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Passive restoration augments active restoration in deforested landscapes: The role of root suckering adjacent to planted stands of *Acacia koa*

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ABSTRACT

Active forest restoration in Hawaii's Hakalau Forest National Wildlife Refuge has produced a network of *Acacia koa* tree corridors and islands in deforested grasslands. Passive restoration by root suckering has potential to expand tree cover and close gaps between planted stands. This study documents rates of encroachment into grassland, clonal stand structure, and tree architecture. Data were collected from random replicate strip transects that started inside 23-year-old koa plantations and ended either in open grassland or in adjacent planted stands. For the former, sucker densities increased from near zero inside planted stands to a maximum of 5–38 stems m^{-2} 5–14 m away from the edge of the plantation canopy, and then decreased to zero–a typical pattern for trees invading grassland. No suckers occurred more than 28 m from the canopy edge on east-facing slopes, or more than 18 m on south-facing slopes. Rates of expansion into grassland ranged from 0.8 to 1.5 m yr^{-1}; suckers had already filled gaps between closely spaced plantation stands located on north-facing slopes. Continued suckering should result in the eventual re-establishment of tree cover on deforested areas between planted tree islands and corridors, and without additional active restoration.

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1. Introduction

Extensive areas of tropical forests have been and continue to be converted to agricultural uses (FAO, 2010). Between 2000 and 2005 an estimated 27 million hectares of humid tropical forest were cleared (Hansen et al., 2008; Asner et al., 2009), a phenomenon driven mainly by rapid urbanization and increasing international demand for agricultural products (Butler and Laurance, 2008; DeFries et al., 2010). The net decline in natural forest area slowed during 2000–2010 (Meyfroidt and Lambin, 2011), an indication that losses were being partially offset by reforestation of abandoned agricultural lands.

Abandonment of degraded and deforested lands is driven by a number of factors, not the least of which is whether the agricultural use is economically viable and sustainable (Cramer et al., 2007; Rey Benayas et al., 2007). Once abandoned, land managers must decide whether restoration is desired to recover lost biodiversity and the suite of other ecosystem service provided by the original forest ecosystem, and if so, how should it be done (Holl and Aide, 2011). Answers vary with the degree of degradation, which will depend on the nature, duration, and intensity of the agricultural practices, the desired rate of recovery, and the desired state of the restored ecosystem (Aide et al., 2000; Holl, 2007). At one extreme are cases of small-scale, short-term subsistence agriculture where forests recover quickly after abandonment without human intervention and with the same species assemblages as formerly (passive restoration or secondary succession). At the other extreme are cases of large-scale, long-term deforestation that occurred when forest landscapes were converted to grasslands either intentionally for cattle pasture or unintentionally as a consequence of the invasive grass-fire cycle (e.g., Mack and D'Antonio, 1998; MacDonald, 2004). The biotic and abiotic legacy of such conversions can be stable alternative ecosystem states dominated by invasive species that resist colonization by native species following abandonment (Kulmatiski, 2006; Suding et al., 2004; Cramer et al., 2007). To speed ecological restoration managers must resort to assisted regeneration (active restoration) (Lamb and Gilmour, 2003), which generally has a negative benefit-cost ratio, except perhaps where the potential environmental cost of doing nothing outweighs the cost of intervention (Lamb et al., 2005; Birch et al., 2010).

Reestablishing of forest cover to deforested landscapes can involve both passive (natural regeneration by seeding, coppice, or root suckers) and active efforts (artificial regeneration by direct

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seeding or planting). Species that can regenerate by root suckering have an advantage over species that regenerate from seed in that they bypass or better cope with many impediments to natural recolonization of deforested landscapes. Those barriers include poor seed dispersal, seed predation, harsh environmental conditions, and competition from introduced grasses (Holl, 2002).

Establishment of tree islands (aka. applied nucleation) within deforested areas has been proposed as a way to overcome those barriers with only modest investment (Rey Benayas et al., 2008; Corbin and Holl, 2012). However, its success depends not only on increased seed dispersal, seedling survival, and species richness within tree islands, but also on the expansion of islands beyond their initial boundaries (Corbin and Holl, 2012). No matter how successful establishment of tree islands might be, if they do not expand into adjacent areas the landscape remains fragmented and only partially restored.

Here we present a case study describing how root suckering (passive restoration) is augmenting planting (active applied nucleation) to reestablish koa forest (*Acacia koa*) in abandoned pastureland. The questions of interest include the following—Might clonal expansion into unplanted grassland eventually close the gaps between planted stands? How long might it take? Are clonal trees and stands different from those of the same age but regenerated from seeds? Does slope aspect influence root suckering?

2. Methods

2.1. Site description

The study site is located inside the Hakalau Forest National Wildlife Refuge at 1980 m elevation (19°14′51″N/155°19′59″W) where the climate is cool and mesic (Scowcroft and Jeffrey, 1999). The Holdridge life zone for the site is Subtropical Montane moist forest (Tosi et al., 2002). Mean daily air temperature ranges from 9 to 14 °C, and freezing temperatures occur near ground level during clear winter nights. Annual rainfall is approximately 2000 mm. Soils are strongly acidic and classified as Medial over hydrous, ferrihydritic, isomesic Acrudoxic Hydrdands.

