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Co-planting of a fast-growing, nitrogen-fixing host tree facilitates regeneration of the root hemiparasitic ʻiliahi (Hawaiian sandalwood)

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ABSTRACT

Root hemiparasitic trees can photosynthesize yet also acquire resources from host plants, which may benefit the long-term survival and growth of the hemiparasite. Experimental evaluation of planting distance between tree hemiparasites and their hosts can lead to biological insights and contribute to practitioner decision making. On an abandoned pasture site in a historically tropical dry forest in Hawaiʻi, we studied the effects of two host species and four planting distances on the survival and growth of ʻiliahi (Hawaiian sandalwood, *Santalum paniculatum*), an endemic root hemiparasitic tree. Treatments included a control with no host or one of two native host species: ʻaʻaliʻi (*Dodonaea viscosa*), a fast-growing shrub, or koa (*Acacia koa*), a fast-growing nitrogen-fixing tree. ʻIliahi and host seedlings were planted at a distance of <0.2, 0.5, 1.0, or 2.0 m from each other. After three years, survival of ʻiliahi seedlings was greatest for ʻiliahi paired with koa at 1.0 m (88 %) compared to the control with no host (53 %) and when paired with koa at 2.0 m (55 %). Height and ground line diameter of ʻiliahi seedlings were greater when paired with koa at closer distances than with ʻaʻaliʻi at any distance or the control with no host. Specifically, ʻiliahi growth was greatest when paired with koa at <0.2 m distance. Foliar nitrogen concentration was greater for ʻiliahi paired with koa at <0.2, 0.5, and 1.0 m distances, whereas the other foliar nutrient concentrations were typically greater for the ʻiliahi control with no host. For sites with few or no pre-established hosts, such as abandoned pastures, ʻiliahi growth can be greatly improved by co-planting in proximity to koa. As with other *Santalum* spp., early and abundant parasitic root connections with a host, especially a nitrogen-fixing host, are likely important for ʻiliahi establishment and early growth.

1. Introduction

Hemiparasitic plants are capable of photosynthesis yet also benefit from host plants by acquiring resources to ensure their long-term survival (Bell and Adams, 2011; Matthies, 2017). Root hemiparasites have specialized root structures called haustoria that connect hosts' roots and transfer resources (Barkman et al., 2007; Bell and Adams, 2011). For example, nitrogen acquired from hosts can comprise large proportions of total nitrogen content in hemiparasites (Cameron and Seel, 2007; Lu et al., 2014; Tennakoon et al., 1997b). Host plants may also be competitors for available resources (Das, 2021a). Host suitability differs by species, as indicated by variable hemiparasitic performance (Irving and Cameron, 2009; Matthies, 2017; Nge et al., 2019). Hosts are classified as suitable when the hemiparasite experiences vigorous performance, i.e., greater survival, height and diameter, compared to performance with other hosts or growing without a host (Brand, 2009; Nge et al., 2019; Ouyang et al., 2015; Teixeira da Silva et al., 2016).

The *Santalum* genus (Santalaceae family), commonly referred to as sandalwoods, is a large group of root hemiparasitic trees and are part of ecosystems in Australia, India, and throughout the Pacific Ocean (Hamilton and Conrad, 1990; Teixeira da Silva et al., 2016; Wagner et al., 1999). Six of the 24 currently recognized *Santalum* spp. are endemic to the Hawaiian Islands (Harbaugh et al., 2010) and locally known as ʻiliahi. The aromatic heartwood imparts cultural and economic

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importance, which has led to the overexploitation of most *Santalum* spp., including ʻiliahi (St. John, 1947; Teixeira da Silva et al., 2016; Thomson et al., 2011). Natural regeneration of many native Hawaiian trees, including ʻiliahi, is limited by several factors. Examples include seed predation, low germination rates, herbivory, competition from invasive plants, decline or loss of pollinators, and greatly increased frequency and spread of wildfire (Friday et al., 2015; Pau et al., 2009; Speetjens et al., 2021; Thaxton et al., 2012). Artificial regeneration (e.g., tree planting) of ʻiliahi, therefore, is necessary to restore populations of ʻiliahi across their natural range. Given the hemiparasitic nature of ʻiliahi and limitations to natural regeneration of native species, success is likely dependent upon the effective establishment of both the hemiparasite and hosts (Das, 2021a). Aspects of hemiparasite and host plant interactions have been researched for other *Santalum* spp. (Pullaiah et al., 2021; Teixeira da Silva et al., 2016), although distance between *Santalum* spp. and their hosts is lacking experimental insight.

