New Forests
DOI 10.1007/s11056-012-9352-6

Parent tree effects on reestablishment of *Acacia koa* in abandoned pasture and the influence of initial density on stand development

Paul G. Scowcroft

Received: 19 August 2011 / Accepted: 19 May 2012
© Springer Science+Business Media B.V.(outside the USA) 2012

Abstract Increasingly private landholders in Hawaii are considering native forest restoration for their lands, and some public agencies have already started such work. Initial efforts have focused on reestablishing *Acacia koa* to recover alien-grass-dominated sites. This study was done in Hakalau Forest National Wildlife Refuge, Island of Hawaii, to determine the efficacy of disk plowing to stimulate natural regeneration of koa from buried seeds. Sites with four different koa parent tree configurations were treated–single live overhead koa canopy, multiple live canopies, downed snags, and no parent koa tree. Tree growth and survival were assessed periodically over 21 years. Average initial stand densities ranged from 100 to 1,500 trees ha^{-1} of scarified land, although some open areas had as few as 20 trees ha^{-1}. The distributions of seedlings with increasing distance from plot center were variable within and between parent tree configurations. Initial seedling density was significantly greater for the multiple-live-parent than for the no-parent configuration. Densities for the single-live and dead configurations differed from the no-parent configuration only when densities were based on the entire scarified area of each plot. Stand densities declined 10–67 % during the next 20 years. Survival was a negative, non-linear function of initial stand density. Initial stand density exerted strong control over stem diameter and crown size at age 21-years, but had little effect on the proportion of trees with single-stems. The relationships between stand basal area and density at 21 years conformed to the existing koa stocking guidelines. While moderate to high densities of natural regeneration can be expected from scarifying around live and dead koa trees, single trees or low density stands are likely in open areas.

Keywords Forest restoration · Natural regeneration · Subtropical montane wet forest life zone · Even-age stands · Soil seed bank · Hawaii

P. G. Scowcroft (✉)
U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Institute of Pacific Islands Forestry, 60 Nowelo Street, Hilo, HI 96720, USA
e-mail: pscowcroft@fs.fed.us

Published online: 08 June 2012

Introduction

In Hawaii, upland areas historically offered the best climate for cattle ranching. Most upland native forests on the islands of Hawaii and Maui were converted to pasture as far back as the mid 1800s (Tummons and Dawson 2002; Pratt and Jacobi 2009). The conversion involved the harvest of commercially valuable trees, the harvest of other trees for fence posts and building materials, the introduction of pasture grasses, the intentional and unintentional introduction of fire, and the release of cattle, which completed the destruction of the forests and assured their continued suppression (Cuddihy and Stone 1990).

Extensive areas of pasture have been abandoned since 1980 on the Islands of Hawaii and Maui as ranching leases expired and profits declined. Landholders have become increasingly interested in reforesting such areas as an investment and to restore the ecosystem services that forests provide. Recent economic models indicate that private investment in forestry might be more profitable than cattle ranching (Goldstein et al. 2006). However, the lack of silvicultural knowledge about koa (*Acacia koa* A. Gray), Hawaii's only native commercial species, has been explicitly identified as hampering private investment in commercial forestry (Pejchar and Press 2006). Public landholders, such as the US Fish and Wildlife Service and National Park Service, are less interested in financial returns: their goals include restoring native biodiversity to speed recovery of endangered species.

One such area of publicly owned land is Hakalau Forest National Wildlife Refuge (NWR). Established in 1985 under the authority of the U.S. Endangered Species Act of 1973 to preserve and protect five species of endangered forest birds and their forest habitat, this Refuge has become a model for landholders interested in reforestation of former pasture land (Maxfield 2003). Initially little information existed about how to reestablish native forest on the nearly 2,000 ha of deforested and open woodland landscapes above 1,600 m elevation. Because these areas were known to have supported a native forest dominated by koa and ohia (*Metrosideros polymorpha* Gaud.) trees, remnants of which were still sparsely present in 1985, the Refuge manager and U.S.D.A. Forest Service researchers decided to focus first on reestablishing koa.

Koa produces abundant although sporadic seed crops. Seed coat dormancy prevents germination of current-year seeds, so soil reserves can build to high levels. Alien grass cover suppresses natural koa seedling regeneration but does not necessarily eliminate recruitment (Denslow et al. 2006). Soil disturbance or fire stimulates germination of the soil seed bank (Scowcroft and Nelson 1976; Scowcroft and Wood 1976; Skolmen and Fujii 1981). Koa is a shade-intolerant species with fast initial height growth (Baker et al. 2009). It is a nitrogen-fixing species that is also colonized by mycorrhizae (Allen and Allen 1936; Koske et al. 1992), so establishment of koa is not inhibited by low soil N and P availability that commonly occurs in tropical pastures (e.g., Cleveland et al. 2003; Scowcroft et al. 2004). Stands of koa reduce biomass of pasture grasses (Scowcroft and Jeffrey 1999), provide habitat and insect prey for native birds (Pejchar et al. 2005; Goldsmith et al. 2007) and protect native understory plants from damage due to winter frost (Scowcroft et al. 2000).

This study reports on the initial effort to promote natural regeneration of koa through mechanical soil disturbance. The objectives of the study were to (1) determine if soil scarification with a disk plow stimulated germination of the existing koa seed bank sufficiently to meet the management goal of restocking sites with an initial density of 50 trees ha^{-1} of treated area; (2) determine whether the presence of koa seed trees affected initial stocking density, survival, and subsequent tree development; and (3) examine the

relationships between initial stand density and survival over time, and between initial density and several tree attributes 21 years after scarification. The hypothesis related to objectives 2 and 3 was that while the presence or absence of parent seed trees would influence initial stocking density, it would be initial density that controlled stand development, including survival, growth, crown architecture and structure of the single cohort, single species stands (Oliver and Larson 1990). Because many public and private lands on Hawaii and Maui have a similar history of degradation and are located in the same climatic zone as the study site, findings should be broadly applicable and thus help landowners decide whether to undertake similar reforestation efforts on their land.

Materials and methods

Site description

The study area (19° 50′ 26″N/155° 18′ 35″W) is located on the eastern flank of the volcanic mountain of Mauna Kea on the Island of Hawaii. A 16-ha ungulate-proof exclosure known locally as the Woodland Exclosure was built in 1987 inside Hakalau Forest NWR at 1,685 m elevation (Conrad et al. 1988). The Holdridge life zone for the site is Subtropical Montane wet forest (Tosi et al. 2002). Mean daily air temperatures at 2 m above ground average about 10 °C. Subzero temperatures and frosts can occur November–April (Scowcroft et al. 2000). Annual rainfall averages approximately 2,500 mm, and trade wind-generated clouds often shroud the study site in fog and mist in the afternoon (Scowcroft 1992). The topography consists of rolling hills with 6–20 % slopes with some shallow wet depressions but no gulches or stream channels. The soil series is Piihonua silty clay loam, which is a well-drained soil formed in volcanic ash (Sato et al. 1973), and it is classified according to the U.S. Soil Taxonomy as hydrous, amorphic, isomesic Acrudoxic Hydrudand (Hue et al. 2006).

Before conversion to cattle pasture in the late 1800s and early 1900s, the area supported a closed, multi-layered koa-ohia montane wet forest (Gagné and Cuddihy 1990). Koa and ohia trees up to 35 m tall formed the emergent tree overstory layer. Native species formed an understory tree layer that was 10–20 m tall and included *Cheirodendron trigynum* (Gaud.) A. Heller, *Coprosma rhynchocarpa* A. Gray, *Ilex anomala* Hook. and Arnott, *Myoporum sandwicense* A. Gray, and *Myrsine lessertiana* DC. *Cibotium* spp formed a tree fern layer at 3–5 m and beneath it were a variety of native species, including the shrubs, *Rubus hawaiiensis* A. Gray, *Leptecophylla tameiameiae* (Cham. and Schlechtend.) F. v. Muell. and *Vaccinium calycinum* Sm., and the fern, *Dryopteris wallenchiana* (Spreng.) Hyl.

