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RESEARCH ARTICLE

Tradeoffs in access to light and root networks of established host trees for restoration planting of the root hemiparasite *Santalum paniculatum*

Emily C. Thyroff[1,2], James B. Friday[1], Travis W. Idol[1], Michael A. Szuter[3], Douglass F. Jacobs[2,3]

Restoration of root hemiparasite trees, such as Hawai‘i's endemic *Santalum* species (‘iliahi), may benefit from underplanting in stands of suitable hosts like the nitrogen-fixing native tree, *Acacia koa* (koa). At a pasture site on Hawai‘i Island previously reforested with koa, we underplanted seedlings of the island-endemic sandalwood species, *Santalum paniculatum*, to examine the tradeoff between access to an established root network (distance to the nearest koa tree) under variable overstory shading (8.8–90.1% canopy openness range) during regeneration establishment. We hypothesized that there is an optimal parasite–host spacing and canopy openness that balance parasitic resource transfer with light availability. ‘Iliahi seedling survival was 96% with no survival treatment differences. ‘Iliahi seedling growth was positively related to canopy openness but negatively related to the distance to the nearest koa tree, and the slope of these relationships increased over time. Leaf photosynthetic light compensation points, light saturation points, and stomatal density mostly followed similar trends as growth. These results demonstrate that ‘iliahi can be successfully underplanted in an established koa stand, which benefits ‘iliahi plantings and contributes to diversifying initial restoration and reforestation plantings. There appears to be a significant tradeoff in planting distance between benefits from and competition with the host; however, the improvement in growth with increased canopy openness appeared to be much greater than the effect of planting distance. Underplanting into an established host stand with sufficient canopy openness can help restore functionally compatible and abundant ‘iliahi regeneration into forests.

Key words: ***Acacia koa*, Hawaiian sandalwood, ‘Iliahi, host plants, mixed species plantings, nitrogen-fixation, tropical forest restoration, underplanting**

Implications for Practice

- Underplanting *Santalum paniculatum* (and potentially other sandalwoods or hemiparasitic trees) in established stands of suitable host trees is recommended for access to well-established root systems.
- Established host roots with sufficient canopy openings provide an optimal tradeoff between benefits and competition from the host.
- While planting ‘iliahi under host trees younger than the 10-year-old koa in our study will provide more light availability, such stands will have less of an established root network, so the distance to the nearest host may be more important to consider. For planting under older hosts, less light may be available, so thinning the host stands to create gaps may be necessary to increase light.

Introduction

Silvicultural and ecosystem restoration techniques such as underplanting, using nurse trees, and enrichment plantings are used to diversify planted forests and to restore forest species with limited natural regeneration (Paquette et al. 2006; Rose et al. 2019; Messier et al. 2022). Specifically, underplanting, that is, the planting of seedlings under an existing forest or canopy cover, may benefit seedlings that thrive later in succession, are shade-tolerant, or are susceptible to browsing by ungulates (Dey et al. 2012; Maltoni et al. 2019; Thyroff et al. 2019). Facilitative interactions, which underplanting promotes, are known to be ecologically important and relevant in development of ecosystem restoration prescriptions (Brooker et al. 2008). The complexity of interactions, and potential cascading effects, between nurse plants (or existing canopy trees) and parasitic beneficiaries implores further investigation of plant community relationships (Melfo et al. 2020).

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Approximately 1% of all angiosperms are parasitic, and most are root hemiparasites (Heide-Jørgensen 2013; Matthies 2017). Hemiparasitic plants are capable of photosynthesis yet rely on their hosts to acquire resources such as water and nutrients to ensure their long-term survival (Bell & Adams 2011; Matthies 2017). Studies have found that hemiparasites photosynthesize at intermediate or relatively comparable rates to non-parasitic plants (Sandquist & Cordell 2007; Těšitel, 2016). Since hemiparasites can photosynthesize at comparable rates, the rate may change under varying light levels and affect performance of planted seedlings. Additionally, there is evidence suggesting that hemiparasites have relatively lower plant water potential to maintain a favorable flow of resources from the host to themselves (Radomiljac et al. 1999; Sandquist & Cordell 2007). Stomatal density may be one way to maintain lower water potential, in addition to stomata size and stomatal conductance. Root hemiparasites physically connect their roots to the roots of other plants with specialized root organs called haustoria (Bell & Adams 2011). Planting hemiparasites under established host plants, rather than planting hemiparasites and hosts simultaneously, may allow the hemiparasites to connect more quickly to host root systems and increase the capacity of resource supply from hosts. There may be tradeoffs, however, between the benefits of resource transfer from the host root system and competition with the host, especially for light (Matthies 1995). Beyond this hemiparasitic perspective, there is a diverse collection of literature regarding the intricate tradeoffs between competition and facilitation between plants in ecosystem restoration settings (Gómez-Aparicio et al. 2004; Brooker et al. 2008; Löf et al. 2014; Fagundes et al. 2023).

