ELSEVIER

Forest Ecology and Management 114 (1999) 447–458

Forest Ecology and Management

Potential significance of frost, topographic relief, and *Acacia koa* stands to restoration of mesic Hawaiian forests on abandoned rangeland

Paul G. Scowcroft[a,*], Jack Jeffrey[b,1]

[a] *USDA Forest Service, Institute of Pacific Islands Forestry, 1151 Punchbowl Street, Room 323, Honolulu, HI 96813, USA*
[b] *USDI Fish and Wildlife Service, Hakalau Forest National Wildlife Refuge, 32 Kinoole Street, Suite 101, Hilo, HI 96720, USA*

Abstract

Beginning in the 1850 s, logging, land clearing, and burning were used to convert high elevation Hawaiian forests to cattle pasture. Recently, declining profits from ranching, the need to expand habitat for endangered species, and diminishing supplies of native saw-timber have prompted interest in restoring native forests. The Forest Service, in cooperation with the Fish and Wildlife Service, is studying climatic, edaphic, and biotic limitations in the reforestation of grassland and savanna in the Hakalau Forest National Wildlife Refuge, island of Hawaii. Frost damage has been implicated in poor survival of *Acacia koa*, a dominant native nitrogen fixing tree, and other endemic plants. Data showed that for some years freezing temperatures were common above 1800 m elevation, and that *A. koa* seedling survival was poorest on micro-topographic sites where freezing temperatures were lowest and most prolonged. Artificial frost protection devices enhanced *A. koa* seedling survival, presumably by reducing radiative cooling. A similar reduction in radiative cooling was observed under a stand of 4 m tall *A. koa*. Such stands also changed soil chemical properties, making them intermediate between those of grassland and forest. Light levels near the ground under *A. koa* were similar to those found in forests, but not as low as those found under pasture grasses. Biomass and nutrient pools of the litter-herbaceous layer were affected by micro-topographic position in the landscape and by the presence of stands of *A. koa*. Using *A. koa* as a nurse crop may create understory conditions favorable for the establishment of other plant components of a mixed-species forest.

Keywords: Reforestation; *Acacia koa*; Montane tropical forest; Nurse crop; Frost damage

1. Introduction

Cattle ranching in Hawaii, which began in the middle of the 19th century, involved the conversion of large expanses of mesic and even some drier montane forests and parklands between 1200 and 2200 m elevation (Cuddihy and Stone, 1990). Mesic forests were dominated by *Acacia koa*, a nitrogen-fixing tree species that was, and still is, the most valuable native hardwood in the state (Jenkins, 1983). Logging this resource not only cleared the forest, but also provided revenues to land owners, as it does today. Fire was used to dispose of slash,

*Corresponding author. Tel.: +1-808-522-8231; fax: +1-808-522-8236; e-mail: pscowcro/psw_ipif@fs.fed.us

[1]Tel.: +1-808-933-6915; fax: +1-808-933-6917; e-mail: john_jeffrey@mail.fws.gov

0378-1127/99/$ – see front matter
PII: S0378-1127(98)00374-0

as evidenced by abundant charcoal in upper soil horizons. Following land clearing, cattle completely suppressed native forest regeneration (Barrera and Kelly, 1974). To complete the conversion and improve pasture, hundreds of alien range species were introduced (McClelland, 1915; Whitney et al., 1939).

The replacement of forest life forms with shallow-rooted herbaceous life forms, along with the impacts of fire and grazing, changed ecosystem structure, and probably many functional characteristics also (Ewel and Bigelow, 1996). Gone were the moss-covered decaying logs needed for regeneration of native species (Scowcroft, 1992) and the tree canopy that moderated light, moisture, and temperature regimes. Productivity, nutrient cycling and water budgets were altered, and forest-dependent animal populations were reduced or eliminated. The physical, chemical and biological properties of soils undoubtedly changed (e.g. Wood, 1977; Piccolo et al., 1994; Prasad et al., 1994; Veldkamp, 1994; Parsons and Keller, 1995). Now, after nearly 150 years, even if grazing is stopped, introduced grasses will probably hold sites indefinitely against all potential native colonizers unless humans intervene.

Large tracts are being withdrawn from cattle ranching for the purpose of restoring native forests. The driving forces behind the current restoration efforts are economic and environmental. Cattle ranching in Hawaii has been only marginally profitable for decades (TenBruggencate, 1991), and land owners are becoming convinced that greater profits can be realized from growing high quality hardwoods, especially *A. koa* (Loudat and Kanter, 1997). In addition, restoration of this habitat is seen as an essential step in the process of recovering certain endangered species (Rubenstein, 1995; Scott et al., 1988). Creation of a forest ecosystem dominated by native species may lessen successful invasion by alien species, which are continually being introduced into Hawaii.

Initial efforts to reforest former ranch lands have been mixed. Planted *A. koa* generally established in grasslands (Rubenstein, 1995). Other native forest species, including *Metrosideros polymorpha*, *Cheirodendron trigynum*, and *Sophora chrysophylla*, failed to survive (Scowcroft, 1992, 1993), perhaps because of competition with grasses, as found in grasslands elsewhere in the world (e.g. Gordon et al., 1989; Bush and van Auken, 1995), or perhaps because of their inability to cope with the high light/UV environment of grasslands (Kobe et al., 1995; Sullivan et al., 1992). *A. koa*'s ability to fix nitrogen and grow rapidly and its requirement for high light may partially explain its greater success. But even koa failed some years at elevations above about 1900 m. These were invariably El Nino years, when winters were dominated by dry, stable air masses resulting in below normal rainfall (Chu, 1989) and frequent clear nights, the latter being conducive to high radiative heat losses and freezing temperatures above 1800 m.