After conversion to pasture, the study area became open woodland dominated by scattered remnant old-growth koa and ohia trees. The native understory vegetation was completely destroyed by 50–100 years of cattle grazing. Introduced grasses, including *Pennisetum clandestinum* Hochst. Ex Chiov., *Anthoxantum odoratum* L., *Holcus lanatus* L. and *Ehrharta stipoides* Labill., became the dominant ground vegetation. The establishment of the Refuge in 1985 brought an end to cattle ranching, and without grazing the understory in the study area was soon covered by a thick thatch of *P. clandestinum*, which is federally listed as a noxious weed (Motooka et al. 2003) that impedes natural regeneration of native plant species, including koa (Denslow et al. 2006).

Design and treatment

The study was originally designed to examine the effect of koa parent tree configuration on initial stocking density and subsequent survival and growth of natural koa regeneration. Four such configurations were recognized inside the exclosure: (1) two or more live old-growth koa trees growing in close proximity with their crowns touching each other (Multiple live), (2) a single live old-growth koa tree (Single live), (3) a dead standing or fallen old-growth koa tree (Dead), and (4) an open area located at least 30 m from the nearest live or dead koa (None). The presence of live trees implies a continual seed rain to counteract losses due to failed germination, disease, and other causes of natural decline in viability. The presence of multiple live trees might produce greater seed rain per unit of ground than an isolated tree. Once a tree dies, the soil seed bank should gradually be depleted. Areas distant from seed trees, including those that show no sign of ever supporting a seed tree (i.e., lack of residual coarse woody debris) should have the fewest viable seed. Thus, the size of the viable seed bank and the density of seedlings emerging following scarification were hypothesized to vary by parent tree configuration in the order of Multiple live > Single live > Dead > None. Areas with only live ohia trees overhead were not considered for scarification, nor were areas that could not be safely treated with the disk plow. All potential sites in each parent tree category were identified: the exclosure contained five multiple live tree plots, 15 single live tree plots, 10 dead tree plots and 10 open area plots. Although five plots for each configuration were chosen at random for scarification, only four single-live-tree plots were actually scarified.

Plots were centered on the tree cluster, single live tree, dead tree or open area. The size and shape of the disturbed areas varied from plot to plot depending on the disk plow operator's judgment about how much of the area around each plot center could be safely scarified. Typically plot centers lay outside each scarified area. Except for open-area plots, the nearest the bulldozer operator got to plot center was 1.8 m. Where possible the scarification extended to twice the radius of the actual or imaginary overhead koa tree crowns. Several passes of the disk plow were made to thoroughly turn over the soil and grass sod to a depth of 12–15 cm without moving either off site. In the open, each scarified area was to have a diameter of approximately 25 m. The ranges in size of disturbed areas were as follows: multiple live, 292–1,911 m^2; single live, 731–1,633 m^2; dead, 763–1,506 m^2; and none, 431–546 m^2. In some cases, plots were adjacent to each other and shared a common border.

Following scarification in July 1987, azimuths and distances from plot center to reference points located around the inner and outer borders of each disturbed area were determined. The size of each area was determined by first converting from polar to rectangular coordinates, ordering them in a counterclockwise direction for outer borders and clockwise direction for inner borders, and then using an R software program (version 2.14.1, Copyright © 2011 The R Foundation for Statistical Computing) and the add-on general polygon clipping routines (Peng 2010) to calculate area. Areas were adjusted to account for unscarified portions within the larger plots.

Staked reference points around the perimeter were used to map the rectangular coordinates of individual seedlings with reference to plot center. Each seedling was assigned a number and marked with a flagged wire pin. Numbered aluminum tags were later used to identify trees within each plot.

The first data–height and crown diameter–were collected in 1988, approximately 1 year after scarification, except for replicate #1 of the Dead configuration, which was measured 4 months after scarification. Crown diameter was the average of two measurements taken

at right angles to each other. All plots were remeasured in 1990–1991 (3.4–4.3 years old) and in 2008 (21 years old). Stem diameter at 1.4 m above ground (DBH) was added to the measurements in 1990–1991. In 2008, two additional attributes were measured: height to the lowest live portion of the main crown, and height above ground to the first live fork. Because some trees had multiple stems at 1.4 m in 2008, the DBH of each was recorded separately but only one tree height and one average crown diameter were recorded per tree. Dead trees were noted for each measurement.

Quantitative analysis

Objective 1

The success of soil scarification to meet the management goal of restocking sites with an initial density of 50 trees ha^{-1} of treated area was evaluated for each parent tree configuration using simple one sample t tests ($P \leq 0.05$). Densities were based on the entire scarified area of each plot.

Objective 2

Although variable size and shape of the plots was an unavoidable consequence of logistical constraints, such variability might bias evaluations of parent tree effects on initial seedling densities if there was a consistent density gradient with distance from plot center, and assuming that plot center was located in the approximate center of the existing or assumed (in the case of the dead configuration) overhead koa canopy. An R software program that called the add-on library routines—'gpclib' (Peng 2010), 'RODBC' (Ripley 2012), and 'sp' (Pebesma and Bivand 2012)—was written to determine if there were discernible within- and between-configuration density gradients (courtesy of Dr. Jim Baldwin, Statistician, Pacific Southwest Research Station, USDA Forest Service, Albany, CA). The program determined seedling density in 5-m-wide bins starting at plot center and progressively moving away in 0.5-m increments until the furthest-most scarified part of each plot was reached. Density was plotted against distance of the mid-point of each 5-m-wide bin from plot center.

Differences in initial stocking density due to parent tree configuration were examined using SAS Proc Mixed (SAS Institute 1996) and log-transformed data to successfully equalize variances. The analysis was repeated using three different data sets to show how differences in initial stocking due to parent tree configuration were affected by changing the size of the sample area. The first data set consisted of densities within plot areas bounded by concentric circles anchored at plot center and with radii of 7.8 and 15 m. All plots had a portion of their area within this band. The second set used the band between 5 and 20 m from plot center. The third set used densities calculated for entire plots. Reported means are the result of back-transforming the least squares means and correcting for bias (Sprugel 1983). Pairwise comparisons among parent tree configurations were performed using Tukey's HSD test ($\alpha = 0.05$).

SAS Proc Mixed and log-transformed data were also used to test differences in the attributes of dominant and co-dominant trees at 21-years-old due to parent tree configuration. The attributes examined included quadratic-mean stem diameter (square root of the sum of DBH squared divided by the number of stems), tree height, number of live stems at breast height, crown diameter, height to the base of the live crown, crown depth (difference between tree height and height to the base of the live crown) and live crown ratio (crown

depth divided by tree height). Pairwise comparisons among parent tree configurations were performed using Tukey's HSD test ($\alpha = 0.05$). Back-transformed and bias corrected means are reported herein.

Objective 3

The effects of initial stocking density on survival, quadratic-mean stem diameter, total tree height, crown diameter, height to the base of the live crown, crown depth and live crown ratio at age 21 years were examined by using the regression fitting feature of SigmaPlot 10 (Systat Software, Point Richmond, CA) to find the best empirical fits to the data. The equations that explained the greatest amount of variation in the data were deemed the best empirical fits.

Lastly, the relationships between stand density and stand basal area (m^2 ha^{-1}) for each 10-cm-wide quadratic-mean stem diameter class at 21-years old were determined using linear regression with intercept at the origin. Enough data points existed to generate regressions for two quadratic-mean stem diameter classes: $15 < DBH \leq 25$ and $25 < DBH \leq 35$. Plots in the no-parent-tree configuration that contained only one open-grown tree were excluded from the regression analyses. Results were overlaid on the preliminary stocking guideline chart developed by Baker and Scowcroft (2005; Fig. 7b) to visually evaluate how well the data in this study fit the model.