The 13,247-ha Hakalau Forest National Wildlife Refuge was established in 1985 to protect and manage endangered Hawaiian forest birds and their rain forest habitat. More than 100 years before establishment, approximately 2020 ha of mesic to wet native forest above 1700 m elevation were converted to pasture for cattle grazing. The vegetation in the deforested area was dominated by alien grasses, including *Pennisetum clandestinum*, which is a C_4 grass adapted to cool, fertile areas (Mears, 1970; Wilen and Holt, 1996), *Ehrharta stipoides*, *Anthozanthum odoratum*, *Holcus lanatus* and *Axonopus fissifolius*. The native grass, *Deschampsia australis*, and the short-stature native shrub, *Vaccinium calycinum*, were sparsely present. Remnant old-growth koa trees were largely confined to steep-sided gulches, although a few isolated individuals occurred elsewhere within the grassland matrix.

The first active reforestation effort was established in 1987 inside a 2.6-ha exclosure that was built that year within the deforested and actively grazed portion of the Refuge. It excluded pigs, goats and sheep as well as cattle. Grazing ended in 1990. Koa was chosen as the native tree species to plant. It was an important structural component of the former forest, and managers believed that it would establish despite grass competition and harsh environmental extremes, and subsequently physically change the abiotic environment, and in so doing directly or indirectly regulate the availability of resource to other species (Wright and Jones, 2006). No naturally occurring koa were present inside the exclosure or located within 0.5 km of it. Thirty blocks of koa were planted inside the Magnetic Hill Exclosure (Scowcroft and Jeffrey, 1999). Within each block, seedlings were planted on a 7 × 7 square grid, using one of two spacing: 2 and 2.5 m (Conrad et al., 1988). All blocks established successfully (Fig. 1a); some were located in drainage bottoms, while others were located on north-, east-, or south-facing slopes (Scowcroft and Jeffrey, 1999). Root suckers were first observed in 1990.

The success of the initial reforestation effort led managers to adopt planting as the method of choice. Active restoration was confined to 10-m-wide corridors, which consisted of three parallel rows of trees that were laid out to link remnant koa trees together and tie them to forest fragments and more densely wooded pastures located at lower elevation (Scowcroft and Jeffrey, 1999; US Fish and Wildlife Service, 2010). The corridor concept was similar in design to that implemented more recently in Columbia (Perfecto and Vandermeer, 2010; Murgueitio et al., 2011), but the intent differed. At Hakalau the intent was to create habitat that was suitable for establishment of native understory plant species, and to provide avenues for species movement into the heart of the deforested landscape. More than 312,000 koa seedlings were planted by 2007 (Unpublished report, 2007 Accomplishments and status – Hakalau Forest NWR, 2 p).

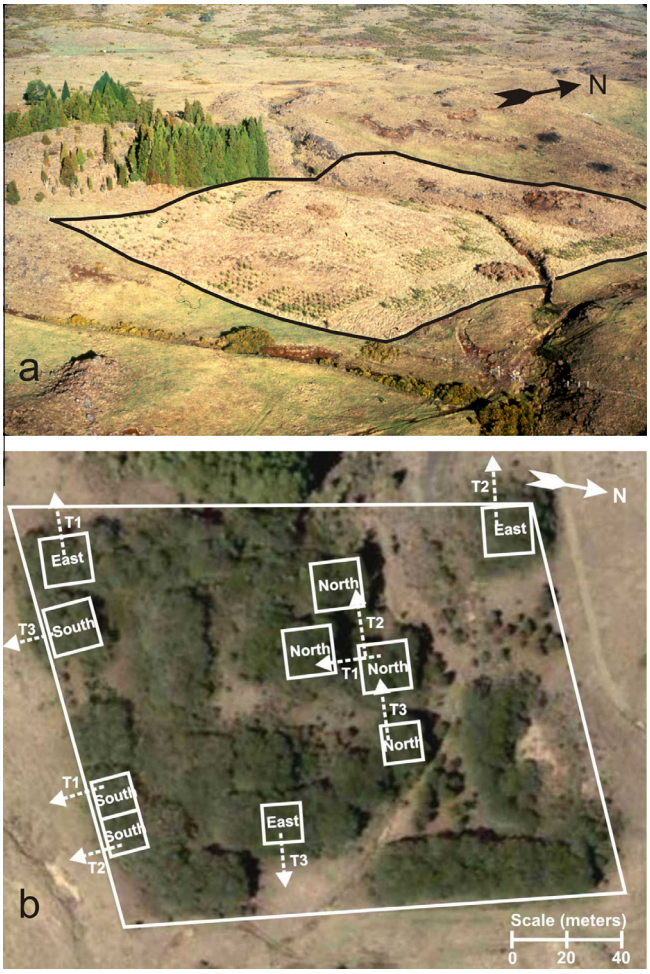


Fig. 1. The 2.6-ha Magnetic Hill Exclosure was the site of the first trial plantings (1987) of *Acacia koa* in deforested portions of Hakalau Forest National Wildlife Refuge. (A) The 7-by7-tree planting blocks were visible from the air in 1990. (B) The original boundaries of individual plantation blocks sampled in this study are shown superimposed on a 2006 Google Earth satellite image: two block sizes are shown depending on spacing (2- by 2-m or 2.5- by 2.5-m). Block labels denote general slope aspect. Dashed arrows denote the direction and approximate location and length of sample transects, which for a given slope aspect were labeled T1 through T3.