Our observations of the pattern of *A. koa* mortality suggested that it was not random, but related to landscape position; specifically, greatest mortality occurred in low lying drainage bottoms. Furthermore, growth of survivors also seemed related to landscape position with greatest growth in drainages, progressively less growth on north, east, and south-facing slopes, and least growth on ridges. We hypothesized that frost was killing and weakening planted seedlings, and that damage should be most severe in low lying areas. We also hypothesized that seedlings planted there would have rapid growth rates possibly due to greater water and nutrient availability. If frost damage was limiting restoration, we hypothesized that establishing a nurse crop of *A. koa* would keep temperatures above freezing. We suspected that artificial frost protection devices could mimic the beneficial effects of a tree canopy and thus improve over-winter seedling survival. As found in studies elsewhere in the tropics, we hypothesized that the nurse crop would also suppress herbaceous competitors (Parrotta, 1993; Guariguata et al., 1995), change soil chemical properties (especially N levels) and nutrient cycling (Parrotta, 1992), and reduce high solar radiation levels, thereby creating an understory microclimate more favorable for establishment of other native species (Fimbel and Fimbel, 1996; Lugo et al., 1993). The benefits of tree nurse crops to native regeneration have also been demonstrated in Hawaii (Harrington and Ewel, 1997). Finally, we hypothesized that the degree to which the nurse crop modified the understory environment would vary according to landscape position, with effects being most pronounced in drainage bottoms.

2. Methods

2.1. Study area

The 13 247 ha Hakalau Forest National Wildlife Refuge was established in 1985 under the authority of the U.S. Endangered Species Act to preserve and protect five species of endangered forest birds and their habitat. It lies between 750 and 2000 m elevation in the face of the trade winds on the northeast slopes of Mauna Kea, one of the five volcanoes that make up the Island of Hawaii. Although most of the Refuge is closed canopy forest, about 2200 ha is former rangeland and consists of wooded pasture and grassland above 1700 m elevation. These former rangelands, which are typical of other such areas on the islands of Hawaii, Maui and Kauai, are targeted for forest restoration.

Rangeland portions of the Refuge are mesic and cool. Mean annual rainfall is about 2000 mm in high-elevation grasslands and about 3000 mm in lower-elevation wooded pastures. Daily movement of the inversion layer frequently results in clear mornings and foggy/misty afternoons. Mean daily air temperature at 2 m ranges from 9 to 14°C, and freezing temperatures occur near ground level during clear winter nights.

Soils throughout the rangeland areas were very strongly acidic and classified as Typic Hydrudands. Derived from volcanic ash, these silt loams and silty clay loams contain large amounts of X-ray amorphous materials and fix large amounts of phosphorus (P. Scowcroft, unpublished data). Organic carbon in the upper 15 cm of soil is about 15% in grassland and as high as 35% in wooded pasture. Total nitrogen in surface horizons is about 1.2% in grassland and up to 2.5% in wooded pasture.

The pre-1790 vegetation of rangelands was open-to-closed uneven-canopied *A. koa/M. polymorpha* montane mesic forest. Above about 1900 m elevation it merged with the open-canopied *A. koa/S. chrysophylla* montane dry forest (Wagner et al., 1990). The understory was rich in native tree, shrub and fern species, including *C. trigynum*, *Coprosma* spp., *Ilex anomola*, *Myoporum sandwicense*, *Myrsine lessertiana*, *Styphelia tameiameiae*, *Rubus hawaiiensis*, *Dryopteris wallichiana* and *Cibotium glaucum*.

Currently, the vegetation is 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*. Even in wooded pasture where scattered tall *A. koa* and *M. polymorpha* survive, these grasses dominate the ground cover. Large woody debris are virtually absent from grasslands, probably due to repeated fires over the last 150 years, and it is sparse in wooded pastures.

2.2. Techniques

2.2.1. Freezing temperatures and survival and growth of A. koa

The effects of topographic position (ridge, side slope and drainage bottom) and aspect on survival and growth of *A. koa* were studied in a treeless grassland area between 1950 and 2010 m elevation. Although *A. koa* was less sensitive to freezing temperatures than other native species, it was the only one available in sufficient quantity for the study. Planting spots were prepared with a sod-scalping three-pronged rake mounted on the blade of a bulldozer; 1×2 m spots were on a grid of approximately 3×3 m. Plots contained at least 30 planting spots each, except for one ridge plot that contained only 25 planting spots. The amount of replication was controlled by availability of microsites in the study area. There were three replicates for plots in drainage bottoms and on north and south facing slopes, and two replicates for plots on ridges and on east- and west-facing slopes. Ridge and drainage bottom plots were not considered to have an aspect.

A. koa seedlings (4 months old) grown from locally produced seeds were planted in April 1993. In late September, 30 healthy seedlings per plot (17 seedlings in one ridge plot) were marked. Height and vigor class (healthy with evidence of recent growth, chlorotic with no evidence of new growth, and dead) were measured in September 1993 (base line data), April and October 1994, March 1995, and April 1996.

Air temperatures were measured with shielded copper–constantan thermocouples at 30 and 60 cm above ground level in one set of adjacent plots representing all topographic positions and slope aspects. Sensors were interrogated every 30 s, and averages were logged hourly using a Campbell Scientific CR10 data logger system coupled with a Campbell Scientific AM416 multiplexer. Daily maximum and minimum temperatures were also logged. Data were collected from January 1994 through May 1996.

Soil chemistry was determined in June 1996 for ridge, drainage, and north-facing plots that were used for temperature measurements. Six intact PVC-contained soil cores, each 15 cm deep and 257 cm^2 in cross-sectional area, were sampled at each microsite. Three were immediately returned to the laboratory and stored for 7 days at 2°C until analyzed at the University of Hawaii Agricultural Diagnostic Service Center. These initial samples were used to estimate soil acidity, organic carbon, total nitrogen, and extractable NH_4–N, NO_3–N, P, K, Ca and Mg. The other sets of core samples were incubated in-situ at ambient temperature for 30 days, collected, and processed like the initial samples, except that extractable NH_4–N and NO_3–N were the only analyses done.

