Propagation of ‘Iliahi (*Santalum paniculatum* Hook. & Arn.), a Valuable Endemic Hawaiian Sandalwood Species

Tawn M. Speetjens, Emily C. Thyroff, Aileen K.F. Yeh, and Douglass F. Jacobs

Sloan Indigenous Graduate Partnership M.S. Student, Purdue University, Department of Forestry and Natural Resources, West Lafayette, IN and Forester, Hāloa ‘Āina Reforestation Project; Ph.D. Candidate, University of Hawai‘i at Mānoa, Department of Natural Resources and Environmental Management, Honolulu, HI; Hawai‘i Island Coordinator, Forester/Horticulturist, Hawai‘i Agriculture Research Center, Hilo, HI; Fred M. van Eck Professor and Director, Tropical Hardwood Tree Improvement and Regeneration Center, Purdue University, Department of Forestry and Natural Resources, West Lafayette, IN

Abstract

Six *Santalum* species are endemic to the Hawaiian Islands where they are known locally as ‘iliahi. ‘Iliahi were once widespread throughout the islands, but most stands were harvested for the valuable heartwood, reducing the distribution by an estimated 90 percent. Limited natural regeneration and a burgeoning interest in ‘iliahi cultivation have prompted the need for reliable propagation systems. One species in particular, *Santalum paniculatum*, has been the focus of interest due to available planting area, relative abundance, and commercial-grade oil quality. We describe methods for seed harvesting, processing, germination, seedling transfer, growth, and field planting of *S. paniculatum*. These methods have successfully produced high-quality seedlings, although further research is needed.

Introduction

Approximately 1 percent of all angiosperms are parasitic, and most are root hemiparasites (Heide-Jørgensen 2013, Matthies 2017). Hemiparasitic plants can photosynthesize yet rely on specialized root structures called haustoria to connect to hosts and extract resources (Bell and Adams 2011, Matthies 2017). Hemiparasites tap into the xylem tissue of host and plants and are capable of extracting water, mineral nutrients, amino acids, and carbon (Govier et al. 1966, Těšitel 2010, Westwood 2013). These species are generally able to parasitize a variety of plant taxa, although nitrogen-fixing legumes are commonly found to be superior hosts, producing greater growth in the parasite (Annapurna 2006, Ouyang 2016). There is evidence of a bi-directional flow of resources, although the dominant direction of flow is towards the parasite, often resulting in reduced growth of the host (Lu et al. 2020, Radomiljac and McComb 1998b, Westwood 2013). Of all hemiparasitic woody angiosperms, most belong to the Oleaceae and Santalaceae families (Veenendaal et al. 1996).

Within the Santalaceae family is the *Santalum* genus, which has species widely distributed from India to Australia and throughout the Pacific Ocean (Teixeira da Silva et al. 2016, Wagner et al. 1999). Members of the *Santalam* genus are collectively known as sandalwood. There are six *Santalum* species and several varieties endemic to the Hawaiian Islands (Harbaugh et al. 2010). The Hawaiian species comprise approximately one-third of the *Santalum* species worldwide (Harbaugh et al. 2010). The six species are derived from two separate founding events, one ancestral group with white flowers and the other ancestral group with red flowers (Harbaugh et al. 2010) (table 1). The five upland tree-like species in Hawaii are locally known as ‘iliahi and the one coastal-growing, shrubby species is known as ‘iliahialo‘e. Additional vernacular names for the ‘iliahi species include ‘a‘ahi, ‘aoa, lā‘au ‘ala, and wahie ‘ala (Wagner et al. 1999). Scientific nomenclature are *Santalum ellipticum* Gaudich (coastal sandalwood), *Santalum freycinetianum* Gaudich. (Freycinet sandalwood), *Santalum haleakalae* Hillebr. (Haleakalā sandalwood), *Santalum involutum* H. St. John, *Santalum paniculatum* Hook. & Arn. (mountain sandalwood), and *Santalum pyrularium* A. Gray (forest sandalwood) (figure 1).

Table 1. Six ‘iliahi species (*Santalum* sp.) and varieties are distributed throughout the Hawaiian Islands (based on Harbaugh et al. 2010).

Scientific name[1]	Common names	Distribution	Flower group
Santalum ellipticum Gaudich	‘iliahi, ‘iliahialo‘e, coastal sandalwood	Kaua‘i, O‘ahu, Maui, Lana‘i, Moloka‘i, Kaho‘olawe, Hawai‘i and Northwestern Hawaiian Islands	White
Santalum freycinetianum Gaudich	‘iliahi, Freycinet sandalwood	O‘ahu	Red
Santalum haleakalae Hillebr	‘iliahi, Haleakala sandalwood	Maui	Red
Santalum involutum H. St. John	‘iliahi	Kaua‘i	White
Santalum paniculatum Hook. & Arn	‘iliahi	Hawai‘i Island	White
Santalum pyrularium A. Gray	‘iliahi	Kaua‘i	Red

[1]Harbaugh et al. (2010) identified species varieties for *S. ellipticum* and *S. haleakalae*. Additionally, some practitioners recognize *S. paniculatum* var. *pilgeri*.

‘Iliahi are broadleaf evergreen, hardwood tree species native to moderately wet to dry Hawaiian forests (Merlin et al. 2006, Wagner et al. 1999). All ‘iliahi species can form a single bole trunk and reach varying heights. *Santalum ellipticum* is most commonly found as a sprawling shrub but can occasionally be found as a short stature tree 3.3 to 16 ft (1 to 3 m) tall (Merlin et al. 2006). The largest species of ‘iliahi (*Santalum paniculatum* and *Santalum freycinetianum*) can reach heights of 43 to 66 ft (13 to 20 m). ‘Iliahi have opposite and simple leaves that can be ovate, elliptic, orbicular, or obovate (Wagner et al. 1999). ‘Iliahi and other *Santalum* species have been, and are still, coveted internationally as sources for the aromatic heartwood that is primarily used for carving, constructing fine furniture, burning in religious practices, and producing sandalwood essential oil (Teixeira da Silva et al. 2016, Thomson et al. 2011). As a result of this resource value, ‘iliahi and other *Santalum* species have been severely exploited throughout their ranges (Kepler 1983, Teixeira da Silva et al. 2016).

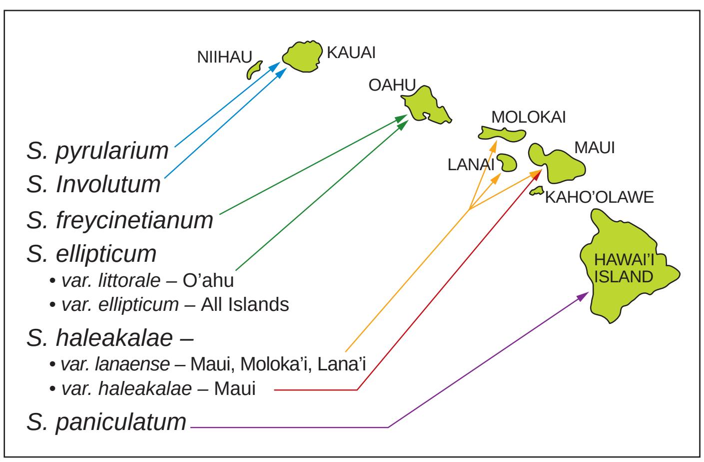

Figure 1. ‘Iliahi species (*Santalum* sp.) and varieties are distributed throughout the Hawaiian Islands (based on Harbaugh et al. 2010).

Native Hawaiians used parts of ‘iliahi in a variety of applications including the construction of traditional stringed instruments (Buck 1964), perfume and preservation of traditional plant fiber cloths (kapa) (Kepler 1983, Kraus 1972), and medicinal treatments for dandruff, head lice, and reproductive ailments (Kraus 1972). Before western contact, native Hawaiians likely affected lowland ‘iliahi populations (below 1,500 ft [457 m] elevation) by burning and clearing to make way for agricultural fields (Kirch 1982). Following western contact, visiting merchants who were familiar with the valuable sandalwood tree being traded in China soon realized there was a substantial supply of these trees in Hawai‘i.

The export of ‘iliahi from Hawai’i to Chinese markets began as early as 1790, after the Hawaiian monarchy became aware of the value of this natural resource (Merlin and VanRavenswaay 1990). Expansion of the ‘iliahi trade was catalyzed by predatory lending practices that involved foreign traders allowing monarchs to purchase foreign luxury items on the promise to be paid in exorbitant amounts of ‘iliahi. The monarchy incurred a substantial ‘iliahi debt and the burden of repayment fell on the shoulders of the common people who were forced to harvest ‘iliahi to repay the merchants. Indeed, the first written law in the Hawaiian kingdom was a sandalwood tax that stated “every man was required to deliver one half of a picul (133.3 lb [60.5 kg]) of sandalwood to the governor of the district to which he belonged, or to pay in lieu thereof four Spanish dollars, on or before September 1, 1827” (Merlin and VanRavenswaay 1990). When easily accessible, lowland ‘iliahi became depleted, native Hawaiians resorted to harvesting trees from distant upland forests, resulting in fatal exposure to the elements and the neglect of food crops. This ultimately contributed to famine and compounded the detrimental effect of alien diseases on native

Hawaiians (Merlin and VanRavenswaay 1990). At its peak, the sandalwood trade in Hawai‘i was so extensive that the islands were known in China as “Tahn Heung Sahn” or “the Sandalwood Mountains” (Kepler 1983). The Hawaiian sandalwood trade had all but ceased by 1940, with the decline attributed to dropping ‘iliahi prices associated with competition from Indian sandalwood sources and poor-quality material sourced from the increasingly depleted Hawaiian forests (Merlin and VanRavenswaay 1990).

