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Can the impact of canopy trees on soil and understory be altered using litter additions?

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Abstract. Trees can have large effects on soil nutrients in ways that alter succession, particularly in the case of nitrogen-(N)-fixing trees. In Hawai'i, forest restoration relies heavily on use of a native N-fixing tree, *Acacia koa* (koa), but this species increases soil-available N and likely facilitates competitive dominance of exotic pasture grasses. In contrast, *Metrosideros polymorpha* ('ōhi'a), the dominant native tree in Hawai'i, is less often planted because it is slow growing; yet it is typically associated with lower soil N and grass biomass, and greater native understory recruitment. We experimentally tested whether it is possible to reverse high soil N under koa by adding 'ōhi'a litter, using additions of koa litter or no litter as controls, over 2.5 yr. We then quantified natural litterfall and decomposition rates of 'ōhi'a and koa litter to place litter additions in perspective. Finally, we quantified whether litter additions altered grass biomass and if this had effects on native outplants. Adding 'ōhi'a litter increased soil carbon, but increased rather than decreased inorganic soil N pools. Contrary to expectations, koa litter decomposed more slowly than 'ōhi'a, although it released more N per unit of litter. We saw no reduction in grass biomass due to 'ōhi'a litter addition, and no change in native outplanted understory survival or growth. We conclude that the high N soil conditions under koa are difficult to reverse. However, we also found that outplanted native woody species were able to decrease exotic grass biomass over time, regardless of the litter environment, making this a better strategy for lowering exotic species impacts.

Key words: Acacia koa; *carbon amendments; exotic grass; forest restoration; Hawai'i; invasive species; litter decomposition;* Metrosideros polymorpha; *nitrogen-fixing trees; plant–soil interactions; soil nitrogen.*

Introduction

Trees are well known to alter soil chemistry and influence soil formation processes (Binkley and Giardina 1998, Hobbie et al. 2006). One of the pathways through which they do so is via the quality and quantity of their leaf litter inputs. Litter inputs can vary dramatically among co-occurring canopy tree species with consequences for soil nutrient availability, pH, and ion exchange capacity (Binkley and Giardina 1998, Waring 2015), particularly in the case of nitrogen (N)-fixing species, which are well known to increase available and total soil N and cycling levels (Vitousek and Walker 1989, Scowcroft and Haraguchi 2004). High litter N (low C:N) can lead to faster leaf decomposition than under co-occurring non N-fixing species, ultimately resulting in greater N availability under the N-fixing tree canopy (Aber and Melillo 1990, August-Schmidt 2018). Alternatively, high litter N may inhibit decomposition depending on the carbon chemistry of the added substrate (Perakis and Matkins 2012*a*).

Changes in soil chemistry driven by changes in tree species dominance during succession can alter understory (here defined as any woody or herbaceous species under the tree canopy) development (Crozier and Boerner 1984), and ultimately, the successional trajectories of forests (Chapin et al. 1994, Hobbie 2015). Therefore, it is imperative to consider tree effects on litter decomposition, soils, and successional outcomes when choosing canopy tree species to plant for reforestation. This is particularly important in the tropics, where N-fixing, early successional tree species are often used in reforestation/restoration projects (Parrotta 1999, Carpenter et al. 2004, Taylor et al. 2017).

Native N-fixing trees and shrubs can become problematic to restoration when the understory is dominated by fast-growing, nitrophilous species or if such species are abundant nearby (Maron and Connors 1996). For example, globally, many tropical and subtropical forests

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have been cleared for agriculture and livestock grazing (Guariguata and Ostertag 2001), and fast-growing exotic grasses have been planted for forage (D'Antonio and Vitousek 1992). When pastures are abandoned and livestock removed, exotic grasses may remain dominant. In this case, managers may plant tree species to "jump start" succession (Holl 1998, Zahawi and Augspurger 2006). However, in the case of N-fixing trees, it has been shown that nutrient rich conditions can facilitate growth or persistence of exotic grasses or other unwanted species in the understory (August-Schmidt et al. 2015, Yelenik 2017, August-Schmidt 2018), rather than leading to a more native dominated state (but see Parrotta 1999, Taylor et al. 2017).

In the case that native N-fixing trees lead to undesirable outcomes, it may be possible to reverse this trend by planting other woody species or adding soil amendments to promote microbial immobilization of N (Blumenthal and Jordan 2003, Prober et al. 2005, Yelenik and Levine 2010). High soil N conditions, however, are sometimes hard to reverse via restoration actions such as carbon amendments, particularly over the long term (Corbin and D'Antonio 2004). Thus, N-fixers can cause long-lasting increased soil N, even if they are removed, other species are planted, or mulch is added to the site (Yelenik and Stock 2004, Haubensak and D'Antonio 2006, Perakis and Sinkhorn 2011, Von Holle et al. 2013).

In Hawai'i, mesic native forests are dominated by two canopy trees, *Acacia koa* (hereafter, koa) an N-fixing Leguminosae, and *Metrosideros polymorpha* (hereafter, 'ōhi'a) a non-fixer (Myrtaceae), with a dense understory of subcanopy trees, shrubs and ferns. Large tracts of Hawaiian forest were cleared and planted with exotic pasture grasses for livestock grazing in the 1900s and these grasses remain persistent after grazer removal, similar to other tropical systems (Fearnalde 1993, Holl 1999, Silver and Ostertag 2001). In an effort to restore vast areas of pasture and create forest bird habitat, managers have planted koa widely because, unlike 'ōhi'a, it is fast growing and easy to propagate. Afforestation goals include creating shade and deep litter layers to reduce exotic grass growth (Cabin 2013), yet surveys show that restoration with koa does not reduce the invasive grass *Cenchrus clandestinum* (hereafter, kikuyu; Yelenik 2017). This may be due in part to elevated soil N (Yelenik 2017), which has been shown elsewhere to benefit kikuyu (Mears 1970, Yelenik et al. 2020). In addition, native woody species are not recruiting in the koa understory, despite avian surveys showing the presence of frugivorous birds (Paxton et al. 2018) and aerial seed rain traps showing dispersal of native understory species' seeds within restoration koa corridors (Rose et al. 2017; Yelenik et al., *in press*).

In contrast to the restoration koa corridors, isolated 'ōhi'a trees can accumulate native understory communities under their canopies (Yelenik 2017, Rehm et al. 2020). This may be in part due to the large quantities of high C:N leaf litter that accumulate at the base of 'ōhi'a trees, which potentially contribute to lower soil available N and favorable low-grass microsites where native seeds can germinate. By inference then, it is possible that adding 'ōhi'a litter can help decrease kikuyu growth and increase the probability that bird-dispersed seed of native understory species are deposited into favorable microsites. While 'ōhi'a litter has a lower C:N ratio than carbon substrates like sawdust, its addition to the forest understory is more "natural" than bringing in an external source. It can be collected locally and may provide other benefits in terms of being a substrate for natural biological activity and seedling recruitment (Yelenik et al., *in press*).