We evaluated nine different frost protection devices during the winter of 1993–1994. The most expensive device was known as the Wall-O-Water; it stood 46 cm tall and surrounded the seedling with 11 l of water. Another commercial device was a Tubex tree shelter, 11 cm i.d., and 60 cm tall. Other devices were as follows: a 60 cm diameter by 1.2 m tall hog-wire cylinder covered with either clear polyethylene sheeting, covered with 'Reemay' polyester fabric, or roofed with 90% black shade cloth; a 60×90 cm^2 piece of 90% shade cloth suspended between stakes on the eastern or western side of the seedling; 60 cm diameter by 5 cm deep redwood bark chips or black plastic sheeting covering the ground around the seedling. Each device was replicated 10 times and there were 10 control seedlings. Seedling height and condition were recorded in November 1993 and in April 1994. The east-side shade cloth device was tested again in the winter of 1994–1995 using 75 protected and 96 unprotected seedlings at 2020 m elevation.

2.2.2. *Climatic, edaphic and biotic conditions under young A. koa stands*

Thirty-one stands of *A. koa*, each containing 49 individuals arranged in a 7×7-grid with 2 m spacing, were planted in 1987 inside a 2.6 ha pig- and cattle-proof exclosure located at 1980 m elevation. All stands were successfully established; some were in drainage bottoms and others on north-, east-, and south-facing slopes. Sample stands were selected at random for study.

Temperature and light regimes under a drainage bottom stand and in an adjacent grassland area were determined between March 1994 and April 1996. High cost prohibited sampling in more than two sites, so we chose drainage bottom sites where we expected coldest temperatures. Towers were erected and copper–constantan thermocouples installed at heights of 5, 10, 20, 40 and 80 cm and 2, 4, 6 and 8 m. These heights allowed intensive sampling of the air layer closest to the ground, where gradients were expected to be greatest, and put sensors at the base of the live crown (2 m), at the top of the canopy (4 m), and above the canopy (6 and 8 m). Light levels were measured with LiCor pyranometers installed in the open above surrounding vegetation, at ground level in grassland and under *A. koa*, and at the base of the live tree canopy. Only *P. clandestinum* shaded the ground-level pyranometer in the grassland; both koa and understory grasses shaded the sensor under tree cover. Data from temperature and light sensors were logged with a Campbell Scientific CR10 data logger and AM416 multiplexer. Sensors were interrogated every 30 s and means output hourly; maximum/minimum temperatures were output daily.

The effects of young *A. koa* on surface soil chemistry were studied by intact core sampling under 9-year-old trees, in adjacent grassland, and in intact mature forest located at the same elevation, but about 1.8 km to the north. Core sampling followed the same procedures as described under Section 2.2.1. The assumption was that soil chemistry in the mature forest represents what the soils would have been like in the grasslands had conversion not occurred.

Reduction of herbaceous competition by the establishment of closed canopy stands of *A. koa* was estimated by comparing biomass of the herbaceous-litter layer under 9-year old trees with that in grassland at 1980 m elevation. All above-ground plant material in the herbaceous-litter layer was sampled in September 1996 from 0.2 m^2 areas that were delineated with a circular plastic ring pressed into the ground. A heavy-bladed knife was used to cut out material within the ring. Three 15×15 m plots were sampled per landscape location under tree cover and in the grasslands. Five random samples were collected from each tree-covered plot, but only one per grassland plot (these were assumed homogeneous). Plant material was separated into live herbaceous tissue, herbaceous-litter, and *A. koa* litter, the latter consisting mainly of phyllodes, but with some fine twigs. Samples were oven dried at 60°C for 72 h and weighed.

Dried samples were composited by plot for chemical analysis at the University of Hawaii's Agricultural Diagnostic Service Center, which included concentrations (dry weight basis) of N, P, K, Ca and Mg. Total N was determined by Kjeldahl digestion and analysis by colorimetric methods (Shuman et al., 1973; Issac and Johnson, 1976). Subsamples used for N determinations were dry-ashed (Issac and Johnson, 1985). K concentrations were determined by Technicon continuous-flow flame-emission spectrophotometry. P, Ca and Mg were determined by inductively coupled plasma emission spectrometry (Perkin Elmer ICP model 6500).

Analysis of variance (ANOVA) was used to examine factor effects, and multiple pairwise comparisons were used to determine significance of factor level effects. For soil data, we used one-way ANOVA to examine chemistry differences among vegetation types (grass, young *A. koa* and mature forest) and among landscape locations (drainage, slope and ridge). For biomass and nutrient distribution in the herbaceous-litter layer, we used two-way ANOVA in which tissue type and landscape location were the two factors. Separate analyses were done for grassland, young stands of trees and each nutrient.

3. Results

3.1. Low temperature limitations

As hypothesized, *A. koa* seedlings planted in the treeless uppermost parts of the Refuge in low-lying drainage bottoms, where cold air settles, experienced higher rates of mortality than those planted on slopes or ridges (Fig. 1(a)). One-half of the seedlings in drainages died during the first winter after planting, and after three winters, mortality had climbed to more than 95%. In contrast, fewer than one-fifth of the seedlings planted on slopes or ridges died during the first winter, and even after two more winters mortality ranged from 40 to 65%. There was no statistical evidence that survival was affected by slope aspect.

