

TREES FOR LIFE IN OCEANIA

CONSERVATION AND UTILISATION OF GENETIC DIVERSITY

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Santalum insulare

Family: Santalaceae

Botanical name: *Santalum insulare* Bertero ex A.DC. In *Prodr.* [A.P. de Candolle] 14(2): 685 (1857).

The specific epithet is from the Latin *insularis*, insular, island, referring to the distribution of the species. Nine varieties are currently recognised in this species: var. *insulare*, var. *alticola*, var. *raiateense*, var. *marchionense*, var. *deckeri*, var. *mitiario*, var. *raivavense*, var. *margaretae* and var. *hendersonense*, but taxonomical revision to come will increase this number up to 10 (2 new varieties to describe and 1 to put in synonymy).

Common names: Polynesian sandalwood (English); *bois de santal polynésien* (French); *a'i* (Cook Islands); *puahi* (Marquesas Islands, French Polynesia); *ahi* (Society and Austral Islands, French Polynesia)

Summary of attributes and why diversity matters

Santalum insulare is a highly valuable, naturally renewable resource for the small isolated islands that make up French Polynesia. It was heavily exploited in the past for its heartwood, rich in fragrant and sought-after santalols, and is now an endangered species over the vast majority of its natural range. All harvesting is now banned in French Polynesia while conservation strategies are implemented and production plantations are established by local communities.

In French Polynesia, up to four traditional varieties of *S. insulare* based on wood colour and fragrance are recognised in each archipelago. *Puahi* is the symbolic tree of the Marquesas archipelago where its uses are numerous, especially as medicine but also for its unique fragrance which is associated with sensuality. Sandalwood oil or *monoï* (*pani puahi*, *mono'i ahi*) can be found in most of the Polynesian markets. While most *S. insulare* populations give commercial santalol-rich heartwood essential oils, three populations from the Marquesas Islands have a different, (Z)-nuciferol chemotype, which has limited or no commercial value.

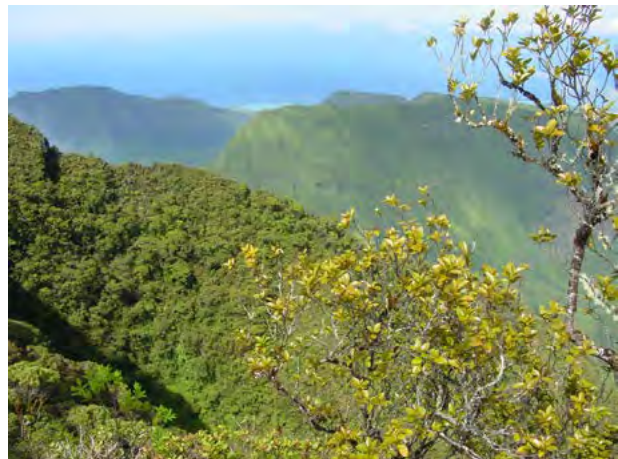
Description

Habit shrub or small tree ≤ 8 –12 m tall, maximally reaching 15 m tall and 50 cm dbh; hemiparasitic with parasitic root haustoria fused to the roots of host plants.

Bark brown-black, becoming fissured in old specimens.

Leaves simple, ovate to elliptic, 3.5–15 cm long, 1.5–9.5 cm wide; new leaves orange in high-elevation

populations, quickly turning dark green at maturity, whereas light green to yellow-green leaves in low-elevation populations; leaf size highly dependent on ecological conditions—small-leaved plants restricted to lower mean temperatures (extra-tropical islands or high-elevation populations) or windy areas, whereas larger-leaved forms at lower elevations on tropical islands. **Inflorescences** terminal or pseudo-axillary panicles. **Flowers** hermaphroditic, shortly pedicellate; tepals (3–)4(–5), ovate to triangular, ≤ 3 mm long; colour ranges from greenish-white through cream white or yellowish to red and brown-red; at higher elevations, the fragrant flowers open whitish before turning red. **Fruit** mature fruit oval, globose to pear-shaped drupe (14–48 mm long, 10–43 mm wide), red to purple and black at maturity, with thick fleshy mesocarp and several petal scars; single, rugose stony shell or endocarp (9–34 mm long,



Santalum insulare var. *alticola* in moist ridge forest, Mount Aorai (2,000 m asl); Tahiti, French Polynesia (Photo: J.-F. Butaud)



Buds and flowers of *S. insulare* var. *mitiario*; Mitiario, Cook Islands (Photo: L. Thomson)



Fruit of *S. insulare* var. *raivavense* from Raivavae (sea level); Austral Islands, French Polynesia (Photo: J.-F. Butaud)

6–31 mm wide) encompassing single seed. *Seed* relatively large and a favourite food of introduced rats.