By the end of the trade, an estimated 90 percent of the natural ‘iliahi stands were harvested (Rock 1974). The most extensive remnant portions are located in the upland mountains of the Kona district on Hawai‘i Island (Rock 1974). All ‘iliahi species are still extant but have smaller ranges due to the harvest history. Other threats to forest health, such as grazing, invasive species, and fire, have suppressed natural regeneration of ‘iliahi stands (Merlin et al. 2006). Poaching is an additional threat given the species’ high commercial value. The discrepancy between possible historic ranges, as modeled by Price et al. (2012), and currently known ranges for ‘iliahi suggest extensive areas for potential restoration of this species.

The economic value of ‘iliahi lends to the potential for it to be a native hardwood forestry crop. Several small operations have reintroduced ‘iliahi products into the global market through salvage harvest operations of dead or dying trees from upland populations. While natural regeneration of ‘iliahi is often minimal, coppicing and root sucker growth are stimulated by salvage harvests. Harvesting the whole tree (trunk and root ball) while leaving lateral roots has resulted in replacement rates of 7 to 10 new coppices or suckers per harvested tree (Senock 2017) (figure 2). Coppice and root suckers produce flowers and seeds within 2 years of emergence compared with 4 years from a seed-planted individual. Coppicing and root suckering cannot, however, expand the current range to the estimated former range because new shoots can only occur in areas where ‘iliahi are already present. Considering this, artificial regeneration is a key strategy for restoring ‘iliahi species beyond the current range. Thus, reliable propagation systems for ‘iliahi must be developed to ensure the long-term success of restoration and commercial cultivation.

Of the ‘iliahi species native to Hawai‘i, *Santalum paniculatum* is an optimal candidate for cultivation due

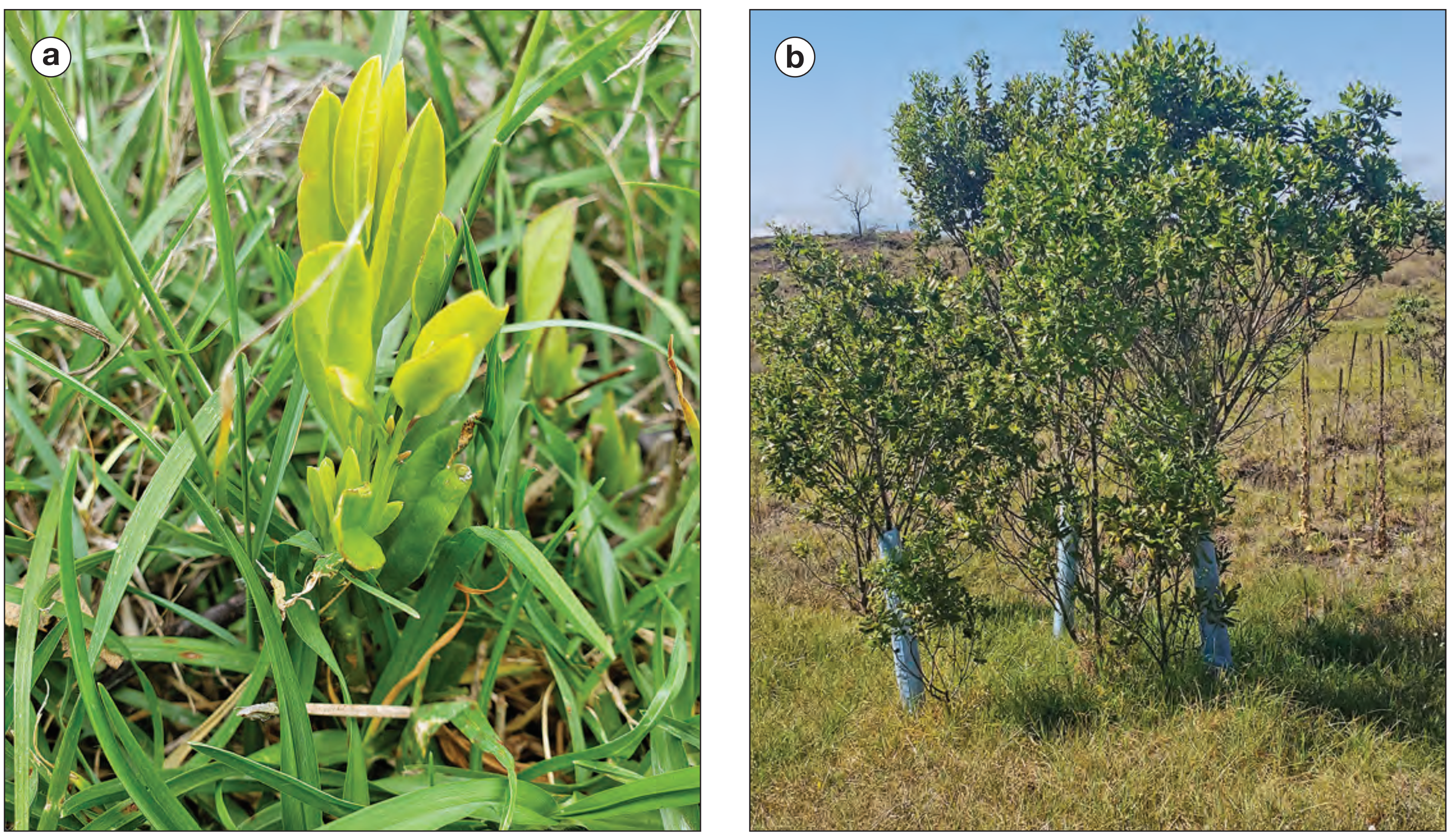

Figure 2. ‘Iliahi regenerates from root suckers such as this (a) 1-month-old ‘iliahi root sucker and this (b) group of 7-year-old root suckers that have regenerated from harvesting a single tree. (Photos by T. Speetjens, 2020)

to its large potential range for restoration, the greatest remnant abundance relative to other species, and its ability to produce commercial-grade oil (Braun et al. 2014, Price et al. 2012, Rock 1974). This article focuses on the propagation of *S. paniculatum*, hereafter referred to as ‘iliahi. Our objective is to provide a detailed and illustrated protocol on the proper care of ‘iliahi seeds and seedlings to help guide future propagation efforts. We provide our recommendations based upon our observations and successes. Each nursery location is different, however, and methods should be adjusted to suit local conditions. Propagating ‘iliahi is an evolving topic and several ongoing research projects currently strive to broaden the understanding of ‘iliahi regeneration to support efforts toward expanding ‘iliahi's current range to be more representative of its former, more abundant distribution.

Step 1: Seed Harvest and Processing

The ‘iliahi fruiting season is highly variable between and within populations. The timing of fruiting depends on the tree health and its geographic location. ‘Iliahi of Hawai‘i Island's south Kona district typically begin to flower in November and will carry fruit into June. Each fruit (drupe) contains a single seed and ripens from green to a mature reddish-purple or black (Wagner et al. 1999, Wilkinson 2007) (figure 3). Fruits should be picked at peak ripeness before the pulp begins to dry. If no fresh fruits are available on the tree, fallen fruits may be viable and suitable for use (Isch 2021). Seeds should be processed immediately to reduce the likelihood of pulp rot and associated negative effects on the seed embryo. If immediate processing is not possible, fruit can be stored between 35 and 39 °F (2 and 4 °C) in a paper bag for up to 1 week.

The first step of seed processing is to remove the pulp from the seed. Seeds should be soaked in water to soften the pulp which aids in its removal (figure 4a). We recommend soaking fresh fruits for a minimum of 1 hour and older, dried fruits for a minimum of 3 to 4 hours. Some propagators have found success in soaking fruits for up to 4 days to aid in pulp removal (Isch 2021). Once soaked, the pulp can then be removed by rubbing fruits against a metal mesh screen with a gloved hand (figure 4). To process large quantities, the seeds can be enclosed in a wire mesh cage and power washed until the majority of pulp is removed (figure 5). After