When underplanting, it is necessary to consider the balance between early access to the host root network and competition with the host, such as competition for light, water, and soil nutrients. For light competition, distance to the nearest host tree must be balanced with the overstory condition and resulting understory light level for the root hemiparasite. Adequate understory conditions depend at least partially on the ecophysiology of the underplanted species (Soto et al. 2017; Rose et al. 2019). Furthermore, shade tolerance of underplanted hemiparasitic trees may be dynamic; for example, a Indian sandalwood (*Santalum album* L.) study reported a range of light environments as seedlings progressed through early development (Barrett & Fox 1994). Seedlings in the highest shade treatment (80% shade) had greater survival and adaptive characteristics to sustain in shaded environments such as thinner, longer, and wider leaves with more chlorophyll than seedlings in the full sun treatment (Barrett & Fox 1994). Phenotypic plasticity, both physiological and morphological, is an adaptive strategy and important in understanding mechanisms that lead to regeneration and restoration success. As ʻiliahi is hemiparasitic, gas exchange and stomata plasticity may relate to photosynthetic capability and water potential maintenance (Benito-Garzón et al. 2013; Lawson & Michler 2014; Cavender-Bares & Ramírez-Valiente 2017; Löf et al. 2019).

Hemiparasitism in Hawaiian forests has been minimally studied, yet hemiparasitism was likely a major forest relationship based upon large estimated historical ranges of endemic *Santalum* spp. (Price et al. 2012), locally known as ʻiliahi or Hawaiian sandalwood. *Santalum* spp. occur throughout Oceania, with approximately a quarter of all *Santalum* spp. endemic to Hawaiʻi (Wagner et al. 1999; Harbaugh et al. 2010; Teixeira da Silva et al. 2016). Internationally, including in Hawaiʻi, *Santalum* spp. have been overharvested as valued sources of sandalwood oil and wood (Thomson et al. 2011). ʻIliahi was historically abundant in dry forests, but this forest type in Hawaiʻi has been reduced by 90% with only dispersed parcels remaining (Medeiros et al. 2014). Natural regeneration is uncommon due to depleted seed banks, limited remaining forest parcels, lack of seed dispersers, seed predators, and non-native herbivores. Given this deforestation legacy in Hawaiʻi and the unique hemiparasitic relationship, reforestation of ʻiliahi at degraded tropical dry forest sites also requires supporting host plant communities. Within the broader underplanting framework, ʻiliahi are anecdotally described as having poor tolerance of high shade levels, but young seedlings may benefit from moderate shade until strong parasitic root connections are made (Merlin et al. 2006). Increased light often encourages the establishment of species in wet forests of Hawaiʻi, but in drier forests, full sun may be detrimental due to increased temperatures and high evapotranspirational demands (Cordell et al. 2002; Inman-Narahari et al. 2013).

Due to its history and value, including cultural and ecological services and functions, there is significant local interest in restoring native Hawaiian forests, including regenerating ʻiliahi. One native plant that ʻiliahi species often pair well with is *Acacia koa* A. Gray (koa) (Merlin et al. 2006; Thomson et al. 2011; Thyroff et al. 2023). *Acacia* spp., overall, are identified as suitable nitrogen-fixing hosts for other *Santalum* spp. (Tennakoon et al. 1997; Brand et al. 2003; Nge et al. 2019). Koa's nitrogen fixation, fast growth, high water-use-efficiency, presence across large rainfall gradients, and tolerance to many abiotic factors (Gugger et al. 2018; Rose et al. 2019) increase its potential as a host for ʻiliahi. Koa is highly valued culturally and economically, and it is also planted widely to increase native bird habitat in forests previously converted to pastures (Friday et al. 2006; Pejchar & Press 2006; Gugger et al. 2018). Koa is often planted at reforestation and restoration sites due to its rapid early growth and ability to overtop remnant pasture grasses and herbaceous weeds (Scowcroft et al. 2008; Funk & McDaniel 2010; Scowcroft & Yeh 2013). Despite casting relatively low shade through its canopy, in part due to the orientation of mature phyllodes, koa is a light-demanding species (Baker et al. 2009; Rose et al. 2019); therefore, the ability of underplanted seedlings to capture available light is of interest. Due to pressures from invasive grasses, without intervening practices such as grass management or underplanting, planted koa in abandoned pastures will likely remain koa and grass with little other diversity (Scowcroft et al. 2008; Rehm et al. 2023). When other limiting factors are accounted for (e.g. removing ungulates), underplanting can be a successful method for diversifying initial reforestation efforts. Specifically, mature koa have relatively sparse canopies, which can be ideal for future underplanting of native species.

While hemiparasitism has been researched for other *Santalum* spp., literature on ʻiliahi is limited. We aimed to improve the survival and establishment of planted ‘iliahi (*Santalum paniculatum* Hook. & Arn., endemic to Hawai‘i Island) seedlings by better understanding how ‘iliahi performs when planted under established host canopies. We hypothesized that there is a tradeoff between canopy openness above the seedling and distance from ‘iliahi to the nearest host tree that would affect early parasitic resource transfer and shading of the seedling. With a denser overstory canopy and closer distance to the nearest host, competition for light, water, and nutrients may offset the increased opportunities for resource transfer via root parasitism. By contrast, lighter overstory canopy and farther distance to the nearest host may result in a less dense root network and exposure to environmental elements that reduces opportunities for root parasitism and increases site stressors. Thus, we predicted ‘iliahi underplanted among established koa with an intermediate canopy openness range, and intermediate distance to the nearest koa, will have better survival and growth due to access to koa roots and increased access to resources such as light availability, water, and nutrients. We also predicted that leaf gas exchange parameters and stomatal density would positively align with growth responses, as the physiological parameters would be a mechanism supporting seedling growth.