A wide diversity of native and non-native plant species co-occur with ʻiliahi in dry forests, potentially serving as hosts. For reforestation and restoration efforts, however, there is a strong impetus to incorporate native species for many reasons, including biocultural and economic values (Friday et al., 2022). Nitrogen-fixing woody plants, such as *Acacia* spp., have been identified as suitable and preferential hosts for many *Santalum* spp. given the importance of acquiring nitrogen for seedling performance (Lu et al., 2014; Nge et al., 2019; Radomiljac et al., 1999a; Veillon and Jaffré, 1995; Woodall and Robinson, 2003). In Hawaiʻi, an endemic nitrogen-fixing tree, koa (*Acacia koa* A. Gray), could be a preferred host species to ʻiliahi and by practitioners. Koa is a common forest restoration species, given its relatively high survival as a planted seedling, fast early growth, and ability to create a suitable understory for other native plants at maturity (Hamilton et al., 2021; Jacobs et al., 2020; Rose et al., 2020; Scowcroft et al., 2008). The native shrub ʻaʻaliʻi (*Dodonaea viscosa* Jacq.) has mixed host suitability reports to *Santalum* spp. (Mwang'ingo et al., 2005; Rocha and Santhoshkumar, 2022; Soosairaj et al., 2005; Thomson et al., 2011). ʻAʻaliʻi is common in Hawaiian dry forests and is planted in restoration projects, given its high survival, growth, and ability to facilitate recruitment of other native plants (Yelenik et al., 2015). Classified as a shrub or small tree, ʻaʻaliʻi could be a less competitive host than the even quicker growing koa. Lastly, many hosts can be paired with ʻiliahi simultaneously, whether to resemble a native forest, in a mixed species plantation, or part of an agroforestry system (Das, 2021b; Goswami, 2014; Lu et al., 2020; Thomson, 2006; van Noordwijk et al., 2001).

When planting hemiparasites with a host plant, the distance between species can vary and is an important consideration (Page et al., 2012). Few studies have experimentally examined host distance, and the effect of distance may depend on the host species (Keith et al., 2004). The distance between the hemiparasite and host may influence how quickly and how many parasitic connections form, and also influence the likelihood that competition for light may diminish benefits of host connections (Keith et al., 2004). While establishing haustoria for resource transfer is likely important for long-term survival and growth of ʻiliahi, there must be balance between parasitic resource transfer and competition both above- and below-ground. Determining an effective spacing between ʻiliahi and its hosts is complicated because the size of the plants, resource requirements, and competitiveness will likely change over time, as observed with other *Santalum* spp. (Hamilton and Conrad, 1990; Thomson et al., 2011).

This study aimed to improve ʻiliahi (*Santalum paniculatum* (Hook. & Arn.), endemic to Hawaiʻi Island) regeneration success through our understanding of ʻiliahi and host interactions. Specifically, survival and growth over three years were assessed when ʻiliahi was co-planted with native dry forest host species (koa or ʻaʻaliʻi) at varying distances from each other. We hypothesized that ʻiliahi seedling performance would be greater when (i) paired with a host compared to no host, (ii) paired with a nitrogen-fixing tree versus when paired with a non-nitrogen-fixing shrub, and (iii) planted closer to the host (e.g., <0.2, 0.5 m).