Results

Effects of parent tree configuration

Soil scarification produced a single cohort of koa seedlings and resulted in monospecific even-age tree islands. Average initial seedling densities ranged from 1,479 ha^{-1} for the multiple-live-parent configuration to 109 ha^{-1} for the no-parent configuration (Table 1, Entire plot data set). Of the four configurations, only the no-parent configuration failed to meet the Refuge's goal of initially restocking sites with >50 trees ha^{-1} of treated area ($P = 0.18$). Densities for the other configurations were all significantly greater than the target: $P = 0.010$, 0.047 and 0.006 for the multiple-live, single-live and dead parent configurations, respectively.

Changes in initial density of koa seedlings with increasing distance from plot center showed several patterns, none of which were consistent either within or between parent tree configurations (Fig. 1). Intuitively, one might expect greatest densities nearest the base of a parent or the center of the overhead canopy, with densities declining with increasing distance. This pattern was present in multiple-, single- and dead-parent configurations, but it was by no means the dominant pattern. A second pattern seen in these configurations was that of densities rising to a peak within 5- to 10-m of plot center and then declining to near zero at distances of 30–50 m, or rising sharply at those same distances. The latter might have indicated that the scarified area was infringing on the zone of influence of a neighboring koa seed tree. A third pattern was densities remaining low at all distances from plot center. This pattern characterized the no-parent configuration, but was also found in the single- and dead-parent configurations.

Initial stocking density varied greatly among plots within a given parent tree configuration, except for the no parent tree configuration (Fig. 2a; note the different y-axis scale for the latter configuration). This was true even when the amount of scarified area used to

Table 1 Effect of parent tree configuration on initial stocking density of *Acacia koa* seedlings as a function of the proportion of each scarified area included in the analyses; and the average size of the included area

Parent configuration	Density (stems ha^{-1})			Sample area (m^2)	
	Mean[§]	Median	SD	Mean	SD
Band 1: 7.6- to 15-m[‡]					
Multiple live	2,068a	1,167	1,779	228	147
Single live	1,549ab	1,460	1,296	337	71
Dead	686ab	631	668	352	68
None	115b	47	148	281	61
Band 2: 5- to 20-m					
Multiple live	1,862a	1,844	849	523	275
Single live	1,133ab	969	1,000	701	162
Dead	449ab	419	385	735	124
None	114b	25	138	424	47
Entire plot (variable band width)					
Multiple live	1,479a	1,316	839	1,228	708
Single live	868a	716	672	1,203	399
Dead	454a	472	146	1,235	322
None	109b	23	127	508	46

Circular sample bands were anchored at plot center and were delineated by concentric circles with the specified inner and outer radii

[§] Within a given band, mean densities for parent tree configurations followed by a common letter are not significantly different (Tukey's test, $\alpha = 0.05$); absence of letters denotes no significant difference

[‡] All plots had a portion of their area within Band 1

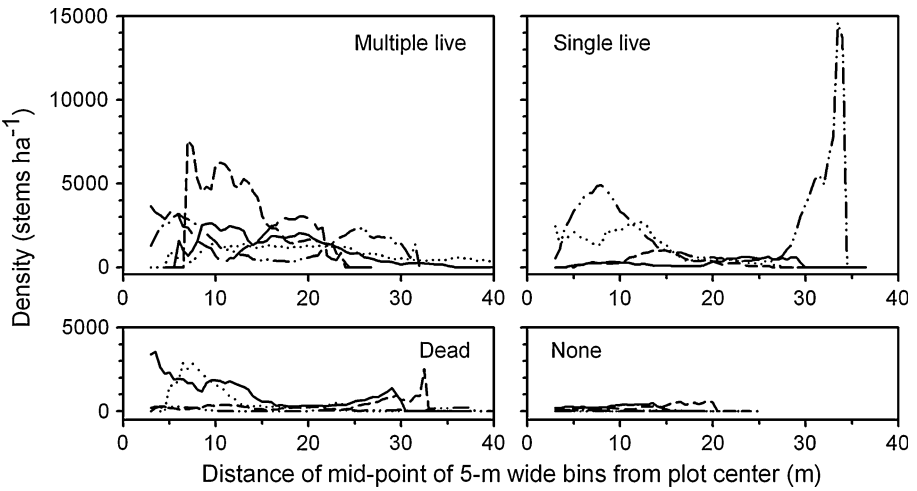

Fig. 1 Change in initial density of *Acacia koa* seedlings as a function of distance from plot center and parent tree configuration; replicates for a given configuration are plotted separately; density was determined for five-meter wide concentric bands that were progressively moved away from plot center in 0.5-m increments until the outermost band reached the end of the scarified area

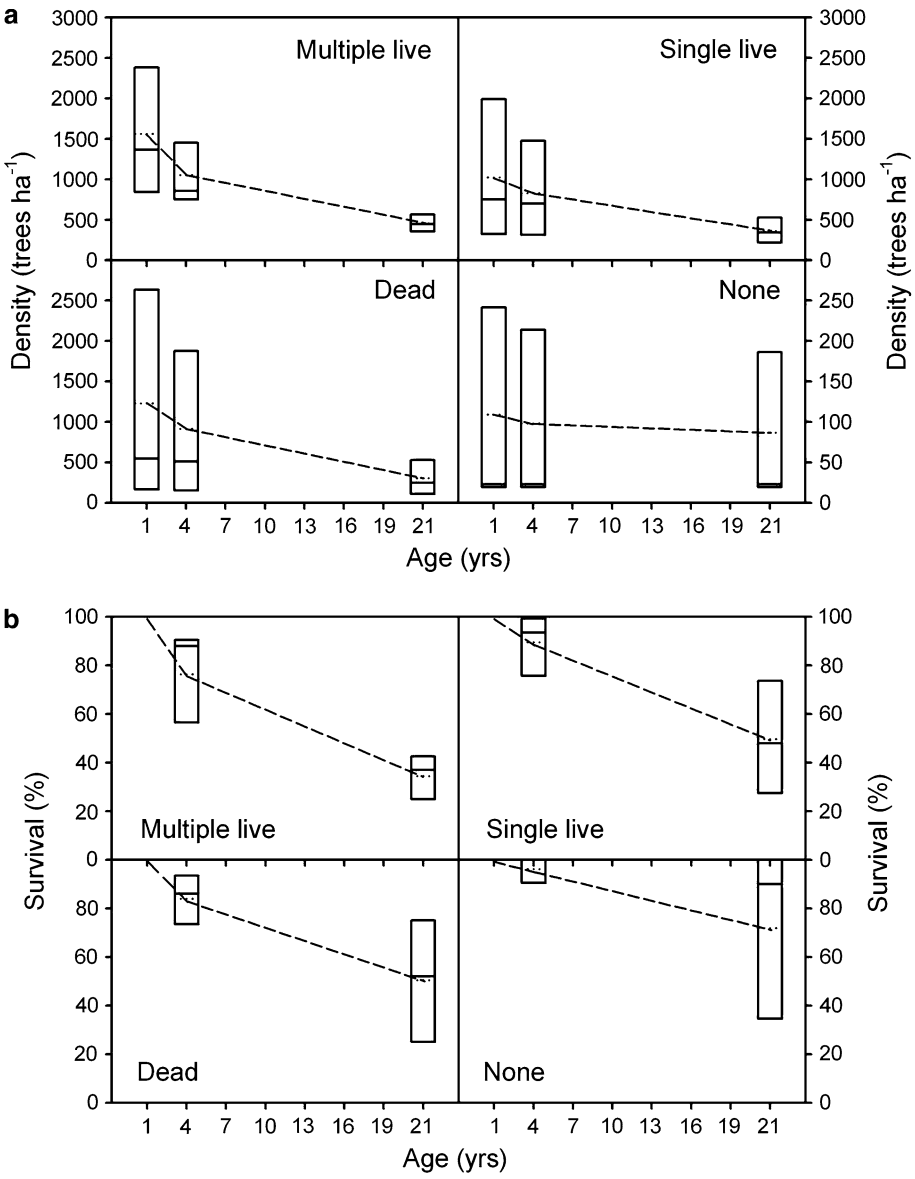

Fig. 2 *Box plots* showing the ranges, medians and arithmetic means of **a** stand density and **b** survival during the first 21 years of development of naturally regenerated *Acacia koa* as a function of the parent tree configuration at the time of soil scarification; *dashed lines* show the trajectories of mean density and survival; n = 5 for *box plots* in the multiple-live and no parent configurations, and n = 4 for *box plots* in the single-live and dead configuration; note the different scale of the y-axis for the no parent tree configuration in panel a

determine densities was restricted to bands at fixed distances from plot centers (Table 1). Consequently, there were no significant differences in initial densities among the multiple, single and dead parent configurations, regardless of the restriction in plot size. The smaller