Methods

Experimental Site

The experiment was conducted at Kealakekua Mountain Reserve, an approximately 3900 ha property designated for forest restoration and sustainable forestry where harvesting, pasture establishment, and grazing have historically inhibited natural regeneration of native forest species, including ‘iliahi and koa. Kealakekua Mountain Reserve is within the ahupua‘a (land division usually extending from the uplands to the sea) of Kealakekua in the Kona moku (district) of Hawai‘i mokupuni (island) on the leeward slopes of Maunaloa (one of the five shield volcanoes comprising Hawai‘i Island), 1,450 m above sea level (Ulukau 2022). This area is considered seasonal mesic to moist mesic lower montane dry forest (Asner et al. 2005; Price et al. 2012), with summer mean daily high and low temperatures of 28.3 and 21.1°C, respectively; winter mean daily high and low temperatures of 24.6 and 10.1°C, respectively; and approximate annual precipitation of 730–830 mm, with a distinct wet season during the summer and dry season during the winter (Giambelluca et al. 2013; U.S. Climate Data 2021). In December 2022, strong winds from a kona low storm (Otkin & Martin 2004) bent and bowed many ‘iliahi. Only a few koa had downed branches. Soils at this site are Puukala medial silt loams: amorphic, isomesic Lithic Haplustands, which are shallow and well-drained soils that formed in basic volcanic ash over pāhoehoe lava (Natural Resources Conservation Service 2021).

In July 2010, a 0.81 ha plot (19.4981°N, 155.8082°W) within an actively grazed area (under previous land stewards) was fenced to exclude livestock and planted with koa seedlings for both native bird habitat and for ranches to have valuable native trees to potentially diversify future income. Pasture grass (*Cenchrus clandestinus* Hochst. ex Chiov.) was uniformly present in the fenced area. Within the fenced enclosed area, planting rows were sprayed with herbicide prior to the koa planting to control the pasture grass. Two hundred and seventy-one koa seedlings grown from local seed sources were planted on an irregular grid along the rows of controlled grass. Koa survival was 77% after the first year. Mortality was attributable to 2010 being one of the driest years on record for Hawai‘i Island (Frazier et al. 2022). Ten years after planting (August 2020), koa survival was 59%. Koa seedling mortality resulted in varying canopy gap sizes, creating a matrix of canopy openness, and resulting understory micro-environments. Anecdotally, presence of native birds at this specific site, especially ‘apapane and ‘amakihi, is an indication of successfully supporting native bird habitat through the establishment of koa stands in open pasture grasses. Of the 160 surviving koa, height and diameter (DBH, taken at 1.37 m) were measured for 68 individual koa (42.5% of all koa trees in the plot). Mean (± SE) koa DBH was 17.9 ± 0.59 cm and mean height was 10.1 ± 0.20 m. Overall, most of the 10-year-old koa trees were uniform in diameter and height as reflected in the small standard errors and were similarly spaced apart.

Plant Material and Experimental Design

Nine-month-old ‘iliahi seedlings grown in 760-cm^3 rectangular containers (028PIFD, Proptek, Belleville, MI, U.S.A.) were underplanted in the koa stand in August 2020. Seedlings were obtained from Hāloa ‘Āina Reforestation Project nursery in Kealakekua, Hawai‘i and grown from a local seed source. From baseline morphology analysis ($n = 20$), mean (± SE) seedling root-collar diameter was 5.5 ± 0.2 mm, height was 31 ± 1.0 cm, and root-to-shoot dry mass (g) ratio was 0.49 ± 0.02. Seedlings were sorted prior to planting and randomly assigned a planting site. Seedlings were hand planted with planting bars.

The underplanting resulted in a gradient of canopy openness above the seedlings. ‘Iliahi seedlings were planted on a precise grid, offset from the irregular koa planting grid, in 18 rows, each with 18 seedlings in a rectangular design with exactly 4.5-m spacing within and between rows (324 total seedlings; Fig. S1). To maintain planting density and intra-specific seedling competition, a perimeter of buffer ‘iliahi seedlings was planted 4.5 m from the research seedlings around the plot. Each ‘iliahi was an independent experimental unit and randomly assigned to a planting site. Pasture grass that had sufficiently grown back from the 2010 herbicide site preparation for koa planting was mechanically cut back using brush saws and hand clippers before planting and then every 3 months afterward for the first year after ‘iliahi seedlings were planted. A circle with a diameter of approximately 0.3 m was hand cleared around each seedling.

Measurements

At every seedling planting site, canopy openness was quantified by taking hemispherical photos with a Sony Mirrorless Digital Camera NEX Series camera (Sony Corporation, Tokyo, Japan) using a Madoka 180 hemispherical lens (Yasuhara, Hiroshima, Japan). All photos were taken 1 m above the ground, at a zero-degree zenith, oriented north, using a tripod-mounted level under homogeneous diffuse sky conditions. Photographs were analyzed with CIMES software (Gonsamo et al. 2011) to determine percent canopy openness. Additionally at each seedling planting site, the distance (m) from ‘iliahi to the nearest koa was recorded.

‘Iliahi seedling ground line diameter (mm) and height to the base of the apical meristem (cm) were recorded at the time of planting (August 2020) and every 6 months for 2.5 years (February 2023). Length of the main stem was used for the height at 2.5 years. At each measurement point ‘iliahi survival was recorded as a binary response; “alive” included seedlings with any number of green leaves.

