



Establishment and heteroblasty of *Acacia koa* in canopy gaps

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ABSTRACT

Acacia spp. are important tropical forest trees but their commercial value may be limited by expression of poor apical dominance and extensive lateral branching. Multiple-aged and gap silviculture may harness the developmental plasticity of phyllodinous *Acacia* spp. to improve regeneration establishment, without sacrificing survival rates, by delaying heteroblasty (transition early in development from true leaves to modified petioles called phyllodes). However, successful development of this system is dependent on knowledge of seedling shade tolerance and ability to establish within canopy gaps. We planted Hawaiian *Acacia koa* (koa) beneath an existing restoration planting with a monospecific overstory canopy of koa on a dry site within koa's natural range. Seedlings originated from a local putative drought-adapted population and a non-local mesic-adapted population, allowing evaluation of responses to a continuous light availability gradient in two populations. Leaf transition rates and the growth and survival impacts of rust fungus infection introduced from the existing canopy were also assessed. We detected significant and positive responses to light availability. Koa exhibited low shade tolerance and cannot sustain overtopping; both height and basal diameter growth increased exponentially with increasing canopy openness. Transition to high-light, drought-adapted mature foliage occurred more rapidly with increasing light availability. High developmental plasticity occurred in response to shading, but we did not find evidence of the adaptive value in that plasticity because of low survival rates and reduced growth in low-light microsites. We detected evidence for a growth-survival trade-off in which the non-local population grew faster overall, yet had reduced survival. Rust infection reduced survival and growth, limiting the possibility of converting degraded koa plantations into multiple-aged, gap silviculture systems. High rust infection rates and impacts on field performance found in this study reflect potential for pathogen-limited growth and survival in gap silviculture.

1. Introduction

The reduced importance of ranching in some tropical areas and the failure of abandoned old fields and ranching lands to regenerate native, productive forests (Cramer et al., 2008; Benayas et al., 2007) has increased interest in production forestry (Scowcroft et al., 2010) and forest restoration (Friday et al., 2015) on degraded agricultural lands. These activities often attempt to balance production and biodiversity (Cramer et al., 2008) or tree cover and understory restoration (Goldstein et al., 2008). This can involve planting trees of high ecological value, either as habitat or food sources for wildlife, before introducing secondary forest species of high timber value that can provide economic returns for restoration activities. Conversely, some practitioners plant early-successional and high-value timber species

prior to introducing understory plants, to balance production and protection by satisfying biodiversity goals over the long-term.

In Hawaii, USA, *Acacia koa* (Gray), or koa, forestry provides a testing ground for these contrasting restoration strategies. Koa is a fast-growing (Earnshaw et al., 2016) dominant or co-dominant canopy tree occurring over a wide range of forest types (Gagne and Cuddihy, 1990) from near sea level to about 2000 m.a.s.l. (Baker et al., 2009), where annual rainfall averages from below 1000 to over 5000 mm. With the reduced importance of ranching, interest in commercial koa forestry (Loudat et al., 1996) and native forest restoration (Scowcroft and Yeh, 2013) have risen. Koa is one of the world's most valuable timbers (Scowcroft et al., 2010) and growth and survival of planted trees respond well to site preparation, including herbaceous control (Pinto et al., 2015), and fertilization (Earnshaw et al., 2016). It is an important

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source of habitat for endemic arthropods (Goldsmith et al., 2007) and endangered birds (Pejchar et al., 2005) and represents the traditional tree species from which Hawaiians made ocean-going canoes (Whistler, 2009). Additionally, because it is a fast-growing nitrogen fixer and the species is tolerant to a wide range of abiotic stressors, likely as a result of high intraspecific diversity (Gugger et al., 2018) and/or high plasticity (Rose et al., 2019), it is a uniquely capable native species for reforestation (Woodcock, 2003) and usually the first planted native tree species on abandoned agricultural fields (Scowcroft and Yeh, 2013) within its range.

Interest in koa as a plantation species has increased but poor stem form and pest and pathogen risks have limited its success (Baker et al., 2009; Scowcroft et al., 2010). Nevertheless, koa has been planted in several large (> 100 ha), single-aged plantations on Hawaii Island during the past decade. Fast growth, the continued value of koa timber (Yanagida et al., 2004), the potential development of new markets for small diameter koa (Lowell et al., 2016), investments in tree improvement (Brewbaker, 1997), improved site preparation techniques for grass-invaded landscapes (Leary and Gross, 2013; Pinto et al., 2015), and experimentation with pruning techniques have incentivized planting. Nevertheless, plantation koa suffers from frequent, low forking that diminishes the economic value of planted stands (Scowcroft et al., 2010). Although pruning has been effective to improve the form of *Acacia mangium* (Beadle et al., 2007) and koa's close relative (Murphy et al., 2010; Brown et al., 2012), *Acacia melanoxylon* (Medhurst et al., 2003), these same gains have not yet been quantified or confirmed for koa (Baker et al., 2009; Scowcroft et al., 2010).

Gap silviculture is an alternative tool to pruning that could improve koa form and early growth (Baker et al., 2009). There is evidence that the historic disturbance regime promoted gap-phased regeneration of koa (Mueller-Dombois, 1981). Additionally, management of a related species (*A. melanoxylon*) using trainer trees suggests the utility of gap silviculture in promoting desirable growth form (Pinkard and Beadle, 2002; Medhurst et al., 2003; Pinkard, 2003). Nevertheless, establishment and recruitment of koa within variably sized gaps, and the role of heteroblasty in facilitating these processes, has not been studied. Identifying canopy cover tolerance for regeneration is a first step in the development of gap silvicultural systems for koa.