In this paper, we explore whether adding large quantities of 'ōhi'a litter can reduce the high soil N under koa trees and whether this subsequently reduced soil N could lower grass biomass and facilitate understory restoration. Alternatively, the high soil N conditions under koa may facilitate 'ōhi'a litter decomposition, resulting in C loss due to respiration and leaving behind ample N.

We specifically ask, (1) does the addition of 'ōhi'a litter to koa-dominated soils alter soil nitrogen and carbon, and does this lead to lower grass biomass? To address this we implemented an experiment in restoration koa corridors where we added 'ōhi'a litter at rates much higher than background litterfall (using both koa litter and no litter added as controls). We also implemented a grass-removal treatment because we were not sure 'ōhi'a litter additions would lower grass biomass, but we wanted to see the effects of lower grass biomass on soil and seedling growth and survival (see Q3). We then tracked soil nitrogen and carbon and grass biomass over time. To better elucidate litter dynamics when 'ōhi'a leaf material is added to koa-dominated plots, we conducted a leaf decomposition study of 'ōhi'a vs. koa leaves under remnant 'ōhi'a and planted koa within the planted koa areas. This allowed us to answer the question, (2) does 'ōhi'a litter added under koa trees decompose faster or slower than koa material, and is this influenced by the immediate canopy (koa vs. 'ōhi'a)? This decomposition study also allowed us to estimate how much C and N are released from these two litter types over a single year and thus how much might be released by our litter-addition treatments. Finally, we asked, (3) does the addition of 'ōhi'a litter facilitate native plant survival and growth? This could happen by lessening the competitive or priority effect of grass. To answer this question, we outplanted native tree and shrub seedlings within the litter-addition, grass-removal experiment to test for treatment effects on native species survival.

Methods

Sites

We conducted our study in the Honohina tract of Hakalau Forest National Wildlife Refuge (19.792° N, 155.322° W) on Mauna Kea Volcano, Hawai'i Island,

Hawai‘i, USA. Hakalau Forest is a 13,240-ha National Wildlife Refuge established in 1985 largely to protect endangered Hawaiian forest birds (U.S. Fish and Wildlife Service 2010). As well as the two canopy dominants, mesic forests in Hawai‘i comprise subcanopy trees including *Cheirodendron trigynum* (‘ōlapa), *Myrsine lessertiana* (kōlea), *Ilex anomala* (kāwa‘u), and *Coprosma rhynchocarpa* (pilo). Common understory shrubs include *Leptecophylla tameiameiae* (pukiawe), *Rubus hawaiensis* (‘ākala), and *Vaccinium calycinum* (‘ōhelo). Soils are ash-derived, well-drained, silty clay loams and are approximately 10,000 yr old on substrate considered to be part of the Laupahoehoe Volcanic Series (data *available online*).[6] Study sites were at 1,700 m elevation, receive an annual rainfall of 2,700 mm and have a mean annual temperature of 12°C (Giambelluca et al. 2013).

Upper portions of Hakalau’s mesic ‘ōhi‘a–koa forest (about 2,000 ha in area) were converted to livestock pasture during the 1800s. After National Wildlife Refuge establishment, cattle and feral animals were removed and between 1987 and 1989, strips of land within the exotic grass pastures were reforested with 390,000 koa seedlings (Jeffrey and Horiuchi 2003, Scowcroft et al. 2004). These strips, which we refer to as koa corridors, are visible as rows of trees leading from intact forest at lower elevation upslope toward the main access road. The study sites were within these corridors and were devoid of remnant koa but scattered remnant ‘ōhi‘a were present. The dominant vegetation is restoration koa trees with thick kikuyu in the understory.

We selected seven replicate sites (approximately 50×50 m in size) in koa restoration forest at least 100 m apart that were similar in terms of elevation, koa size (diameter at breast height [DBH] = 47.36 ± 1.63 cm [mean $\pm$ 1SE] for experimental trees), light conditions, and that contained at least one large remnant ‘ōhi‘a. We used these sites for the litter addition, outplanting, and decomposition experiments.

Passive litter collection

To place our litter additions into context, we quantified litterfall using litterfall traps. We measured litterfall biomass and determined C and N inputs. At each of the seven sites, we placed five 0.5×0.5 m mesh-bottomed traps under one restoration koa, and another five traps under one nearby remnant ‘ōhi‘a in December 2015. Litter was collected from the traps approximately every 2 months for 1.5 yr, bulked per tree species and site, and dried for 48 h at 70°C. Because we were interested in C and N inputs, and litter fractions vary widely in their C:N values, we separated samples into component parts (leaves of focal tree, leaves of any other species, woody material, flowers, and lichens/moss) prior to weighing. A subsample of each litter fraction from the first collection date was ground and sent to University of Hawai‘i Hilo for percent C and N analysis (Costech Elemental Analyzer, Valencia, California, USA). Litterfall values were summed across the 1.5 yr before converting to rates expressed as $g \cdot m^{-2} \cdot y^{-1}$. We used the species-specific, litter-fraction-specific percent C and percent N to calculate inputs of C and N added via litterfall under koa vs ‘ōhi‘a over 1 yr. Finally, we used a Wilcoxon signed-rank test to evaluate how annual litterfall mass, C, N, and litter fractions (leaves, flowers, etc.) differed between koa and ‘ōhi‘a ($n = 7$ per tree type as there was one tree per seven transects).

Litter-addition, grass-removal experiment

We selected four restoration koa trees at each site that were at least 10 m apart from each other, with similar DBH, and randomly assigned them to one of the following treatments: (1) control, (2) ‘ōhi‘a litter addition (live and ground material), (3) koa litter addition (live only), or (4) grass removal. We added koa litter, the predominant species of litter falling in these sites, as a control for the experimental manipulation of adding litter. We used a grass-removal treatment because we were not certain our ‘ōhi‘a litter addition would lower grass biomass, but we wanted to see the effect of lower grass on outplant survival (see “Understory outplanting survival and growth”).

For litter additions, we used live koa clippings because they are readily available due to abundant suckering stems, making this method the easiest possible restoration treatment. This included some green stem material. ‘Ōhi‘a litter was added in the first two rounds of additions as live clippings from the ends of lower ‘ōhi‘a branches, which were leaves and woody stem material. To supplement this, we also added litter found on the ground under large ‘ōhi‘a trees. Here, litter tends to form thick layers that seem to decompose slowly, and are not quickly covered by grass. After research emerged showing that a new fungal pathogen (*Ceratocystis* spp.) was entering ‘ōhi‘a trees through wounds (Keith et al. 2015), we switched to using 100% litter from the soil surface for ‘ōhi‘a so that we were not creating wounds on living trees.