Seedlings were assigned to one of five categories of canopy openness: 0–20, 20–40, 40–60, 60–80, or 80–100%. A subsample of 16 seedlings in each category of canopy openness was randomly selected for physiological measurements, resulting in 80 total sampling units.

Leaf gas exchange and stomatal density were measured 1 year after planting (August 2021). Leaf gas exchange was measured with a portable LI-6800 (LI-COR Biosciences, Lincoln, NE, U.S.A.) to create light response curves. One upper-canopy, fully expanded, recently mature leaf per tree was measured between the 10:00 and 14:00 hours. Light response curves were determined by measuring net CO_2 assimilation from 0 to 1600 μmol m^{-2} s^{-1}. Infrared gas analyzers of the LI-6800 (IRGAs; reference and sample) were matched at the beginning and end of each light curve measurement. Relative humidity (approximately 60%), vapor pressure deficit (<3.0 kPa), and temperature (leaf and block) were monitored for consistency. The gas exchange data point was taken after sample gas values (H_2O and CO_2) and net CO_2 assimilation were stable, based on coefficient of variation. If ‘iliahi leaves did not completely fill the 3 × 3 cm LI-6800 leaf chamber, gas exchange measurements were adjusted for actual leaf areas. Leaf areas were determined from a photo of the leaf in the chamber using ImageJ (National Institutes of Health, Bethesda, MD, U.S.A.). Light response curves were created by plotting net CO_2 assimilation (A_N, μmol CO_2 m^{-2} s^{-1}) against photosynthetically active radiation (PAR). The curves were fitted to a non-rectangular hyperbola (SigmaPlot V11.0, Systat Software, San Jose, CA, U.S.A.). Methodology to calculate final parameters from the model followed Chartier and Prioul (1976). Final parameters were used to calculate light compensation and light saturation points (μmol m^{-2} s^{-1}).

Stomatal density was calculated for the same 80 ‘iliahi seedlings used for gas exchange measurements using the same upper-canopy, fully expanded, recently mature leaf. Impressions of the adaxial and abaxial leaf surfaces were made in the middle of each leaf, midway between the midrib and the leaf margin. Leaf impressions were made on microscope slides using cyanoacrylate. Five leaf impression images (DCM 900 microscope CMOS Camera, Oplenic Optronics, Hangzhou, China) were taken of a 0.19 × 0.14 mm (0.0266 mm^2) area under 40× magnification using a microscope (BH-2 Microscope, Olympus, Tokyo, Japan). Stomatal counts were conducted using ImageJ and the cell counter plug-in (Kurt De Vos, University of Sheffield). For unbiased counting, all whole stomata were counted within the impression image area and stomata partially within the image were only counted on the top and right sides of the image area. Stomatal density (mm^{-2}) was calculated by dividing the number of stomata in the image by the image area. Leaf gas exchange and stomatal density parameters can provide insight to performance metrics and in cases increased parameters suggest better viability.

Statistical Analyses

All data were analyzed with R software version 4.2.0 (R Core Team 2022). Polynomial regression models were initially used for growth and physiological measurements with canopy openness as the continuous independent factor and distance to nearest koa as a covariate. Only the first linear terms were significant; therefore, linear models were subsequently used. Height and diameter were analyzed using linear mixed-effects models (lme function from the nlme package; Pinheiro et al. 2018) with canopy openness by time as a continuous independent variable, distance to the nearest koa by time as a continuous covariate, and individual tree identity as the random variable. For light compensation, light saturation, and stomata density, linear models were used with canopy openness as the independent variable and distance to nearest koa as the covariate. For survival, Kaplan–Meier was used to estimate the survival of seedlings over time. We note that with high survival at every time point, there were few mortality events to incorporate into the Kaplan–Meier estimate.

Fitted curves for each response variable were used to estimate the nature and significance of the relationship at $\alpha = 0.05$ level. Residuals from all response variables were tested to ensure normality and homogeneity of variance. Due to the use of continuous independent variables, a linear mixed-effects model was used to evaluate the effect of canopy openness and koa distance, instead of a repeated measures analysis of variance (ANOVA). The assumption of sphericity was not met for the data, but we concluded it was acceptable to proceed with the analysis because sphericity is not considered to be strictly necessary for mixed models, but compound symmetry is the more important aspect (Armstrong 2017; Muhammad 2023). Linear mixed-effects models allow for specification of the covariance structure to meet the assumption of compound symmetry. For our model, we specified a hierarchical covariance structure with time nested within subjects, allowing for analysis of the changes of treatment effect over time.

Results

Plot Characteristics

Canopy openness derived from the hemispherical photographs had a mean value of 35.9%, median value of 25.7%, and a range of 8.8–90.1%. Most seedlings in the canopy openness, especially the higher percent canopy openness, received direct

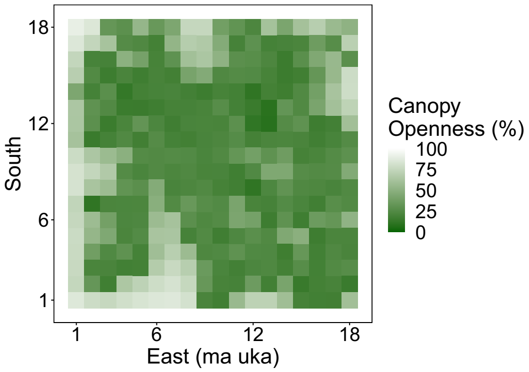

Figure 1. Heat map of the field site. Each square represents an ʻiliahi seedling. Canopy openness ranged from 8.8 to 90.1% with darker squares representing lower canopy openness and lighter squares representing higher canopy openness. The "1," "6," "12," and "18" axis labels reference the ʻiliahi planting design of 18 rows with 18 ʻiliahi seedlings per row.