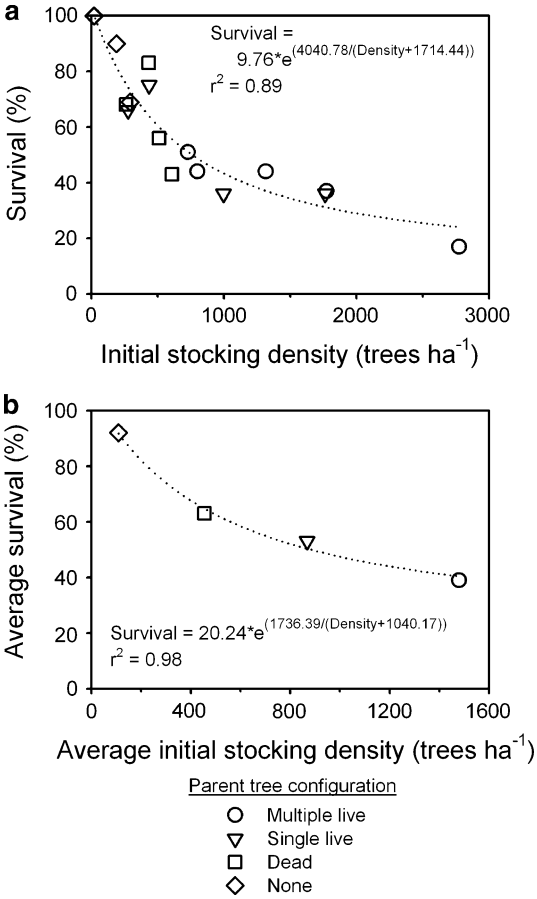

Fig. 3 Effect of initial stocking density on 21-year survival of naturally regenerated *Acacia koa* on sites with different parent tree configurations; *dotted lines* are empirically fitted regressions for **a** individual plot data and **b** data averaged by parent tree configuration (excludes the outlier for the dead configuration)

variation within the no-parent configuration accounts for its having a significantly lower density than the multiple-live configuration across all plot sizes. Only when densities were based on entire plots was the no-parent configuration significantly different from all three of the other configurations ($P = 0.017$).

Over time, residual stocking densities decreased and became less variable (Fig. 2a). Twenty-one years after scarification, average densities calculated on the basis of entire plots were 715, 535, 325 and 79 trees ha^{-1} for multiple-live, single-live, dead and no parent configurations, respectively. These values correspond to declines in stocking of 65, 44, 67 and 9 %. The only significant difference in 21-year stocking density was between the multiple-live and no parent configurations (adjusted $P = 0.043$).

Time had the opposite effect on variability in survival–within a given parent tree configuration variability increased even as average survival decreased (Fig. 2b). In general, survival did not decrease significantly during the first 3 years after scarification. However, by the 21st year, it had decreased significantly for all configurations except the no-parent configuration. Survival averaged 39, 54 and 55 % for multiple-live, single-live and dead parent tree configurations, respectively, and 92 % for the no-parent configuration.

These stand dynamics were the result of greater mortality in plots with greater initial stocking density, irrespective of parent tree configuration (Fig. 3a). As a result of density-

dependent mortality, plot densities converged with time, such that after 20 years, the range in density had declined from 20–4,390 to 20–765 trees ha^{-1}.

Although initial stand density exerted major control over survival (Fig. 3a), parent tree configuration also exerted some control because of its relationship to initial stand density. The far right data point in Fig. 3a was an outlier when compared to other points for the dead parent tree configuration. When it was dropped, and average initial stocking densities and average 21-year survival rates were computed and plotted for the four parent tree configurations, it was apparent that parent tree configuration predictably affected both variables (Fig. 3b).

Parent tree configuration had little influence on growth rates. Periodic annual stem diameter increments between the ages of 4 and 21 years ranged from 1.1 (±0.1) cm $year^{-1}$ for the multiple-live configuration to 1.7 (±0.7) cm $year^{-1}$ for the no-parent configuration, and averaged 1.4 (±0.2) cm $year^{-1}$ for all configurations combined. Periodic annual height increment varied little among configurations, and the combined average was 0.50 (±0.02) m $year^{-1}$. Periodic crown diameter increments averaged 0.18, 0.18, 0.27 and 0.30 m $year^{-1}$ for multiple-live, single-live, dead, and no-parent configurations, respectively. As a result, trees in the no-parent configuration had significantly wider crowns than those in the other configurations at 21 years. Height to the first live fork at 21-years-old was significantly less for the no-parent configuration than the other configurations, 1.4 m (±0.3) versus 2.1 m (±0.3) to 2.4 m (±0.2), respectively.

Parent tree configuration had no effect on the average height or quadratic-mean stem diameter of dominant/co-dominant 21 years old trees. It did, however, affect five other attributes of such trees (Table 2). Those in the no-parent configuration had significantly larger crown diameters, crown depths and LCRs, but shorter heights to the base of live crowns than trees in the other configurations. Differences in these attributes among the other three configurations were not significant. Dominant/co-dominant individuals in the no-parent configuration had an average of 2.2 live stems at breast height, which was significantly more than the 1.6 stems $tree^{-1}$ in the single-live configuration. None of the other paired comparisons were significant.

Table 2 Effect of parent tree configuration on average quadratic-mean stem diameter, height, number of live stems at breast height, and several crown attributes for only dominant and co-dominant, 21-year-old *Acacia koa* trees that were naturally regenerated by disk plowing in sparsely wooded abandoned pasture

Tree attribute	Parent tree configuration			
	Multiple live	Single live	Dead	None
Stem diameter (cm)	28.8	32.7	33.0	43.9
Height (m)	12.9	13.0	12.7	13.1
Live stems @ 1.4 m	1.7ab[§]	1.6b	1.6ab	2.2a
Crown diameter (m)	5.7b	5.4b	5.3b	9.2a
Height to crown (m)	8.6a	9.3a	8.4a	4.7b
Crown depth (m)	5.2b	4.8b	4.7b	9.4a
Live crown ratio	0.43b	0.39b	0.40b	0.66a

Averages are the result of back-transforming the least squares means and correcting for bias introduced by the log transformation

[§] Within a given tree attribute, least squares means followed by a common letter are not significantly different (Tukey's test, $\alpha = 0.05$); absence of letters indicates no difference among means

Effects of initial stand density

Independent of parent tree configuration, stem diameter, height and crown attributes of 21-year-old trees were highly correlated ($P < 0.001$) with initial stocking density (Fig. 4). Empirically derived, biologically meaningful fits to the data showed that initial density accounted for approximately 90 % of the variation in quadratic-mean stem diameter, 80 % of the variation in crown diameter, and 65 % of the variation in crown depth and live crown ratio (LCR). The regression for height, although significant ($P = 0.016$), indicated that density accounted for only 27 % of the variation in average height. Height to crown was unrelated to initial density.