If gap silvicultural methods are to be successful in regenerating and recruiting koa, heteroblastic development is likely to play a role in its success. Phyllodinous *Acacia* spp. are heteroblastic; the dominant leaf form transitions early in development, usually during the first year, from true, horizontally oriented, and compound leaves to modified, vertically oriented petioles called phyllodes. Past research suggests that physiological and morphological differences between true leaves and phyllodes, where true leaves are associated with fast growth in gaps and phyllodes with drought tolerance, could have adaptive significance in field settings. Although light response curves are identical for koa's true leaves and phyllodes (Pasquet-Kok et al., 2010) and despite similar photosynthetic plasticity in response to changes in photosynthetic photon flux density (Walters and Bartholomew, 1990), true leaves have higher photosynthetic rates by mass and lower water use efficiency (Hansen, 1996), probably as a result of reduced stomatal control with decreasing soil water potential (Pasquet-Kok et al., 2010). Furthermore, both light and water availability have been shown to affect ontogenetic trajectories of koa in the greenhouse (Rose et al., 2019). These results have led to the conclusion that true leaves are more adaptive in low light conditions and advantageous for fast growth and light acquisition at a lower carbon cost in gap-phased regeneration. Phyllodes, conversely, are advantageous for "persistence" (Hansen, 1996) or stress tolerance, the most important of which for koa on drier sites would be drought tolerance.

It is unknown, however, whether delays in transition to phyllodes are associated with maintained survival in partially shaded conditions found within canopy gaps. If koa cannot be regenerated and established within canopy gaps, the hypothesized disturbance regimes of koa

forests (Mueller-Dombois, 1981) may need to be reconsidered; if koa can be regenerated and established within canopy gaps, future steps can be taken to evaluate methods for recruitment and the effects of this management regime on stem form, ultimately leading to a new silvicultural system for the management of koa.

To address the issue of regeneration and establishment of koa within forest gaps, we conducted a study in which we planted koa from two populations under an existing, irregular koa overstory canopy. We tested the following hypotheses: (1) increased light availability would increase survival and growth, and koa would show low plasticity across both parameters in response to light; (2) the local population would be more adapted to water stress and experience higher survival rates, but lower growth rates; and (3) the local population would have reduced developmental plasticity in response to shade, leading to a faster transition to phyllodes across shade levels; and an increase in survival and reduced growth except in the most open microsites. A fourth hypothesis was developed following discovery of koa rust (*Endoraecium* spp.; Berndt, 2011) infections of seedlings shortly after planting: infection rates of rust would be low, limiting rust effects on seedling survival and growth.

2. Methods

2.1. Site description

The study was located atop the Puu Waawaa cinder cone (19.7737N, -155.8331W) at an elevation of 1150 m.a.s.l. within the Puu Waawaa Cinder Cone State Park on Hawaii Island, USA. During the previous century, the cone has been deforested and grazed by cattle, sheep, and goats (Giffin, 2003). Since 2003, some parcels have been fenced and planted with native trees for restoration. The study was conducted on approximately 0.6 ha within a 36-ha fenced area free from grazing.

The soil of the cone is classified as a Waawaa medial silt loam where the B-horizon is a medial silty clay loam. These soils are slightly acidic to neutral in pH, well-drained with moderate soil water storage, and deep (> 2 m). They are classified as medial, amorphous, isothermic Pachic Haplustands. They are productive soils with an estimated CEC at a pH of 7 of 83.3 meg 100 g⁻¹ at 0–30 cm depth (Soil Survey Staff, accessed 20170307). A soil sample, aggregated from ten soil subsamples taken within the 0.6-ha study area to a depth of 20 cm, was sent for nutrient and texture analysis at the Agricultural Diagnostic Service Center at the College of Tropical Agriculture and Human Resources at the University of Hawaii at Manoa. This soil was classified as an Andisol and was not air-dried before analyses. Because soil pH was above 7.0, extractable phosphorus was quantified using the Olsen method (Olsen and Sommers, 1982) and was estimated to be 43 ppm. Calcium (12,288 ppm), magnesium (784 ppm), and potassium (2,379 ppm) were measured using standard methods. Total nitrogen (0.77%) was quantified using dry combustion (Burt, 2004). Particle size was determined according to Kettler et al. (2001). These results showed the site to be slightly alkaline, whereas most of koa's range is slightly acidic to acidic (Soil Survey Staff). Estimated percent clay from the NRCS Soil Survey is 20% at 0–10 cm (Soil Survey Staff), but the composite soil sample estimated soil texture to be 41.1% sand and 53.0% silt, probably underestimating clay (6.0%) as a result of the dispersion method used to quantify clay in an Andisol (Silva et al., 2015).