overhead sunlight; therefore, they received higher rates than a typically understory would receive. Canopy openness varied throughout the underplanting grid (Fig. 1); however, there were more instances of lower canopy openness indicated by skewness of the distribution of canopy openness (Fig. S2A). The mean distance of ʻiliahi planting sites to the nearest koa was 3.3 m, median was 2.8 m, and with a range of 0.4–13.0, with a similar skewness of closer distances of ʻiliahi to the nearest koa (Fig. S2B). Canopy openness and distance to the nearest koa were highly correlated with an r^2 of 0.67 ($F_{[1,322]} = 666.2, p = <0.001$; Fig. 2). This collinearity between the fixed effects may cause some reduction in statistical power. However, we believe this is mitigated by the high number of planting sites (i.e. seedlings) in our study. Additionally, our models were within an acceptable range of variance inflation factor levels and our model estimators ran adequately.

Seedling Performance

Initial height and diameter of planted ʻiliahi were similar across canopy openness (Table S1). Over time, a relationship emerged between ʻiliahi growth and both canopy openness and distance to the nearest koa (Table S1). Canopy openness became a significant predictor of seedling diameter 1 year after planting; distance to nearest koa became a significant predictor of both height and diameter 2 years after planting (Table S2). Most notably, the model canopy openness coefficients were positive, while the distance to the nearest koa coefficients were negative (Table S1). These significant predictors are illustrated in Figure 4 with the final measurements taken 2.5 years after underplanting ʻiliahi seedlings. After 2.5 years, ʻiliahi survival was 96.0%; that is, of the 324 planted, only 13 died with no treatment differences for either canopy openness or distance to the nearest koa ($z = 0.11, p = 0.920; z = -0.50, p = 0.610$). After 2.5 years, height ranged from 22 to 359 cm (mean of 154 cm) and ʻiliahi diameter ranged from 4.5 to 48.2 mm (mean of 18.2 mm) with significant relationships for both canopy openness and distance to the nearest koa (Table S2; Figs. 3 & S3).

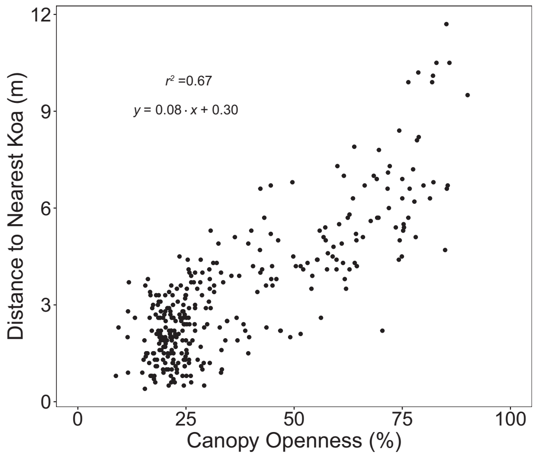

Figure 2. Scatterplot of distance to nearest koa (m) by canopy openness (%). The resulting r^2 value was 0.67 and linear equation of $y = 0.08 \cdot x + 0.30$.

Physiology Measurements

For gas exchange parameters, there were significant positive linear relationships for both light compensation ($F_{[2,72]} = 11.64$, $p = 0.001$) and light saturation points ($F_{[2,72]} = 51.69$, $p < 0.001$) with canopy openness (Fig. 4). Though both were significant, the relationship was relatively stronger for light saturation point ($r^2 = 0.41$) and weaker for the light compensation point ($r^2 = 0.13$). For the light compensation model, the distance to the nearest koa covariate did not significantly contribute to the model ($p = 0.986$), whereas for the light saturation model, the covariate did significantly contribute to the model ($p = 0.052$). Light response curves followed a similar trend (Fig. 5). From the leaf impressions, there were detected stomata on the abaxial (i.e. lower) leaf surface and stomatal density ranged from 7 to 33 mm^2. There were no detected stomata on the adaxial (i.e. upper) leaf surface. There was a significant positive relationship between stomatal density and canopy openness ($F_{[2,72]} = 11.64, p = 0.001, r^2 = 0.40$; Fig. 6). For the stomatal density model, the distance to nearest koa was on the margin of being a significant covariate ($p = 0.069$).

Discussion

Our research demonstrates that ʻiliahi, a hemiparasitic tree, can be successfully underplanted in a reforested stand of koa trees as indicated by overall high survival and growth rates. Variation in canopy openness due to koa mortality provided opportunities to plant ʻiliahi under conditions that favor rapid early growth. Koa stands have a relatively sparse canopy, canopy architecture with vertically oriented leaves, and low leaf area index (Pearson & Vitousek 2001; Denslow et al. 2006; Scowcroft et al. 2008). This could help to explain high survival even in the densest part of the experimental stand. Nevertheless, our results suggest that higher light environments facilitate greater ʻiliahi growth.