Although large tracts of treeless pasture still exist between the koa corridors, the Refuge is counting on passive restoration (i.e., exclusion of ungulates, prevention of wildfires, and natural regeneration) to ultimately close the gaps. This hope is partly based on the observation that, three years after the initial 1987 trial planting, prolific koa root suckering began to occur in areas adjacent to the original planting trial. Similar suckering has since been observed next to planted koa corridors throughout the Refuge.

2.2. Sample design

Root sucker data were collected during June and July 2010 from 10 of the 30 planted blocks established inside the exclosure. The main criterion for plantation block selection was that it be situated so as to allow a strip transect to be run from the middle of the plantation out into open grassland until root suckers no longer occurred. These were necessarily located along the perimeter of the exclosure. Plantation blocks located near the access road were excluded to avoid potential effects on suckering. Only nine blocks met the criteria: four were located on east-facing slopes, four on south-facing slopes and one located in drainage bottom. Lack of replication eliminated the latter block. Three replicate east-facing and three south-facing blocks were randomly selected for sampling. In addition, four interior blocks on a north-facing slope were selected because of their close proximity to each other (Fig. 1b). The expectation was that rapid colonization of the narrow gaps between them would result in different size trees and stand structures than found in the other sample areas.

One 2-m wide strip transect was laid out for each block located on the east- and south-facing slopes. There were six possible transect locations within a given block (one between each row of trees), and one was randomly selected. Each transect consisted of contiguous 2-by-2 m subplots that extended from the center of the original plantation block into the open pasture until the last subplot contained no root suckers. Transect locations for blocks on the north-facing slope were not selected at random but were constrained by the relative position of each pair of blocks (Fig. 1b). Transects still ran from the center of one block across the intervening gap and to the center of the other block. This design yielded three strip-transects each for east-, south- and north-facing slopes.

2.3. Measurement variables

All koa root suckers within each subplot were measured for height, diameter at 10 cm above ground and breast height (DBH), crown height (i.e., height of base of crown above the base of the trunk), and average crown diameter. The distance between the edge of the plantation canopy and the center of each subplot was also recorded.

2.4. Data analysis

Total root sucker density (stems m^{-2}) was calculated for each subplot along a given transect. Histograms were constructed for each transect to show how stem density changed with distance of subplot centers from the outer edge of the plantation canopy.

The rates of expansion of root suckers into grassland (m yr^{-1}) for transects on east- and south-facing slopes were estimated by dividing the distance between the outermost row of planted trees in the original plantation and the outer edge of the last subplot with root suckers by the elapsed time since root suckering was first observed (i.e., 1990). One-way ANOVA (SYSTAT 12 Software, San Jose, CA) was used to test the hypothesis that expansion rates were the same for east- and south-facing slopes.

An R software script (R Development Core Team, 2012) that called the add-on Generalized Additive Model library package, 'gam' (Hastie, 2012), was written to fit trend lines showing the effects of distance of subplot centers from the edge of the plantation canopy on mean and median sucker heights, basal stem diameters and crown diameters within subplots (script courtesy of Dr. Jim Baldwin, Statistician, Pacific Southwest Research Station, USDA Forest Service, Albany, CA). Separate fits were obtained for east-, south- and north-facing slopes. For the latter, each transect was divided so that each segment started at the center of a plantation block and ended in the center of the gap between adjacent blocks.

To assess structural similarities of root sucker and planted koa stands, the relationships between stem DBH and tree height was determined for each aspect. For planted stands, only dominant and co-dominant interior trees at ages 3, 5, 11, and 21 years were used. For root suckers, all individuals with measureable DBH were used. Based on the year when root sucker first was observed (1990) and the time needed for an individual to be tall enough to have a measurable DBH, the age range for root suckers was assumed to be 3–19 years. Data were fit to the 4-parameter, sigmoidal model: $y = y_o + a/(1 + \exp(-(x-x_o)/b))$ (Sigma Plot 10, Systat Software, Inc., San Jose, CA).

Data on tree heights, DBHs, crown diameters, ratios of DBH to height, and live crown ratios of the tallest root suckers located within 2 m of the edge of the plantation canopy were compared to corresponding data for 21-year-old trees regenerated (a) from seed following disk plowing in the Woodland exclosure (Scowcroft, 2012) and (b) from nursery stock planted in the Magnetic Hill exclosure. As noted above, the tallest root suckers were assumed to be 20 years old. The effect of type of koa regeneration on tree size was examined using general linear model procedure (SYSTAT 12, Systat Software, Inc., San Jose, CA). Post-hoc pairwise comparisons were done using Tukey's Honestly-Significant-Difference test ($\alpha = 0.05$).

3. Results

On east- and south-facing slopes where clonal expansion into open grassland was unrestricted by nearby tree plantings, root sucker densities increased to a maximum with increasing distance beyond the edge of the plantation canopy and then decreased to zero—a typical invasion front (Fig. 2a and b). Density distributions varied considerably in shape between transects even when located on the same slope aspect. In general, suckers were found deeper within and further away from edges of plantations located on east- than south-facing slopes. No root suckers occurred more than 28 m from the canopy edge on east-facing slopes, or more than 18 m on south-facing slopes. On east-facing slopes, maximum densities ranged from 5 to 30 stems m^{-2}. Those maximums were reached 5–7 m from the canopy edge on two transects, and 12–14 m on the other transect. On south-facing slopes maximum densities ranged from 14 to 38 stems m^{-2}. Those maximums were reached 5–7 m from the canopy edge on two transects, and 9–11 m on the other transect.