The region is arid and within the lower range of annual precipitation requirements for koa (Baker et al., 2009). According to a nearby Remote Automated Weather Station (RAWS) station at the base of the cone, average annual precipitation during 2005 through 2013 was 326 ± 57 mm. Average monthly precipitation from June 2004 through May 2014 was variable throughout the year without a clear pattern. As a result of increased elevation, the top of the cone, where the study was located, receives more precipitation than that of the area around the RAWS station, which is 441 m lower in elevation and about 2.7 km from

the study site. For mean average daily temperature by month from 2004 through 2014, August was the warmest month (21.31 °C) and February, the coolest (17.87 °C). Precipitation data during the study was obtained from two stations, a RAWS station at the base of the hill at 709 m.a.s.l. (N19° 47' 42", 155° 50' 43"; [RAWS 2017](#)) and a USFS weather station in the nearby Puu Waawaa Bird Sanctuary at 1659 m.a.s.l. (Lat 19.72544, Lon -155.87389; [Hawaii Permanent Plot Network \(2017\)](#)). Between July 1, 2014 and July 31, 2016, precipitation at the base of the hill was 1000 mm. During the same period, in the Bird Sanctuary, precipitation was over 2000 mm.

In October 2013, a mixture of 1.5% glyphosate and 2.5% imazapyr were applied in 1-m² circles to 672 potential planting locations along 28 transects oriented with the contour of the slope (24 circles per transect). This site preparation strategy was implemented in order to achieve a long-term reduction in grass competition without endangering non-target trees planted within the restoration area on top of the cone. At the time of planting, the planting site was clear of herbaceous competition. To minimize differences in grass competition in shaded vs. non-shaded areas, a mixture of 0.28% fluzafop and 0.27% quizalofop p-ethyl was applied 6 and 12 months after planting.

2.2. Experimental design

Seeds were from two populations: Puu Waawaa (local, dry site) and Kaumana City (non-local, wet site). Seeds from Puu Waawaa were collected in July 2013 from 17 trees on the cone, all spaced at least 100 m apart. The Kaumana City population (19.6910 N, 155.1821 W, elevation 600 m.a.s.l., annual precipitation 5700 mm ([Giambelluca et al., 2013](#))) consisted of seeds from 11 mother trees spaced approximately 100 m apart.

Seedlings for outplanting at the site were grown at the DLNR/DOFAW State Tree Nursery in Kamuela on Hawaii Island. They were germinated during the first week of February 2014 and transplanted into D16 treepots (Stuewe & Sons, Tangent, OR), using a mixture of sand, vermiculite, and a soil:perlite mix (1:1). They were transported and planted at Puu Waawaa on July 6, 2014.

The study used a randomized design underneath koa planted within the previous ten years creating a gradient of shade levels for underplanted koa. Trees were planted on a grid with 24 planting points within 28 transects along the contour of the slope. A total of 652 seedlings from the 17 Puu Waawaa and 11 Kaumana City families were randomly planted to the 672 planting locations. At the time of planting, 315 seedlings from Kaumana City and 337 seedlings from Puu Waawaa were planted. The final number of plants in the study was 556 (238 and 318 from Kaumana City and Puu Waawaa, respectively) because of poor planting or lost ID tags.

2.3. Measurements

Plant survival, performance, developmental stage, and the presence of rust were assessed six times during the two years of the study: at planting and 16, 36, 52, 81, and 108 weeks after planting. Performance measures included height and diameter at ground level. The measurements for diameter taken at two years included two perpendicular subsamples to account for elliptically shaped trunks. In order to estimate relative water content (RWC) of leaves and phyllodes one year after planting (August 12, 2015), 50 mL Falcon centrifuge tubes (Falcon Scientific, Seaton Delaval, UK) were weighed before representative leaves (and phyllodes, if present) from every third surviving seedling were collected, and immediately enclosed in the vial and placed on ice. Samples were returned to the lab and weighed for fresh weight before being rehydrated for four hours in separate cups. Leaves were then returned to their original vials and weighed for saturated weight. They were then dried at 40 °C for 48 h before being weighed for dry weight. RWC, expressed as a proportion, was calculated as the difference between the fresh weight and dry weight, divided by the difference

between the saturated weight and dry weight.

Developmental state was assessed at all six measurement times for the presence or absence of phyllodes. For all presence/absence censuses, rust-induced production of mature tissue was not counted as a positive occurrence of phyllodes. Beginning at week 52, we also assessed the proportion of the plant crown that was phyllodinous. This was categorized into four equal bins (0–24%, 25–49%, etc.). Rust was first noted during the second census and thereafter the presence or absence of rust was recorded during each census.

Rainfall data was obtained from the nearby RAWS and USFS weather stations. Individual canopy openness measurements were determined for each seedling using hemispherical photography. In September 2014, photos were taken with a Canon EOS40 camera (Canon U.S.A., Melville, NY, USA) using a Sigma 8 mm hemispherical lens (Sigma Corp. of America, Ronkonkoma, NY, USA). All photos were taken 1 m above, and perpendicular to, the ground and oriented towards the local zenith using a tripod-mounted level. All photos were taken where the top of the photo pointed towards to true north. Binary images of all photos were created using ImageJ Software ([Schneider et al., 2012](#)). Canopy openness, or proportion of the sky that is unobstructed, was calculated for the full photo and at the following zenith angles in order to assess the importance of overall canopy openness versus the presence of overhead gaps: 2.5°, 17.5°, 37.5°, 47.5°, 57.5°, 77.5°, and 87.5°. Canopy openness was calculated using CIMES software ([Gonsamo et al., 2011](#)).