Research with *Santalum album* suggested shade is beneficial for early survival with mixed effects on growth (Barrett &

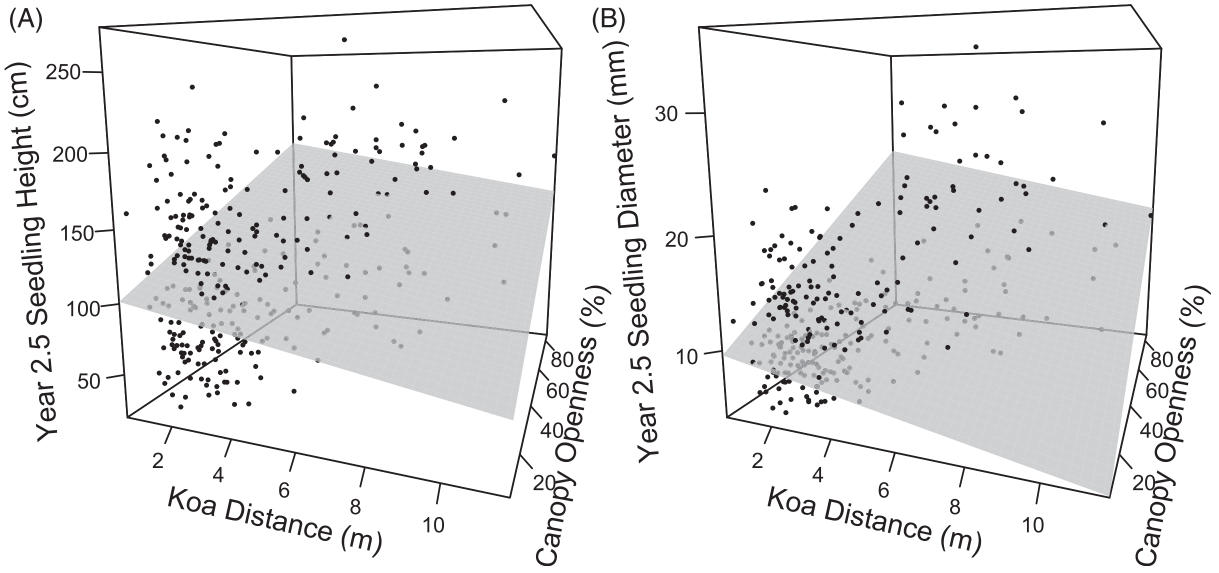

Figure 3. (A) Height (cm) and (B) diameter (mm) measured at 2.5 years after planting in relation to the distance to nearest host plant and canopy openness. The gray planes represent the least-squares regressions.

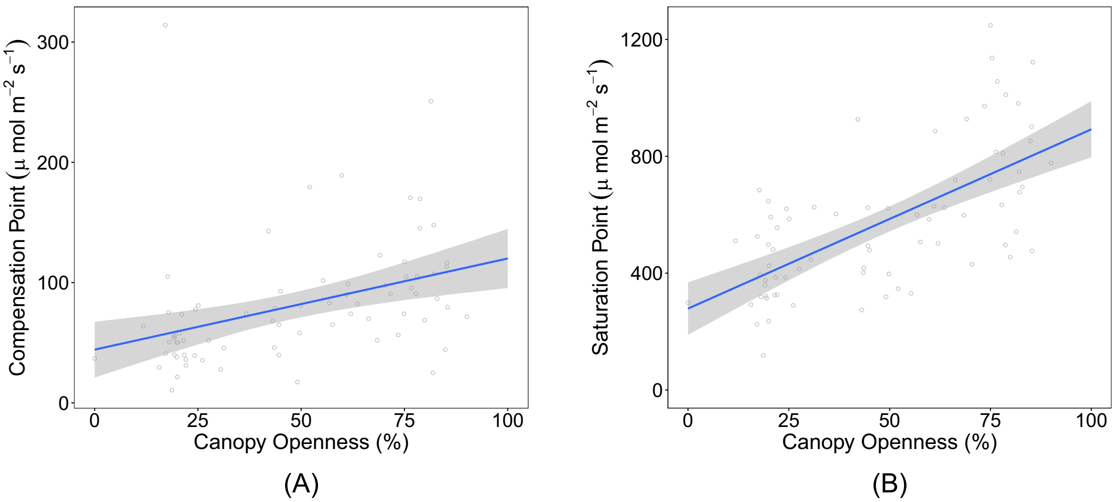

Figure 4. (A) Light compensation and (B) saturation points (μmol CO_2 m^{-1} s^{-1}) by canopy openness (8.8–90.1%) of ‘iliahi seedlings 1 year after planting. Gray shading indicates 95% CI. Gray points represent individual seedlings.

Fox 1994). Barrett and Fox (1994) hypothesized this was from less water loss due to reduced leaf temperature, transpiration, and soil evaporation. Merlin et al. (2006) also anecdotally suggested that the shade and protection from high temperatures provided by nearby established trees would benefit ‘iliahi until strong parasitic root connections could be made. Our results, however, showed linear growth and increased physiological responses with canopy openness. The increased growth, even in high canopy openness, may be due to the presence of an abundant and relatively uniform host root network, although the negative effect of the koa distance covariate indicated that proximity to the host is beneficial and dampens the positive relationship with canopy openness. Similar to other studies, seedlings were able to increase both photosynthesis and growth by using the increased available resources associated with increased canopy openness (Gómez-Aparicio et al. 2006; Soto et al. 2017; Thyroff et al. 2019).