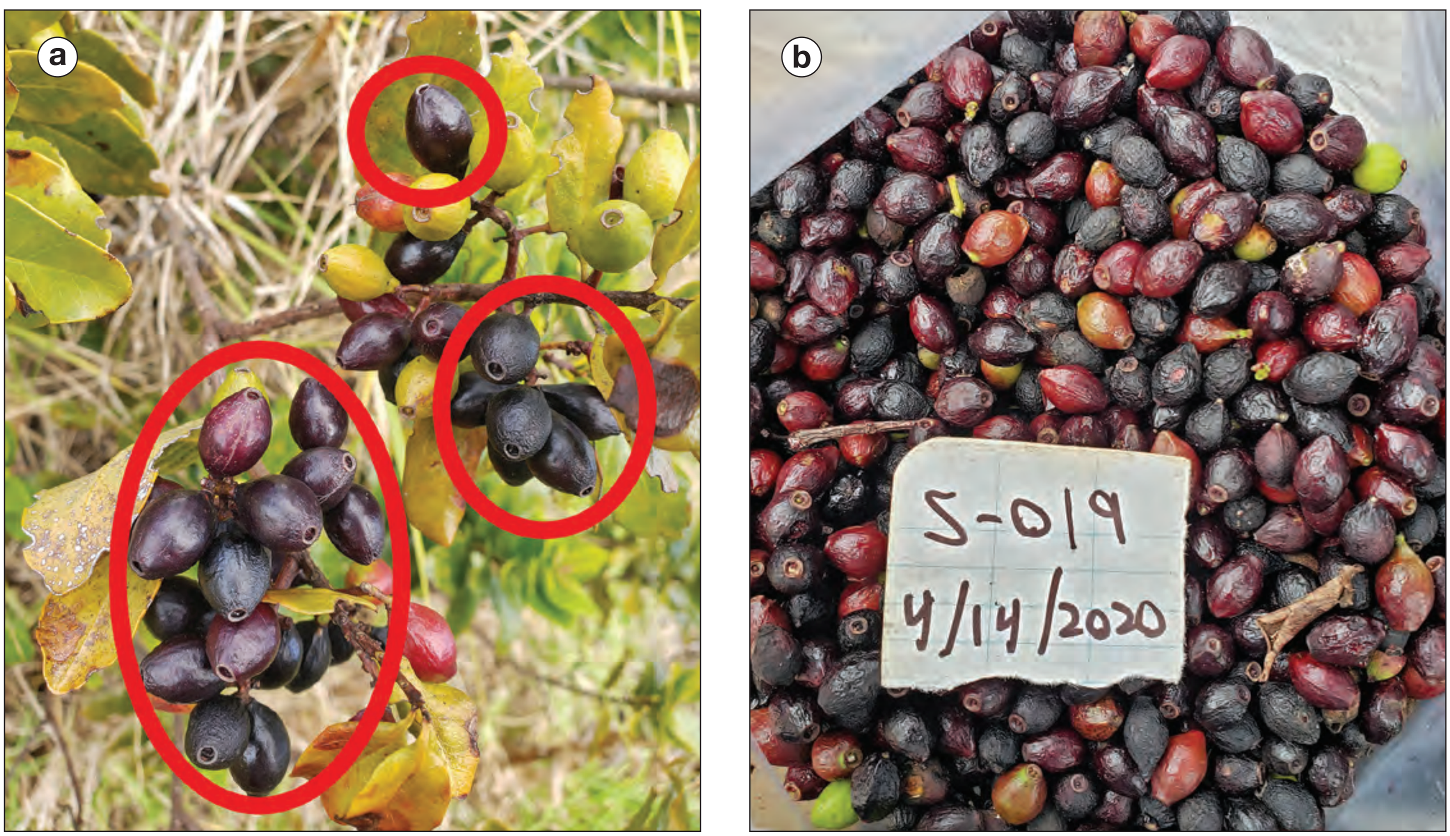

Figure 3. During seed collection season, ‘iliahi trees can have both (a) green unripe fruits and dark purple ripe fruits. (b) Fruits should be collected when they are ripe. (Photos by T. Speetjens, 2020).

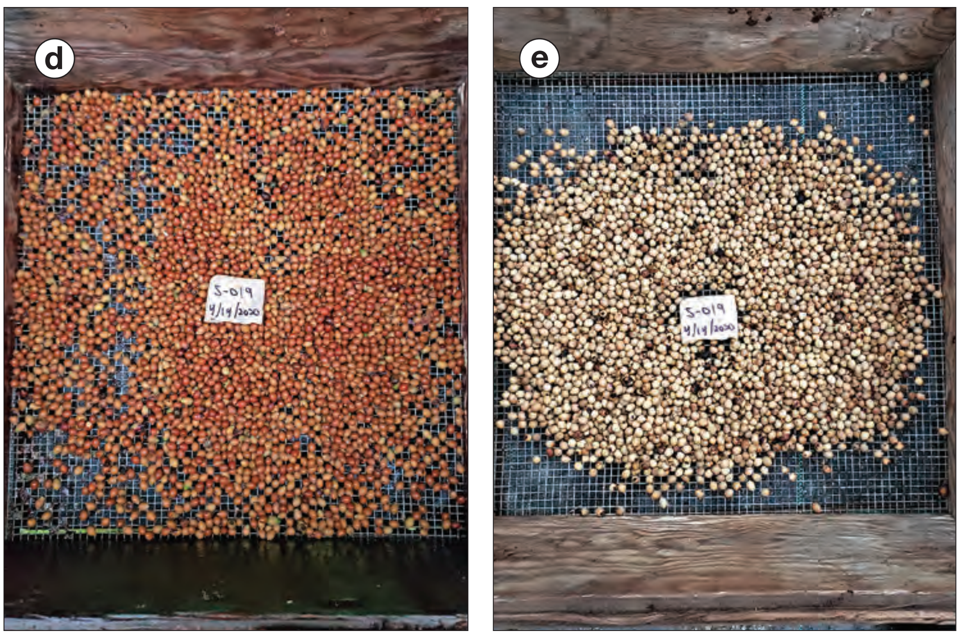

Figure 4. The first step in processing ʻiliahi seeds, is to remove the pulp. (a) Fruits are soaked in water for 3 to 4 hours to soften pulp. (b) A wood box with a mesh screen bottom can then be used for pulp removal by (c) repeatedly rubbing fruits against the mesh screen and rinsing so the pulp falls through the screen. The process is continued until (d) all pulp is removed from the seed. Seeds should be sown immediately or (e) dried for storage by placing on a wire mesh or cloth weed mat to be air dried for 3 to 5 days. (Photos by T. Speetjens, 2020)

power washing, it is often necessary to remove any remaining pulp with the metal mesh screen method. For all methods, it is important not to crack the seed coat and expose the embryo. Some propagators have found success sowing seeds with pulp still on when the seed is fresh (Shigematsu 2021), although we recommend removing the pulp for storage preparation and to reduce the amount of material available for potential fungal growth.

Once the pulp has been removed, the seeds should be sown immediately or properly stored. Seed can be dried for 1 to 3 days (and up to 7 days) to 8 percent moisture (figure 4e) and stored at 39 °F (4 °C) in airtight containers or bags for several years (Elevitch and Wilkinson 2003, Wilkinson 2007). ʻIliahi species have been identified as likely freeze sensitive (Chau et al., 2019), indicating that more research would be beneficial in guiding long-term storage and seed banking.

Step 2: Seed Germination

We have observed variable germination rates from 10 to 90 percent and variable germination time from 4 months to 2 years depending on seed treatment (Elevitch and Wilkinson, 2003, Wilkinson, 2007).