Despite greater crowding in high density stands, the proportion of single-trunk koa at 21 years old was essentially the same across a wide range of initial stocking densities

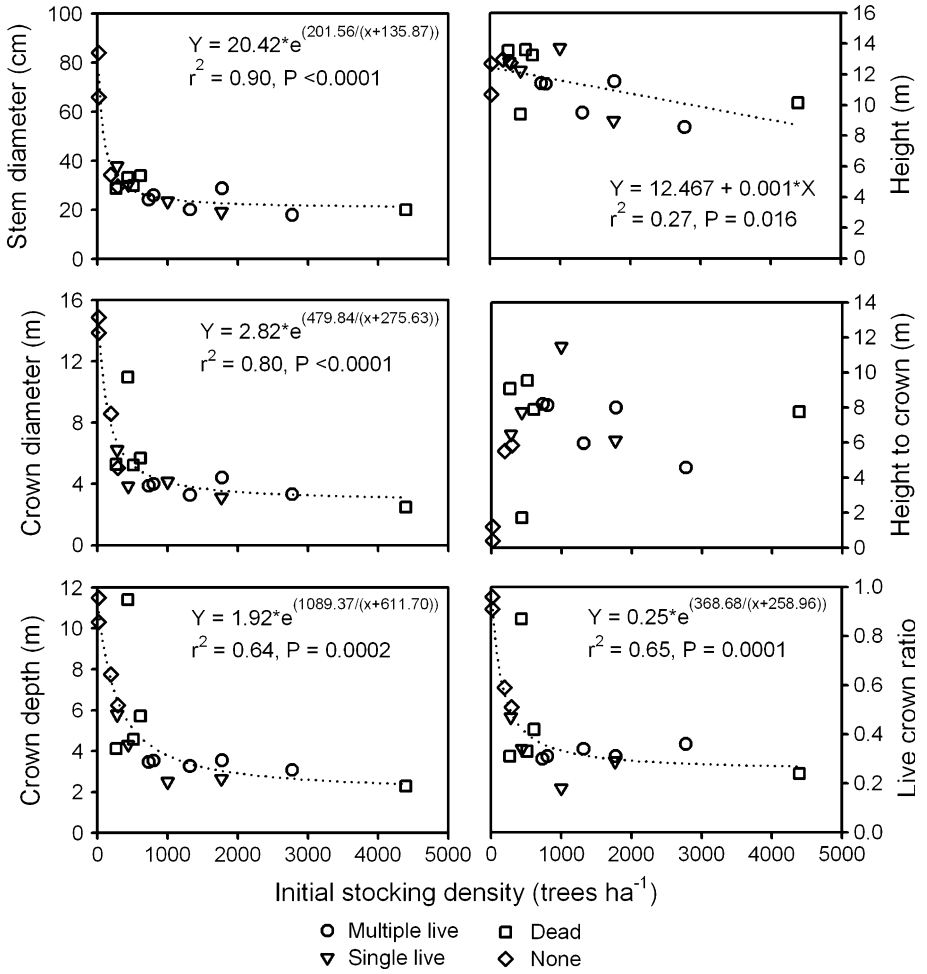

Fig. 4 Effects of initial stocking density on average quadratic-mean stem diameter, and average height and crown attributes of naturally regenerated *Acacia koa* trees 21 years after stand initiation on sites with different parent tree configurations

(Fig. 5a). Only when density fell below about 250 trees ha^{-1} did the proportion decline sharply. The number of trunks $tree^{-1}$ was significantly correlated with average height to the base of the live crown (r = 0.92), average crown depth (r = 0.95) and average live crown ratio (r = 0.93) (Fig. 5b). While average crown diameter tended to increase with increasing number of stems, the correlation was not significant. Average fork height was little affected by initial stand density (data not shown).

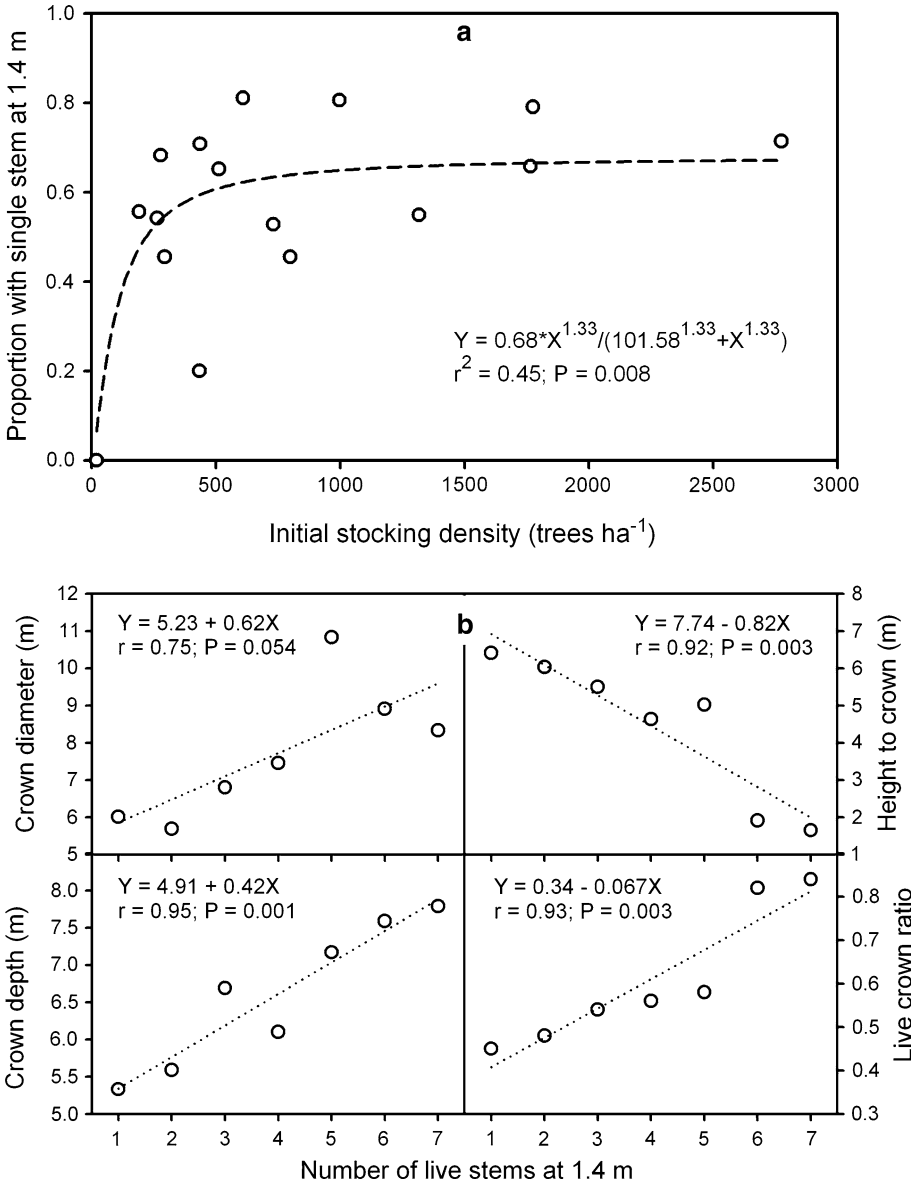

Fig. 5 Relationships between **a** initial stocking density and the proportion of trees with single stems at breast height and **b** number of live stems at breast height and four crown attributes for stands of 21-year-old, naturally regenerated *Acacia koa*

Stand structure

Linear regressions of stand basal area against stand density at 21-years-old were significant for both quadratic-mean DBH classes ($P < 0.001$). The slope was 0.033 ($r^2 = 0.97$) for plots where $15 < \text{DBH} \leq 25$ cm and 0.067 ($r^2 = 0.98$) for those where $25 < \text{DBH} \leq 35$ cm (Fig. 6). In both cases, the fitted lines lay near the mid-point of their respective diameter classes, and were parallel to the guideline (Baker and Scowcroft 2005). Also in both cases, some of the plots lay above and below the maximum stocking level shown in the guideline. The one stand in the $35 < \text{DBH} \leq 45$ cm class was correctly positioned, and lay within the 80 % stocking level. The open-grown trees associated with the no-parent configuration lay below the 40 % stocking level.