There is substantial polymorphism in fruit and seed size with the smallest seed being produced by plants in windy sites at high elevation (>1,600 m asl) on Tahiti (var. *alticola*) and the largest seed by plants at rainy sites of intermediate elevation (700–1,100 m asl) on Nuku Hiva (var. *nov.*), Marquesas Islands. This polymorphism

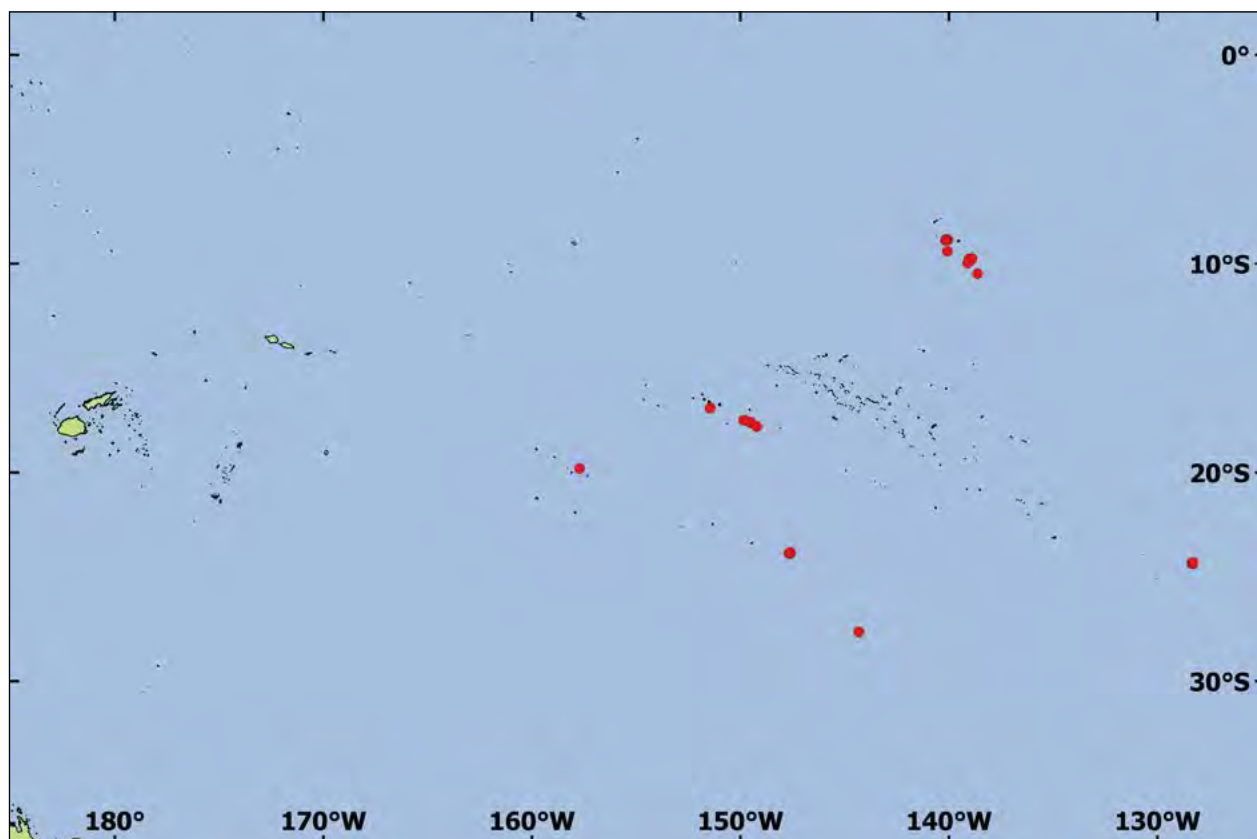
in fruit size can also be correlated with the size of fruit-dispersing pigeons and doves.

Distribution

Santalum insulare is endemic to eastern Polynesia and occurs as nine different botanical varieties in French Polynesia (10 islands in 3 archipelagos), the Cook Islands (var. *mitiario* on Mitiaro Island) and Pitcairn Islands (var. *hendersonense* on Henderson Island). In French Polynesia, var. *marchionense* and var. *deckeri* are known in the Marquesas Islands of Nuku Hiva, Ua Pou, Hiva Oa, Tahuata and Fatuiva; var. *insulare* and var. *alticola* are endemic to Tahiti; var. *raiateense* is restricted to Moorea and Raiatea in the Society Islands; and var. *raivavense* and var. *margaretae* grow on Raivavae and Rapa, respectively, in the Austral Islands. A planned taxonomic revision will affect Marquesan varieties with var. *marchionense* (syn. var. *deckeri*) on Nuku Hiva, Ua Pou, Hiva Oa and Tahuata, a first new variety for high-elevation populations from Nuku Hiva, and a second for Fatuiva populations.