2. Materials and methods

2.1. Experimental site

This experiment was conducted at Kealakekua Mountain Reserve, an approximately 3,900-ha property designated for tropical dry forest restoration and sustainable forestry where forest harvesting, pasture establishment, and grazing have inhibited natural regeneration of native forest species, including ʻiliahi. Non-native pasture grass (kikuyu, *Cenchrus clandestinus* Hochst. ex Chiov.) dominate the experimental site (19.4960° N, −155.80841° W). Kealakekua Mountain Reserve is within the ahupuaʻa[1] of Kealakekua in the Kona moku[2] of Hawaiʻi mokupuni[3] on the slopes of Maunaloa[4], 1,450 m above sea level. Overall, the slope does not exceed 5 %, but slope is locally heterogenous due to the underlying lava flow terrain. This area is considered lower montane dry forest (Asner et al., 2005), with mean wet season (i.e., summer in Kona) maximum and minimum temperatures of 28.3 and 21.1 °C, respectively; mean dry season (i.e., winter in Kona) maximum and minimum temperatures of 24.6 and 10.1 °C, respectively; and mean annual precipitation is 736 mm (U.S. Climate Data, 2021). The experimental site is on a lava flow estimated to be 1,500 – 3,000 years old (Sherrod et al., 2021). Soils are a mixture of Puʻukala medial silt loams (medial-skeletal, amorphic, isomesic Lithic Haplustands), and Kēkake organic soils (euic, isomesic, micro Lithic Ustifolists) (NRCS, 2021). Both are shallow and moderately- to well-drained soils formed in variable amounts of organic material mixed with basic volcanic ash over pāhoehoe lava (NRCS, 2021).

2.2. Plant material

The three native plants used in this experiment were ʻiliahi, koa, and ʻaʻaliʻi (Table 1). The source used for all three species were open-pollinated seeds from Hawaiʻi Island (Kona moku[2]) and germinated based on a June 2019 planting date (Table 2). All seedlings were grown in hard-walled plastic containers at the Maui Native Tree Nursery in Kula, Hawaiʻi. Seedlings were sorted for consistency prior to planting.

2.3. Experimental design and treatments

This experiment was established as a completely randomized design and structured with 40 columns spaced 3 m apart (Supplemental Fig. 1). Columns were oriented 60 °/240 ° along the contour to account for site topography. Each column had nine rows spaced 6 m apart resulting in 360 experimental units. One of nine treatments, with 40 replicates per treatment, were randomly assigned to each experimental unit: ʻiliahi with (1) no woody host (control), (2) koa at <0.2 m, (3) koa at 0.5 m, (4) koa at 1.0 m, (5) koa at 2.0 m, (6) ʻaʻaliʻi at <0.2 m, (7) ʻaʻaliʻi at 0.5 m, (8) ʻaʻaliʻi at 1.0 m, and (9) ʻaʻaliʻi at 2.0 m. The planting distances were implemented within set ranges. The closest distance, <0.2 m, was as close as possible. The next distance was set between 0.25 and 0.5 m, followed by 0.75–1.0 m, and lastly 1.75–2.0 m. If the treatment had an assigned host, then the host was planted within the column with its respective treatment distance on the western (ma kai) side of the ʻiliahi seedling. This planting arrangement resulted in a uniform distance of 3 m between columns and a variable distance between experimental units within a column depending on the distance the host was planted from ʻiliahi; however, regardless of the ʻiliahi-host distance, the minimum distance between experimental units within a column was 4 m. Each column had a koa seedling at the eastern (ma uka) end to account for

[1] ahupuaʻa: land division usually extending from the uplands to the sea (Ulukau, 2022).

[2] moku: district (Ulukau, 2022).

[3] mokupuni: island (Ulukau, 2022).

[4] Maunaloa: one of five shield volanoes comprising Hawaiʻi Island.

Table 1
Common name, scientific name, family, host-parasite relationship, nitrogen-fixing, and stature at maturity for the three species in the experiment: ʻiliahi, koa, and ʻaʻaliʻi.

Common name	Scientific name	Family	Host-Parasite Relationship	Nitrogen-fixing	Stature at maturity
ʻiliahi	*Santalum paniculatum*	Santalaceae	Hemiparasite	No	Large tree
koa	*Acacia koa*	Fabaceae	Host	Yes	Large tree
ʻaʻaliʻi	*Dodonaea viscosa*	Sapindaceae	Host	No	Shrub/ small tree

Table 2
Common name, outplanting age (months), nursery container, and initial height (cm) and diameter (mm) (±SE) for the three species in the experiment: ʻiliahi, koa, and ʻaʻaliʻi. D40 and SC10 nursery containers are cylindrical containers with volumes of 656 and 164 mL, respectively (Stuewe & Sons, Inc., Tangent, OR, USA).