Litter was added in a 3-m radius plot around the individual koa trees, seven times over the course of 2.5 yr, starting in December 2015 and culminating in January 2018. Natural litterfall occurs all year at these sites. We tracked approximate litter quantity added over time by collecting it into a 90-L plastic bin and noting how many bins of litter were added per tree. On the first litter-addition date, we also collected five replicate 90-L bins of each litter type (live koa, live ‘ōhi‘a, ground ‘ōhi‘a), which was then dried at 70°C for at least 48 h, and separated into leaves and woody material. We then weighed each fraction and took subsamples for percent C and N. We used fraction-specific litter amounts (e.g., grams of live koa leaves per bin) and percent C and percent N values of the different fractions from this initial collection

[6] http://websoilsurvey.nrcs.usda.gov/.

to estimate grams of C and N added over the course of the experiment (Appendix S1: Table S1). We added relatively large quantities of litter to help make experimental effects detectable within the time frame of the study. Over 2 yr, we added approximately 2,070 g/m^2 of koa litter and 6,590 g/m^2 of ʻōhiʻa litter to their respective treatment plots (Appendix S1: Table S1). We estimated that this was equivalent to 1.5 and 4.7 times passive litterfall for koa and ʻōhiʻa, respectively, at this site (Table 1). For koa, we added 2.3 and 1.5 times passive N and C inputs, respectively. For ʻōhiʻa, we added 4.7 and 4.5 times passive N and C inputs, respectively. Ideally, we would have added similar multipliers of litter for each species, but we did not have the passive litterfall data when the experiment was launched.

To create the grass-removal plots, we used a one-time application of 1% Roundup Pro (EPA Reg #524-475, Monsanto, St Louis, Missouri, USA), 0.5% Polaris AC (EPA Reg #228-570, Nufarm, Alsip, Illinois, USA) and water (Pinto et al. 2015) mixture in February 2016 to kill all exotic grasses within a 4-m radius around study trees. Herbicide was applied with a backpack sprayer (235 L/ha).

To determine how litter and grass-removal treatments altered grass biomass, litter, and soil inorganic N (NH_4^+ and NO_3^-), we sampled soils before treatments began (October 2015), as well as in June 2017 and July 2018. We sampled multiple time points to see possible incremental effects of litter additions on outplant growth (see "Understory outplanting survival and growth"). Grass was clipped at the soil surface within a haphazardly placed 0.5 × 0.5 m quadrat, and any woody species' litter that was found was included in the sample. Grass was reclipped in July 2018 in the same manner, except that one quadrat was placed in between experimental outplants as above, and one quadrat was placed under the largest outplanted individual in the plot because we noticed that grasses seemed to be thinning under the canopy of the outplants. For most sites, this was *C. rhynchocarpa* (pilo) but, under one tree, the largest outplant was *C. trigynum* (ʻōlapa). Samples from both time points were dried at 70°C for 48 h and sorted into grass (predominantly kikuyu) and woody species litter. Subsamples of grass and litter were ground and analyzed for percent C and percent N. We also took two 3.8 cm diameter × 10 cm deep soil cores from the soil surface (including the organic horizon) and bulked these into a single sample per tree. For all sample dates, we took soils from between outplants. Soils were refrigerated for 4 d then sieved to 2 mm. We extracted 10 g of sieved soil with 50 mL of 2 mol/L KCl for 1 h, filtered extracts with a Whatman #1 filter, and took them to the University of Hawaiʻi Hilo Analytical lab for inorganic N analysis (Lachat Quikchem 8500, Hach Company, Loveland, Colorado, USA). At the final time point, we also evaluated soil for percent C and percent N on a dried, sieved, and ground subsample as above.

All analyses were conducted in R version 3.3.1. We modeled grass biomass at the final time point against the fixed effects of the seedling outplants (under or not under a seedling) and treatment (litter addition/grass removal) using a generalized linear model. Total soil inorganic N (NO_3^- and NH_4^+) over time was modeled using a generalized linear mixed effects model (lme4 package [Bates et al. 2014]) with fixed effects of treatment, sample date, and their interaction with a random effect of site. We used AIC model selection to determine the most parsimonious model (Anderson and Burnham 2002). We considered a model to be better than other models if it was at least 2 AIC units lower than the next competing model. If two models were within 2 AIC units of each other, we considered the simpler model to be the preferred model. To ask how total soil N (inorganic + organic), total soil C, and soil C:N differed across treatments at the end of the experiment, we used one-way ANOVAs with treatment as a fixed effect, and post hoc Tukey's Honestly Significant Different (HSD) tests to compare treatments.

Litter decomposition study

To evaluate how rates of litter decomposition and N and C release differed between ʻōhiʻa and koa within restoration corridors, as well as how microhabitat affected these rates, we established a reciprocal decomposition experiment. We placed litter bags with koa or

Table 1. Passive litterfall, N, and C inputs for ʻōhiʻa and koa.

Statistic	Conspp leaves	CWD	Flowers	Moss and lichen	Hetspp leaves	Total litterfall	Total litterfall N	Total litterfall C
Koa								
Mean	430.48	154.63	53.59	14.47	3.37	656.54	11.59	310.83
SE	20.87	24.33	6.72	2.97	0.68	33.57	0.57	15.76
ʻŌhiʻa								
Mean	394.37	117.88	124.00	8.59	11.13	655.98	5.86	306.55
SE	27.17	15.29	8.42	2.21	4.30	34.50	0.32	16.14
P	0.38	0.47	**0.016**	0.30	0.17	0.94	**0.016**	0.94

Notes: *P* values from Wilcoxon signed rank test with tree species as a fixed effect; significant *P* values (<0.05) are shown in boldface type. Abbreviations: ConSpp, conspecific; CWD, coarse woody debris; HetSpp, heterospecific. $N = 7$. All units are g·m^{-2}·yr^{-1}.