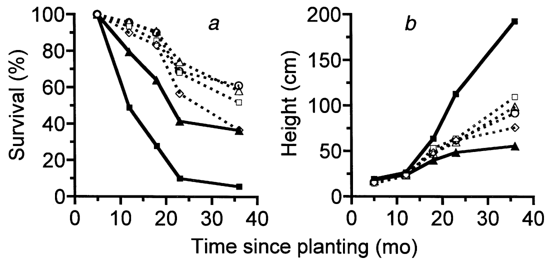

Fig. 1. Effect of aspect (north, ···○···; east, ···△···; south, ···□···; and west, ···◇···) and topographic position (drainage bottom —■— and ridge top —▲— on (a) mean survival and (b) height of *Acacia koa* seedlings planted in grassland at 1980 m elevation, Hakalau Forest National Wildlife Refuge.

Topographic position had the opposite effect on height growth of surviving seedlings, with those in drainages growing more rapidly than those on slopes or ridges (Fig. 1(b)). Three years after planting, seedlings in drainages averaged about 2 m in height, while those on slopes averaged about 0.8 to 0.9 m and those on ridges 0.5 m. More favorable soil moisture and nutrient availability in drainage bottoms probably accounted for better growth of *A. koa* seedlings. Analyses showed that total N and extractable NH_4–N were significantly greater in surface soil from drainage bottoms than from other locations (Table 1). Likewise, extractable P, Ca, and Mg were significantly greater in drainage bottoms than elsewhere, except Mg on the northern slope.

Radiative cooling during dry cloudless nights produced freezing temperatures near the ground. Cold air flow into drainage bottoms created freezing conditions that were both more intense and longer lasting than those produced on ridges or side slopes. For example, on the night of 22 December 1994, temperatures at 30 cm above the ground in a drainage bottom fell below freezing for more than three hours and reached a low of −4°C (Fig. 2). Even at 60 cm temperatures in the drainages were below freezing for 2–3 h although by no more than 2°C. Conditions on ridges and slopes were not as severe or long lasting. Fog moved in after 2:00 pm causing temperatures to climb above freezing; otherwise temperatures would probably have been lower. Freezing temperatures at 10 cm above ground in drainages occurred 24% of the days between December and March during the winter of 1994–1995.

Table 1
Chemical properties of the upper 15 cm of grassland soils located at three different topographic positions in the landscape at 1890 m elevation, Hakalau Forest National Wildlife Refuge

Attribute	Drainage bottom	North slope	Ridge top
pH	5.2 a[a]	5.1 a	5.3 a
Organic carbon (g kg^{-1})	189.0 a	161.0 a	154.0 a
Total nitrogen (g kg^{-1})	13.0 a	9.0 b	9.0 b
Extractable NH_4–N (mg kg^{-1})	28.0 a	8.0 b	10.0 b
Extractable NO_3–N (mg kg^{-1})	7.0 a	3.0 a	2.0 a
Net N mineralization (μg g^{-1})	24.0 a	13.0 a	6.0 a
Extractable P (mg kg^{-1})	135.0 a	34.0 b	37.0 b
Extractable K ($cmol_c$ kg^{-1})	0.3 a	0.2 a	0.2 a
Extractable Ca ($cmol_c$ kg^{-1})	1.5 a	0.8 b	0.5 b
Extractable Mg ($cmol_c$ kg^{-1})	0.8 a	0.5 ab	0.1 b

[a] Means within a row followed by the same letter are not statistically different (α=0.05).

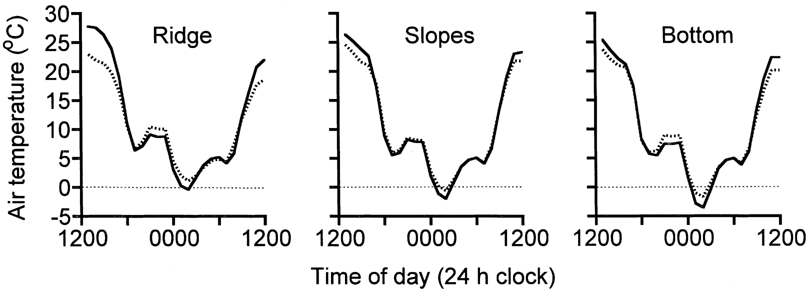

Fig. 2. Air temperatures during the 24 h period from 12:00 pm 22 December to 12:00 pm 23 December, 1994 at 30 cm (———) and 60 cm (· · ·) above the ground on ridge, side slope and drainage bottom sites at 1980 m elevation, Hakalau Forest National Wildlife Refuge. Horizontal dotted line is a zero degree reference line.

At 30 cm the proportion was 7% and at 60 cm it was 3%. Similar values for side slopes were 15%, 10% and 4%; while those for ridges were 9%, 3% and 2%. The lowest temperature recorded during the study was −5.4°C at 10 cm.

Results of the winter of 1993–1994 tests of frost protection devices showed that one of the least expensive devices, a single layer of shade cloth placed on the eastern side of seedlings, offered as good protection from damage as the most expensive Wall-O-Water; survival in both cases increased from 15% to 100%. The results of a second test of the east-side shade cloth in the winter of 1994–1995 confirmed the first test: 89% of the 75 protected seedlings survived compared to only 16% of the 96 unprotected seedlings. Why should this be true if damage was caused by ice crystals forming in leaf tissue? The east-side shade cloth should have had no influence on clear-night leaf temperatures, whereas the Wall-O-Water should have kept leaf temperatures above freezing by radiating heat stored in the water surrounding the seedling. Two other devices that shielded seedlings on the eastern side, the polyethylene and Reemay cylinders, also improved survival to 100%. Significantly, shade cloth placed on the western side of a seedling offered less protection (50% survival) than when placed on the eastern side.