Common name	Outplanting age (months)	Nursery container	Initial height (cm)	Initial diameter (mm)
ʻiliahi	12	D40	45 (0.7)	4.7 (0.05)
koa	3	SC10	38 (0.6)	3.1 (0.05)
ʻaʻaliʻi	8	SC10	28 (0.5)	2.6 (0.04)

potential border host effects. There was a 5-m buffer between the experimental site and other reforestation plantings.

Site preparation was completed in June 2019. Using an excavator, the grass was removed, and the ground scraped to expose soil from lava rock. As the grass grew back, competition and potential parasitism with the grass were assumed to be homogenous across each ʻiliahi planting. One year after planting, a grass-specific herbicide (24.5 % active ingredient fluazifop-P-butyl, Fusilade® DX, reg. no. 100–1070, Syngenta Crop Production LLC, Greensboro, NC, USA) was aerially applied to the experimental site and surrounding area to reduce grass competition.

2.4. Measurements

At the time of planting (June 2019), height (cm) to the base of the apical meristem and ground line diameter (mm) were measured for all seedlings (ʻiliahi and hosts). Height and diameter were re-measured three years after planting for all plants. Survival of both ʻiliahi and hosts was recorded as a binary response (i.e., alive or dead). Foliar nutrient concentration (%) (i.e., N, P, K, Ca, Mg, S) was assessed for a subsample of ʻiliahi seedlings. For each subsample, 3–5 leaves from the upper one-third portion of the plant were collected and dried at 60 °C for 48 h. Dried samples were composited, pulverized, and analyzed at the University of Hawaiʻi at Hilo Analytical Lab.

2.5. Statistical analyses

All data were analyzed with R software version 4.2.0 (R Core Team, 2022). Because we included a no host control treatment, the experimental design was not a full factorial between host species and planting distance and we could not analyze the data with a two-way ANOVA. Therefore, the independent variable was treatment with nine levels. ʻIliahi survival was analyzed with a logistic regression. ʻIliahi height, diameter, and foliar nutrients were analyzed with one-way ANOVA with treatment as the fixed factor. Koa and ʻaʻaliʻi height and diameter were analyzed separately with one-way ANOVA with planting distance as the fixed factor. Regressions were used to compare ʻiliahi growth and host growth for each treatment. Residuals from all response variables were tested to ensure normality and homogeneity of variance. ʻIliahi diameter was log-transformed to meet assumptions. If a significant treatment effect was detected ($p \leq 0.05$), the multcomp package (Hothorn et al., 2008) was used to run Tukey's HSD test for pairwise comparisons ($\alpha = 0.05$ level).

The hemiparasitic nature of ʻiliahi added noteworthy methods and statistical considerations. First, ʻiliahi could be parasitizing the pasture grass; however, because grass cover was relatively uniform across the site, if the grass was parasitized, we assumed this equally affected all treatments. Second, we removed ʻiliahi from the dataset for instances where ʻiliahi survived, but its host died, n = 19. Third, we removed ʻiliahi from the dataset for instances where koa naturally regenerated and likely affected treatments by introducing an additional host(s), n = 7.

3. Results

Initial height and diameter of planted ʻiliahi were similar across all treatments with an overall mean height of 45 ± 0.7 cm ($F_{8,343} = 1.27$, $p = 0.257$) and an overall mean diameter of 4.7 ± 0.05 mm ($F_{8,343} = 1.90$, $p = 0.585$; Table 2). After three years, ʻiliahi survival was only significantly greater when paired with koa at 1.0 m distance than ʻiliahi with no host and ʻiliahi paired with koa at 2.0 m ($X^2_{8,344} = 22.20$, $p = 0.005$; Fig. 1).