The effect of distance from edge of the plantation canopy on sucker density was less pronounced on north-facing slopes because clonal expansion had filled the gaps between stands years before this study was done. Within the narrow gaps between planted blocks, maximum sucker densities ranged from 2 to 4 stems m^{-2} (Fig. 2c). The maximums occurred close to the center of the gaps.

Few root suckers occurred under the canopy of the plantations, regardless of slope aspect (Fig. 2). That there were any present at all was due to gaps in the planted stands caused by early seedling mortality. Such canopy gaps eventually closed, and surviving

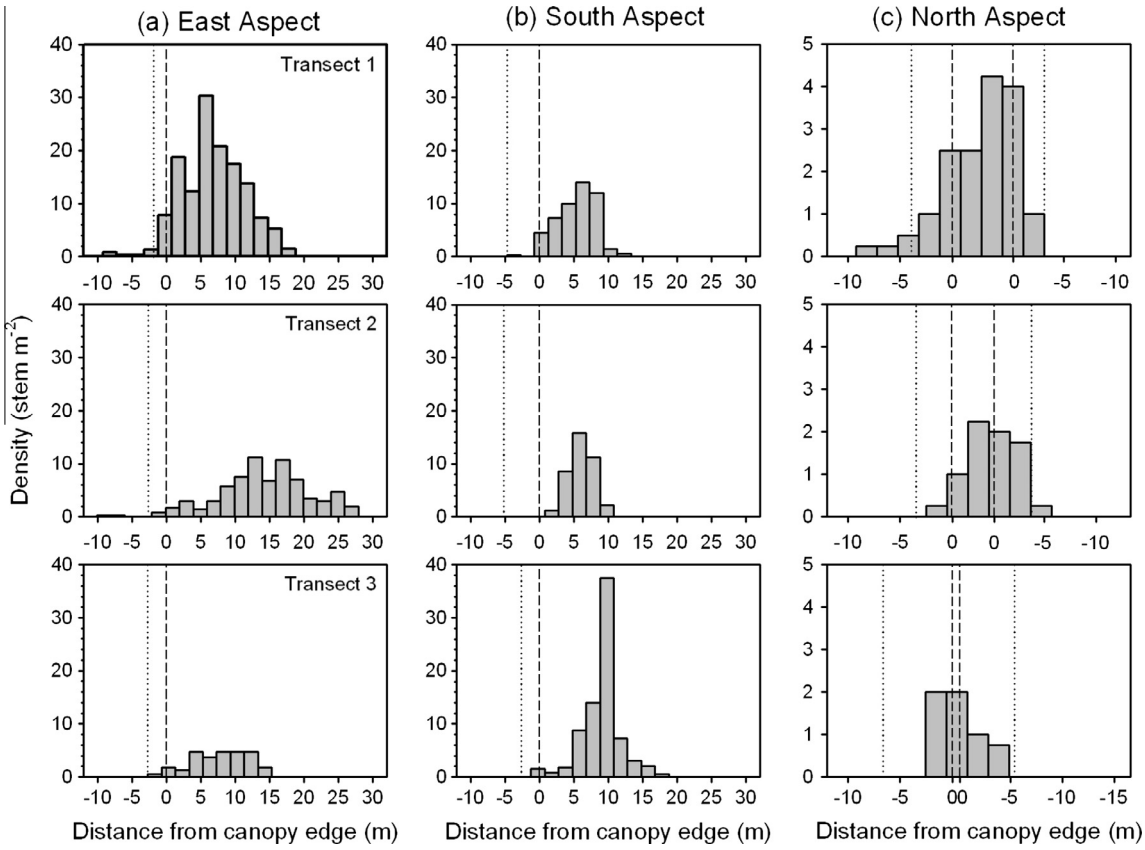


Fig. 2. Density of *Acacia koa* root suckers in 4-m^2 subplots 20 years after suckering was first observed (1990) as a function of distance of subplot centers from the edge of the canopy of the original plantation stands (dashed vertical lines) located on (a) east and (b) south aspects where colonization was extending tree cover into open grassland, and (c) a north-facing slopes where the gaps between closely spaced tree islands were being colonized. The dotted vertical lines denote the location of the stems of the outermost row of planted trees for a given stand. The scale for the *X* and *Y* axes of north-facing slopes differs from those used for east- and south-facing slopes because while transects for the latter started in the center of planted stands and ended in open grassland areas, those for north-facing slopes started and ended in the centers of adjacent planted stands.

suckers were suppressed, of low vigor, and unlikely to survive and grow into full size trees.

Root suckers expanded into grassland at rates of 0.9–1.5 m yr^{-1} on east-facing slopes and 0.8 to 1.0 m yr^{-1} on south-facing slopes. The difference between east- and south-facing slopes was not significant ($P = 0.200$). The leading edge of the invasion front was found an average of 20.3 m beyond the edge of the plantation canopy on east-facing slopes and 13.0 m on south-facing slopes. On north-facing slopes, the gaps between planted stands, which originally ranged from 11 to 14 m wide, were fully occupied by root suckers in 2008 (Fig. 2c). Consequently, it was not possible to estimate rates of expansion for northern slopes. However, if the rates of expansion were comparable to those found on east- and south-facing slopes, the gaps between planted stands would have been colonized by suckers within 4–9 years the start of suckering. Expansion of plantation canopies occurred at the same time as clonal expansion, and by 2008, 21 years after establishment, sizes of the canopy-free gaps were down to 0.2, 4.5, and 6.3 m (Fig. 2c).

