the availability of wood and oil increases, various industries associated with Sandalwood would also start functioning and undoubtedly Sandalwood has a brighter horizon.

There is a huge global requirement; hence, cultivation of Indian Sandalwood is increasing. To harness this bioresource potential, it is important to utilize the latest tools of information and communication technology coupled with a space-based observation from indigenous or other open-source satellite datasets. The vast information that is already existing and extensive information that is expected in future needs meaningful synthesis into a farmer-friendly content which would become a handholding tool in the future. The application of artificial intelligence supports better management of plantations and sustained harvest of Sandalwood (Pujar et al. Chap. 33). Considering the threats in the changing environment and using species distribution model, 79 and 60% of the predicted suitable habitats of Sandalwood in India and Indonesia, respectively, has been converted to croplands, and only 2% of the remaining natural habitats fall in protected areas. Considering the climate change impacts, and using suitable modelled distribution, Sandalwood would not be adversely affected due to climate change in most of its natural range by 2050. However, continuous efforts are to be nurtured in conserving and sustained utilization of Sandalwood both in India and Indonesia (Jalonen et al. Chap. 32).

The demand for Indian sandalwood oil has stood the test of time, and there is an expectation that this will continue. The probable option to meet this demand is to encourage large-scale cultivation as a sustainable and socially acceptable substitute for the supply from the wild. Parallelly, the remnants of natural populations need to be protected to serve as sources for future plantations. An International Network Programme is the need of the hour. Plantations are being raised in different parts of the globe can serve as base populations for developing tree improvement strategies. Exchanging genetic material and establishing multi-country provenance trials to identify suitable planting material for diverse environmental contexts would also be useful. Sandalwood plantations as an industry can be a successful venture despite its numerous constraints. Its adaptability in areas not identified as its natural habitat can be tested globally. Variation in environmental conditions to assess differently adapted populations, and region-specific populations need to be delineated. Such populations can later serve as seed zones.

With modern infrastructure and technology in place, this can be easily achieved. However, long term studies on the impact of various issues include lack of seed supply, difficult soils, rain-fed conditions, invasives, fire, biotic and abiotic stresses. Once there is sufficient heartwood and oil availability, all the allied research fields and associated industries/sectors would also progress.

Though protection of Sandalwood plantations is an important aspect specially in India and adjoining countries, it has not been considered in this compendium as we feel that traditional way of having solar fencing, maintaining equipped security guards, using dog squad or through technological interventions using drones, microchips or radio frequency identification, and combinations of these may provide a temporary relief but at a considerable cost. We firmly believe that to have a strong in-built protection system for Sandalwood cultivation, it is essential to have a participatory approach in the form of 'social fencing' where several growers in a community can volunteer themselves and enhance mutual trust and interdependence which would foster not only in protection of the valuable Sandalwood tree, but also generate substantial financial gains which would be a win–win situation for all.

We end this chapter with a passionate note, Sandalwood is truly a global species with diversified uses regardless of the country, creed or the religion. All of us involved in this compendium along with the wide spectrum of the global society, who are associated directly or indirectly to the minutest level with the Indian Sandalwood must join with reverence to save the venerated tree ensuring its perfumed eternal future for the benefit of humanity.