There was a significant treatment effect for both height ($F_{8,246} = 9.77$, $p < 0.001$) and diameter ($F_{8,246} = 5.71$, $p < 0.001$). After three years, mean ʻiliahi seedling height and diameter were consistently greatest when paired with koa at <0.2 m (Fig. 2). Height and diameter were next greatest with koa at 1.0 m. ʻIliahi height and diameter when paired with ʻaʻaliʻi was comparable to the control (Fig. 2).

For the host plants, average host survival three years after planting was 85.6 % for koa and 91.9 % for ʻaʻaliʻi. Koa height and diameter was 563.43 ± 10.86 cm and 105.10 ± 1.96 mm three years after planting. ʻAʻaliʻi height and diameter was 181.84 ± 6.28 cm and 34.33 ± 1.01 mm three years after planting. Host position did not affect height or diameter for either koa ($F_{3,101} = 1.48$, $p = 0.225$; $F_{3,101} = 2.67$, $p = 0.058$, respectively) or ʻaʻaliʻi ($F_{3,110} = 0.70$, $p = 0.553$; $F_{3,110} = 1.40$, $p = 0.246$, respectively), nor were there significant regression relationships between ʻiliahi growth and growth of either host when analyzed separately for each of the four distance treatments.

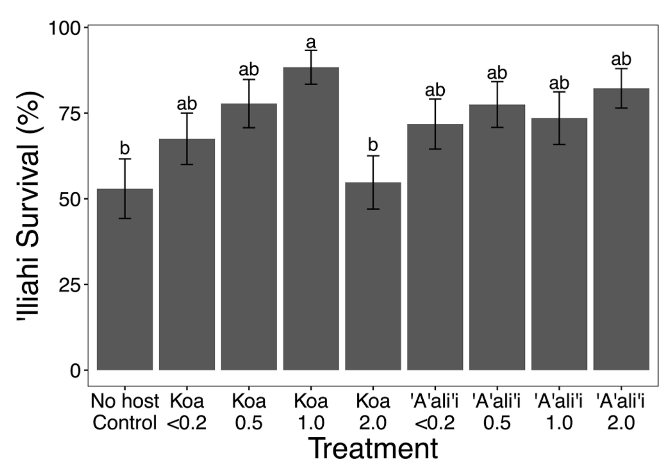
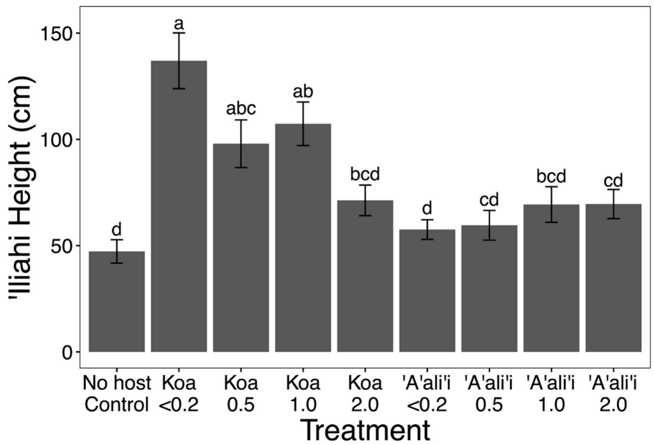


Fig. 1. Mean percent survival (%) (±SE) of ʻiliahi seedlings three years after planting. ʻIliahi seedlings were planted either by itself with no host or with koa or ʻaʻaliʻi at four distances (<0.2, 0.5, 1.0, or 2.0 m away from ʻiliahi). Different letters indicate significant differences among the nine treatments ($\alpha = 0.05$).