3.2. *Moderating influence of Acacia koa stands*

3.2.1. *Air temperature profiles*

The freezing night temperatures found in the grasslands were eliminated under stands of *A. koa*. Although the stands were only 15 m wide and were located in a drainage bottom with grassland both above and below, pre-dawn temperatures close to

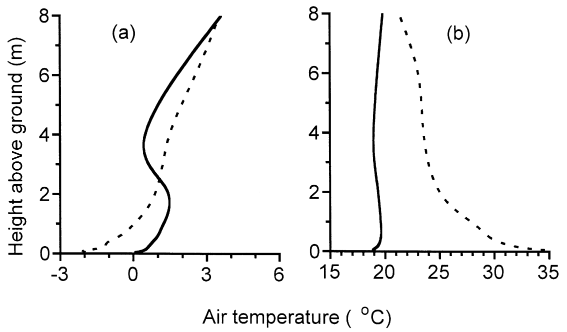

Fig. 3. Typical pre-dawn (a) and midday (b) temperature profiles from ground level to 8 m in a 5-year-old stand of *Acacia koa* (———) and in adjacent grasslands (– – –) during December 1993 at 1980 m elevation, Hakalau Forest National Wildlife Refuge.

the ground remained above freezing while those in the open fell below freezing (Fig. 3(a)). The thickness of the layer of freezing air in the December example was about 1 m in grassland. The S-shaped temperature profile in the stand of *A. koa* was a distinctive and real phenomenon; the top of the S curve, where temperatures again began to increase with height corresponded to the top of the tree canopy. Not surprisingly, tree cover also moderated the high temperatures experienced at midday near the ground (Fig. 3(b)).

3.2.2. Soil chemistry

Certain chemical properties of the surface 15 cm of soil changed within 10 years after *A. koa* became established in the grasslands. Soil acidity and total OC and N, while not significantly greater than that of the grasslands, had increased to levels not significantly different from those of nearby intact forest (Fig. 4). As expected, the amount of extractable NO_3–N was significantly increased for soil under the young N-fixing trees, although levels were still less than one-half of those in forest soil. The concentration of extractable Ca for soils under young *A. koa* was not significantly greater than that for grassland soil, and it was much less than that for forest soil. The amount of extractable P, which was tightly bound in the amorphous-rich soils, was unaffected by the establishment of *A. koa*, and levels were less than one-third of those in the forest soil. These findings are consistent with results in other tropical regions (e.g. Montagnini and Sancho, 1990).

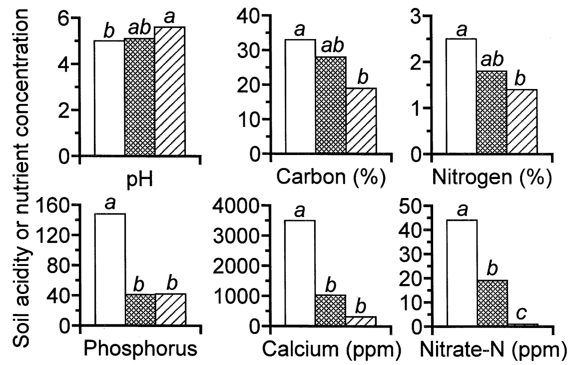

Fig. 4. Mean soil acidity, total organic carbon and nitrogen, and extractable calcium and nitrate–nitrogen under an old growth *Acacia koa* forest (□) under a 9-year-old *Acacia koa* stand growing on abandoned grassland (▩), and in grassland (▨) at 1700 m elevation, Hakalau Forest National Wildlife Refuge. For each graph, bars capped with a common letter were not significantly different (α=0.05).

3.2.3. Herbaceous-litter layer biomass

The establishment of closed canopy *A. koa* stands changed some structural aspects of the herbaceous-litter layer. Two-thirds of the total biomass under trees was *A. koa* litter, 23% was herbaceous-litter, and 10% was live herbaceous material. In grassland, 77% of the biomass was herbaceous-litter and the remainder was live grasses and forbs. The ratio of live to dead herbaceous material under trees (1:2.8) was not significantly different from the ratio in grassland (1:2.3). However, tree cover significantly suppressed herbaceous productivity; standing herbaceous biomass was only 2.45 Mg ha^{-1} under *A. koa*, three and one-half times less than in the open. Total biomass of the herbaceous-litter layer under tree cover was not significantly different from that in grassland, 7.50 and 8.55 Mg ha^{-1}, respectively.

Distribution of biomass in the herbaceous-litter layer was significantly affected by position in the landscape, but only under tree cover (Fig. 5). Total biomass under *A. koa* exceeded 11.30 Mg ha^{-1} for microsites located in drainage bottoms compared to 5.00–6.15 Mg ha^{-1} for microsites located on slopes. The difference was due to the accumulation of two to three times more tree litter on sites located in drainages. There was also a significant difference in the ratio of live to dead herbaceous material in drainages under *A. koa*: it was 1:1 in drainages versus 1:3 to 1:5 on slopes. The difference was due to a significantly

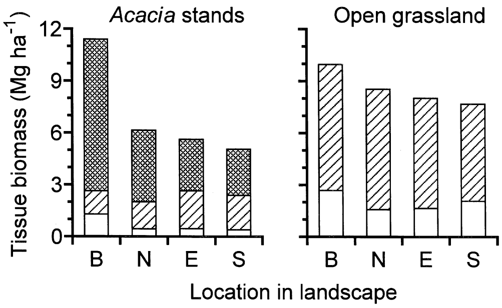

Fig. 5. Biomass of fine *Acacia* litter (▩), herbaceous litter (▨) and live herbaceous material (□) in the herbaceous-litter layer beneath 9-year-old stands of *Acacia koa* and in grassland at 1980 m elevation, Hakalau Forest National Wildlife Refuge, by location in the landscape (B=drainage bottom, N=north-facing slope, E=east-facing slope, and S=south-facing slope).

greater standing crop of live herbaceous material in drainage bottoms. Neither total nor dead herbaceous biomass were significantly affected by the position in the landscape, whether under tree cover or in grassland.