ʻōhiʻa leaves under both conspecific and heterospecific trees (that were different trees than the litter addition and outplanting trees) at each of the seven replicate litter-addition sites. Fully expanded leaves were collected from several koa and ʻōhiʻa trees at each site, bulked per tree species across all sites, and placed in a drying oven at 34°C for 2 weeks. Five subsamples were ground and analyzed for initial percent C and percent N. Dried koa or ʻōhiʻa leaves (2 g) were then placed into 10-cm^2 sown mesh (1.13 × 1.30 mm) bags, and 12 bags per species were strung together into a single strand such that one bag could be removed per month for 1 yr. One koa and one ʻōhiʻa strand of bags were placed under one remnant ʻōhiʻa (which was surrounded by restoration koa) at each site by moving the standing litter pool aside, making sure each bag in each strand had contact with the soil surface but not with other strands of bags, and replacing the litter layer above the strand. The same was done under one restoration koa tree per site. Bags were placed into the field in February 2016. One bag per strand was returned to the lab each month and dried at 70°C for 48 h. The remaining leaf material was separated from soil and mesh with a brush, and weighed, ground, and analyzed for percent C and percent N. By 12 months, some of the bags had too little leaf material to analyze for nutrients. These were considered as zero values.

We calculated litter decay constants (k) for mass loss (g) and remaining N (mg) using the equation

$$\ln\left(\frac{x_0}{x_t}\right) = kt$$

where x_0 equals the initial litter mass or nitrogen amount, x_t is the mass or N remaining at time t. We calculated k values for each litter species (koa and ʻōhiʻa) under each overstory tree species (restoration koa or remnant ʻōhiʻa) at each of the seven sites. Initial mass of litter was 2 g for every bag but initial N amount varied with site and litter species. Differences in k were assessed using a generalized linear model (glm) with fixed effects of litter species, overstory species, and their interaction. We then performed model selection using AIC selection as described.

We modeled the change in litter percent C and percent N using generalized linear mixed effects models (glmer) in the lme package (Pinheiro et al. 2019), with fixed effects of litter species, overstory tree species, time, and all combinations of two-way interaction with site entering as a random effect. Interactions were included to determine if changes in litter percent C or percent N varied with litter species based on the overstory tree species, with litter species over time, or with a given overstory tree species with time. Model selection proceeded as above.

To ask how remaining litter quantities differed at the end of the decomposition experiment, we summed litter quantity for the last two collection dates, (after 11 and 12 months of decomposition) because there was little material left after 12 months, particularly for ʻōhiʻa. We then used two-way ANOVAs with litter species and canopy species as fixed effects.

Understory outplanting survival and growth

We planted five common fruiting understory species within experimental treatment plots (control, koa litter, ʻōhiʻa litter, and no grass) to test if litter additions and grass removal affect survival and growth over 2 yr (Appendix S1: Fig. S1). Species were chosen because they are often used in restoration projects and provide habitat and food for birds, a primary goal of Hakalau Forest. Plants at this site grow relatively fast and an effect should therefore be apparent quickly. Seeds were collected and plants grown in greenhouses at Hakalau Forest. Due to varying phenology and times to germination (Lilleeng-Rosenberger 2005), seedlings were of varying sizes at the time of outplanting. The first plants to emerge and be planted were *C. trigynum* (ʻōlapa), and *C. rhynchocarpa* (pilo); four of each were planted per plot in June 2016, three months after herbicide application. We then planted three *M. lessertiana* (kōlea), three *V. calycinum* (ʻōhelo), and two *I. anomala* (kāwaʻu) in October 2016, for a total of 16 plants per plot (16 trees per 28 m^2). Plants were randomly assigned to regularly dispersed planting sites located within 3 m of the base of the tree. All seedlings were checked 1 month after planting and those that died due to transplant stress (<10 total) were replaced. They were checked again in October 2018 for survival.

Survival of outplanted seedlings was modeled using a glm with a binomial distribution and fixed effects of plant species, litter-addition–grass-removal treatment, their interaction, and plant initial biomass. Model selection then proceeded as described previously. The initial biomass for each individual was calculated from the basal diameter and height at initial planting following allometric equations from Aplet and Vitousek (1994) and was included to account for any possible effects that initial plant size has on survival. Equations were available for all species except *V. calycinum,* for which we used the equation for *L. tameiameiae* (previously called *Styphelia tameiameiae*), a shrub in the same family with similar growth form to *V. calcycinum*. We then used a Tukey's HSD test to look for pairwise differences of significant main effects using the multcomp package (Hothorn and Bretz 2008).

We chose to analyze plant growth slightly different than survival because plant growth forms varied and therefore plant growth rates would inherently be different among species. Plant growth was calculated as the relative growth rate (RGR) of each individual as $\ln(B_2/B_1)/T_2 - T_1$, where B_1 and B_2 are biomass (g) at initial planting date (T_1) and final resurvey date (T_2), respectively. For each species, we then modeled RGR with the fixed effect of treatment in a glm.

Results

Passive litter collection

Total annual passive litterfall rates under remnant ʻōhiʻa and restoration koa trees were similar, leading to closely matched C inputs due to percent C of litter being comparable (Table 1). However, because koa leaves, woody material, and flowers in litter contained at least twice the concentration of N as in ʻōhiʻa (Appendix S1: Table S2), annual input of N was greater under the koa trees (Table 1). In terms of different fractions making up the litter, the only difference between koa and ʻōhiʻa was the quantity of flowers, which was over twice as high in passively falling litter under ʻōhiʻa as koa trees (Table 1).

Litter-addition, grass-removal experiment

Soil inorganic N did not differ among plots before the treatments were implemented (one-way ANOVA with treatment as fixed effect, $F_{3,28} = 0.47$; $P = 0.76$). Model selection revealed that only litter treatment and grass removal had an impact on soil inorganic N change over time, with inorganic N being higher in plots where ʻōhiʻa litter was added than in the no-litter control treatment (Table 2). Plots with ʻōhiʻa litter added showed a 50% increase in inorganic N after 1.5 yr as compared to control plots although this difference was not as dramatic after 2.5 yr (Table 2).

Adding tree litter to plots also affected their soil percent N and percent C (Table 3). Koa litter-addition plots had greater soil percent N than control plots, whereas percent C increased in both the ʻōhiʻa and koa litter-addition plots compared to the control plots. The soil percent N did not increase significantly in ʻōhiʻa litter-addition plots. Overall, this led ʻōhiʻa litter-addition plots to have soils with the greatest C:N ratios at the end of the study.

Grass biomass results

The only treatment that affected grass biomass was grass removal by herbicide, where grass biomass was near zero (Fig. 1, Appendix S1: Table S5). After 2.5 yr, we started seeing some regrowth in these plots but otherwise they remained relatively grass free (Fig. 1). Within plots, we found that grass biomass was significantly lower under the largest outplant compared to biomass in adjacent areas in between outplants (Fig. 1, Appendix S1: Table S5). This was true across all treatments suggesting a localized effect of the woody plantings on grass growth.