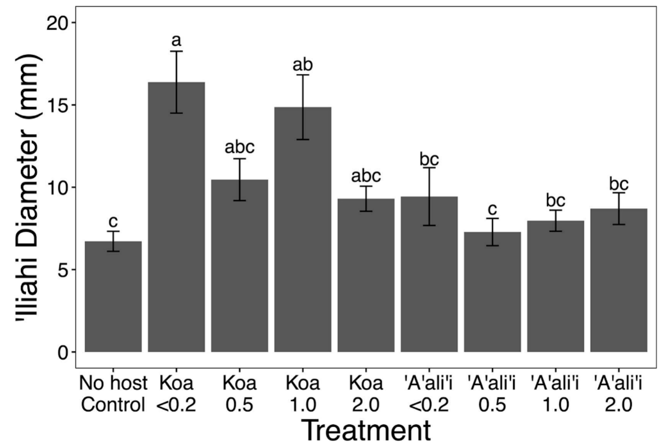


Fig. 2. Mean (a) height (cm) and (b) diameter (mm) (±SE) of ʻiliahi seedlings three years after planting. ʻIliahi seedlings were planted either by itself with no host, ʻaʻaliʻi, or koa at four distances (<0.2 m, 0.5 m, 1.0 m, or 2.0 m away from ʻiliahi). Different letters indicate significant differences among the nine treatments (α = 0.05).

Mean concentration (%) of foliar nitrogen (N) was greater for ʻiliahi paired with koa at distances of <0.2, 0.5, and 1.0 m ($F_{8,142} = 4.68$, $p < 0.001$; Table 3). The other nutrients had different patterns with observed phosphorous (P) and calcium (Ca) greater for ʻiliahi paired with ʻaʻaliʻi than when paired with koa at certain distances ($F_{8,142} = 7.18$, $p < 0.001$; $F_{8,142} = 3.01$, $p = 0.004$, respectively), potassium (K) greater for ʻiliahi without a host than with either host ($F_{8,142} = 4.78$, $p < 0.001$), and magnesium (Mg) and sulfur (S) greater for ʻiliahi without a host or with most ʻaʻaliʻi distances than with koa ($F_{8,142} = 5.09$, $p < 0.001$, $F_{8,142} = 2.62$, $p = 0.011$, respectively; Table 3).

Throughout this experiment, we observed notable variability between how ʻiliahi responded within a treatment (Supplemental Fig. 2). Each treatment had a few ʻiliahi seedlings that experienced proficient growth and a few ʻiliahi with slow growth rates. Overall, koa pairings resulted in higher ʻiliahi survival and growth compared to ʻaʻaliʻi and the no host control; furthermore, shorter distances to the koa host also generally resulted in greater growth.

4. Discussion

For restoration sites with no pre-established hosts, koa co-planted at a closer distance was a key advantage for early ʻiliahi growth, whereas koa co-planted at an intermediate distance was advantageous for ʻiliahi survival. Greater survival and growth results for ʻiliahi paired with koa partially support hypothesis (i) that ʻiliahi performance would be greater with a host than with no host. In full support of hypothesis (ii), ʻiliahi seedling growth and foliar nitrogen were greater when paired with koa (the nitrogen-fixing host) than with an ʻaʻaliʻi host. The absence of significant difference for ʻiliahi paired with ʻaʻaliʻi may indicate a reduced host suitability or at least comparable to the effect of the pasture grass. ʻAʻaliʻi potentially possesses characteristics (e.g., allelochemicals) that may restrain the growth of other plants (Rowshan et al., 2014). Additionally, ʻaʻaliʻi shrub characteristics may affect ʻiliahi differently than koa, such as foliar shade affecting light quality. In addition to being reported as a suitable host for Indian sandalwood, ʻaʻaliʻi has been ambiguously reported as an unsuitable host to Indian sandalwood (Rocha and Santhoshkumar, 2022) and African sandalwood (Mwang'ingo et al., 2005).

The ability of koa to promote greater ʻiliahi performance as a host is likely due to koa being a nitrogen-fixing tree. ʻIliahi's greater foliar nitrogen concentration when paired with koa is likely advantageous and contributed to increased height and diameter growth for ʻiliahi paired with koa. The benefit of a nitrogen-fixing host has been identified for other hemiparasitic plants (Irving and Cameron, 2009; Matthies, 2017; Nge et al., 2019) including other *Santalum* spp. (Brand et al., 2000; Lu et al., 2014; Nge et al., 2019; Radomiljac et al., 1999a; Veillon and

Table 3
Mean nutrient concentration (%) (±SE) for ʻiliahi paired either with no host, koa, or ʻaʻaliʻi three years after planting at <0.2, 0.5, 1.0, or 2.0 m distances. Nutrients include: nitrogen (N), phosphorous (P), potassium (K), calcium (Ca), magnesium (Mg), sulfur (S). Within each nutrient parameter, different letters indicate significant differences among the nine treatments (α = 0.05).