The effect of distance from the outer edge of the plantation canopy on height, basal stem diameter and crown diameter of suckers was different for each slope aspect. On the east, mean and median trend lines started at high levels deep within plantations, remained nearly level up to the edge of the canopy, and then declined at nearly a constant rate to the leading edge on the colonization front (Fig. 3a). On the south, few suckers occurred under the plantation, so trend lines started closer to the canopy edge and at levels higher than those for eastern slopes (Fig. 3b). The lines showed no initial flat trajectory but immediately declined, and at a steeper rate than found on eastern slopes. Finally they leveled off at about 12 m away from the canopy. On the north, trend lines started within plantations, and trajectories were (1) nearly flat for tree height, (2) sinusoidal for basal stem diameter, and (3) rising to a maximum for crown diameter (Fig. 3c). The trend lines started and ended high; the ending values for the northern suckers were consistently greater than those for either eastern or southern suckers.

The ranges of heights, basal stem diameters and crown diameters were large where there was no overhead plantation canopy (Fig. 3). For east and south-facing slopes the large ranges persisted until the leading edges of the colonization fronts were approached. Because the colonization front on north-facing slopes had disappeared many years ago, the large ranges in sizes did not change with distance for the canopy edge.

Suckers >2 m tall occupied the zone between −2 and 15 m of the canopy edge for the east aspect; between −2 and 7 m for the south aspect; and between −6 and 7 m for the north aspect. Short suckers, ⩽10 cm tall, were not found under the plantation canopy (Fig. 3). They were found all along east-facing transects starting at the canopy edge and ending as far as 26.7 m into the grassland (Fig. 3a). The south aspect supported short suckers between 5 and 15 m from the canopy edge (Fig. 3b). Short suckers were absent throughout the length of north-facing transects; the single exception was the result of dieback and regrowth (Fig. 3c).

Sigmoidal curves fitted to height and DBH data for plantation trees and root suckers had large r^2 values and all were significant with $P < 0.0001$ (Fig. 4). Curves for suckers were already flattening out having reached heights <6.5 m at DBHs ranging from 7 to 10 cm. In contrast, curves for planted koa continued upward with maximum heights projected to range between 14 and 17 m.

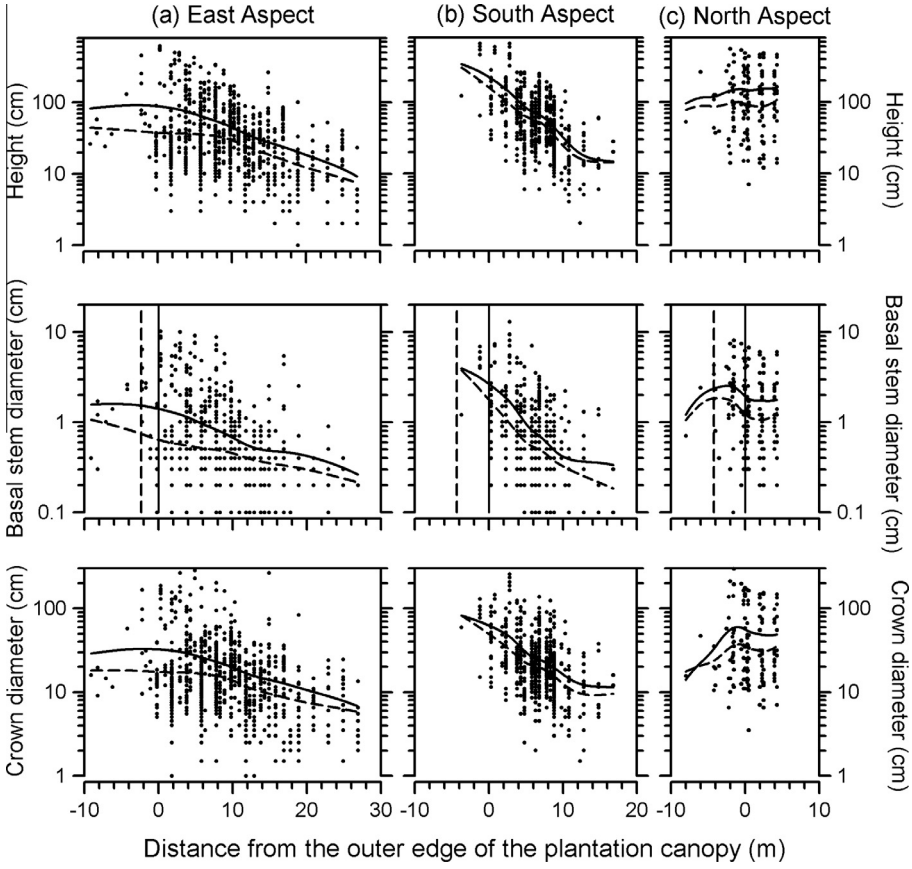
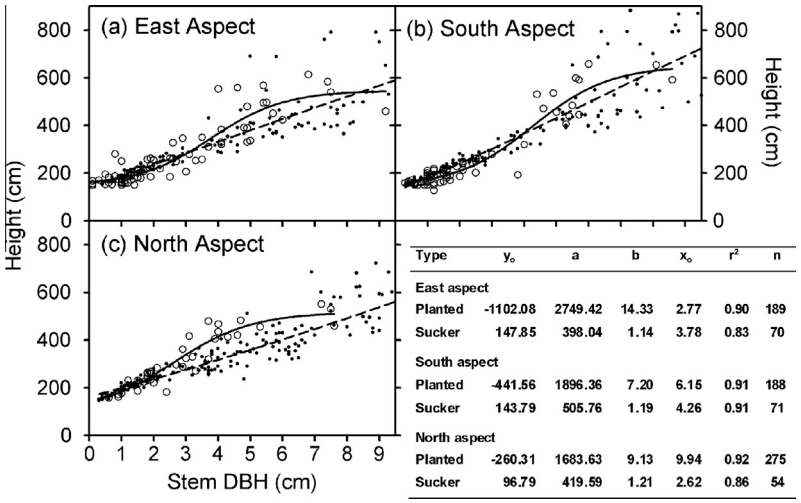