2.4. Statistical analyses

All statistical analyses were performed using R Software (R Core Team 2016). For all models, the response was first tested across the range of zenith angles in order to identify the zenith angle most important for the response. Zenith angle for models was selected using `selMod()` function in R, following selection criteria from [Anderson et al. \(2001\)](#) and [Burnham and Anderson \(2002\)](#). Relative growth, instead of absolute growth, was modeled because of significant differences in the size of wet- and dry site populations at the time of planting. At planting, the wet site population was taller than the dry site population (44.7 ± 0.7 cm and 27.5 ± 0.8 cm, respectively). The wet site population also had a larger basal diameter at the time of planting (4.4 ± 0.2 mm and 3.1 ± 0.2 mm, respectively). For combined populations, average height at planting was 37.4 ± 0.6 cm and average basal diameter, 3.7 ± 0.04 mm. A zenith angle of 87.5° was used for relative growth models for the first year, whereas a zenith angle of 57.5° was used for relative growth models for the full two years of the study. If models performed equally well for a given response variable in a given year, zenith angles were chosen for consistency across models. Following model selection for zenith angle, model selection was then performed on the remaining independent variables. Correlations between canopy openness and rust presence at six months, across all possible zenith angles, was used to evaluate the relationship between those parameters.

Survival was analyzed using Cox proportional hazards models. Two survival models were tested. The first included the full time-series but did not include rust because it was not assessed until the third census. The second model, consequently, assessed survival for those that had survived until the third census and included the effect of rust presence at six months post-planting. This second model used a zenith angle of 87.5° and included the interaction between rust presence and canopy openness. Performance measures were modeled using relative growth indices calculated as the change in height and basal diameter between the time of measurement and the reference point, divided by the reference point. This was multiplied by 100 to achieve a relative growth measurement in the form of a percentage. Both height and basal diameter relative growth response variables were log-transformed. Relative water content (RWC) was analyzed as a linear model with population, leaf type, and openness as fixed effects. Heteroblasty was

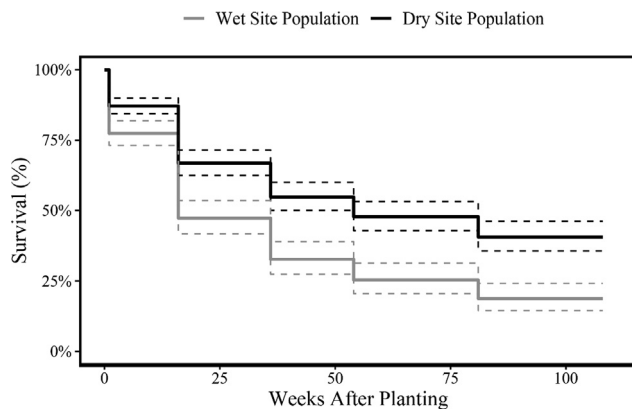


Fig. 1. Survival of two populations of koa seedlings (dry site and wet site, respectively) outplanted in a dry site. Dotted lines show the 95% confidence bands. This survival analysis used a constrained view of the sky, with a zenith angle of 57.5°, to test the effect of overtopping on survival.

analyzed in two ways. First, it was assessed using a Cox Proportional Hazards Model, following methods from Rose et al. (2019). This model included the effects of population, canopy openness, and their interaction. Second, heteroblasty was assessed using multinomial logistic regressions at one year, one and a half years, and two years. Models assessed the probability of having a canopy with 0% phyllodes, 1–24% phyllodes, 25–49% phyllodes, 50–74% phyllodes, and greater than 75% phyllodes. Models evaluated main effects of population, canopy openness (CO, as proportion), and their interaction, but this interaction was removed when not significant ($\alpha = 0.05$).

3. Results

3.1. Survival and relative water content

Survival models were run using a canopy openness parameter calculated from a zenith angle of 57.5° for the full two years and 87.5° for survival after six months. Survival using the full two years of data was affected by POPULATION ($p < 0.001$) and OPENNESS ($p < 0.001$) (Figs. 1 and 2). For trees that had survived at least six months, POPULATION did not affect survival ($p = 0.6867$) during the following year and a half. The presence of RUST at six months ($p < 0.001$) and OPENNESS ($p < 0.001$) both affected survival rates: RUST infection reduced survival and survival was positively related to OPENNESS. The interaction between RUST and OPENNESS was weakly non-significant (Fig. 3; $p = 0.0632$). In contrast to survival, RWC of leaves and phyllodes at one year was not affected by OPENNESS ($p = 0.1197$), but the

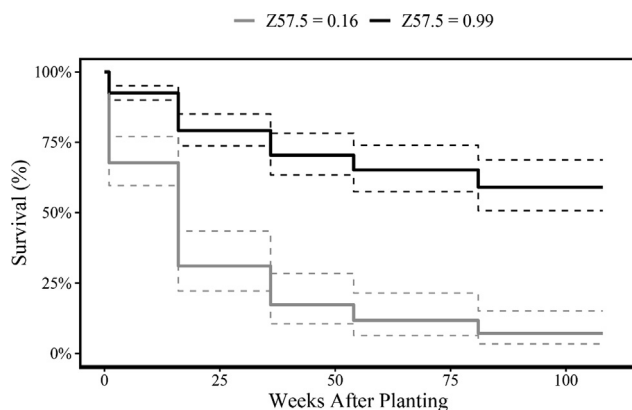


Fig. 2. Canopy openness effect on survival at the maximum and minimum openness (0.16 and 0.99) values at a zenith angle of 57.5°. The dotted lines show the 95% confidence bands for each covariate level.