Litter decomposition study

Decay constants of litter mass loss and nitrogen loss were greater for ʻōhiʻa than koa leaf litter, and the tree canopy species under which decomposition bags were placed did not affect loss rates (Fig. 2, Appendix S1: Tables S3, S4). The amount of litter material left at the end of the decomposition experiment was about three times greater for koa (103.6 ± 39.9 mg/bag) than ʻōhiʻa (45.7 ± 21.2 mg/bag) despite starting at the same initial mass. Similarly, litter N remaining after 11 and 12 months was five times greater for koa (3.3 ± 1.4 mg/bag) than ʻōhiʻa (0.7 ± 0.4 mg/bag) litter. Nonetheless, the total amount of N released by koa compared to ʻōhiʻa was greater because koa litter had much more N in it at the outset.

Table 3. Soil percent N, percent C, and C:N averaged across each treatment.

Treatment	N (%)	C (%)	C:N
Control	$2.23^{a} \pm 0.14$	$31.97^{a} \pm 2.00$	$14.41^{a} \pm 0.22$
Koa litter	$2.66^{b} \pm 0.12$	$38.37^{b} \pm 2.03$	$14.39^{a} \pm 0.20$
ʻŌhiʻa litter	$2.48^{a,b} \pm 0.13$	$38.71^{b} \pm 2.19$	$15.60^{b} \pm 0.37$
Grass removal	$2.36^{a,b} \pm 0.14$	$33.96^{a} \pm 2.07$	$14.37^{a} \pm 0.12$
df	3, 54	3, 54	3, 54
P	**0.014**	**0.004**	**<0.001**

Notes: Data were from last soil sampling date, July 2018. All values are means ± SE. Different letters represent significant differences between individual treatments at a level of $P < 0.05$ using post hoc Tukey tests. Values in boldface type indicate $P > 0.05$. We note that there was one lost soil sample (ʻŌhiʻa litter, in between outplants), leading to a df = 54.

Table 2. Soil inorganic N (μg/g dry soil) over time in litter and grass treatments.

Treatment	Soil inorganic N 1.5 yr	Soil inorganic N 2.5 yr	Parameter estimate	SE	*P*
Control (intercept)	41.4 ± 5.8	26.5 ± 2.0	34.76	4.57	$\mathbf{4.94 \times 10^{-11}}$
Koa litter	47.0 ± 6.3	40.0 ± 4.9	8.55	6.47	0.1902
ʻŌhiʻa litter	62.0 ± 6.9	41.6 ± 4.8	16.33	6.47	**0.0136**
Grass removal	37.6 ± 5.5	31.1 ± 5.1	0.51	6.47	0.9363

Notes: All values are means ± SE (standard error). Litter-addition and grass-removal treatments were compared to control treatments (no litter added or grass removed) using generalized linear mixed effects models (df $t = 80$) with fixed effects of treatment, sample date (pre-treatment, 1.5 yr, and 2.5 yr time point) and their interaction with a random effect of site. Parameter estimates represent model outputs for the best selected model that only included litter and grass treatment on soil inorganic N. Boldface values indicate $P < 0.05$. While sample date was not a significant factor in the model, we present soil inorganic N values at both dates for completeness.

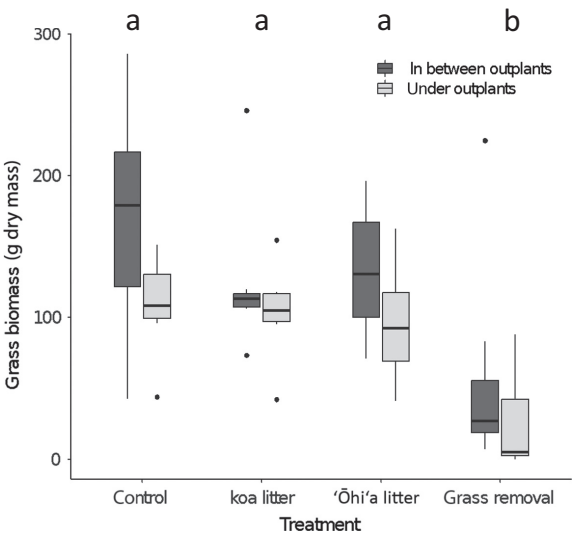

FIG. 1. Box plots of grass biomass in different litter-addition or grass-removal treatments, where biomass was sampled directly underneath the largest outplant in the plot (light gray), or in between outplants (dark gray). Biomass is in grams per 0.25-m^2 plot. The best fit model indicated a difference in grass biomass in between and under outplanted seedlings and between litter treatments (see statistics in Appendix S1: Table S5 for full description). Different letters above plots represent significant ($P \leq 0.05$) differences between litter treatments. Box mid line shows the median; box edges show the first and third quartiles. Whiskers extend from first and third quartiles $\pm$ 1.5 $\times$ interquartile range. Points represent outliers.

Percent carbon of litter varied over time depending on species. ʻŌhiʻa litter had lower percent C than koa litter under both overstory species at the outset. It gained in percent C over time under both tree canopies, while koa litter gained percent C only under the ʻōhiʻa canopy (Fig. 2, Appendix S1: Table S3). In addition, under the koa canopy, percent C of ʻōhiʻa litter began at much lower values than that of koa, but by the end of the experiment ʻōhiʻa litter percent C was greater than that of koa.

As with percent C, ʻōhiʻa litter percent N began at lower values than koa litter percent N, but ʻōhiʻa litter gained percent N over the time, while koa litter maintained a similar percent N level over time (Fig. 2). This resulted in a time $\times$ litter-species interaction (Appendix S1: Table S3). Canopy tree also affected litter percent N, with ʻōhiʻa litter increasing in percent N to a greater degree under koa than under ʻōhiʻa canopies.

Understory outplanting survival and growth

Seedling survival was 82.7% across all species and treatments (Fig. 3). Survival was best predicted by species and experimental treatment, but the interaction of these factors was not significant. Post-hoc comparisons showed that *C. trigynum* had higher survival than all other species (Appendix S1: Table S6). *Myrsine lessertiana* had higher survival (96.0%) than *C. rhynchocarpa* (85.1%) and *I. anomala* (83.3%). *Vaccinium calycinum* had the lowest survival (44.4%). Across all species, the only difference in survival among treatments was in grass-removal plots where seedling survival was higher than the control. This relationship was likely largely driven by high survivorship of *V. calycinum* and *I. anomala* in the grass-removal plots and poor survival of that species in all other treatments.