Despite an assumed uniform host root network, when modeling canopy openness and koa distance together, we found that height, diameter, light saturation, and stomatal density increased significantly when ‘iliahi were planted closer to koa hosts. This effect of koa distance within the height and diameter models was not significant until the seedlings were 2 years old, 1 year longer than the detection of a significant relationship between ‘iliahi

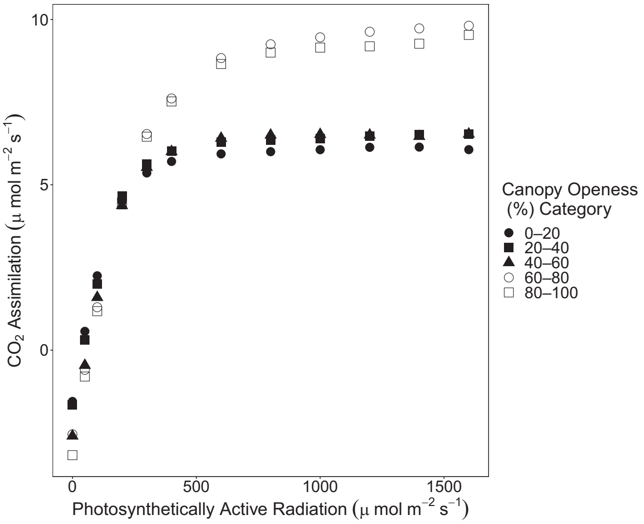

Figure 5. Mean light response curves for five canopy openness categories: 0–20, 20–40, 40–60, 60–80, 80–100%, $n = 16$.

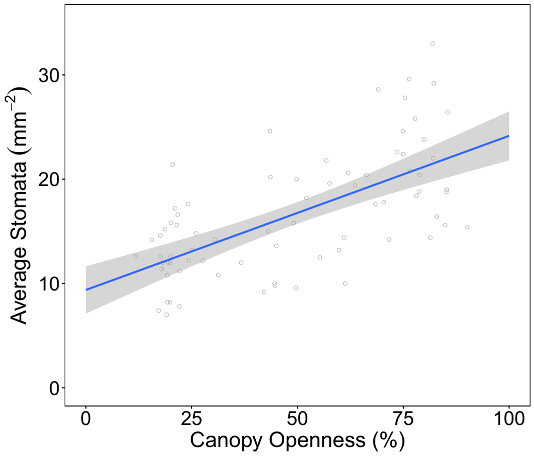

Figure 6. Stomatal density (mm^{-2}) on the abaxial (i.e. lower) leaf surface by canopy openness (8.8–90.1%) of ‘iliahi seedlings 1 year after planting. Gray shading indicates 95% CI. Gray points represent individual seedlings.

growth and canopy openness. This may suggest “early” parasitic root connections still require more than a year to become important enough to affect growth. This could also be due to reduced statistical power because of the collinearity between host distance and canopy openness. The significant physiological parameter differences after 1 year, when the growth parameters were not yet significant, may indicate treatment effects were already impacting seedling physiology, which in turn contributed to the significant seedling growth differences after 2 years. Similar trends in the beneficial effect of closer planting distance with a host on ‘iliahi growth were observed in a simultaneous ‘iliahi and host planting study (Thyroff et al. 2023). Underplanting within a well-established stand of koa seemed to mitigate this tradeoff between increased resources in higher canopy openness yet less root availability. ‘Iliahi, therefore, performed like most tree species by increasing growth with increasing light availability (Walters & Reich 1996; Sevillano et al. 2016; Rose et al. 2019). Koa is a notably fast-growing Hawaiian forest species (Scowcroft et al. 2007; Baker et al. 2009), which may rapidly provide a large and uniform enough root network for haustoria connections. Additionally, root hemiparasites are strong belowground resource competitors but appear to be relatively weak competitors for light (Atsatt & Strong 1970; Matthies 1995). With parasitic root connections, we hypothesize that the limiting factor for ‘iliahi seedling growth when underplanted shifted from belowground resources to primarily light-limited.

Physiology measurements also followed a linear response to canopy openness with higher light compensation, light saturation, and stomatal density with increased canopy openness, which supports the growth results. In particular, increased light saturation and stomatal density provided greater photosynthetic potential. This demonstrated plasticity could be beneficial for ‘iliahi to acclimate to different underplanting environments. Plasticity can also promote survival under environmental changes, particularly for sub-tropical and tropical broad-leaf evergreen trees (Lusk et al. 2008; Cavender-Bares & Ramírez-Valiente 2017). Underplanted ‘iliahi from this experiment had similar A_{net} (μmol m^{-2} s^{-1}) to ‘iliahi surveyed at a lowland dry forest site (Sandquist & Cordell 2007). Detection of stomata only on the abaxial leaf surface aligns with the results of Stemmermann (1980), who reported on several ‘iliahi species and varieties. *S. album* growing in western Australia also only had abaxial leaf surface stomata. In contrast to our results, Barrett and Fox (1994) found significantly more stomata for *S. album* in shaded treatments. Our growth and physiology results support other studies of successful seedling establishment in tropical dry forest canopy gaps likely due to ameliorated dry conditions (Lieberman & Li 1992; Cordell et al. 2002; Yelenik et al. 2015). We also acknowledge that had this study occurred over a time of water stress or drought rather than over a typical rainfall period (Jared et al. 2021), water relationships, including competition for water, may have been an important factor of consideration.