Fig. 3. Variations and trends in heights, basal stem diameters and crown diameters of *Acacia koa* root suckers in 4-m^2 subplots as a function of distance of subplot centers from the existing edge of the canopy of the original plantation stands (solid vertical lines) located on (a) east-, (b) south- and (c) north-facing slopes 20 years after suckering began in 1990. Solid curves were fitted using general additive model and the R statistical package. Dashed vertical lines denote the locations of the stems of the outermost row of planted trees.



Type	y_o	a	b	x_o	r^2	n
East aspect						
Planted	-1102.08	2749.42	14.33	2.77	0.90	189
Sucker	147.85	398.04	1.14	3.78	0.83	70
South aspect						
Planted	-441.56	1896.36	7.20	6.15	0.91	188
Sucker	143.79	505.76	1.19	4.26	0.91	71
North aspect						
Planted	-260.31	1683.63	9.13	9.94	0.92	275
Sucker	96.79	419.59	1.21	2.62	0.86	54

Fig. 4. Relationships between stem diameter at breast height and tree height for 5- to 21-year-old planted koa (dashed lines and dots) and 5- to 19-year-old koa root suckers (solid lines and open circles) growing on east-, south- and north-facing slopes inside the Magnetic Hill exclosure, Hakalau Forest National Wildlife Refuge. Data were fit to the 4-parameter, sigmoidal model: $y = y_o + a/(1 + \exp(-(x - x_o)/b))$; $P < 0.0001$ for all fitted curves.

The largest suckers, which as noted above were near the canopy edge of plantations, were consistently and significantly smaller than their planted and naturally regenerated counterparts despite being close to the same age (Table 1). The average height of suckers was approximately 2.5 times less than that for trees of seed origin ($P < 0.001$). Average sucker stem diameter was 5–6 times smaller ($P < 0.001$), and average crown diameter was 3.5–4.8 times smaller ($P < 0.001$). Suckers had more slender trunks for a given height than trees of seed origin ($P < 0.001$). Live crown ratio of suckers was the same as planted koa ($P = 0.8$), but one-half that of naturally regenerated trees ($P = 0.004$).

Table 1
Comparison of average (s.e.) height, DBH, DBH:height ratio, crown diameter and live crown ratio for 15- to 19-year-old koa root suckers and 21-year-old planted trees at Magnetic Hill exclosure and naturally regenerated trees inside the Woodland exclosure, the latter located at 1700 m elevation in Hakalau Forest National Wildlife Refuge.

Attribute	Root sucker[a]	Planted[b,c]	Natural[c]
Initial density (stems m^{-2})	2–37.5	0.16–0.25	0.028–0.28
Sample size	15	55	398
Height (m)	5.0 (0.4)a[d]	12.4 (0.3)b	12.8 (0.1)b
DBH (cm)	4.9 (0.5)a	25.6 (1.0)b	30.1 (0.6)c
Crown diameter (m)	1.2 (0.1)a	4.3 (0.2)b	5.8 (0.1)c
DBH:Height (m/m)	0.010 (0.001)a	0.021 (0.001)b	0.024 (<0.001)c
Live crown ratio	0.23(0.04)a	0.27 (0.02)a	0.41 (0.01)b

[a]The individuals used in this calculation had heights >2 m and were growing between −1.2 and 0.8 m of the edge of the plantation canopy.
[b]From the same plantation stands used in this study to sample root suckering.
[c]Only dominant and codominant trees were used.
[d]Within row means followed by a common letter were not significantly different (Tukey's Honestly-Significant-Difference Test, $\alpha = 0.05$).

4. Discussion

Corbin and Holl (2012) stated that expansion is necessary for applied nucleation to be an effective restoration technique. The present study showed that passive restoration by means of root suckering successfully augmented active restoration by causing planted tree islands and corridors to expand beyond their original boundaries. The rate of sucker expansion into grassland at Hakalau (0.8–1.5 m yr^{-1}) was toward the lower end of the 0.5–2.5 m yr^{-1} range report for mountain parkland areas of Hawaii Volcanoes National Park after cattle grazing and goat browsing were controlled (Mueller-Dombois, 1967; Cuddihy, 1984). Lack of injury due to grazing, browsing and trampling in the present study might have contributed to slower rates. Nevertheless, suckering appears to be common where koa becomes re-established in a grassland matrix, and it shows no sign of stopping as long as uncolonized open areas exist. The implication for managers is that a 100-m gap between planted koa corridors inside the Refuge will close in 35–65 years without additional management intervention.