3.2.4. Herbaceous-litter layer nutrient pools

Nutrient concentrations of above-ground herbaceous-litter layer plant material differed among tissue types and among landscape locations (Table 2). Tissue type×landscape location interaction was not significant. Both *A. koa* litter and live herbaceous tissues had N concentrations of about 23 g kg^{-1}, which were significantly greater than that in herbaceous litter. Concentrations of P and K were greatest in live herbaceous tissues and least in bulk *A. koa* litter. The latter contained five times more Ca than herbaceous-litter and ten times more than live herbaceous material. Nitrogen concentration for herbaceous-litter layer material produced in drainage bottoms was about 22 g kg^{-1}, but this was not significantly different from that produced on north- and south-facing slopes. The concentration of P was significantly greater in material produced in drainage bottoms (1.2 g kg^{-1}) than in material produced on slopes. Differences for the other nutrients were small.

Nutrient pool sizes as a function of types of herbaceous-litter layer material and landscape positions under *A. koa* stands are shown in Table 3. Bulk tree-litter consistently accounted for the greatest proportion of N and Ca on the forest floor. The tree-litter N pool under stands in drainage bottoms (217 kg ha^{-1}) clearly exceeded that of stands on slopes (<100 kg ha^{-1}). The same was true for P, Ca and Mg pools in drainages compared to slopes. Even for K the largest pool was found in drainages, but in this case it was the live herbaceous material that had the most K. With this exception, nutrient pool sizes for live and dead herbaceous material were generally small compared to those for tree litter.

In grassland, N pool sizes were greater for herbaceous-litter than for live material, and location in the landscape did not significantly affect them (Table 4). P pool sizes did not vary between tissue types either, but live P pool size was significantly greater in drai-

Table 2
Effects of tissue type and position in the young *Acacia koa*-dominated landscape on mean nutrient concentrations of above-ground plant material in the herbaceous-litter layer at 1950 m elevation, Hakalau Forest National Wildlife Refuge

Factor	Nutrient concentration(g k^{-1})				
	N	P	K	Ca	Mg
Tissue type					
Acacia-litter	23.0 a[a]	0.5 c	0.3 b	23.4 a	3.4 a
Herbaceous-litter	15.5 b	0.8 b	1.6 b	4.7 b	1.9 b
Live herbaceous	23.3 a	1.5 a	13.2 a	2.3 b	3.0 a
Aspect or topographic position					
Bottom	22.1 a	1.2 a	5.3 a	11.1 a	3.4 a
North slope	21.9 a	0.9 b	5.5 a	10.6 a	2.7 a,b
East slope	18.9 b	0.9 b	4.5 a	9.8 a	2.8 a,b
South slope	19.4 a,b	0.8 b	4.8 a	9.0 a	2.2 b

[a] Data were analyzed by two-way ANOVA; factor level means within columns followed by a common letter were not significantly different (α=0.05).

Table 3
Effects of type of plant tissue and location in the young *Acacia koa* dominated landscape on mean nutrient contents (kg ha^{-1}) of above-ground plant material in the herbaceous-litter layer at 1950 m elevation, Hakalau Forest National Wildlife Refuge

Tissue type	Aspect or topographic position			
	Drainage bottom	North slope	East slope	South slope
	Nitrogen			
Acacia-litter	217.4 a,a	90.6 b	67.4 b,c	59.2 b,c,d
Herbaceous-litter	26.4 c,d,e	24.9 c,d,e	29.9 c,d,e	24.9 c,d,e
Live herbaceous	27.2 c,d,e	12.5 d,e	9.5 e	7.6 e
	Phosphorus			
Acacia-litter	6.3 a	2.0 b	1.4 b	1.2 b
Herbaceous-litter	1.6 b	1.1 b	1.7 b	1.4 b
Live herbaceous	2.0 b	0.7 b	0.7 b	0.4 b
	Potassium			
Acacia-litter	0.6 b	2.8 b	1.2 b	0.2 b
Herbaceous-litter	2.5 b	2.4 b	3.3 b	3.1 b
Live herbaceous	15.0 a	6.3 b	5.6 b	4.5 b
	Calcium			
Acacia-litter	219.8 a	100.8 b	68.1 bc	56.8 c
Herbaceous-litter	7.3 d	6.8 d	9.5 d	8.5 d
Live herbaceous	2.8 d	1.2 d	0.9 d	0.8 d
	Magnesium			
Acacia-litter	34.2 a	15.0 b	10.8 b,c	8.7 b,c
Herbaceous-litter	3.2 c	2.6 c	3.9 c	3.0 c
Live herbaceous	5.2 b,c	1.3 c	1.5 c	0.8 c

[a]Data were analyzed using two-way ANOVA; for a given nutrient, means followed by a common letter were not significantly different (Bonferroni pairwise comparisons, $\alpha \leq 0.05$)

Table 4
Effects of type of plant tissue and location in the grassland landscape on mean nutrient contents (kg ha^{-1}) of above-ground plant material in the herbaceous-litter layer at 1950 m elevation, Hakalau Forest National Wildlife Refuge

Tissue type	Aspect or topographic position			
	Drainage bottom	North slope	East slope	South slope
	Nitrogen			
Herbaceous-litter	74.2 a[a]	62.6 a	45.8 a	41.0 a
Live herbaceous	37.3 b	23.5 b	22.2 b	28.2 b
	Phosphorus			
Herbaceous-litter	8.7 a	5.6 a,b	4.5 ab	2.8 b
Live herbaceous	7.5 a	2.4 b	3.0 b	2.5 b
	Potassium			
Herbaceous-litter	12.4 b	10.4 b	8.9 b	4.5 b
Live herbaceous	29.2 a	28.2 a	33.7 a	20.5 a
	Calcium			
Herbaceous-litter	20.4 a	21.6 a	17.8 ab	16.3 a,b
Live herbaceous	4.6 b	3.1 b	5.3 b	5.2 b
	Magnesium			
Herbaceous-litter	6.5 a	5.6 a	5.1 a	5.6 a
Live herbaceous	6.4 a	2.7 a	2.8 a	5.4 a

[a]Data were analyzed using two-way ANOVA; for a given nutrient, means followed by a common letter were not significantly different (Bonferroni pairwise comparisons, $\alpha \leq 0.05$).