Growth rates of individual species were not strongly affected by treatments overall. The treatment with the most marked effect compared to controls was the no-grass treatment. Consistent with survival, *V. calycinum* benefited from the no-grass treatment (Fig. 3; Appendix S1: Table S7). *Ilex anomala* also had a positive trend ($P = 0.0744$) with grass removal. Conversely, *Coprosoma* sp. was negatively affected by grass removal. The only litter-addition effect observed was a positive trend of koa litter addition on two species (*C. trigynum*, $P = 0.092$ and *I. anomala*, $P = 0.0714$).

DISCUSSION

We added 4.7 times the amount of naturally falling ʻōhiʻa litter to our study plots, which we expected would decrease soil N given its relatively high C:N content, and we anticipated that this would lead to a decrease in grass biomass. However, we found no decrease in soil available N or grass biomass compared to plots without ʻōhiʻa litter added. In fact, ʻōhiʻa litter addition led to a 50% increase in soil inorganic N as compared to control plots, and a 4% increase as compared to koa litter-addition plots. We note, however, that we only added 1.5 times the natural litterfall rate in the koa litter-addition plots, making direct comparisons between the two types of litter-addition difficult. Nonetheless, ʻŌhiʻa litter did not reduce available N relative to the control, which was consistent with a lack in reduction of grass biomass between no-litter control and litter-addition treatments. Not surprisingly then, there was also no difference in understory outplant survival between treatments. Taken together, these results suggest that the high available soil N conditions created by monocultures of koa (Scowcroft et al. 2004, Yelenik 2017) are not readily reversed, at least while koa is still present as in our study. As a result, the positive effects of soil N on species such as kikuyu will persist under current conditions, unless understory species are planted, which can decrease grass biomass through shading after just 2.5 yr. As such, the continued planting of monocultures of koa (Goldstein et al. 2006, Pejchar and Press 2006, Baker and Scowcroft 2009, McDaniel and Ostertag 2010, McDaniel et al. 2011, Scowcroft and Yeh 2013, Yelenik 2017) across Hawaiʻi may be creating persistent conditions that favor an exotic grass understory, even if efforts are made to reduce available soil N via soil amendments or the planting of ʻōhiʻa seedlings.

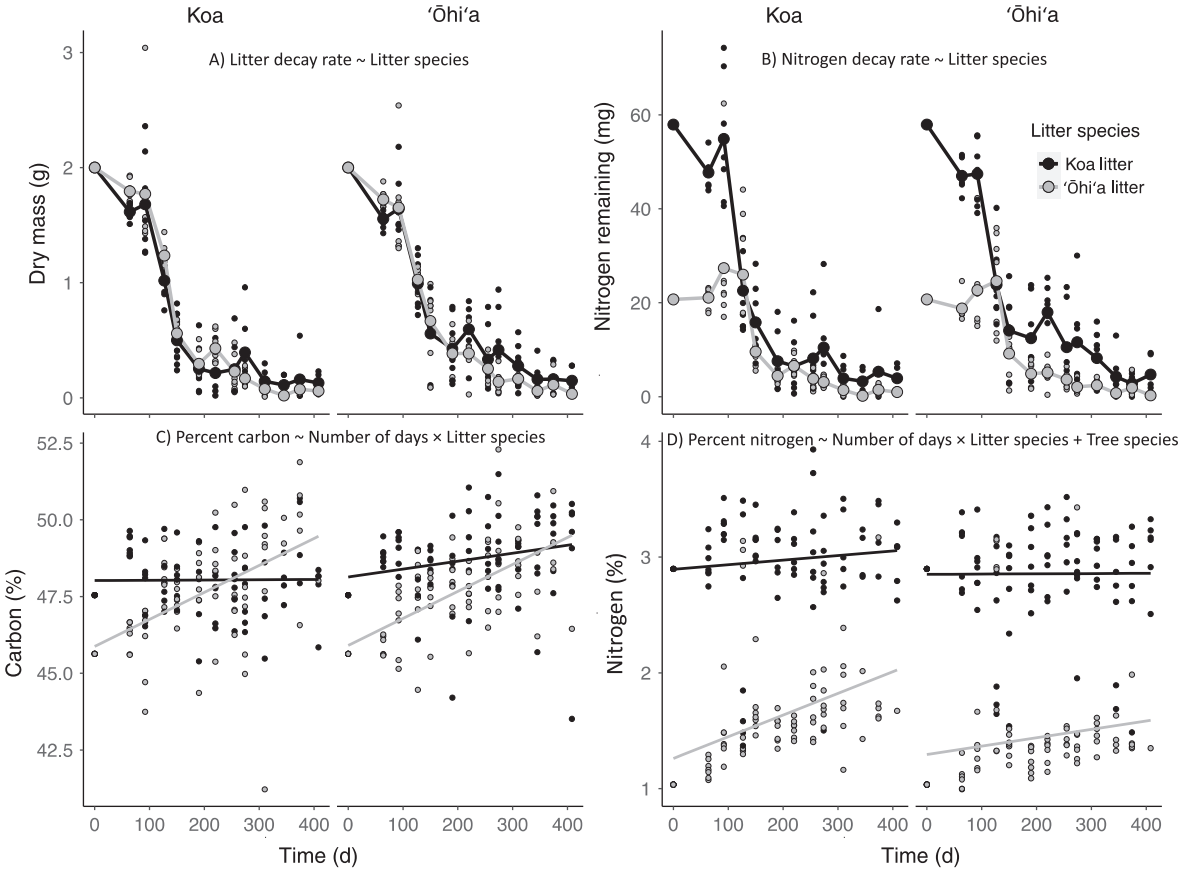

FIG. 2. Litter decomposition of ʻōhiʻa and koa litter under ʻōhiʻa and koa canopy trees over 12 months. (A) Dry mass loss over time, (B) nitrogen mass remaining, (C) percent carbon remaining, (D) percent nitrogen remaining. In each panel, overstory treatment is denoted by koa on the left and ʻōhiʻa on the right. Litter type is denoted by black (koa litter) or gray (ʻōhiʻa litter) color. In panels A and B, the large points represent mean values for that sampling period and small points represent actual data points. The model given in each panel is the best-fit model as determined by model selection. For a full description of models and statistics, see Appendix S1: Table S3 for decay rates, Appendix S1: Table S4 for statistics, and Appendix S1: Fig. S2 for decay rates expressed as a proportion of remaining mass or N.