There are many other potential contributing factors to underplanting success, such as the age and development of the host canopy. For example, we recognize that canopy openness changes over time, so the effect of the gap that ‘iliahi experiences likely also changes over time.

In western Australia, *Santalum spicatum* was successfully established with 1- to 2-year-old *Acacia acuminata* (Brand et al. 2000). With a much younger host, the host canopy effects and host root development could become the primary limiting factor for establishment of planted seedlings. Naturally regenerated koa stands reached peak leaf area index around the age of the established koa in this study (Pearson & Vitousek 2001); therefore, koa hosts older than 10 years (as in our study at time of planting ‘iliahi) likely would not alter the observed effect on the planted seedlings as much as younger hosts would. The reasons for koa mortality in this stand are unknown. Drought was most likely a factor for the early koa mortality, given the dry period during the year the koa were planted (Giambelluca et al. 2013; Frazier et al. 2022). These rocky soils likely vary in stoniness and depth, which would affect water-holding capacity and thus susceptibility to drought. Wind also could have affected koa mortality given strong wind patterns in this area, especially during Kona low storms and in open grass pastures with no wind breaks. Even with mature koa, ʻiliahi seedlings still suffered from strong windstorms. Being underplanted could have exacerbated the effects of wind due to rapid growth and potentially lower root-to-shoot ratios because of rapid height growth in the understory.

As natural and artificial regeneration of koa can be very dense (Scowcroft et al. 2007; Friday 2011; Hamilton et al. 2021), underplanting ʻiliahi in a koa stand with little overstory mortality may result in uniformly low canopy openness. In this situation, to address just how dense koa can regenerate, another approach to establishing ʻiliahi under koa could be to pre-commercially thin the koa before underplanting ʻiliahi. This has been evaluated to improve productivity of selected koa trees (Scowcroft et al. 2007; Baker et al. 2009; Idol et al. 2017). ʻIliahi could then be planted in the canopy gap near released crop trees to optimize planting distance with canopy openness. This approach, however, requires determining harvesting logistics and likely a group selection final harvest to reduce potential damage.

Similar to results with *S. album* (Das 2021), ʻiliahi appears to grow well under partial shade during the establishment phase of regeneration. Root parasites and even root hemiparasites, such as *Santalum* (sandalwood) spp., can also weaken and kill the host, so it is common when establishing sandalwood plantations to plant multiple hosts, including at least one "intermediate host" that is not expected to live more than a few years (Radomiljac et al. 1999; Page et al. 2012). This may be another benefit of underplanting a root hemiparasite, as the much larger host should be able to survive parasitic resource transfer for many years and share the burden among a number of hosts as the root hemiparasite grows. Two and a half years after planting, our results indicate that relatively low canopy openness may be suitable to establish ʻiliahi, yet higher canopy openness promotes early growth. Proximity to host trees also appears to be beneficial and indicates a balance between light availability and access to host root networks is required for underplanting hemiparasitic seedlings. It will be interesting to follow whether ʻiliahi can tolerate shade in later establishment stages, as does *S. album* (Das 2021). To relate our underplanting results to a control (i.e. ʻiliahi not underplanted), we can tentatively draw comparisons to Thyroff et al. (2023). In that study, only 250 m away from this underplanting study, ʻiliahi seedlings of a similar size were planted simultaneously with koa seedlings at different distances. The second-year mean measurements for ʻiliahi seedlings simultaneously planted with koa seedlings across distances were lower at 78% survival, 79 cm height, and 9.6 mm diameter than the second-year measurements of this underplanting study at 98% survival, 118 cm height, and 12.5 mm diameter. This anecdotal comparison lends further support to underplanting as an effective silvicultural technique for establishing *Santalum paniculatum* and other ʻiliahi in Hawaiʻi.

Our study results contribute to a better understanding of ʻiliahi establishment within gaps of established hosts and help improve silvicultural efforts to restore functionally compatible and diverse native forests in Hawaiʻi. The contrasting positive canopy openness and negative koa distance effects help illustrate the complexity of hemiparasitism. These effects, as well as many other potential variables in this study, make specific planting recommendations more complex. However, our results suggest that underplanting ʻiliahi would be successful and appropriate in many naturally and artificially regenerated koa stands, particularly for those persisting in an overly simple koa and grass system (Scowcroft et al. 2007; Friday 2011; Hamilton et al. 2021). By planting ʻiliahi under established trees with an abundant root network to connect to, the focus can turn toward increasing the amount of light reaching ʻiliahi. Planting ʻiliahi can begin the diversification process, and if one of the goals is to support ʻiliahi, identification and planting of other beneficial hosts would continue to increase diversity.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. (A) Drone image of koa stand in 2020, the same year the ʻiliahi were planted (B) drone image of koa stand with illustrative rendering of the ʻiliahi grid overlaid.

Figure S2. (A) Histogram of canopy openness data (B) histogram of distances to the nearest koa data.

Figure S3. (A) ʻiliahi in lower canopy openness and (B) ʻiliahi in lower canopy openness 2.5 years after planting, February 2023.

Table S1. General linear mixed model equations for data collected at the time of planting and then 6 months, 1 year, 1.5 years, 2 years, and 2.5 years after planting.

Table S2. Associated t values, *p* values, and degrees of freedom (DF) derived for height and diameter models for data collected at the time of planting and then 6 months, 1 year, 1.5 years, 2 year, and 2.5 years after planting.

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