Discussion and implications for reforestation

Effects of parent tree configuration

Using soil scarification to successfully establish islands of koa trees in abandoned pasture clearly worked because a buried soil seed bank still existed. The target level of 50 trees

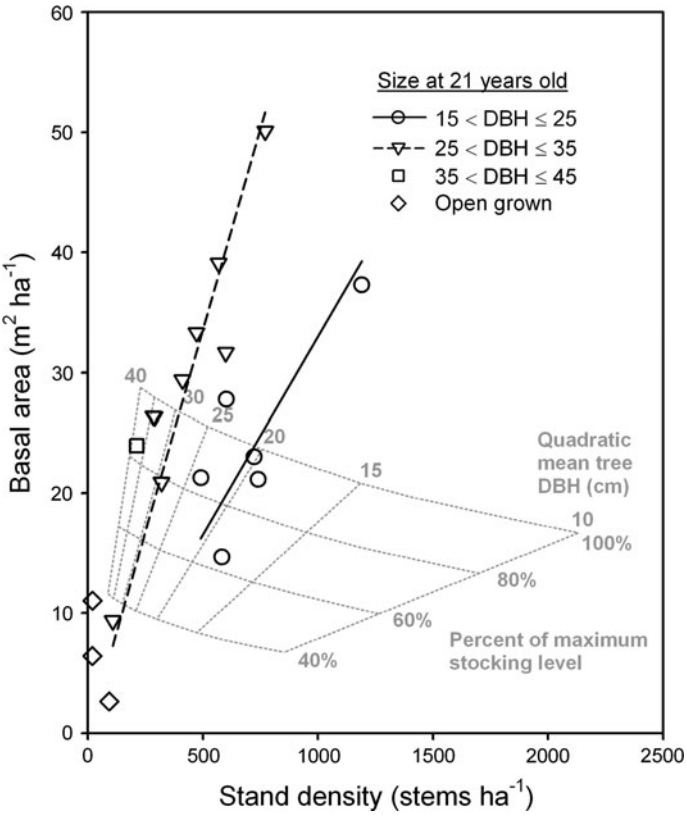

Fig. 6 Relationships between density and basal area of 21-year-old *Acacia koa* stands as a function of quadratic-mean stem diameter class, and how those relationships compare with previously published stocking density guidelines for windward areas of Hawaii Island (Baker and Scowcroft 2005)

ha^{-1} was exceeded in all but three of the 19 areas scarified in this study, and those three were in open areas distant from the nearest potential seed source. These findings indicate that in areas lacking mature koa trees or skeletal remains seed reserves might be very low or entirely depleted. Where there has been a history of fire along with cattle grazing, depletion should be expected because fire stimulates germination of buried seeds (Scowcroft and Wood 1976) and cattle then eat the seedlings. In such circumstance, planting will be the only option for reforestation. However, if some old live koa or skeletal remains are present then managers will want to focus their soil scarification efforts on those areas.

The spatial distribution of seedlings around parent trees is mainly dictated by seed dispersal patterns, although seed dormancy can play a role too (e.g., Wilson 1993; Ribbens et al. 1994). Koa seeds are not usually dispersed by birds or water. As they fall to the ground, wind can transport the large, heavy seeds and pods a short distance away from their point of origin (Baker et al. 2009), but neither is morphologically adapted for wind dispersion. Although studies to quantify dispersal distances and patterns have not been done for koa, research on other large-seeded species indicates that the seed rain should be greatest close to the parent and follow a negative exponential or log-normal distribution with increasing distance from the parent (e.g., Wilson 1993; Ramos et al. 2005; Santos et al. 2006; Catellanos and Stevenson 2011). So in the case of sparsely wooded pastures, managers should generally expect a decline in overall stocking density as scarification is extended to areas further from the parent.

For the multiple-, single- and dead-parent configurations, the spatial distributions of seedlings around plot centers in this study generally conformed to the distributions described above, but there was no consistent pattern either within or between configurations. Radial symmetry of seedling density around plot center was absent, suggesting that the soil seed bank was patchy or that seeds were redistributed during scarification or that plot centers were not always coincident with the center of overhead koa crowns. The no-parent tree configuration showed no pattern of seedling distribution, which was expected because plot center was established without reference to a potential seed source. The sizes of seedling shadows were greater for the multiple- than for single- or dead-parent configurations because the projected crown areas of the former were large relative to plot center. The density of seedlings close to plot center for the multiple-parent configuration also tended to be greater than the other configurations because the seed shadows of individuals within clusters overlapped (Clark et al. 1999). The increase in density toward the outermost portions of several plots (Fig. 1) might have been due to overlapping seed shadows from nearby or long-lost trees that contributed seeds to those locations (Sato and Hiura 1998).

Parent tree configuration only broadly influenced initial stand densities in the decreasing order hypothesized: Multiple > Live > Dead > None. Within each configuration there was a wide range of initial densities, except for limited variation within the no-tree configuration. The outlier plot for the dead tree configuration (Fig. 2a) greatly exceeded the maximum density observed for the most dense multiple-live-tree plot, 4,400 and 2,800 trees ha^{-1}, respectively. Inspection of aerial photographs for 1965 revealed that the tree in question was still alive at that point. Aside from the relatively recent death of the parent tree, there is no explanation for the exceptionally high stocking density. The lack of multiple-live or even single-live configurations on a given parcel should not prevent landowners from working with what they have.

Effects of initial stand density

The role of initial stand density in subsequent tree growth, architecture and stand dynamics of even-age, single-species secondary forests has been well summarized by Oliver and

Larson (1990). Spacing determines crown growing space. Trees in denser stands are shorter and have smaller crowns at canopy closure than trees in less dense stands. Suppression and mortality begin sooner in dense stands, and this leads to stand density trajectories that converge over time on those for less dense stands. The earlier onset of crown restriction in dense stands has several consequences, all of which are related to the ability of competing neighbors to produce photosynthate for respiration and growth. Denser stands have slower stem diameter growth, smaller live crown ratio, slower rates of crown expansion, and for species with weak apical control of lateral terminals, such as koa, slower height growth. For even-age monocultures, tree size at any age will generally be smaller for high- than low-density stands (e.g., Thoranisorn et al. 1990).

In this study, parent tree configuration only broadly influenced survival during the 20 year study in the same order noted above. Primary control was exerted by the density of individual stands independent of parent tree configuration. Proportionately greater mortality in more dense stands caused highly variable initial stand densities to converge over time, a tendency that has been observed in other stands of koa, some having densities exceeding 20,000 trees ha^{-1}, and in even-age temperate forests (Peet and Christensen 1987; Baker et al. 2009, p 48; Scowcroft unpublished data). Within 20–30 years, naturally regenerated even-age koa stands should have similar stocking densities due to density-dependent mortality, despite large variation in initial densities. Investment in artificial thinning is not needed unless the landowner wants to (a) increase wood volume increment of select individuals with potential for future merchantable wood, (b) create canopy gaps to favor establishment and growth of planted ohia and understory species or (c) encourage more rapid development of large-crown koa for bird habitat.

Initial stand density was the main determinant of size of dominant and co-dominant trees at 21-years old. Parent tree configuration played a role only as it broadly influenced initial stand density as noted above. More than 80 % of the variation in stem diameter and crown diameter at 21-years-old was explained by initial density. Although less of the variation in height was explained by initial density, trees were $\sim$2 m shorter in stands whose density was >1,000 trees ha^{-1}. So, while landowners should expect high survival, large stem diameters and large tree crowns in low density stands and individual open-grown trees, they should also expect lower survival and smaller stem diameters (5–7 cm smaller) and crowns of trees (1–1.5 m smaller) in high density stands.