Litter decomposition

Our results suggest that koa litter loses N quickly for the first five months of decomposition, and then rates of decomposition become comparable to ʻōhiʻa litter, similar to Scowcroft (1997). But by the time the slowing occurs, large amounts of N have been released. Fast N release early in decomposition is linked to the higher percent N content in koa litter and lower C:N, while slower decomposition over time may be due in part to complex secondary compounds in koa litter such as polyphenolics and complex lignin and the fact that most of the N has been lost (Aber et al. 1990, Talbot and Treseder 2012). Lignin has been found to be greater in foliage of koa than ʻōhiʻa in seasonal submontane woodlands on Hawaiʻi Island (August-Schmidt 2018) perhaps because koa "foliage" consists of phyllodes, which are technically expanded stems. In addition, high soil N conditions, as occur under koa trees more generally, may actually slow lignin decay (Fog 1988). Slower rates of decomposition of koa litter material may also relate to the high phenol content of koa vs. ʻōhiʻa relative to N (Peñuelas et al. 2010). The overall pattern of rapid initial decomposition and N release in koa resembles other N-fixing trees and can foster a plant–soil feedback that reinforces persistent high soil N availability (Perakis and Matkins 2012*b*).

The high N availability in koa corridor soil is likely maintained by large amounts of continually falling koa litter with its rapid initial N release. Because decay rates slow after the initial release, koa litter is likely to build up over time, leading to large coarse O and A horizon organic matter pools. This is consistent with various studies showing an increase in organic matter and soil C under koa stands relative to nearby open grassy sites (Scowcroft et al. 2004, August-Schmidt 2018) and is common among N-fixing trees (Binkley and Cromack 1994). Observationally, kikuyu roots appear to use the thick partially decayed leaf litter layer as a growing medium, and in general it was difficult to dig down to

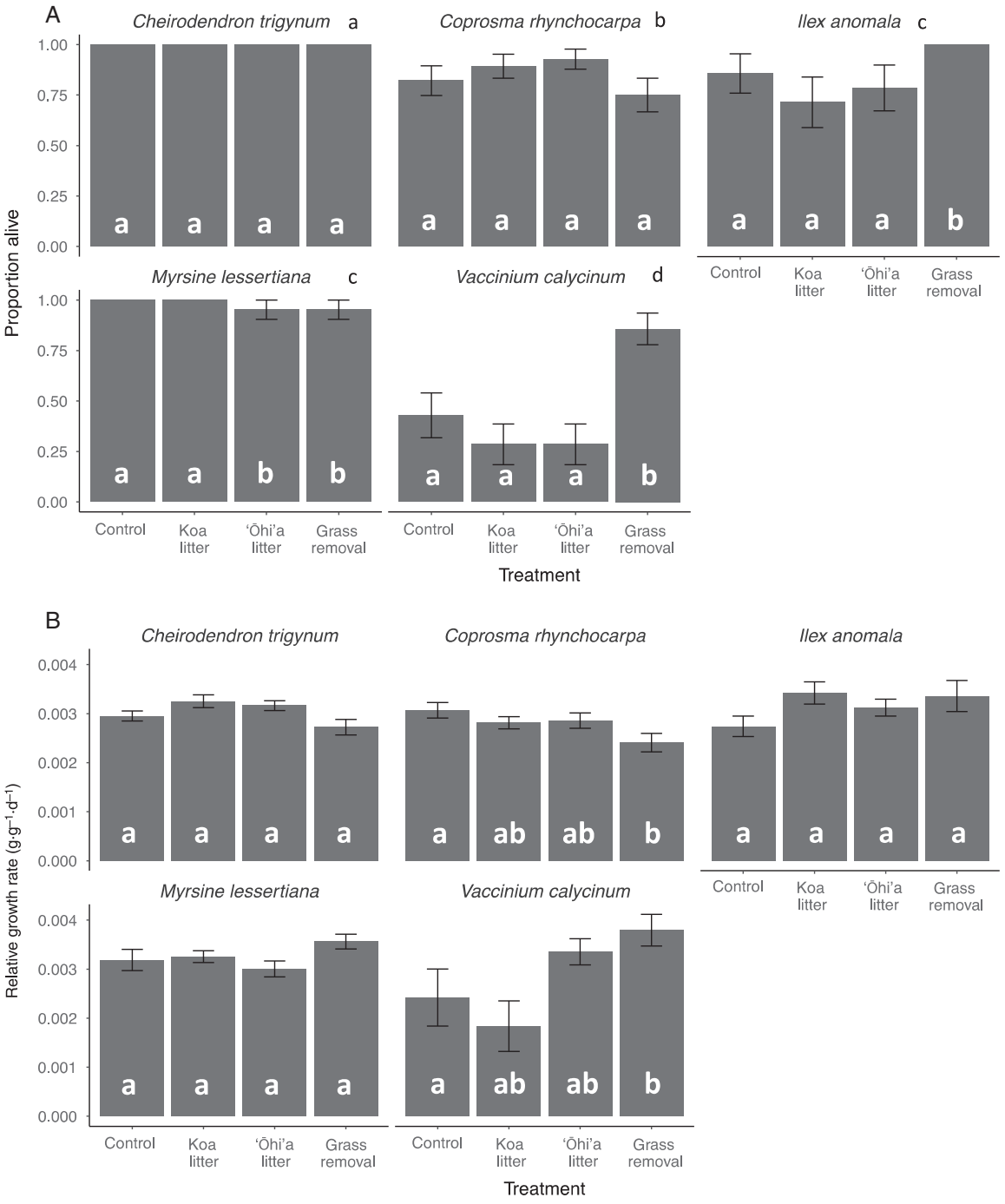

FIG. 3. (A) Survivorship and (B) growth of individual seedlings of different native woody species under different litter-addition and grass-removal treatments. Bars are means ± SE. Lowercase letters above each top panel indicate significant differences ($P \leq 0.05$) in survival between species across all treatments and letters on bars represent significant differences in treatments compared to controls within each species. Lowercase letters on bars in bottom panel indicate significant differences in growth rate of treatments compared to the control within a given species (see statistics in Appendix S1: Tables S6 and S7). Additional post hoc comparisons of all contrasts between all treatments can be found in Appendix S1: Fig. S3.

mineral soil under koa (S. G. Yelenik, C. M. D'Antonio, E. M. Rehm, *personal observations*). Previous work within these sites under individual koa and ʻōhiʻa trees has shown greater organic matter under ʻōhiʻa than koa in the A horizon, although both soils were highly organic (koa = 57%; ʻōhiʻa = 65%; Yelenik 2017).

The high density of koa trees in the koa corridor areas was not comparable to "intact" forest sites.

Indeed, litterfall from randomly placed litterfall traps in intact forest plots at 1,600 m in elevation (Giardina et al. 2014) showed substantially lower koa than ʻōhiʻa litterfall rates. In contrast, litterfall rates of koa and ʻōhiʻa were similar to each other in our sites. The high koa density and subsequent litterfall in the restoration corridors are likely sustaining a widespread high soil mineral N pool not representative of intact forest.