Changes in root sucker density across the invasion fronts in the present study were similar to those observed for trees invading grasslands through seed rain and seedling establishment. For instance, Dovčiak et al. (2008) reported that densities of *Picea abies* germinants and seedlings were low near the forest edge, increased to a maximum part way along the invasion front, and then decreased to low levels at the leading edge. They attributed the pattern to the combination of seed rain and environmental factors that influenced successful establishment of seedlings with the latter being the main determinant. The low densities of suckers near the established plantations in the present study are probably due to the negative influence of the koa overstory. The decline in sucker density between the point where density peaks and the edge of the plantation canopy probably reflects density induced mortality. The increase in density from the leading edge of invasion front back to the point of maximum density reflects a favorable environment capable of supporting far more suckers and with a greater range of sizes than initially emerge at the leading edge.

Clonal expansion of tree cover into surrounding grassland occurred independent of effects of tree islands on increasing seed dispersal and/or seedling survival, and it thus bypassed many of the obstacles facing seedling regeneration (Holl, 2002). Although neither seed-focused process was examined in the present study, existing literature strongly suggests that neither process would play a role in expanding koa tree cover into adjacent areas. Koa pods/seeds are not animal dispersed. Planted koa can sporadically produce large seed crops. However, because (1) the heavy seeds are not animal dispersed and have a limited dispersal distance (Baker et al., 2009), (2) intense competition from introduced grasses, particularly kikuyu grass (*P. clandestinum*), inhibits establishment (Denslow et al., 2006), and (3) subfreezing winter temperatures severely damage or kill seedlings growing in the open (Scowcroft and Jeffrey, 1999), colonization of and expansion into grassland adjacent to planted tree corridors and islands is unlikely.

In the short term, koa islands established in abandoned pasture might not serve as plant recruitment foci for other native forest species because the understory of the young stands contains no fruit bearing shrubs and trees that would otherwise attract frugivorous birds. On the other hand, koa corridors connect deforested areas to less degraded wooded pasture, and thus provide a tree-covered pathway that frugivores might explore, depositing seeds in the process. The 'Ōma'o (*Myadestes obscurus*) is the primary endemic species involved in dispersal of seeds of fleshy-fruited plants. The endemic Hawaii 'Amakihi (*Hemignathus virens*) can also disperse seeds, but fruit comprises a small portion of its diet (Mitchell et al., 2005). The most common introduced frugivores that might carry seeds from neighboring forested areas to koa corridors and tree islands are the Japanese White-eye (*Zosterops japonicus*) and Red-billed Leiothrix (*Leiothrix lutea*) (Foster and Robinson, 2007). Feral cattle and pigs might also move seeds into koa corridors and tree islands, but they were eradicated before the start of restoration and kept out. Rats (mainly *Rattus rattus*) can disperse seeds too (Sugihara, 1997), but they are also seed predators (Shiels and Drake, 2011). *R. rattus* has a small home range (e.g., <4 ha), and its preference for arboreal habitat (Shiels, 2010) would likely limit dispersal to the narrow ecotone between existing forest and abandoned pasture.

Even if seeds of other native plant species did make it into tree islands and corridors, subsequent spread onto open areas would be difficult due to intense competition with alien grasses. Enrichment plantings (active restoration) to increase understory species diversity is underway to enhance the attractiveness of planted stands, but there will be a lag before fruit production starts. Even then the likelihood of the understory species establishing outside the confines of the tree islands and corridors is low because they are even more susceptible to frost damage than koa (e.g., Scowcroft et al., 2000).

This study confirmed the observation that koa root suckering rarely occurs beneath an established canopy of koa. Those struggling suckers that were found there originated in canopy gaps that had since closed. Whether reduced light levels and/or belowground competition or some other factor prevents establishment of root suckers is unknown. The exclusion phenomenon is not restricted to koa. Trembling aspen (*Populus tremuloides*) shows similar patterns of root suckering with production of suckers being inhibited in the shaded understory of healthy stands (Peltzer, 2002). Although light is not needed for aspen sucker initiation, it is essential for growth and establishment (Shepperd, 2001). That might be true for koa root suckers as well, and could account for the lack of suckers inside plantation stands of koa.

Grass competition is known to be a main impediment to recolonization of grassland by trees and other woody species in many biomes (Holl, 2002; Bond, 2008). It limits koa seedling recruitment (Denslow et al., 2006), but the extent to which it limits root sucker recruitment is unknown. Tunison et al. (1995) speculated that alien bunch grasses such as *Andropogon virginicus*, *A. odoratum* and *H. lanatus*, which dominated most grassland at their sites, are less competitive with root suckers than are other introduced grasses such as kikuyugrass and meadow ricegrass (*E. stipoides*), both of which occur in abandoned pastures and the understory of koa plantations. Perhaps the large variability in sucker density

observed in this study reflects differences in grass species composition and competition. Nevertheless, the presence of suckers across the range of microsites at the Magnetic Hill site indicated that whatever grass competition existed, it did not prevent suckering.