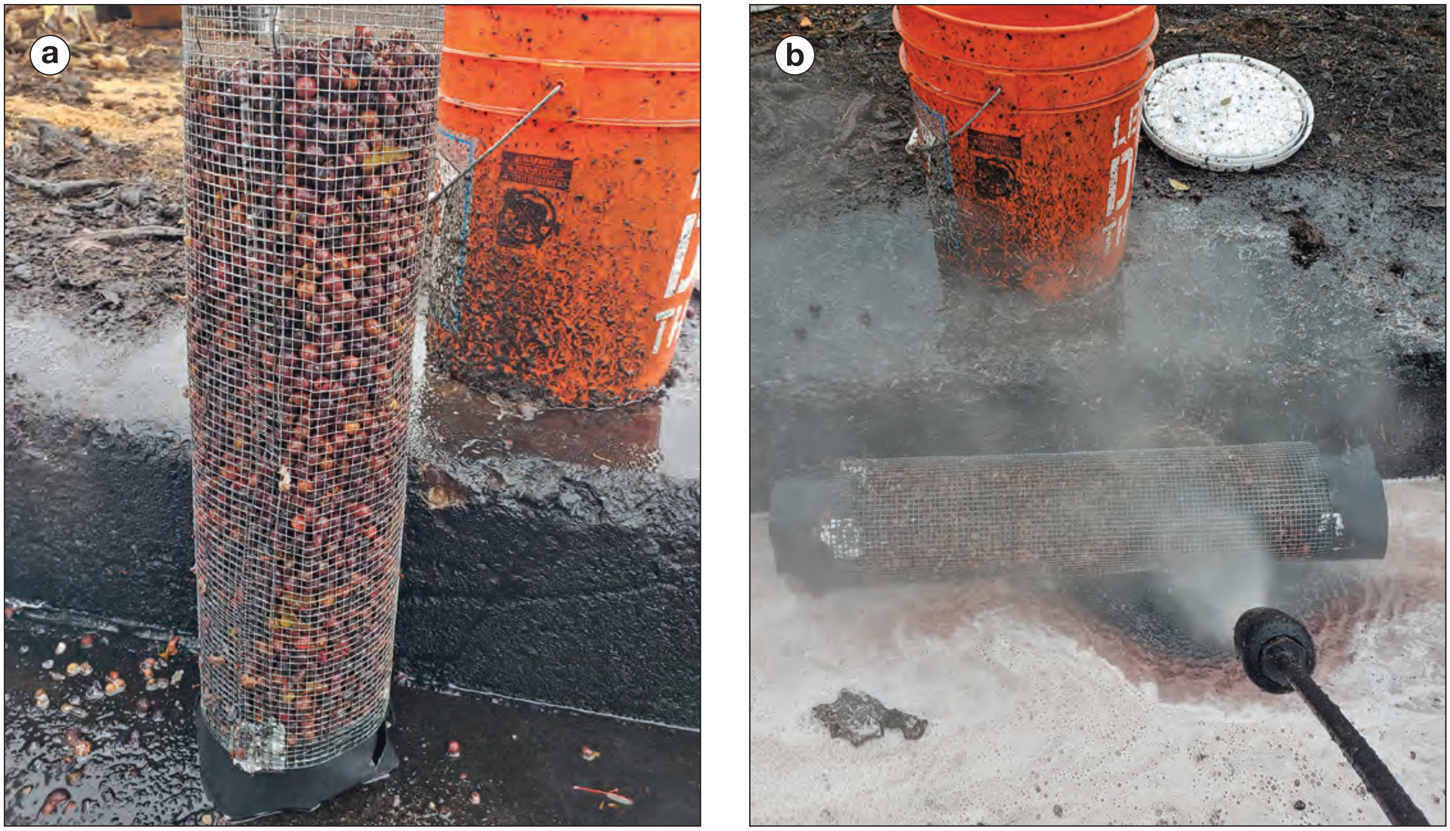

Figure 5. To remove large quantities of ‘iliahi seeds, fruit can be (a) placed in a mesh cage and then (b) washed with a power washer until the majority of pulp is removed. (Photos by T. Speetjens, 2019)

Sandalwood seeds have a hard, semi-permeable seed coat, a large endosperm, and a reduced embryo. Viable seeds will have a crisp, white-colored endosperm when split and the radicle will emerge at the seed apex when germinating (figure 6). Indian sandalwood (*Santalum album* L.) seeds exhibit morphophysiological dormancy, meaning seeds require treatment with the plant hormone gibberellic acid (GA_3) to overcome physiological aspects of dormancy (Jayawardena al. 2015). This type of dormancy appears to hold true

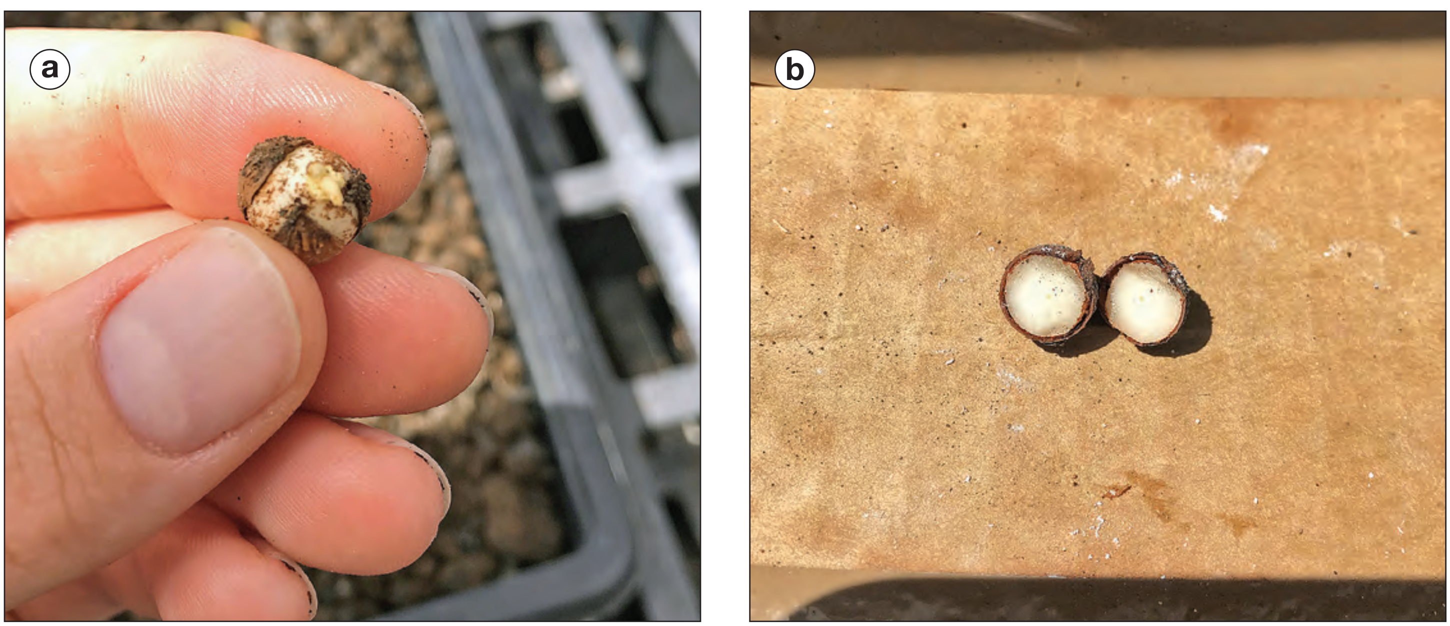

Figure 6. (a) A radicle will emerge from the large seed endosperm of a viable seed as it germinates. (b) Viable seeds have a crisp white embryo when split. (Photos by E. Thyroff, 2020)

for other *Santalum* species, including ‘iliahi, although further studies are needed to confirm this. Confirmation of morphophysiological dormancy would imply the seed coat is permeable to water and that scarification (e.g., clipping the tip of the seed coat or using sandpaper abrasion) is not necessary. Some Hawai‘i propagators have had variable success with physical scarification improving germination rates, although extreme care should be taken not to expose or damage the embryo. Exposing the embryo can potentially increase the chances of the seed rotting before germination.

Treating seeds with GA_3 is known to assist many plant species in overcoming physiological dormancy by altering the GA_3 and abscisic acid (ABA) ratio within the embryo (Kucera et. al, 2005). Many studies have shown that GA_3 reduces germination time and increases germination success for Indian and Australian sandalwood (*Santalum accuminata* A.DC.) (Das and Tah 2013, Jayawardena et al. 2015, Teixeira da Silva et al. 2016). GA_3 can be purchased in a powder or a pre-dissolved liquid form. The powder form must be dissolved in water (preferably deionized water) to reach the target concentration using a reference formula: (mg/ml)*1000 = ppm, or (ppm*ml)/1000 = mg, or (oz/fl oz)*1000 = ppm, or (ppm*fl oz)/1000 = oz. For example, to mix 500 ml (16.9 fl oz) of 500 ppm GA_3, use 250 mg (0.00882 oz) GA_3 powder. Mix the GA_3 powder and water in glassware using a magnetic mixer for 2 hours to ensure the powder is fully dissolved (figure 7).

Research with Indian and Australian sandalwood species found 100 to 500 ppm GA_3 was effective for stimulating germination (Lu et al. 2014, Ouyang et al. 2015, Radomiljac, 1998). A study at Lyon Arboretum with *Santalum ellipticum* found comparable germination success between 200 and 600 ppm (Kroessig and Chau 2021). We have found that ‘iliahi seeds treated with a 24-hour soak at 400 to 500 ppm GA_3 begin to germinate within 30 to 45 days, and most viable seeds germinate within 180 days. After treating with GA_3, we observed that two ‘iliahi species (*S. ellipticum* and *S. freycinetianum*) appear to have similar germination timelines to *S. paniculatum*, whereas another ‘iliahi species (*S. haleakalae*) appears to take longer. Further studies are needed to confirm and compare germination rates within ‘iliahi species in response to GA_3. After GA_3 treatment, seeds should be sterilized by soaking for 1 minute in a 10-percent bleach solution, rinsed,

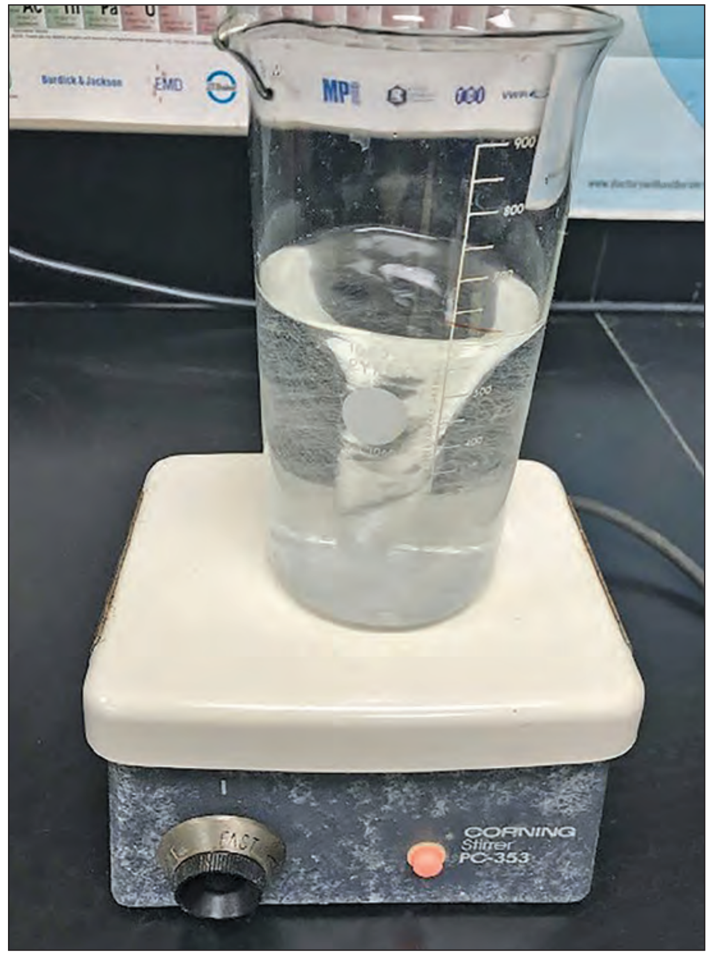

Figure 7. A magnetic mixer can be used to stir deionized water and gibberellic (GA_3) powder into solution. (Photo by E. Thyroff, 2020)

then coated with powdered sulfur and/or Captan® fungicide to reduce the risk of embryo rot (Elevitch and Wilkinson 2003, Hirano 1990, Wilkinson 2007, personal observations).