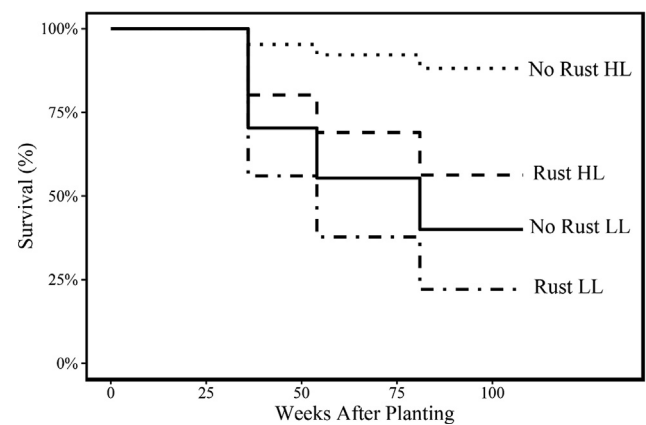


Fig. 3. Canopy openness effect on survival at representative high light (0.6; HL) and low light (0.3; LL) microsites with and without rust infection at 6 months using a zenith angle of 57.5°. Note that only effects for seedlings that had survived at least 6 months were modeled.

wet site population had a higher RWC regardless of leaf type ($86.7\% \pm 0.007\%$ vs $84.1\% \pm 0.006\%$, respectively; $p = 0.0025$). Phyllodes had a higher RWC than true leaves ($p < 0.001$), but the effect size was similar to POPULATION.

3.2. Growth

Relative height growth was modeled for first year growth using a canopy openness parameter calculated from a zenith angle of 87.5°. For the full two-year period, a zenith angle of 57.5° performed best. Relative height growth after one year was affected by POPULATION ($p < 0.001$), OPENNESS ($p < 0.001$, Fig. 4), and RUST at six months ($p < 0.001$) whereby the wet site population grew faster ($320.7 \pm 40.2\%$ vs. $194.0 \pm 14.7\%$) and rust presence at six months reduced height growth after one year ($250.7 \pm 18.7\%$ vs. $139.6 \pm 19.6\%$). For the full two years of the study, POPULATION ($p < 0.001$), OPENNESS ($p < 0.001$, Fig. 4), and RUST presence at six months ($p < 0.001$) affected relative height growth. The interaction between POPULATION and OPENNESS was not significant ($p = 0.0667$). The wet site population's growth rate far exceeded the dry site population ($p < 0.001$): $943.7 \pm 96.7\%$ vs. $483.1 \pm 31.5\%$, respectively. The presence of rust after six months was not correlated with OPENNESS for zenith angles of 2.5° ($r = -0.01$), 17.5° ($r = 0$), 37.5° ($r = 0.03$), 47.5° ($r = 0.05$), 57.5° ($r = 0.06$), 77.5° ($r = 0.08$), 87.5° ($r = 0.07$), or 90° ($r = 0.07$). However, the presence of it at six months post-planting reduced relative height growth after two years from $661.1 \pm 46.6\%$ to $434.9 \pm 62.4\%$.

Relative diameter growth (RDG) for the first year used a canopy openness parameter calculated from a zenith angle of 87.5°. The full two-year RDG model utilized a zenith angle of 57.5°. For the first year, the dry site population's basal diameter increased slightly faster than the wet site population ($278.5 \pm 34.3\%$ vs. $204.2 \pm 14.5\%$; $p = 0.0122$). Basal diameter growth responded positively to increasing OPENNESS ($p < 0.001$, Fig. 5). The interaction between POPULATION and OPENNESS was not significant, although the wet site population tended to maintain growth better in shaded conditions (0.084). RUST infection at six months reduced basal diameter growth during the first year from $241.0 \pm 16.9\%$ to $167.2 \pm 22.3\%$ ($p = 0.004$). For the full two years, the dry site population had lower basal diameter growth than the wet site population ($p < 0.001$). Basal diameter increased in both populations with increasing OPENNESS ($p < 0.001$), but the wet site population had increased growth at lower OPENNESS levels compared to the dry site population ($p = 0.003$, Fig. 5). RUST presence at 6 months reduced basal diameter growth after two years from $730.8 \pm 49.6\%$ to $576.0 \pm 75.5\%$ ($p < 0.001$).