Fifteen- to 20-year-old suckers were shorter, had smaller DBHs and crowns, and had more slender trunks for a given tree height than planted and naturally regenerated trees of comparable age (Table 1). The reduced size of suckers was probably due to prolonged maintenance of high sucker stand density. They remained connected to the parent tree which allowed them to obtain essential resources from a well-developed root system. In contrast, seedlings have to fend for themselves. The integrated root system of suckers might make them more tolerant of abiotic stressors (Peltzer, 2002) and intraspecific competition. As a result, stem densities potentially can be maintained for a long time. But the potential disadvantage of high sucker density is that it is likely to reduce resource availability for height growth of any one individual (Midgley, 1996). Eventually surviving root suckers should develop their own root system and become independent of the genet tree (Jeník, 1994), and then they might have more resources for growth and be able to develop into canopy trees of a stature similar to that found in the original forest.

Reliance on clonal expansion to passively reach the goal of restoring forest bird habitat will depend on the ability of clonal stands to develop a structure similar to the original forest. Clonal koa can reach large size given enough time in some areas. Tunison et al. (1995) found that mature clonal trees had become established 50 years after release from cattle browsing in Hawaii Volcanoes National Park. They also reported that several clonal stands had all size classes represented (i.e., suckering was ongoing) while one stand was made up of only pole size and larger trees with no young suckers or saplings. In the present study, relationships between DBH and height indicated that clonal koa will not reach the stature attained by the original koa-ohia forest, at least not as long as stand densities remain at 20,000–370,000 stems ha^{-1}. The data indicate that sucker densities do decline, however it is equally clear that new suckers continue to be produced even under a developing root sucker overstory, which contradicts the finding that suckers are excluded by a plantation overstory. Although the long-term implications of short stature and small crowns on suitability for bird habitat are largely unknown, those bird species that require large trees for survival and reproduction, such as the Hawaii ʻAkepa, *Loxops coccineus coccineus* (Freed, 2001; Fretz, 2002; Camp et al., 2010), will not be advantaged.

Slope aspect influences above- and belowground physical environments, and those in turn affect vegetation and site productivity (e.g., Stage, 1976; Sternberg and Shoshany, 2001; Desta et al., 2004; Stage and Salas, 2007). In the northern hemisphere, south-facing slopes are hotter and drier than other aspects. East-facing slopes tend to be cooler and moister that west-facing slopes and north-facing slopes are generally cooler and wetter than other aspects (Spurr and Barnes, 1980, p. 208). Mast et al. (1997) reported that pine tree invasion of grassland in the Colorado Front Range was more rapid on north than south-facing slopes. Although the Refuge is located on the east flank of Mauna Kea, undulating terrain has west-, south- and north-facing as well as east-facing slopes. In the present study, aspect had modest effects on changes in height, basal stem diameter and crown diameter with increasing distance from the plantation canopy. While trees nearest the plantation were larger on south- than east-facing slopes, the rates of decline with increasing distance were steeper on the south. The width of the zone occupied by suckers was smaller on the south than on the east. The modest effect of aspect on koa root suckers compared to the strong effect on pine seedling invasions reported by Mast et al. (1997) may be due to suckers having multiple root linkages that buffer individual suckers against harsh localized environmental conditions. Despite these differences, the important point is that root suckers colonized all aspects.

Expansion of forest cover through root suckers raises concerns about long-term effects on genetic diversity. Will genetic diversity of clonal stands be reduced compared to stands originating solely from seeds; and if so by how much and with what consequences? Generally, genetic diversity of clonal stands is reduced because many stems are identical (Del Tredici, 2001; Bettinger et al., 2009). When active restoration is the necessary precursor to passive clonal restoration, any reduction in genetic diversity can be minimized by employing thousands of planted trees grown from local seed sources during the active phase of restoration (Leakey, 1987). The clonal stands produced as hundreds of thousands of suckers fan out around tree islands and across gaps between corridors should have far more genetic diversity than stands used in production forestry, where only one or a few genotypes are used. A related question is whether genetic diversity within clonal stand can be increased as ramets themselves produce seeds and seedlings are recruited (Eriksson, 1989; Olejniczak, 2003)? In the case of koa at Hakalau Refuge, remnant old-trees are sparsely found throughout the reforestation area and old-growth forest exists to the north and east, thus affording opportunity for interbreeding with sexually mature ramets. Research is needed to quantify the loss of genetic diversity, and to determine if and when stands of root suckers are able to reproduce sexually, and thus to offset some of the clonally caused loss in genetic diversity.

5. Conclusions

At Hakalau Refuge, investments in active restoration have resulted not only in the establishment of koa tree islands and corridors, but also, and unexpectedly, in development of root sucker stands. Koa root suckers have been continuously and successfully colonizing open pasture areas for nearly 20 years despite the lack of disturbances that normally trigger suckering and despite potential grass competition. It seems likely that grass-dominated open areas between planted koa islands and corridors will eventually be colonized. The amount of time to close the gaps can be estimated from knowledge of the distance between corridors and observed rates of expansion (0.8–1.5 m yr^{-1}). The ultimate characteristics of mature clonal koa stands and their suitability as bird habitat and regeneration sites for establishment of native understory species in Hakalau Forest NWR have yet to be determined.

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