Seeds are sown in germination trays onto the surface of the germination medium at approximately 2 to 4 seeds per in^2 (2 to 4 per 6.5 cm^2) in a single layer (figure 8a). The size of ‘iliahi seeds may vary, which will affect sowing density (figure 8b). A layer of black cinder (0.5 to 0.75 in [1.3 to 1.9 cm]) should be applied over the seeds to minimize weeds (figure 8c).

We have used a variety of media for germinating ‘iliahi seeds including: 1) 5:1:1 ratio of perlite:coconut coir:vermiculite topped with black cinder; 2) 5:1 ratio of perlite:vermiculite, 3) 1:1 ratio of perlite:potting soil topped with black cinder; 4) all vermiculite; and 5) 1:1 ratio of perlite or vermiculite: *Sphagnum* peat moss. Perlite used in soil mixtures should have a particle size of 0.25 to 0.38 in (6.4 to 9.5 mm; i.e., #2, classic super coarse). Further studies are required to

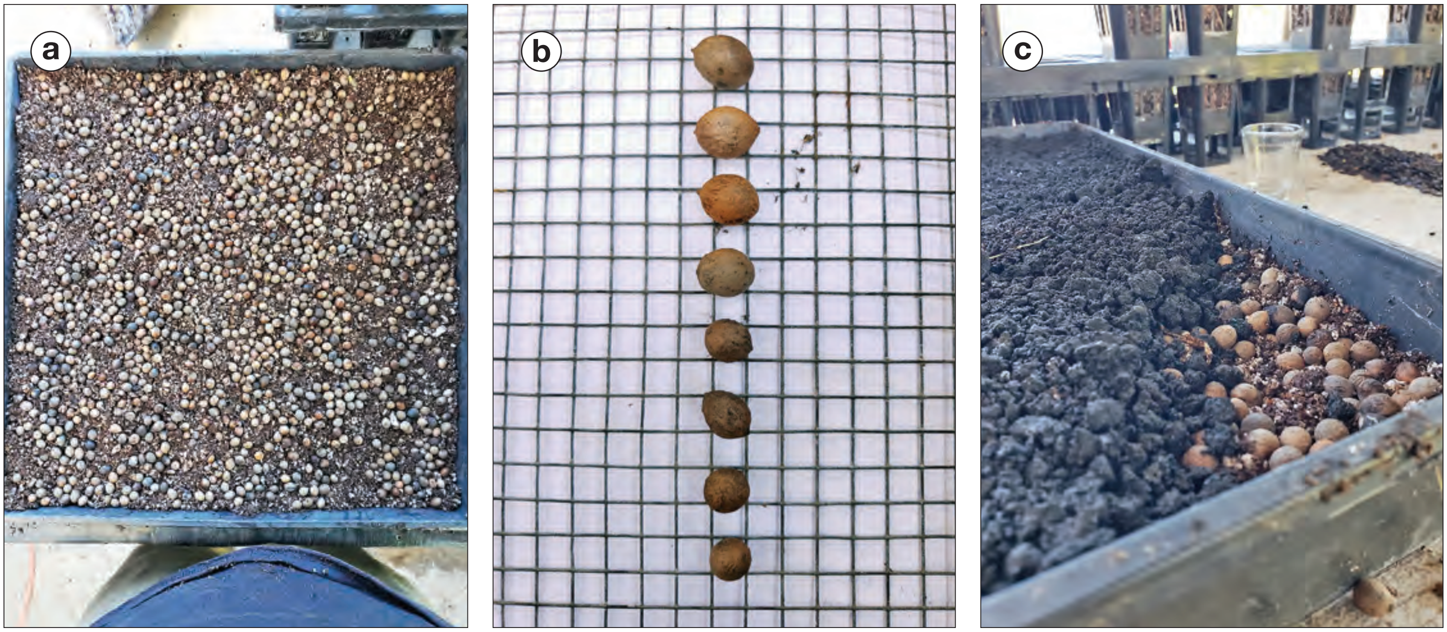

Figure 8. (a) ʻIliahi seeds should be sown in a single layer on medium composed of equal parts perlite and potting soil. (b) Sowing density will be affected by the variable seed sizes. (c) Seeds can be covered with a layer of fine, black cinder to prevent establishment of weeds. (Photos by T. Speetjens, 2019)

determine an ideal germination medium. Regardless of the medium used, it is critical to maintain proper moisture to aid in seed imbibition while also minimizing fungal infection and fungus gnat infestations. The medium should not remain completely saturated for multiple days and should be allowed to partially dry before rewatering. We recommend irrigation trials to determine the best frequency and duration for a given medium based on the nursery or greenhouse conditions (e.g., sunlight and temperature) where the germination trays will be located.

Step 3: Seedling Transfer and Growth

Young seedlings should be transplanted out of germination trays within 1 to 2 months of emergence when germinants have reached the 2 to 6 true-leaf stage (figure 9). Transplanting at this stage ensures the seedling will have sufficient roots although not enough to tangle with neighboring seedlings in the germination tray. Transplanting seedlings too early could result in compromised survival, while transplanting seedlings too late increases the risk of root stress and transplant shock.

Similar to the germination tray media, there are several recommendations for container media. A few examples include: 1) 1:1:1 perlite:coconut coir:vermiculite; 2) 1:1:1 perlite:fine black cinder:potting soil; and 3) 1:1 perlite:potting soil. Wilkinson (2007) recommended a 14-14-14 (N-P-K) controlled-release fertilizer, dolomite, and gypsum integrated into the growing medium. We recommend the medium and fertilizer regime used by the Hāloa ʻĀina nursery (Kealakekua, Hawaiʻi) which consists of equal parts perlite, potting soil, and fine black cinder with controlled-release fertilizer (Osmocote® Plus 15-9-12 + micros) and organic fertilizer (Espoma® Organic Plant-Tone 5-3-3) incorporated into the medium at a rate of 10.54 lbs per yd^3 (6.2 kg per m^3). We also recommend applying a 0.4 oz (1.2 ml) ethylenediamine (EDDHA) chelated iron powder to the surface of each container at least 30 days after transplanting (applying earlier has been observed to kill some seedlings). The chelated iron powder should be watered in immediately and reapplied every 2 to 3 months. The chelated iron treatments appear to be necessary for sustained seedling growth (Hirano 1990, Wilkinson 2007, personal observations). Trials are currently being conducted to explore potential interactions of chelated iron and controlled-release fertilizer on ʻiliahi seedling quality. In addition to nutrient applications, it is good practice to inoculate ʻiliahi seedlings with local mycorrhizae to help improve growth rates, increase stress resistance, and improve nutrient uptake, especially with phosphorus (Binu et al. 2015, Davies 2000, Miyasaki 1993).

As a hemiparasite, ʻiliahi seedlings will ultimately need to attach to a host, but pairing with a host