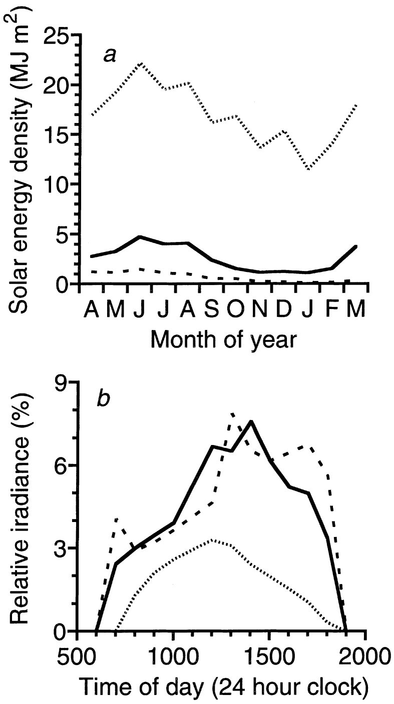

Fig. 6. Moderating effects of a stand of 7- to 8-year old *Acacia koa* on (a) relative irradiance (% of full sun) at 2 m above ground level under the tree canopy and at ground level under *Pennisetum clandestinum* in the open (1 September 1994–15 October 1994), and (b) mean daily solar energy density at and 2 m above ground level under tree canopy (1 April 1995–31 March 1996). Line patterns are as follows: ground level under trees (– – –); ground level under grass for relative irradiance or full sun for solar energy density (· · · · ·); and 2 m above ground under trees (———). Data collected at 1980 m elevation, Hakalau Forest National Wildlife Refuge.

nage bottoms than on slopes. The amount of K in live tissues was always significantly greater than that in litter across all landscape positions. Live plant Ca pools were three to five times smaller than litter pools. Landscape location had no significant influence on Ca pool sizes.

3.2.5. Light level under trees and grass

The canopies of young stands of *A. koa* intercepted 80% to 90% of the incident solar energy at the 1980 m elevation study site in Hakalau (Fig. 6(a)). Full-sun solar energy densities ranged from 22 MJ m^{-2} in June 1995 to 11 MJ m^{-2} in January 1996. In comparison, at the base of the live tree canopy, solar energy densities ranged from 5 MJ^{-2} in June to 1 MJ $^{-2}$ in January. Even lower levels of incident radiation were observed at ground level under *A. koa*.

The percentage of full-sun radiation penetrating tree and grass cover (relative irradiance) during the course of a day late in the summer of 1994 is shown in Fig. 6(b). Illumination at ground level under *P. clandestinum* was delayed 1 h compared to that under tree cover; it peaked at noon and it never exceeded 3% of full sun. At the base of the live crown under *A. koa*, relative irradiance peaked near 2 pm at about 8%. Relative irradiance at ground level under tree cover paralleled that at 2 m, except for early in the morning and late in the afternoon. At those times, the sun angle was low enough for direct light to reach the ground inside the 15 m wide stands where the sensor was located. We expected light levels to be reduced on the forest floor by herbaceous growth and litter. This did not happen, possibly because herbaceous growth was insufficient to allow the full recovery of trodden-down herbaceous vegetation after instrument installation. Indeed, following an additional year of recovery, solar energy densities at ground level in the *A. koa* stand were only 10% of those at 2 m above ground (Fig. 6(a)).

4. Discussion

Our findings provide strong circumstantial evidence for the hypothesis that frost was limiting reforestation of grasslands within the Refuge. Microsites with the coldest air temperatures suffered the greatest seedling mortality, and some frost protection devices were effective at increasing over-winter survival, presumably by moderating radiative heat loss. Additional support for the hypothesis comes from the work of Dr. Goldstein, physiological ecologist, University of Hawaii. In laboratory studies, he found that ice nucleation occurred at −6°C in leaves of *M. polymorpha* seedlings from Hakalau, and that irreversible tissue damage occurred at −7.5°C (unpublished data). Our data showed freezing temperatures near −6°C, but not as low as −7.5°C. Dr. Goldstein also showed that *S. chrysophylla*, which occurs in the Refuge and forms tree line on Mauna Kea at 2900 m elevation, suffered irreversible tissue damage at −8°C.

Results of the test of frost protection devices indicated that in addition to frost damage, some other low-temperature phenomenon may be weakening or killing seedlings. One possibility is that seedlings may fail to meet the transpiration demand in early morning sunlight due to small root systems, small stem water storage capacity, reduced root and xylem conductivity, and increased viscosity of water at temperatures near freezing. Low soil moisture caused by below normal rainfall or grass competition, and a steep leaf-to-air water potential gradient in dry air, would exacerbate the situation. Such water stress could reduce carbon gain and seedling vigor.

Mortality was not just a winter phenomenon. As indicated in Fig. 1, some *A. koa* mortality occurred between April and October 1994 the second year after planting. On the slopes, 20% of the 1994–1995 mortality occurred during summer; on ridges and in drainage bottoms 45% to 50% of the year's mortality occurred during the growing season. The cause was not frost, at least not directly. On ridges, low soil moisture probably contributed to summer mortality. In drainages, the seedlings may have been so weakened by low winter temperatures that they succumbed to competition with *P. clandestinum*, the dominant grass in such microsites. We suspect that competition for P was particularly intense. Not only did the soils have a high capacity to fix P into plant-unavailable forms, but the grasses were highly endo-mycorrhizal enabling them to effectively scavenge for P, while nursery grown seedlings were not initially mycorrhizal and after planting such associations developed slowly (Habte, personal communication). More long lasting control of grasses than is achieved by spot scalping at time of planting may be essential to successful seedling establishment.