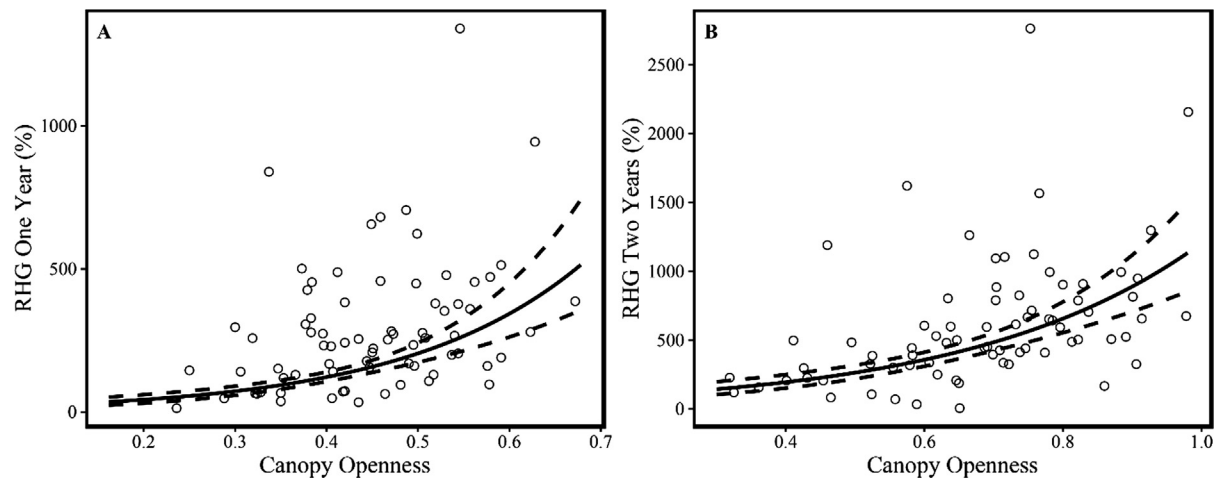


Fig. 4. The effect of canopy openness, using a zenith angle of 87.5° the first year (A) and 57.5° after two years (B), on relative height growth (RHG) at one- and two-years post-planting. Dashed lined represent 95% confidence intervals for modeled responses.

3.3. Heteroblasty

A Cox Proportional Hazards Model evaluating canopy openness (zenith angle 57.5°), population, and their interaction effects on transition to phyllodes (at least one fully developed phyllode) indicated that OPENNESS ($p < 0.001$), POPULATION ($p < 0.001$), and their interaction ($p = 0.001$) all affected the rate of transition (Fig. 6). Multinomial logistic regression models evaluating heteroblasty used a zenith angle of 77.5°. After one year, POPULATION ($p = 0.0178$), OPENNESS ($p < 0.001$), and their interaction ($p = 0.0011$) affected leaf transition rates over time. Increasing OPENNESS increased transition to phyllodes, but trees from the wet site population had transitioned more rapidly than the dry site population across OPENNESS levels. The dry site population had a stronger response to OPENNESS. At one and a half years, only OPENNESS affected the rate of transition ($p < 0.001$), but POPULATION ($p = 0.1074$) and the interaction between POPULATION and OPENNESS was not significant ($p = 0.1253$). After two years (Fig. 7), both POPULATION ($p < 0.001$) and OPENNESS ($p < 0.001$) affected transition rates but their interaction did not ($p = 0.6609$). OPENNESS had a positive effect on transition, but the trees from the wet site population had higher rates of transition across OPENNESS levels.

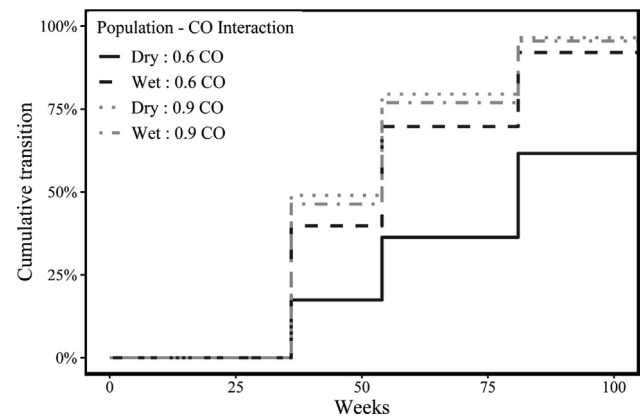


Fig. 6. Survival curves showing the rate of transition (cumulative) in the interaction between population and canopy openness (CO) using two populations of koa. Curves are predicted values from a Cox Proportional Hazards model using data for wet- and dry-sites in large-sized (0.9 CO) and medium-sized gaps (0.6 CO).

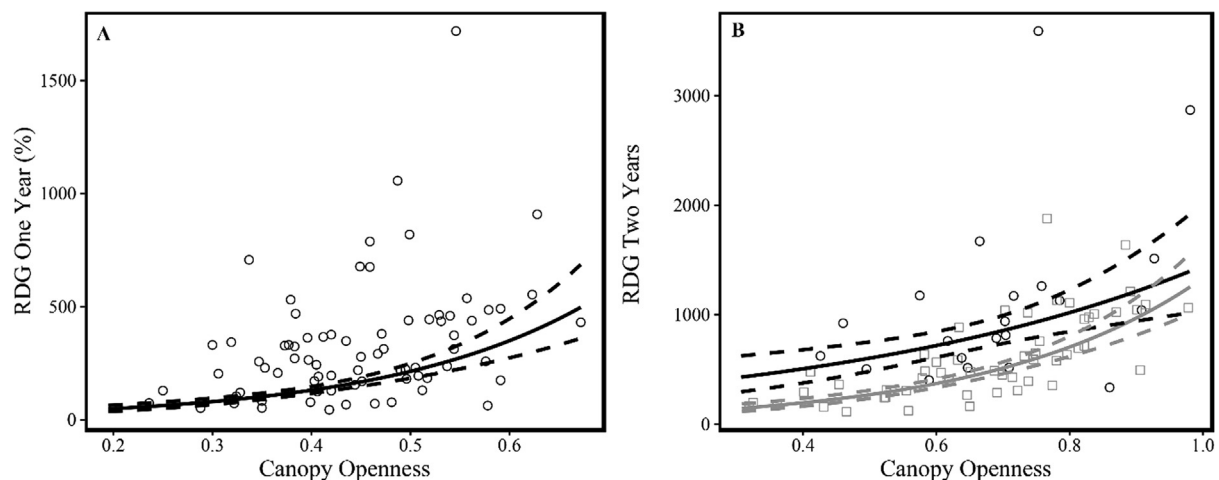


Fig. 5. The effect of canopy openness, using a zenith angle of 87.5° the first year (A) and 57.5° after two years (B), on relative diameter growth (RDG) at one- and two-years post-planting. The two-year plot (B) includes interaction effects between canopy openness and population (Dry Site Population = gray, Wet Site Population = black). Dashed lined represent 95% confidence intervals for modeled responses.