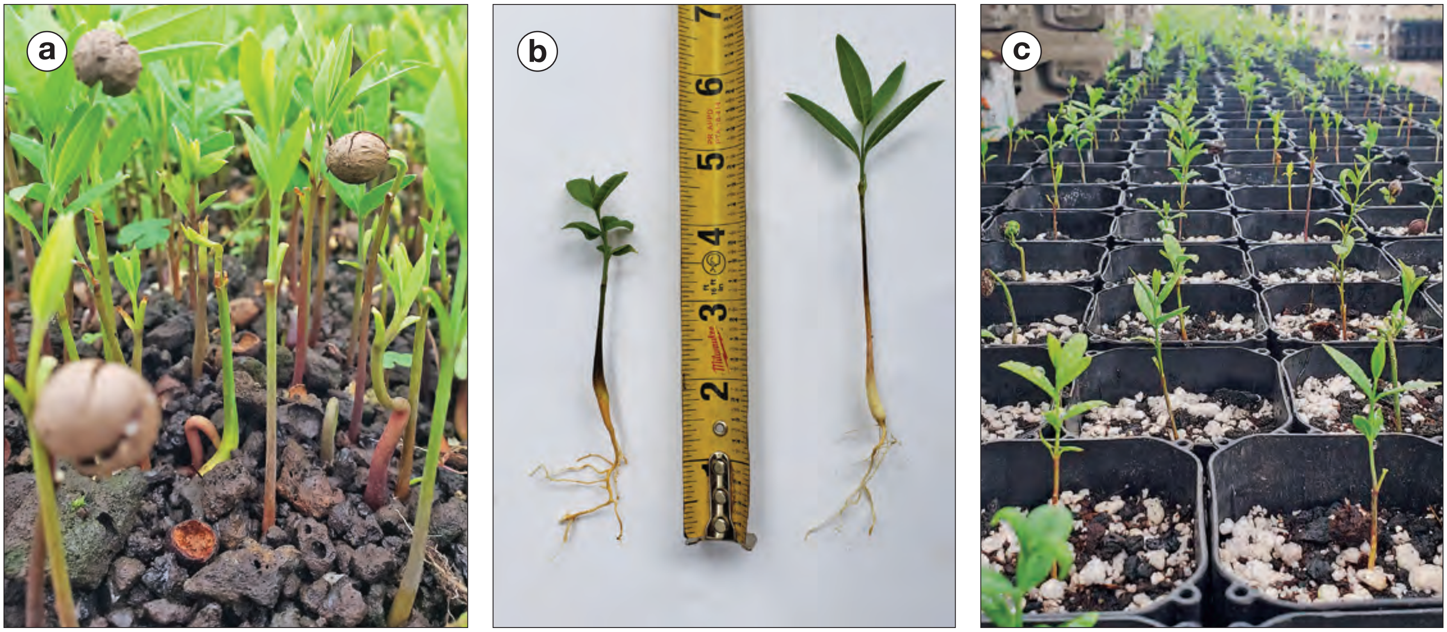

Figure 9. (a) ʻIliahi seeds treated with GA_3 will germinate in a uniform flush over 2 to 6 months and are ready to transplant when (b) seedlings have 2 to 6 true leaves. (c) ʻIliahi seedlings can be transplanted into individual containers. (Photos by T. Speetjens, 2019)

during nursery cultivation is not necessary to produce healthy growth if seedlings are fertilized sufficiently. The effect of growing ʻiliahi with a container host, in combination with fertilizer treatments, however, is not well understood. While ʻiliahi can survive without a container host, the presence of a host may help with haustoria development and long-term outplanting success. A study on Indian sandalwood showed that a non-leguminous host did not provide any benefit to growth in the nursery but significantly affected outplanting success (Radomiljac and McComb 1998a). Growing ʻiliahi with container hosts is complicated by the potential for the container host to out-compete the ʻiliahi seedling if the parasitic connection is not formed. We have observed that ʻiliahi seedlings without container hosts have good survival (more than 90 percent) when planted in areas with pre-established, 4-year-old, koa (*Acacia koa* A. Gray) host trees. We recommend not using a container host if the intended field planting area has long-term hosts established. When planting in barren areas such as a pasture, we recommend using a container host due to the likelihood of improved outplanting success. If container hosts will be used, ʻiliahi seedlings should be grown for a minimum of 3 months before introducing a host. This 3-month period will allow the ʻiliahi seedling to become established and help it compete against hosts which typically grow more vigorously. Container hosts can be introduced by sowing host seeds or by transplanting host germinants. Introducing a host via seed sowing is preferred because it reduces the risk of damaging existing ʻiliahi root structure. Seed sowing is most effective for host species with high seed viability such as koa and ʻaʻaliʻi (*Dodonaea viscosa* Jacq.). Host seeds should be treated in the manner appropriate to the species to maximize germination rates. If the seed viability of the host is poor or unknown, then we recommend germinating host seedlings in a separate flat and transplanting into ʻiliahi containers as soon as it is appropriate for the given species. When transplanting host seedlings, it is important to minimize the impact to ʻiliahi roots by using a fine point instrument to create the transplant holes.

A host suitability study on Indian sandalwood found that low-lying, prostrate legumes are the most effective at improving parasite growth during nursery propagation due to limited light competition and increased nitrogen availability (Annapurna et al. 2006). Several studies have shown that a leguminous host species usually will provide better overall growth than non-leguminous hosts (Ouyang et al. 2015, Radomiljac and McComb 1998b). We recommend using koa as a container and field host, although it may need to be top pruned in either application to reduce light competition. Although koa is not a low-lying species, it is leguminous and commonly found in association with ʻiliahi on

Hawai‘i Island. Trials are underway to explore the host suitability of other native forest species and to examine the effect of a container host in nursery propagation and outplanting performance.

Depending on growing medium composition and nursery climate, ‘iliahi plants should be watered 1 to 3 times per week. Similar to germination trays, medium should be saturated evenly, then allowed to partially dry before rewatering. Excessive soil moisture can lead to root rot and stunt seedling growth. Environmental conditions vary among plant nurseries. Again, we recommend irrigation trials to determine the ideal watering regimen during this propagation stage. For lighting, we recommend 60 to 80 percent shade during the active growth period. Indian sandalwood seedlings grown under 80 percent shade developed favorable characteristics while those grown in full sun had the lowest survival rates (Barrett and Fox 1994).

Containers should be large enough to allow sufficient root development during the 10-to-12-month growth period in the nursery. The Hāloa ‘Āina nursery uses 46 in^3 (760 cm^3) containers with root pruning air-holes (028PIFD, Proptek Inc.; 3-in [7.6-cm] diameter by 8-in [21.6-cm] depth) to grow seedlings to maturity within 1 year (figure 10a). The air pruning holes reduce root bunching and circling at the bottom of the container and can improve new root growth formation after outplanting (Marler and Willis 1996). Indian sandalwood grown in 37 in^3 (600 cm^3) containers produced larger seedlings, compared with seedlings grown in polybags of equal or greater volume (Annapurna et al. 2004). An ‘iliahi stocktype trial is currently underway to evaluate other container types and sizes (figure 10b). When growing ‘iliahi with a container host, a larger container may be beneficial to accommodate the host’s root mass and to reduce light competition by placing seedlings farther apart.

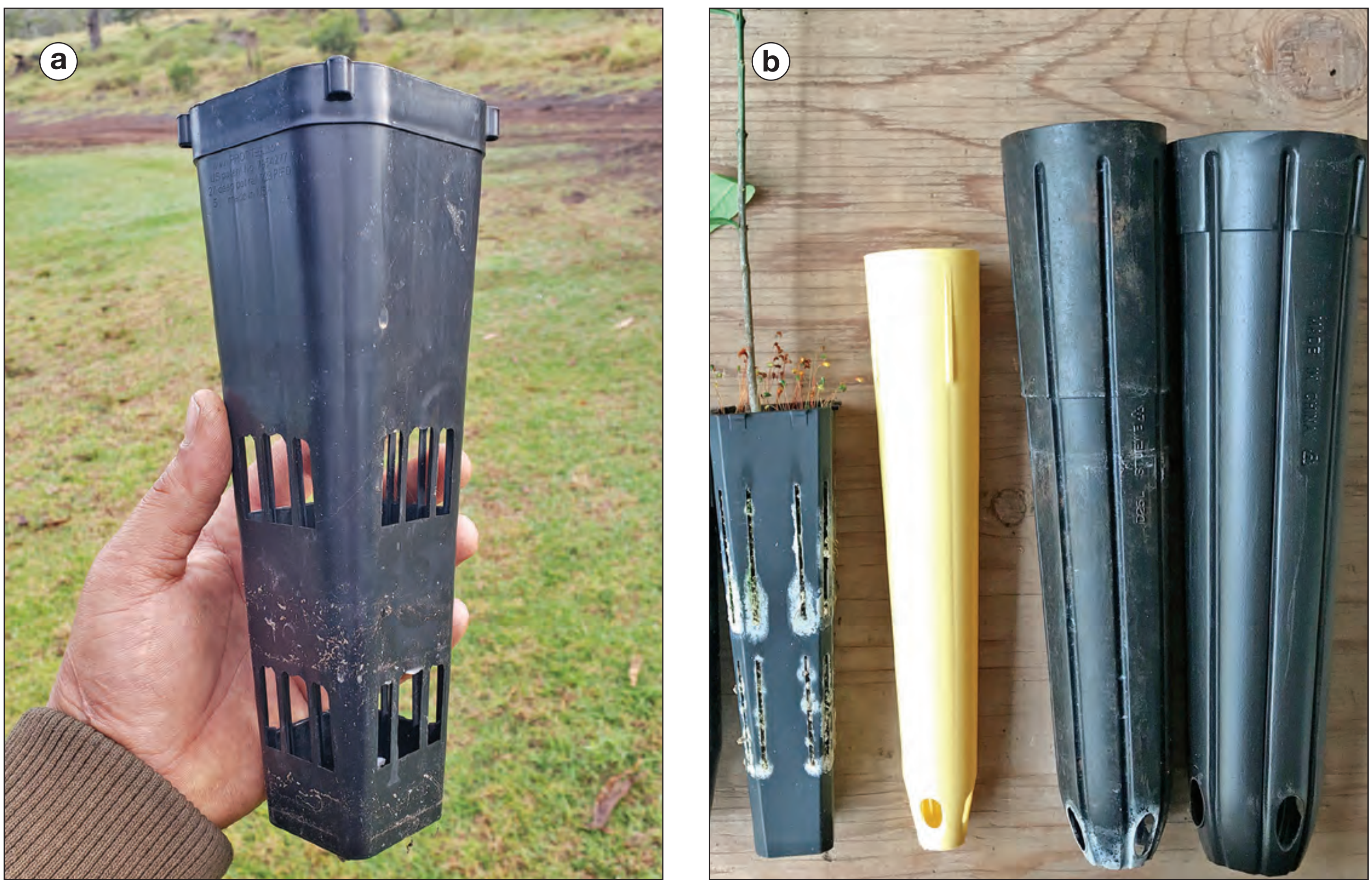

Figure 10. (a) Proptek 028PIFD containers (46 in^3 [760 cm^3]) have root pruning air holes that reduce root circling and bunching and have been used to grow ‘iliahi seedlings successfully. (b) Iliahi has also been successfully grown in other containers (left to right: Side Slit 150, Ray Leach SC10U, Deepot 25L, and Deepot 40L; Stuewe & Sons, Inc.; container specifications available at https://stuewe.com) and additional research is underway to further evaluate ‘iliahi growth in these containers (Photo a by T. Speetjens, 2019; photo b by E. Thyroff, 2020)