Canopy tree identity did not affect overall litter decomposition in terms of mass lost, even under koa canopies (Appendix S1: Table S4). It is possible that the buildup of koa phyllodes and concomitant tannins or phenolics (Peñuelas et al. 2010) constrains the effect of high mineral N on microbial organisms. It may also be that carbon quality directly constrains microbially mediated decomposition, similar to Hobbie and Vitousek (2000), who found that fertilization with N (akin to ʻōhiʻa litter being placed under the koa canopy) only had small effects on litter decomposition rates in Hawaiʻi. Finally, it is possible that because our sites only had scattered remnant ʻōhiʻa within the koa corridors, the soil there was influenced by high koa densities and thus sites were not as different as if we were to compare koa and ʻōhiʻa in a typical forest where ʻōhiʻa dominates. Importantly our data suggest that ʻōhiʻa litter coming into a koa plantation or restoration site will decompose rapidly whether under koa or ʻōhiʻa, thus supporting our result that ʻōhiʻa litter addition did not lower N availability.

Addition of C to reduce available N

Numerous managers and investigators have attempted to reduce available N in N-rich soils by adding an external source of carbon (reviewed in Perry et al. 2010), typically sugar or sawdust. Beneficial results of C addition on native perennial grasses, for example, were found in a subtropical system invaded by exotic grasses in Australia (Prober et al. 2005). The goal of these studies was to free microbes from C limitation so that they become N limited and immobilize mineral N. This, in turn, should tip competitive interactions away from nitrophilous invasive plants like kikuyu (e.g., Blumenthal et al. 2003, Perry et al. 2010).

Our addition of ʻōhiʻa litter was based on a similar premise: a relatively high C:N litter of ʻōhiʻa compared to koa (i.e., C:N = 53.2 vs. 28.8) would stimulate microbial immobilization of soil N (Johnson and Cheng 2000), which is otherwise highly available under koa (Scowcroft et al. 2004, Yelenik 2017). We expected that an available N reduction in turn would reduce kikuyu growth, which has been shown elsewhere to benefit from high soil N (Colman and O'Neill 1978). We chose to use ʻōhiʻa litter because it can be collected on site, has a higher C:N ratio than koa (Appendix S1: Table S2), can be an important substrate for woody plant germination and seedling growth (Rehm et al. 2020), and does not require bringing in an external source of materials in this remote environment. ʻŌhiʻa is also a species sometimes planted as seedlings into koa monocultures by managers; thus over time, its litter should build up (Yelenik 2017).

Yet, we saw no evidence of reduced available soil N in ʻōhiʻa litter-addition plots despite adding litter at a rate quadruple that found under lone ʻōhiʻa trees (Table 2). In fact, we saw increased available N in the ʻōhiʻa litter-addition plot soils, suggesting we had not released microbes from C limitation. Nonetheless, we found an increase in soil C:N in ʻōhiʻa litter-addition plots from around 14.4 to 15.6 (Table 3) suggesting that the added litter is already changing organic matter pools, but that this change is not yet substantial enough to generally immobilize N. Springob and Kirchmann (2003) suggest that soil C:N ratios between 15 and 17 represent the breakpoint between high and very low N mineralization. Since it took about 2.5 yr to achieve an 8% change in the soil C:N, it would take approximately 1.5 more years of our litter additions to reach a C:N of 17 (assuming a linear rate of change).

The increase, rather than decrease, in available soil N that we observed at the final time point, is inconsistent with the observed increase in C:N and suggests more detailed studies are needed to understand carbon chemistry and controls over N availability in this system. It is possible that C in the added litter is quickly respired by microbes with the rapid decomposition in this mesic environment, leaving behind N because of the large amounts of litter added. It is also possible that the elevated soil N was due to a priming effect (Kuzyakov 2010) whereby N added by naturally falling koa litter (which we did not exclude) enhanced N release from the added ʻōhiʻa litter. Finally, it is possible that the added ʻōhiʻa litter stimulated asymbiotic N-fixation, which can be associated with the O-layer and decomposing native plant leaves in other parts of Hawaiʻi (Ley and D'Antonio 1998, Crews and Farrington 2000).

Treatment effects on associated plant species

Recently we have shown that ʻōhiʻa litter is an important substrate in which native woody plants recruit in the intact forest understory near this site (Yelenik 2017, Rehm et al. 2019). Yet here, the addition of ʻōhiʻa litter had no measurable effect on grass growth nor did it increase native woody seedling survivorship or growth. In fact, the litter disappeared quickly (consistent with our decomposition study) and did not build up enough to offer substrate for woody plant recruitment or to create a physical barrier to impede kikuyu growth.

Results of our study suggest that native woody seedlings can survive and grow reasonably well in kikuyu under koa, even though no woody seedlings are naturally found in the dense grass that typifies the koa corridor understory (Yelenik 2017), despite seed rain (Yelenik et al., *in press*), presumably due to inability to germinate and survive. Most of our seedlings were as tall as the

grass canopy when outplanted, and thus did not suffer light attenuation from kikuyu. The one exception was ʻōhelo (*V. calycinum*), which was below grass height when planted, potentially accounting for its higher survival and better growth when grass was removed. Overall, however, we found that most native woody plants can thrive under koa. Indeed, our results are evidence that saplings ultimately may begin to limit grass growth (Fig. 1), and that it is light competition, rather than changes in soil nutrients that will drive forest succession. Active restoration of native woody understory could help to control exotic grasses (McDaniel and Ostertag 2010). Once that happens, passive recruitment of native woody plants may begin to occur, a possibility we are exploring. Indeed, dense plantings of native understory leading to further passive restoration has been seen in other tropical and subtropical systems (Holl 1998, Parrotta 1999, Carpenter et al. 2004, Zahawi and Augspurger 2006).

Management implications

Our data suggest that adding litter of a common non-N-fixing tree species to the high N conditions under koa will not readily reverse this condition. Thus, litter amendments or planting of non-N-fixing trees such as ʻōhiʻa will not quickly reverse the soil conditions that occur under unnaturally high koa densities such as those in the restoration forests at Hakalau Forest (Hart 2010). However, we also show that the survival of planted native understory species is high, particularly if the plants are at least as tall as the dominant grass understory. Over time, these outplants may decrease grass growth via light, water, or nutrient competition. We planted understory species at higher densities than is standard at Hakalau Forest. It is possible that such higher density plantings may increase the rate at which grass biomass decreases and thus more quickly create forest stands where native woody seedlings can regenerate, though this question has yet to be addressed in Hawaiian restoration projects.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2477/full

Open Research

Data (Yelenik and Rehm 2020) are available in the U.S.G.S. ScienceBase data catalog at https://doi.org/10.5066/P9XY3LLI.