The natural range of the species has contracted through human-related factors, such as harvesting and introduction of the black rat (*Rattus rattus*): *S. insulare* is now presumed extinct on several islands; namely, Ua Huka in the Marquesas Islands, Makatea in the Tuamotu Islands and Tubuai in the Austral Islands.

Santalum insulare occurs from sea level on coralline soils up to 2,200 m asl on volcanic soils, under various temperature and rainfall conditions, from semi-dry to cloud forests.



Uses

Although sandalwood was already used by Polynesians, sandalwood traders overharvested *S. insulare* resources from the Austral and Marquesas archipelagos between 1810 and 1830. Remaining populations are sorely depleted today as a result of those activities and traditional harvesting of the species.

Wood and non-wood—the main traditional uses of *S. insulare* involved its fragrant heartwood. Most traditional uses required the production of wood shavings or powder which were soaked in coconut oil for several days to obtain *mono'i ahi* or *pani puahi* (sandalwood *mono'i*). The heartwood was gathered from natural populations which sometimes could only be reached after several days of walking. The heartwood harvest was destructive as each tree was uprooted to obtain the heartwood in major roots, as well as the trunk and larger branches.

Puahi/ahi heartwood is widely used in traditional medicines for the treatment of several ailments. Heartwood powder is mixed with coconut water or *mono'i* for internal or external remedies: skin diseases, wounds, earache, sinusitis, rheumatic pains, conjunctivitis and throat infection. Moreover, massages with sandalwood *mono'i* are often applied for muscle pains, tiredness, chills or stretch marks. Sandalwood *mono'i* is also widely used as a cosmetic in skin and hair care. In Tahiti, babies of royal lineage were massaged at birth with *mono'i ahi*, as is the common practice nowadays for Marquesan babies using *pani puahi*. The benefits of these traditional uses, mainly for medicinal purposes, have recently been supported by the identification of antibacterial and antifungal constituents in the heartwood of *Santalum* species.

Some special bark clothes called *'aeu pipi* or *kaeu pipi* were perfumed with sandalwood powder in Marquesas Islands as were some *hei* or necklaces called *hei keka'a*, *kumu hei* or *'umu hei*. In these *hei*, pineapple eyes are sprinkled with sandalwood powder. Handicrafts in sandalwood have been recently developed, mainly in response to the demand for souvenirs by tourists and expatriates. *Tiki* (statuettes), bowls and hair sticks are some of the items fashioned out of sandalwood. In the Society and Marquesas archipelagos, sandalwood powder and *mono'i* were used in the embalming process for the deceased of important families. Sandalwood was also burnt during the burial rituals to purify the atmosphere and repel evil spirits. Sandalwood was also revered as a vital, if not sacred, and precious material in weddings, and is recorded in traditional songs (*rari o te puahi*) in Marquesas Islands. Nowadays, continuance of traditional uses is at risk due to the scarcity of the natural stands and the complexity of sustainable management of this depleted natural resource.



Handicrafts from *S. insulare* heartwood—tiki figures surrounded by garland in wood shavings (Photo: J.-F. Butaud)

In the Marquesas Islands the seed was sometimes eaten by Polynesians, while in Tahiti the bark was used as a red dye. The fragrant flowers were possibly also used in *hei* (floral wreaths).

Diversity and its importance

Santalum insulare is morphologically highly variable (adaptive diversity), probably due to its wide natural distribution and the diversity of ecological conditions under which it grows. This has resulted in the differentiation of 10 morphologically distinctive varieties, each being endemic to a particular archipelago. In addition, typically about three traditional varieties are recognised in each archipelago mainly on the basis of heartwood quality (colour, fragrance and toughness).

Chemical studies showed that the diversity of heartwood sesquiterpenoid composition is organised into two general chemotypes characterised by the distinct carbon skeletons of their main constituents: the typical santalol chemotype of commercial quality in most of the natural populations; and a new (Z)-nuciferol chemotype of limited commercial value restricted to three populations of Marquesas Islands. Moreover, some minor variations exist within the santalol chemotype and tend to differentiate several provenances linked with geographical distribution. Thus, these moderate variations between populations conjugated with important variations within populations support the conclusion



Above: Morphotypes of *S. insulare* seed from French Polynesia (Photo: J.-F. Butaud)

Left: Three-year-old seed orchard of *S. insulare* var. *marchionense* from Nuku Hiva planted at sea level in Taiohae; Nuku Hiva, Marquesa Islands, French Polynesia (Photo: J.-F. Butaud)



of the occurrence of a stabilising selection. Other chemical studies indicate that flavonoids—in particular, C-flavonoid glycosides—can be used as chemotaxonomic markers for *S. insulare*, whereas fatty acid seed oils could be useful to investigate diversity in the genus.