Figure 11. (a) ʻIliahi seedlings can be grown to outplanting size without a pot host in 1 year if fertilized appropriately. (b) ʻIliahi seedlings grown under suitable conditions for 1 year are ready to move to a hardening area where they will remain for at least 1 month before outplanting. (Photos by T. Speetjens, 2020)

Step 4: Field Planting

ʻIliahi seedlings are generally ready for outplanting 1 year after transplanting from the germination flat to the individual containers (figure 11). Ideally, seedlings ready for outplanting will have new shoot growth, root systems that fully occupy the container, adequate hardening (at least 1 month), and active haustoria development before outplanting (figure 12). Hardening should consist of moving seedlings from partial shade to full sun and reducing irrigation frequency without subjecting seedlings to harmful desiccation.

The target plant concept can be used to improve seedling survival and growth by matching seedling characteristics to the outplanting site (Dumrose et al. 2016). The ideal outplanting window is determined by expected precipitation timing for the specific outplanting site. Given ʻiliahi's hemiparasitic nature, it will ultimately require a host in the field to survive and thrive. Unfortunately, there is limited data on ʻiliahi field planting and interaction with hosts after outplanting. For Indian sandalwood, a field host provides supplemental water and nutrients, resulting in higher carbon assimilation rates (Rocha et al. 2014). Additionally, hosts of Indian sandalwood seedlings appear to aid in reduced drought stress as indicated by higher pre-dawn water potential for hosted sandalwood seedlings (Rocha et al. 2014).

Ideally, ʻiliahi should be planted next to an established host, but if no established hosts are present, then a container host should be used, and additional hosts should be planted concurrently (figure 13). The container host alone will not sufficiently support the parasitic need of ʻiliahi, so additional hosts will be needed to support long-term ʻiliahi seedling growth (Wilkinson 2007). Australian planting guidelines recommend planting at least 3 hosts per sandalwood (Brand 2005). As a general rule, distance between ʻiliahi and field hosts should not exceed the height of the host plant to optimize the chance ʻiliahi roots will

Figure 12. (a and b) Active haustoria formation, as shown on this 1-year-old ʻiliahi paired with mamane (*Sophora chrysophylla*), is desired at the time of outplanting and indicates the parasitic connection has been formed. (Photos by T. Speetjens, 2019)

encounter host roots. Additionally, ʻiliahi should also be planted on the south side of the host to reduce shading during dawn and dusk. In a plantation cultivation setting, Indian sandalwood has often been planted at a 10- to 20-ft (3- to 6-m) spacing with host plants interspersed (Page et al. 2012, Wilkinson 2007). Exploring the suitability of the large number of native plant species that could serve as hosts to ʻiliahi may be beneficial to long-term ʻiliahi restoration efforts (figure 13d). Several potential host species identified by anecdotal observations of nursery propagation, planting trials, and plant communities within remnant ʻiliahi stands. These potential hosts species include koa, koaiʻa, (*Acacia koaia* Hillebr.), ʻaʻaliʻi, ʻōhiʻa lehua (*Metrosideros polymorpha* Gaudich.), and māmane (*Sophora chrysophylla* [Salisb.] Seem.).

In Hawaiʻi, there are many limitations to restoration work including the need to protect seedlings from herbivory (Friday et al. 2015). This herbivory concern necessitates the protection of both ʻiliahi and its host.

Given the opportunities for forest restoration in Hawaiʻi, and considering ʻiliahi's once expansive range, there is great potential for ʻiliahi to be incorporated into many restoration projects and to be cultivated commercially. Various publications and guides for other sandalwood species worldwide may be complementary to efforts with ʻiliahi (Lu et al. 2020, Neil 1990, Noordwijk et al. 2001, Surata and Butarbutar 2008).

Pests of Concern

Several pests present major challenges to ʻiliahi cultivation. Rats (*Rattus* sp.) eat ʻiliahi seeds and can also kill seedlings by gnawing on the stem. Seeds in trees should be protected from rat predation using metal tree bands installed around the trunk of the tree to prevent rats from climbing up the tree trunk to reach seeds (figure 14a). Rats should also be excluded from germination trays using wire mesh cages (figure 14b). If left unchecked, a single rat can eat dozens of seeds per night.

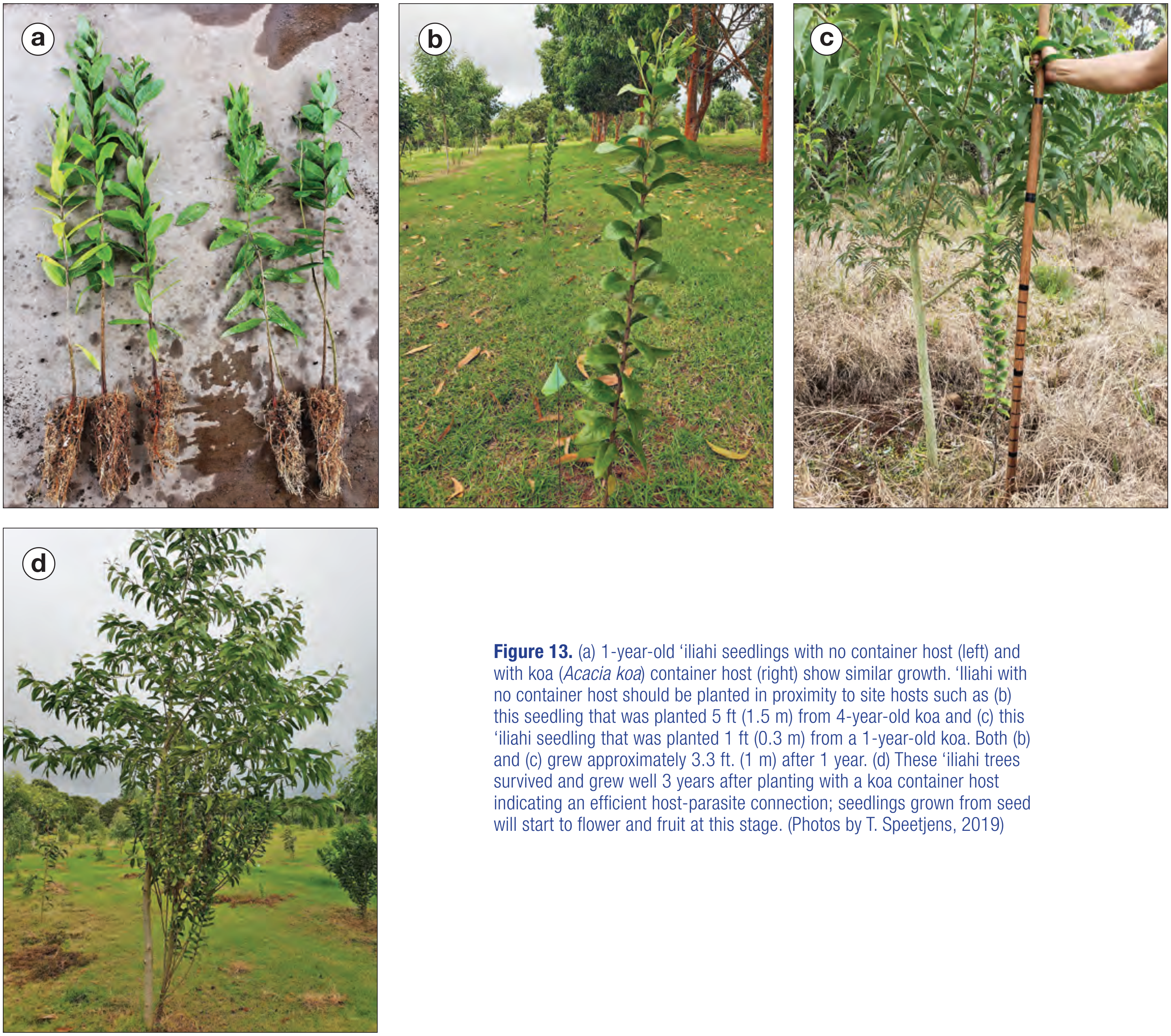

Figure 13. (a) 1-year-old ʻiliahi seedlings with no container host (left) and with koa (*Acacia koa*) container host (right) show similar growth. ʻIliahi with no container host should be planted in proximity to site hosts such as (b) this seedling that was planted 5 ft (1.5 m) from 4-year-old koa and (c) this ʻiliahi seedling that was planted 1 ft (0.3 m) from a 1-year-old koa. Both (b) and (c) grew approximately 3.3 ft. (1 m) after 1 year. (d) These ʻiliahi trees survived and grew well 3 years after planting with a koa container host indicating an efficient host-parasite connection; seedlings grown from seed will start to flower and fruit at this stage. (Photos by T. Speetjens, 2019)