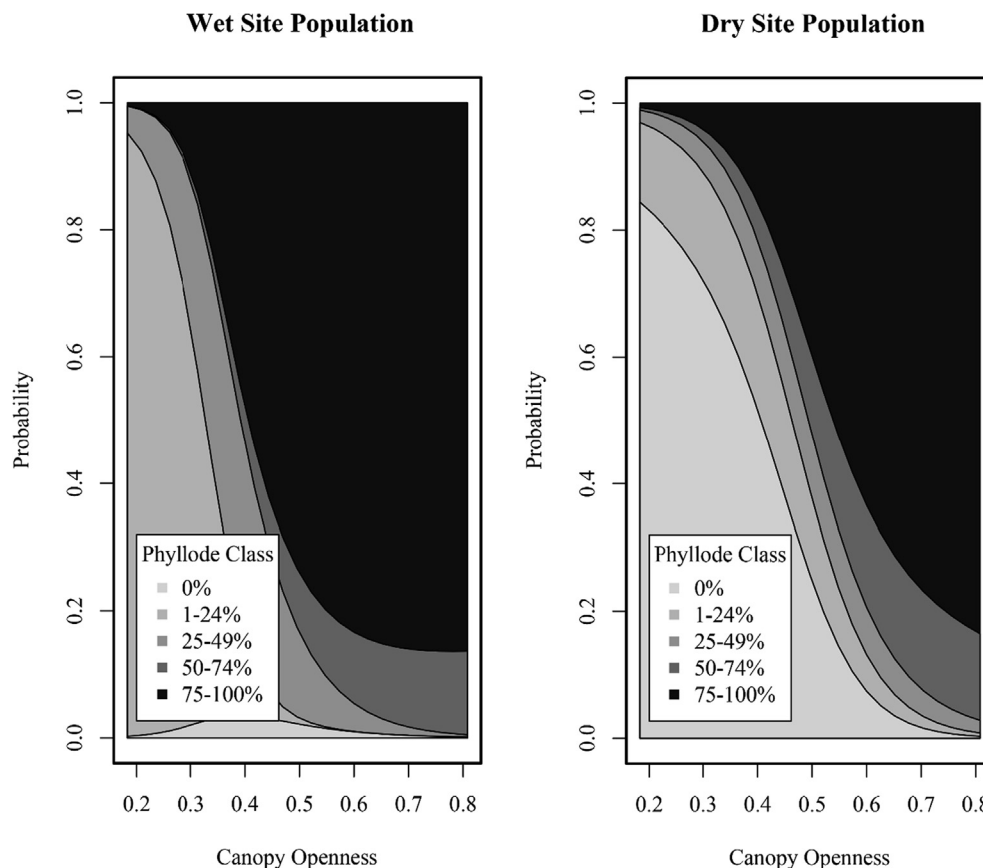


Fig. 7. The effect of canopy openness on transition rates to a phyllodinous canopy at 2 years post-planting for the dry site population wet site population. Canopy openness was calculated at a zenith angle of 77.5° (a constrained view of the sky). Phyllode Class refers to the proportion of the leaves that are phyllodes.

4. Discussion

Some have proposed introducing gaps into overgrown koa progeny tests and failed plantations (Baker et al., 2009) because the historic disturbance regime across much of koa's range probably led to a gap-phased regeneration strategy (Mueller-Dombois, 1981; Asner and Goldstein, 1997). Such treatments have been hypothesized to result in form improvements (Baker et al., 2009), as seen in plantations of *A. melanoxylon* using trainer trees (Medhurst et al., 2003). Although form improvements could be realized in the absence of pests and pathogens, the growth and survival losses seen across both populations in our study, in both high and low canopy openness conditions, as a result of koa rust represents an important finding and evidence against our fourth hypothesis. As a result of the high diversity of rust fungi, it is difficult to identify the specific species of rust that infected koa in our study, but the most common genus of rust in Hawaii on koa is *Endoraecium*, of which there are two main native species, *E. phyllodiorum* and *E. kauaianum* (Berndt, 2011). Although rust infection has been noted in Hawaii previously (Gardner, 1978) and reduced the productivity of *Eucalyptus* spp. (Coutinho et al., 1998) and the more closely related *A. mearnsii* and *A. mangium* (Wingfield et al., 2011), the impact of these rusts on koa forestry have not previously been reported or quantified. Although the interaction between rust presence and openness was not significant for survival after six months, predicted curves for the lowest and highest range in openness values for a zenith angle of 87.5° (0.16, 0.68) showed no effect of rust for the lowest openness and a large effect for the highest openness level (Fig. 3). We have presented results for canopy openness levels of 0.3 (Low Light; LL) and 0.6 (High Light; HL), in which the effect of rust is similar regardless of canopy openness.