Tree mortality can be caused by a variety of factors, including pathogens, insects, mechanical damage and ungulates (e.g. Lutz and Halpern 2006). Neither disease—e.g., *Fusarium oxysporum* (Daehler and Dudley 2002), nor eruptions of insects–e.g., *Scotorythra paludicola* Butler (Stein and Scowcroft 1984; Haines et al. 2009), have been observed in the study area. Although high winds do occur in Hakalau (Baker et al. 2009) and might have killed a few trees, suppression of smaller trees by larger ones probably accounted for most of the mortality. Whether expressed as survival or average annual mortality (data not shown) between 1988 and 2008, initial stand density explained $\geq$89 % of the variation in both statistics.

Stand structure

The naturally regenerated, unmanaged koa stands examined in this study conformed well to the only koa stocking guideline in existence (Baker and Scowcroft 2005). Denser stands tended to have smaller quadratic-mean stem diameters than less dense stands. Some of the unmanaged stands were over-stocked while others were under-stocked. Five of the eight stands with quadratic-mean stem diameters in the range of 25–35 cm appeared to be overstocked. The productivity of such stands might be increased by reducing stand density.

If harvest of some trees at maturity is desired, landowners will need to consider selecting and favoring through silvicultural treatments those individuals with the greatest potential yield of merchantable wood. Without such stocking control, growth rates will decline and potential crop trees might not survive the self-thinning process (Baker et al. 2008). Potential crop trees can be identified in stands as young as 8-years old (Martinez Morales 2010). Typically they will be dominant or co-dominant individuals that have single stems at breast height and a clear butt logs >2 m long. Few such trees will be found in very low density stands, or as open-grown individuals, like some of those in the no-parent tree configuration. Crop trees will usually have smaller crowns and LCRs than their multiple-stem neighbors, so they might not survive the self-thinning process as well as their large-crown neighbors. Even if they survived, wood volumes will be less without than with silvicultural intervention (Scowcroft et al. 2007).

As has been observed elsewhere in the tropics, islands of native trees within a sea of alien grasses can induce changes in above- and belowground environments, and that is true of koa (Scowcroft and Jeffrey 1999; Scowcroft et al. 2004). Frost damage is greatly reduced under a koa tree canopy. Consequently, Hakalau Refuge continues to use tree islands and planted tree corridors to reintroduce and successfully establish native understory plants, including endangered species (Jeffrey and Horiuchi 2003; Jeffrey and Glynn 2009). The presence of young koa stands with their mix of healthy, dying and dead trees and branches has allowed reestablishment of cerambycid beetle populations (Goldsmith et al. 2007), which are an important food of the endangered bird, *Hemignathus munroi* (Ralph and Fancy 1996; Pejchar et al. 2005). Certain native and introduced bird species have already benefited from reforestation of former pasture in Hawaii (Camp et al. 2009).

In conclusion, soil scarification of abandoned pasture will stimulate natural regeneration of koa where a viable seed bank still exists. The pasture areas that will most likely meet this condition are in the immediate vicinity of remnant old growth individuals, snags and downed trees. In open areas at least 30 m distant from such remnants, scarcity of viable seeds will limit regeneration. If such areas are to be reforested, planting should be the method of choice. Survival, growth, tree size and crown architecture of unmanaged tree islands created by soil scarification will be controlled mainly by initial stand density. Although few trees will have a growth form suitable for high wood volume yield, the understory habitat of tree islands will be suitable for establishment of other native plant species by means of planting (Scowcroft et al. 2000; Jeffrey and Glynn 2009; US FWS 2011). Furthermore, managers interested in forest restoration will likely find that tree islands in abandoned pasture enhance natural forest recovery by moderating microclimatic extremes, shading out grasses and increasing bird-mediated seed dispersal as has been reported elsewhere in the tropics (Holl et al. 2000; Holl 2002).

Acknowledgments The author acknowledges Dr. Richard Wass, manager of Hakalau Forest NWR for establishing the Woodland exclosure, arranging for disk plowing of plots and providing access and logistical support for the field work; Gene Conrad for assistance in study design and establishment; Sami Frietas, David Fujii, Don Goo, Jan Haraguchi, Tats Kimoto, and Alan Urakami for data collection; Drs Jim Baldwin, John J Ewel, James B Friday, Christian Giardina and two anonymous reviewers for helpful comments on earlier drafts. The 2008 field work was conducted under Hakalau Forest NWR Special Use Permit SUP12516-08001.

References

Allen ON, Allen EK (1936) Root nodule bacteria of some tropical leguminous plants: II. Cross inoculation tests with the cowpea group. Soil Sci 47:63–76

Baker PJ, Scowcroft PG (2005) Stocking guidelines for the endemic Hawaiian hardwood, *Acacia koa*. J Trop For Sci 17:610–624

Baker PJ, Robinson AP, Ewel JJ (2008) Sudden and sustained response of *Acacia koa* to crown release in stagnant stands. Can J For Res 38:656–666

Baker PJ, Scowcroft PG, Ewel JJ (2009) Koa (*Acacia koa*) ecology and silviculture. Gen Tech Rep PSW-211, Albany, CA, US Dept Agric, Forest Service, Pac SW Res Stn. Available via http://www.fs.fed.us/psw/publications/documents/psw_gtr211/psw_gtr211.pdf. Accessed 29 Feb 2012

Camp RJ, Pratt TK, Gorresen PM, Jeffrey JJ, Woodworth BL (2009) Passerine bird trends at Hakalau Forest National Wildlife Refuge, Hawaii. Tech Rep HCSU-011, Hawaii Cooperative Studies Unit, University of Hawaii, Hilo

Catellanos MC, Stevenson PR (2011) Phenology, seed dispersal and difficulties in natural recruitment of the canopy tree *Pachira quinata* (Malvaceae). Rev Biol Trop 59:921–933

Clark JS, Silman M, Kern R, Macklin E, HilleRisLambers J (1999) Seed dispersal near and far: patterns across temperate and tropical forests. Ecology 80:1475–1494

Cleveland CC, Townsend AR, Schmidt SK, Constance BC (2003) Soil microbial dynamics and biogeochemistry in tropical forests and pastures, southwester Costa Rica. Ecol Appl 13:326–414

Conrad CG, Scowcroft PG, Wass RC, Goo DS (1988) Reforestation research in Hakalau Forest National Wildlife Refuge. Trans W Sec Wildl Soc 24:80–86

Cuddihy LW, Stone CP (1990) Alteration of native Hawaiian vegetation: effects of humans, their activities and introductions. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu

Daehler CC, Dudley N (2002) Impact of the black twig borer, an introduced insect pest, on *Acacia koa* in the Hawaiian Islands. Micronesica Suppl 6:35–53

Denslow JS, Uowolo AL, Hughes RF (2006) Limitations to seedling establishment in a mesic Hawaiian forest. Oecol 148:118–128

Gagné WC, Cuddihy LW (1990) Vegetation. In: Wagner WL, Herbst DR, Sohmer SH (eds) Manual of the flowering plants of Hawaii. University of Hawaii Press, Honolulu, pp 45–116

Goldsmith S, Gillespie H, Weatherby C (2007) Restoration of Hawaiian montane wet forest: endemic longhorn beetles (Cerambycidae: *Plagithmysus*) in koa (Fabaceae: *Acacia koa*) plantation and in intact forest. Southwest Nat 52:356–363

Goldstein JH, Daily GC, Friday JB, Matson PA, Naylor RL, Vitousek P (2006) Business strategies for conservation on private lands: koa forestry as a case study. Proc Natl Acad Sci USA 103:10140–10145

Haines WP, Heddle ML, Welton P, Rubinoff D (2009) A recent outbreak of the Hawaiian koa moth, *Scotorythra paludicola* (Lepidoptera: Geometridae), and a review of outbreaks between 1982 and 2003. Pac Sci 63:349–369

Holl KD (2002) Tropical moist forest. In: Perrow MR, Davy AJ (eds) Handbook of ecological restoration. Cambridge University Press, Cambridge, pp 539–558