Host	Distance (m)	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	S (%)
Control	—	1.20	0.13	3.72	0.62	0.38	0.29
No host		(0.12) b	(0.02) abc	(0.36) a	(0.04) ab	(0.02) a	(0.03) a
Koa	<0.2	2.31	0.10	1.62	0.30	0.14	0.12
		(0.14) a	(0.01) c	(0.18) b	(0.06) b	(0.03) c	(0.01) b
Koa	0.5	2.33	0.10	2.29	0.46	0.21	0.18
		(0.19) a	(0.01) c	(0.29) b	(0.07) ab	(0.03) bc	(0.02) b
Koa	1.0	2.56	0.12	2.21	0.48	0.21	0.18
		(0.33) a	(0.01) bc	(0.21) b	(0.08) ab	(0.03) bc	(0.01) b
Koa	2.0	1.90	0.10	2.59	0.45	0.27	0.17
		(0.52) ab	(0.02) bc	(0.22) b	(0.04) ab	(0.03) bc	(0.01) b
ʻAʻaʻliʻi	<0.2	1.44	0.17	3.12	0.69	0.37	0.25
		(0.20) b	(0.03) a	(0.25) b	(0.09) a	(0.05) ab	(0.07) ab
ʻAʻaʻliʻi	0.5	1.74	0.14	3.05	0.61	0.29	0.19
		(0.25) ab	(0.02) ab	(0.36) b	(0.06) ab	(0.04) bc	(0.02) b
ʻAʻaʻliʻi	1.0	1.99	0.21	2.64	0.51	0.37	0.26
		(0.22) ab	(0.02) a	(0.44) b	(0.10) ab	(0.07) ab	(0.05) ab
ʻAʻaʻliʻi	2.0	1.65	0.16	3.13	0.68	0.40	0.24
		(0.22) ab	(0.01) ab	(0.46) b	(0.10) a	(0.05) ab	(0.04) ab

Jaffré, 1995; Woodall and Robinson, 2003). Since nitrogen is noted as an important resource hemiparasites acquire from hosts (Cameron and Seel, 2007; Lu et al., 2014; Pageau et al., 2003; Tennakoon et al., 1997a), nitrogen transfer is a likely benefit from nitrogen-fixing trees. Koa's host suitability could also be due to other characteristics, such as fast growth and development (Scowcroft et al., 2007) leading to a higher probability of haustoria connections. Rapid growth of the host (e.g., koa) during the establishment phase also seems to be of a net benefit that outweighs any competitive inhibition to hemiparasites (Hautier et al., 2010; Radomiljac et al., 1998). Additionally, koa's fast growth and canopy development may facilitate ʻiliahi establishment by ameliorating harsh site conditions (e.g., high light, dry periods), thereby increasing ʻiliahi performance.

Given the hemiparasitic nature of ʻiliahi, there are likely additional ecological trade-offs between competition with the host for resources and facilitation through root parasitism (Keith et al., 2004; Matthies, 1995). In partial support of our final hypothesis (iii), ʻiliahi growth when paired with koa was greatest at the closest distance (Fig. 2). This result aligns with host considerations for Indian sandalwood of maximizing functional haustoria and minimizing competition for aboveground resources (Rocha et al., 2014). Earlier connections forged between the closest pairings could explain the koa host distance effect. For Indian sandalwood, earlier connections forged between a nursery container host yielded greater growth after planting (Radomiljac et al., 1998). The intermediate spacings, however, may be close enough to encourage early connections and sufficient growth enhancement, yet not too close where seedlings quickly become intertwined and compete for limited resources, such as light. The intermediate spacings also align to the growers' guide for Vanuatu sandalwood (Page et al., 2012). The response at 0.5 m distance may indicate reduced haustoria connections (compared to <0.2 m) and increased competition (compared to 1.0 m). The 1.0 m intermediate spacing with koa was also the only significantly different treatment for ʻiliahi survival results compared to no host control or koa at 2.0 m. The difference between ʻiliahi survival for 1.0 and 2.0 m koa distances may be indicative of the greater distance lacking haustoria benefits. This result also supports that while hemiparasites can survive independently of a woody host, suitable long-term hosts may increase survival and growth of the hemiparasite (Těšitel, 2016). The different response of survival and growth to distance may similarly be due to trade-off differences between benefits from haustoria formation and competition from hosts.