These results have important implications for gap-phased

silviculture of tropical *Acacia* spp. in failed plantations when overstory pathogens are present. Overstory pathogens have reduced regeneration success across climate and forest types (Augspurger, 1984; Hawksworth and Johnson, 1989; Stanosz, 1989; Ferguson, 1994). Our study shows that, similarly, failing to account for rust in the overstory, as is the case in mature stands of koa on Hawaii Island (Nelson, 2009), could lead to survival and growth decreases. Although the only other study of koa regeneration in native-dominated forests (Friday et al., 2008) did not identify rust as a predictor of survival, the recommendation to plant koa and similar shade intolerant species in gaps (Scowcroft et al., 2010) may need to be tempered by the caveat that this system could have limitations if the surrounding canopy has a high rust infection rate. These factors should be considered when designing multiple-aged or gap silviculture systems, especially in native forests where species diversity is low and pathogen vectors are present that could inhibit growth and survival of regenerating trees (Janzen, 1970; Hyatt et al., 2003).

Our study also indicated that gaps that provide koa seedlings conditions with less than 80% canopy openness (zenith angle 57.5°) are unlikely to result in acceptable growth and survival rates. Most tree species will increase growth and survival with increasing light availability, including shade-tolerant species, such as *Fagus sylvatica* (Sevillano et al., 2016), *Chamaecyparis obtusa* (Ito et al., 2017) and *Betula papyrifera* (Walters and Reich, 1996), and shade-intolerant species (Ito et al., 2017), but shade intolerant trees cannot survive prolonged shaded conditions. In our study, the results confirmed the first hypothesis: both populations exhibited shade intolerance where survival and growth (height and diameter) declined with increasing canopy cover despite demonstrating developmental plasticity in response to light (Figs. 4 and 5). Nevertheless, the results indicate that high survival and growth in medium- to large-sized gaps is possible. The

constrained zenith angle (57.5°) evaluated the proportion of the sky open to the seedling more directly overhead and more closely evaluated the requirement of a gap than the requirement of open-grown conditions.

Despite this, the populations differed in both survival and growth rates in contrasting ways. The local seed source from the dry site experienced lower average relative growth rates over the two years of the study, but also had a higher probability of survival. Whereas the population from a dry site was able to survive at a slightly higher rate than the population from a wet site after two years, the surviving seedlings from the wet site population outperformed the RHG of the local population, nearly doubling the local's populations growth rate after two years (944% vs. 483%).

This suggests a growth-survival trade-off to explain the increased growth performance for the non-local population at the cost of reduced survival. Although we are unaware of this trend being field-tested between populations of the same species (and we strongly remind the reader that there was no ecotypic replication of populations in this study), this trade-off is well-established in forests and has helped to explain the distribution of species across space and successional stages (Grubb, 1977; Poorter and Kitajima, 2007; Coomes et al., 2009). Our results could be the result of random variation throughout the species, but also highlight the need for more research examining the vulnerability of different ecotypes to increased stress and reduced performance and survival because of climate change; adding more data points is important for developing prescriptions for seed transfer, forest management, and forest restoration in Hawaii (Gugger et al., 2018). Our results, using representative populations from two sites within distinct koa ecotype zones (Gugger et al., 2018), are in line with the idea that drier ecotypes will favor survival over performance. Within this context, the reduced growth plasticity of the dry site seed source could be a remnant of historical disturbance regimes and selection pressures that required resiliency over performance.

As in our study, attempts to demonstrate or test the adaptive significance of heteroblasty in the field, and its relationship to stress tolerance, have brought mixed results (Winn, 1999; Darrow et al., 2002; Gamage and Jesson, 2007; Ostria-Gallardo et al., 2015). The developmental response to light availability found in our study suggests that heteroblasty in koa is both adaptive and in harmony with previous work on koa (Rose et al., 2019) and other *Acacia* spp. (Forster and Bonser, 2009), but without controlling for ontogeny (Zotz et al., 2011) it is difficult to say that delays in transition translated to maintained growth and survival or changes in ontogenetic trajectory. Moreover, we did not find evidence for our third hypothesis, however; the wet site population transitioned faster than the dry site population. Because the wet site population grew faster than the dry site population, and poor performers had lower survival rates, it likely reached a transition point dependent on ontogeny faster than the dry site population (Rose et al., 2019).

5. Conclusions

Our results suggest that koa can grow in forest gaps, but cannot sustain canopy overtopping. Importantly, rust may reduce both growth and survival and decrease the potential of mixed-age management of koa. These considerations are important for the design and implementation of gap silviculture for koa and potentially other shade-intolerant species, especially in monotypic stands of the same species. Nevertheless, *Acacia* spp. represent significant sectors of the forest industry in the tropics (Pinkard and Beadle, 2002; Krisnawati et al., 2011) and use of mixed-age, gap silviculture in *Acacia* spp. may provide both economic (Medhurst et al., 2003) and societal (O'Hara, 2001) benefits. Preliminary results testing effects on two populations suggest that future work should test more populations on multiple sites representing a wide rainfall gradient to better understand the role of developmental plasticity in phyllodinous *Acacia* spp. as an adaptive trait. This has

particular importance in the face of climate change, which is predicted to reduce annual precipitation or increase stochasticity across many sites in koa's range (Chu et al., 2010) and the tropics in general where *Acacia* spp. are economically important (Allen et al., 2010).

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