Holl KD, Loik ME, Lin EHV, Samuels IA (2000) Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. Restor Ecol 8:339–349

Hue NV, Uehara G, Yost RS, Ortiz-Escobar M (2006) Distribution of soil orders in Hawaii. J Haw Pac Agric 14:17–28. Available via http://www.uhh.hawaii.edu/academics/cafnrm/research/documents/hawaii_soils706.pdf. Accessed 30 Sept 2009

Jeffrey J, Glynn J (2009) Hakalau Forest National Wildlife Refuge: a conservation model for the Big Island. Hawaii For J 4:3–5

Jeffrey J, Horiuchi B (2003) Tree planting at Hakalau Forest National Wildlife Refuge—the right tool for the right stock type. Nativ Plants J 4:30–31

Koske RE, Gemma JN, Flynn T (1992) Mycorrhizae in Hawaiian angiosperms: a survey with implication for the origin of the native flora. Am J Bot 79:853–862

Lutz JA, Halpern CB (2006) Tree mortality during early forest development: a long-term study of rates, causes and consequences. Ecol Monogr 76:257–275

Martinez Morales R (2010) Differentiation of forest stands, assessment of forest health and silvicultural guidelines for growing and managing the native Hawaiian hardwood *Acacia koa*. PhD dissertation, University of Hawaii, Honolulu, 129 pp

Maxfield B (2003) Hakalau Forest National Wildlife Refuge. Endanger Species Bull 28(1):9–11

Motooka P, Castro L, Nelson D, Nagai G, Ching L (2003) Weeds of Hawaii's pastures and natural areas: an identification and management guide. College of Tropical Agriculture and Human Resources, University of Hawaii, Honolulu

Oliver CD, Larson BC (1990) Forest stand dynamics. McGraw-Hill, Inc., New York

Pebesma E, Bivand R (2012) Package 'sp': Classes and methods for spatial data, version 0.9–95. Available via http://cran.r-project.org/web/packages/sp/sp.pdf. Accessed 22 Feb 2012

Peet RK, Christensen NL (1987) Competition and tree death. Bioscience 37:586–595

Pejchar L, Press DM (2006) Achieving conservation objectives through production forestry: the case of *Acacia koa* on Hawaii Island. Environ Sci Policy 9:439–447

Pejchar L, Holl KD, Lockwood JJ (2005) Hawaiian honeycreeper home range size varies with habitat: implications for native *Acacia koa* forestry. Ecol Appl 15:1053–1061

Peng RD with contributions from Duncan Murdoch and Barry Rowlingson (2010) Package 'gpclib': General polygon clipping routines for R based on Alan Murta's C library, version 1.5-1. Available via http://cran.r-project.org/web/packages/gpclib/gpclib.pdf. Accessed 22 Feb 2012

Pratt TK, Jacobi J (2009) Loss, degradation, and persistence of habitats. In: Pratt TK, Atkinson CT, Banko PC, Jacobi JD, Woodworth BL (eds) Conservation biology of Hawaiian forest birds, implications for island avifauna. Yale University Press, New Haven, pp 137–158

Ralph CJ, Fancy SG (1996) Aspects of the life history and foraging ecology of the endangered 'akiapōlā'au. Condor 98:312–321

Ramos FN, Silva Matos DM, Santos FAM (2005) Spatial distribution of seeds and juveniles of *Enterolobium glaziovii* Bentham (Leguminosae, Mimosoideae) in the Atlantic forest, Brazil. Acta Bot Braz 19:609–614

Ribbens E, Silander JA Jr, Pacala SW (1994) Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. Ecology 75:1794–1806

Ripley B (2012) Package RODBC: an ODBC database interface, version 1.3–4. Available via http://cran.r-project.org/web/packages/RODBC/RODBC.pdf. Accessed 22 Feb 2012

Santos BA, Melo FPL, Tabarelli M (2006) Seed shadow, seedling recruitment, and spatial distribution of *Buchenavia capitata* (Combretaceae) in a fragment of the Brazilian Atlantic forest. Braz J Biol 66:883–890

SAS Institute (1996) SAS/STAT software changes and enhancements through release 6.11. SAS Institute, Inc., Cary

Sato H, Hiura T (1998) Estimation of overlapping seed shadows in a northern mixed forest. For Ecol Manage 104:69–76

Sato HH, Ikeda W, Paeth R, Smythe R, Takehiro M Jr (1973) Soil survey of Island of Hawaii, State of Hawaii. USDA Soil Conservation Service in cooperation with University of Hawaii Agric Exp Sta

Scowcroft PG (1992) Role of decaying logs and other organic seedbeds in natural regeneration of Hawaiian forest species on abandoned montane pasture. In: Conrad CE, Newell L (tech coord) Proceedings of the Session on Tropical Forestry for People of the Pacific, 17th Pacific Science Congress. Gen Tech Rep GTR-129, Albany, CA, pp 67–73. Available via http://www.fs.fed.us/psw/publications/documents/psw_gtr129/psw_gtr129_scowcroft.pdf. Accessed 29 Feb 2012

Scowcroft PG, Jeffrey J (1999) Potential significance of frost, topographic relief, and *Acacia koa* stands to restoration of mesic Hawaii forests on abandoned rangeland. For Ecol Manage 114:447–458

Scowcroft PG, Nelson RE (1976) Disturbance during logging stimulates regeneration of koa. USDA Forest Service Research Note PSW-306, Berkeley, CA

Scowcroft PG, Wood HB (1976) Reproduction of *Acacia koa* after fire. Pac Sci 30:177–186

Scowcroft PG, Meinzer FC, Goldstein G, Melcher PJ, Jeffrey J (2000) Moderating night radiative cooling reduces frost damage to *Metrosideros polymorpha* seedlings used in reforestation in Hawaii. Restor Ecol 8:161–169

Scowcroft PG, Haraguchi JE, Hue NV (2004) Reforestation and topography affect montane soil properties, nitrogen pools and nitrogen transformations in Hawaii. Soil Sci Soc Am J 68:959–968

Scowcroft PG, Friday JB, Idol T, Dudley N, Haraguchi J, Meason D (2007) Growth response of *Acacia koa* trees to thinning, grass control and phosphorus fertilization in a secondary forest in Hawaii. For Ecol Manage 239:69–80

Skolmen RG, Fujii DM (1981) Growth and development of a pure stand of koa (*Acacia koa* Gray) at Keauhou-Kilauea. In: Smith CW (ed.) Proceedings of 3rd Conference in Natural Science. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu, pp 301–319

Sprugel DG (1983) Correcting for bias in log-transformed allometric equations. Ecology 64:209–210

Stein JD, Scowcroft PG (1984) Growth and refoliation of koa trees infested by the koa moth *Scotorythra paludicola* (Lepidoptera: Geometridae). Pac Sci 38:333–339

Thoranisorn S, Sahunalu P, Yoda K (1990) Density effects and self-thinning in even-aged pure stands of *Eucalyptus camaldulensis* Dehn. Bot Mag Tokyo 103:283–295

Tosi JA Jr, Watson V, Bolaños R (2002) Life zone maps of Hawaii. Joint venture of the Trop Sci Center, San Jose, Costa Rica and the Institute of Pacific Islands Forestry, USDA Forest Service, Pac SW Res Sta, Hilo, HI. Available via http://www.fs.fed.us/psw/topics/ecosystem_processes/tropical/restoration/lifezone/. Accessed 23 Sept 2009

Tummons P, Dawson T (2002) Cattle in Hawaiian forests: two centuries of loss. Environ Hawaii 13(3):1–22

US Fish and Wildlife Service (2011) Hakalau Forest National Wildlife Refuge Comprehensive Conservation Plan. Available via http://www.fws.gov/hakalauforest/Hakalau%20Forest%20NWR%20Final%20CCP.pdf. Accessed 9 Jan 2012

Wilson MF (1993) Dispersal mode, seed shadows, and colonization patterns. Vegetatio 107(108):261–280