Fungus gnats are a major contributor to embryo and cotyledon rot for young seedlings (figure 15). Fungus gnats (*Bradysia* sp.) thrive in excessively wet media containing organic matter. We observed less damage from fungus gnats in winter months at the high elevation Hāloa ʻĀina nursery at (4,500 ft [1,370 m]), suggesting fungus gnats may be negatively affected by colder temperatures (40 to 50 °F [4.4 to 10 °C]). Preventative measures against fungus gnats include controlling media moisture, top dressing with Growstone® gnat nix™, treating germination media with azadirachtin (AzaMax™), applying *Bacillus thuringiensis* var. *israelensis* to growing media, and placing a fine-mesh weed mat at the bottom of the germination flat. Gnat nix™ is a silica-based granule applied over the surface of the germination tray in place of gravel. This product acts as a mechanical control by creating an inhospitable physical barrier between the fungus gnats and the germination media. The fine mesh weed mat deters fungus gnat adults from entering the underside of germination flats. When using the weed mat, seedlings must be transplanted before the main root grows into the weed mat to avoid root damage upon extraction. *Bacillus thuringiensis* var. *israelensis* is an organic larvicide biocontrol available in pellet and powder form. This product kills fungus gnat larvae and is applied to the surface of media and watered in. The azadirachtin is applied as a drench at a concentration

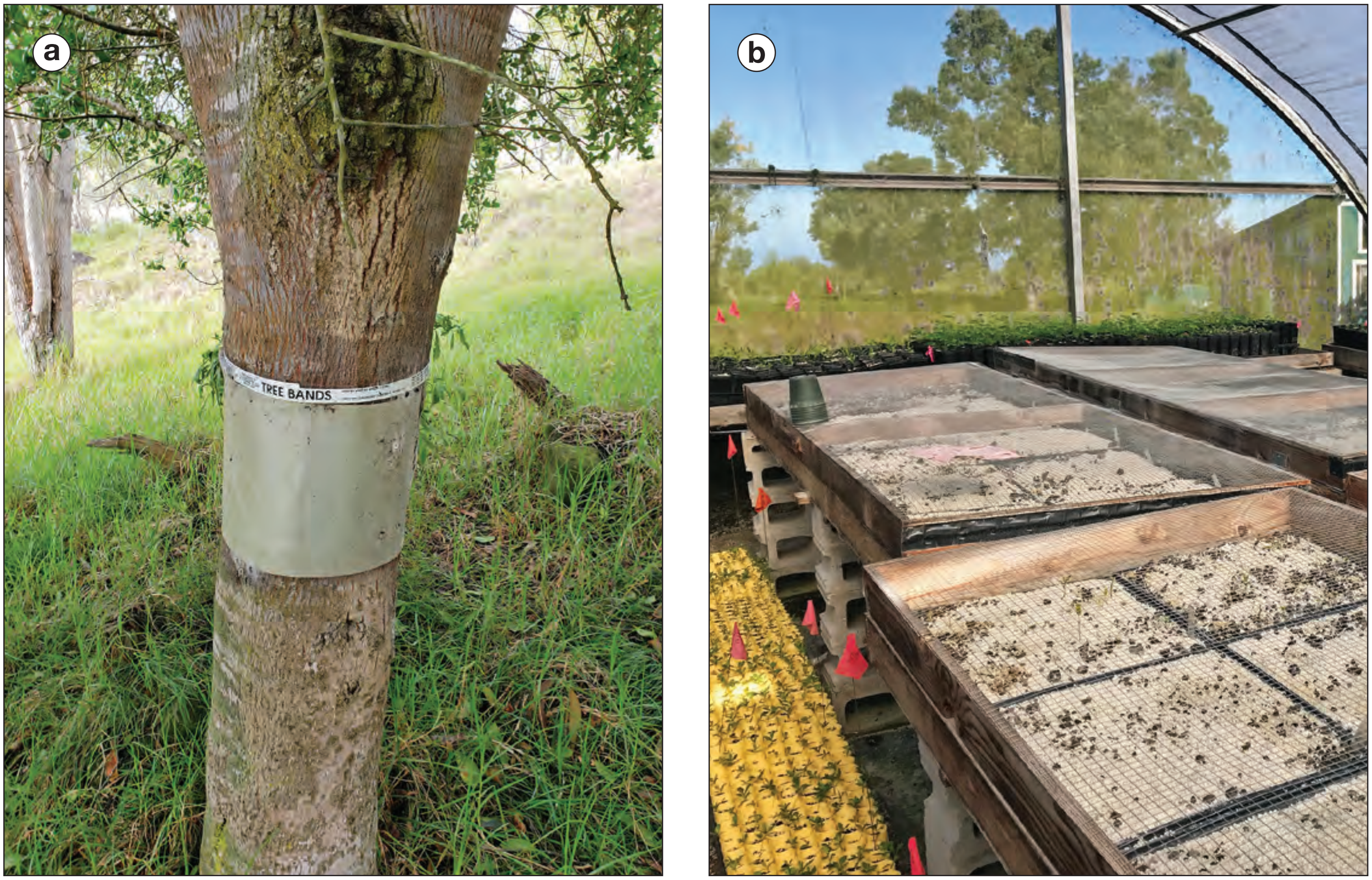

Figure 14. (a) Productive ‘iliahi (*Santalum paniculatum*) seed trees are fitted with metal bands around the trunk to prevent rats from climbing into the canopy and feeding on seeds. To protect ‘iliahi seeds from rodent predation in the nursery, (b) germination flats should be enclosed in a box with wire mesh screen covers. (Photos by E. Thyroff, 2020)

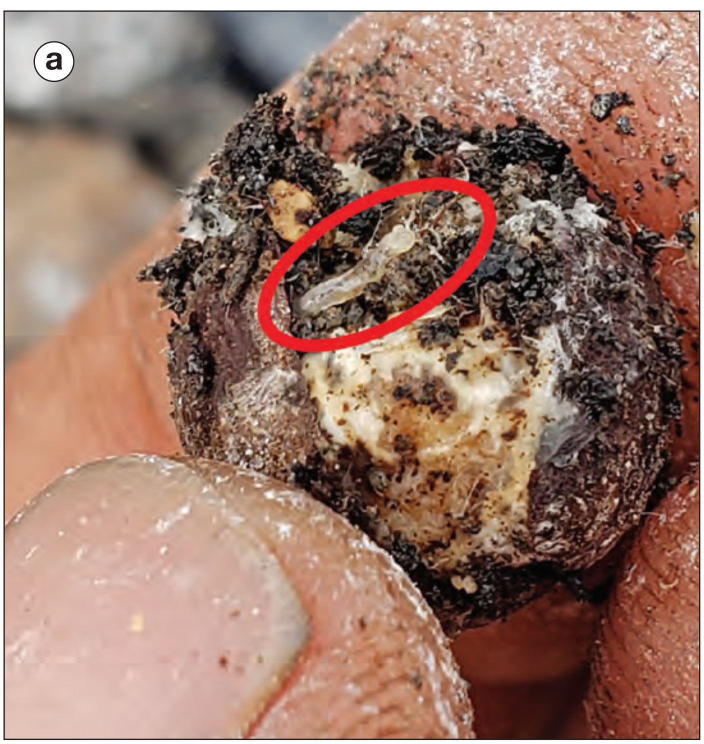

Figure 15. (a) Fungus gnat larvae will feed on ‘iliahi seed embryos, especially in association with embryo rot. (b) Seedling meristem rot is a common occurrence in germination flats infested with fungus gnat. (Photos by T. Speetjens, 2020)

of 0.04 to 0.08 percent every 2 to 3 weeks and can be used instead of a watering day. High concentrations of azadirachtin can burn radicals. Be sure to read and follow the label directions for all products.

Future Work

While foundational information exists for other sandalwood species within the *Santalum* genus, there is still a need for improved knowledge for ‘iliahi. The methods described in this article are the best recommendations at this time for producing healthy *Santalum paniculatum* seedlings and may be applicable to other ‘iliahi species. Some of these methods are anecdotal, however, and require further research. Propagators are encouraged to determine what methods work for specific ‘iliahi species, environmental conditions, and other factors (e.g., host species, climate, elevation, and light intensity).

Future research is much needed on ‘iliahi species to better understand seed dormancy, germination treatments, fertilizer response, vegetative propagation, stand management, host suitability, oil quality, genetics, and biocultural importance. Currently, the Tropical Hardwood Tree Improvement and Regeneration Center (https://www.trophtirc.org/) has several ongoing research projects that will expand our knowledge and recommendations for propagation and management of this valuable native species.

Address correspondence to—

Tawn Speetjens, PO Box 1118 Honoka‘a, HI 96727; email: tawnspeetjens@gmail.com; phone: 808-464-1234.

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