Genetic studies using chloroplast and nuclear microsatellite markers showed: moderate diversity; a high proportion of clones (60%) explained by vegetative multiplication (root suckering); and differentiation into four metapopulations (evolutionarily significant units) in French Polynesia corresponding to archipelagos or islands separated by large oceanic barriers; namely, Marquesas Islands, Society Islands, Raivavae island and

Rapa island. These characteristics can be interpreted as the consequence of the insular syndrome due to the small founder effect (one or few individuals), subsequent limited gene flows and high genetic drift.

Thus, whereas speciation processes mainly occur at the archipelago scale, substantial morphological and chemical diversity is observed at the island scale. This diversity impacts on both wood quality and artificial regeneration, with seed size and provenance habitat influencing nursery practices.

Conservation of genetic resources (including threats and needs)

Although sandalwood was already used by Polynesians, the first documented threats to *S. insulare* came from the sandalwood trade with European settlers and visitors from Australia, USA and France. Furthermore, sandalwood from Austral and Marquesas archipelagos was overexploited for incense production in China between 1810 and 1830. Remaining populations constitute relics from

that period and the different varieties are here assessed as either Endangered or Critically Endangered. A negative selection has occurred with the extirpation of the best-quality sandalwood populations (shape of the tree and quality of the wood) leaving a residue of inferior-quality trees (shrubby and faintly fragrant heartwood).

The introduction of the black rat at the beginning of the 19th century prevented natural reproduction by seed, a favourite rat food source, and contributed to the drastic decline in *S. insulare* populations. Moreover, these rats and other introduced predators (cats, swamp harriers and even humans) have contributed to the extinction of several species of fruit-eating birds which aided *S. insulare* seed dispersal and regeneration. In addition, modification of natural Polynesian ecosystems by humans (fire, agriculture and urbanisation), introduced herbivores (goats, horses and cattle) and/or invasive plant species has led to the extirpation of many *S. insulare* populations and contributed to its rarity throughout its natural range. In some islands, natural ecosystem processes can be restored but, in others, ongoing human intervention and management is now necessary to preserve remnants of former *S. insulare* populations.

In order to preserve and sustainably manage the sandalwood resource, the Government of French Polynesia has, since 1998, been implementing a management program for *S. insulare* in the Marquesas, Society and Austral archipelagos.

This program is based on several preliminary studies undertaken by several collaborators:

- inventory of populations and ecological studies on the 10 islands where *S. insulare* occurs in French Polynesia (Rural Development Service—SDR)
- investigations of variation in heartwood chemistry (University of French Polynesia—UPF)
- analyses of the genetic diversity and structure of most of the populations (International Cooperation Centre in Agronomic Research for Development—CIRAD).

Legal protection has been provided to the more threatened varieties (i.e. var. *margaretae*, var. *alticola*, var. *insulare*, var. *marchionense* and var. *deckeri*). Physical

protection is also practised with the enclosure of small populations (mainly to protect plants from wild goats and cattle) and rodent control to permit fruit production and harvest. Our observation of major genetic differentiation between populations has led to the definition of management units based on evolutionarily significant units. Thus, exchanges of plant material between these units are banned to minimise future hybridisation.

Santalum insulare nurseries have been established in each unit in order to conserve local provenances (seed orchards, conservatory plantations and enrichment of small natural populations) and promote their cultivation by communities. Indeed, *S. insulare* is a highly valuable, naturally renewable resource for the small isolated islands that make up French Polynesia. A particular case involves trees/populations representing the rarest chemotype with no actual commercial value. These populations have not been multiplied for production plantations but are only protected from the feral herbivores by enclosure and several conservation plantations have been established in Marquesas Islands (two on Nuku Hiva and one on Hiva Oa) and in the Society Islands (one on Tahiti, two on Moorea and one on Tahaa).

This program will be complete once conservation plantations have been established and are well managed in each management unit and production plantations have been made by the local communities. Experience has shown that the success of such conservation activities, for a great part, depends upon the enthusiasm of key persons in each island. Indeed, *S. insulare* plantations are a long-term investment given the long rotation (>30 years) and are unattractive to most farmers who have the option, for example, of growing fruit trees that may produce a commercial harvest within a few years. Agroforestry could be a way to make sandalwood cultivation in French Polynesia more attractive; for example, in mixed plantings with *noni* (*Morinda citrifolia*) or *Citrus* species.

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