While parasitic plants have the potential to affect the plant communities that they inhabit (Cameron and Phoenix, 2013), similar to Brand et al. (2000), we did not detect an influence of ʻiliahi on the survival or growth of the hosts themselves. It is interesting that even though there was an effect of distance for ʻiliahi paired with koa, there was not an apparent negative effect of parasitism on koa growth. Perhaps the effect of ʻiliahi on host plant survival and growth is beyond the scope of early establishment. Nitrogen-fixation on site by koa is highly likely because nitrogen was the prominent exception to the trend of ʻiliahi with no host having greater foliar nutrient concentration than ʻiliahi paired with either host. Lower observed P, K, Mg, and S concentrations in ʻiliahi paired with one or both hosts could potentially be due to a dilution effect of ʻiliahi growing faster with hosts or due to competition for mineral nutrients, whereas N was likely more available given koa nitrogen-fixation. Results from past studies have supported transfer of several other mineral nutrients (e.g., Ca, K, P, Na, Cu) between *Santalum* spp. and hosts when a hemiparasitic connection is made (Radomiljac et al., 1999b; Struthers et al., 1986). This result could also be due to the complexity behind ʻiliahi acquiring nutrients auto- and heterotrophically as seen with Indian sandalwood and two nitrogen-fixing hosts in a plantation setting (Lu et al., 2020).

Management of mixed species stands with ʻiliahi need to consider several future directions depending on site goals. For example, deciding whether to keep, remove, or prune hosts if hosts are too competitive for resources (e.g., light, mineral nutrients) or entangled with ʻiliahi. Further work on this experimental site must account for root systems expanding past the 3-m spaced rows and 6-m spaced planting positions; therefore, a larger experimental scale of interacting trees and an increasing role of competition both above- and below-ground would be beneficial to following the trees over time.

5. Conclusions

Our research contributes to knowledge of hemiparasitic plants broadly regarding the role of hosts and co-planting proximity of hemiparasites to their host. Few studies have experimentally examined host distance, and our results support those of Keith et al. (2004) that the effect of distance depends on host species. In our study, koa was a more effective host for early ʻiliahi establishment than ʻaʻaliʻi. Host proximity has trade-off's for hemiparasites between the cost of competition from a host and the benefit of resource acquisition from a suitable host. Even though the closest distance for ʻiliahi paired with koa resulted in the greatest growth, planting at an intermediate distance (e.g., 1.0 m) still yielded increased growth relative to the farthest distance (2.0 m), had the greatest survival, and provides the plants physical room to grow and avoid entanglement. Consideration of secondary hosts at farther distances will likely be necessary for continued survival and growth of ʻiliahi beyond the early establishment phase. Additional research may help to understand how unaccounted site effects (e.g., soil characteristics, microclimate, soil compaction) may interact with host species and co-planting distances and thereby increase variation within the results.

6. Data availability

Data available upon request to corresponding author.

CRediT authorship contribution statement

Emily C. Thyroff: Methodology, Data curation, Formal analysis, Investigation, Visualization, Funding acquisition, Writing - original draft, Writing - review & editing. **Kyle M.E. Rose:** Conceptualization, Data curation, Methodology, Writing - original draft, Writing - review & editing. **Travis W. Idol:** Resources, Investigation, Visualization, Supervision, Funding acquisition, Writing - original draft, Writing - review & editing. **Quinn Moon:** Data curation, Visualization, Writing - original draft, Writing - review & editing. **Owen T. Burney:** Conceptualization, Formal analysis, Writing - original draft, Writing - review & editing. **Douglass F. Jacobs:** Conceptualization, Methodology, Resources, Investigation, Visualization, Supervision, Project administration, Funding acquisition, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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