Our results supported the hypotheses that an established stand of *A. koa* prevents freezing temperatures, provides a shaded but not too dark light regime for establishment of native understory species, makes soil chemical properties more like those found in an intact forest, and reduces competitor biomass. These findings may have significant management implications. Although *A. koa* is susceptible to low temperature damage, other native species appear to be more susceptible. In a 1987 field trial, only one out of hundreds of planted *M. polymorpha* survived, and that on a south-facing slope (Scowcroft et al., 1993). Most *A. koa* seedlings planted at the same time survived; the resulting stands were used in this study. So except for unusually cold years, *A. koa* can be successfully established, and the resulting stands may serve as nurse crops for other understory species.

Finally, the results of our study support the hypothesis that landscape position is a determining factor in the degree to which *A. koa* modifies herbaceous-litter layer nutrient pools and reduces understory herbaceous competitors. Additional studies are planned to determine what impact such nurse crop-landscape interactions have on establishment of other native plants.

Acknowledgements

We thank David Fujii, Donovan Goo, Janis Haraguchi, and Alan Urakami for their invaluable help in installing instrumentation, collecting weather data, measuring plants, and generally supporting all phases of the work reported here. We also thank Kathy Ewel, Robin Harrington and two anonymous reviewers for thoughtful comments on an earlier draft manuscript. This research could not have been done without the logistical support and encouragement of Richard Wass, manager, Hakalau Forest National Wildlife Refuge.

References

Barrera, W., Jr., Kelly, M., 1974. Archaeological and historical surveys of the Waimea to Kawaihae Road corridor, island of Hawaii. Hawaii Historic Preservation Rep. 74-1, Anthropology Department, B.P. Bishop Museum, Honolulu, HI, p. 84.

Bush, J.K., van Auken, O.W., 1995. Woody plant growth related to planting time and clipping of a C_4 grass. Ecology 76, 1603–1809.

Chu, P-S., 1989. Hawaiian drought and the southern oscillation. Int. J. Climatol. 9, 619–631.

Cuddihy, L.W., Stone, C.P., 1990. Alteration of Native Hawaiian Vegetation: Effects of Humans, Their Activities and Introductions. Cooperative National Park Resources Studies Unit, University of Hawaii, Honolulu, HI, p. 138.

Ewel, J.J., Bigelow, S.W., 1996. Plant life-forms and tropical ecosystem functioning. In: Orians, G.H., Dirzo, R., Cushman, J.H. (Ed.), Biodiversity and Ecosystem Processes in Tropical Forests, Ecological Studies, vol. 122, Chap. 6, Springer, Berlin, Germany, pp. 101–126.

Fimbel, R.A., Fimbel, C.C., 1996. The role of exotic conifer plantations in rehabilitating degraded tropical forest lands: a case study from the Kibale Forest in Uganda. For. Ecol. Manag. 81, 215–226.

Gordon, D.R., Welker, J.M., Menke, J.W., Rice, K.L., 1989. Competition for soil–water between annual plants and blue oak (*Quercus douglasii*) seedlings. Oecologia 79, 533–541.

Guariguata, M.R., Rheingans, R., Montagnini, F., 1995. Early woody invasion under tree plantations in Costa Rica: Implications for forest restoration. Restor. Ecol. 3, 252–260.

Harrington, R.A., Ewel, J.J., 1997. Invasibility of tree plantations by native and non-indigenous plant species in Hawaii. For. Ecol. Manag. 99, 153–162.

Issac, R.A., Johnson, W.C., 1976. Determination of total nitrogen in plant tissue using a block digester. J. Assoc. Offic. Anal. Chem. 59, 98–100.

Issac, R.A., Johnson, W.C., 1985. Elemental analysis of plant tissue by plasma emission spectroscopy-collaborative study. J. Assoc. Offic. Anal. Chem. 68, 449–505.

Jenkins, I., 1983. Hawaiian Furniture and Hawaii's Cabinet Makers, 1820–1940. The Daughters of Hawaii, Editions, Honolulu, HI, p. 350.

Kobe, R.K., Pacala, S.W., Silander Jr., J.A., 1995. Juvenile tree survivorship as a component of shade tolerance. Ecol. Monog. 5, 517–532.

Lugo, A.E., Parrotta, J.A., Brown, S., 1993. Loss of species caused by tropical deforestation and their recovery through management. Ambio 125, 263–280.

Loudat, T.A., Kanter, R., 1997. The economics of commercial koa culture. In: Ferentinos, L., Evans, D.O. (Eds.), Koa: A Decade of Growth, Proceedings of the Hawaii Forest Industry Association's 1996 Annual Symposium, 18–19 November 1996, Honolulu, HI, pp. 124–147.

McClelland, C.K., 1915. Grasses and forage plants of Hawaii. Hawaii Agric. Expt. Stn., University of Hawaii, Honolulu, HI, Bull. 36, p. 43.

Mears, P.T., 1970. Kikuyu-(*Pennisetum clandestinum*) as a pasture grass – a review. Trop. Grasslands 4, 139–152.

Montagnini, F., Sancho, F., 1990. Impacts of native trees on tropical soils: A study in the Atlantic lowlands of Costa Rica. Ambio 19, 386–390.

Parrotta, J.A., 1992. The role of plantation forests in rehabilitating degraded tropical ecosystems. Agric. Ecosys. Environ. 41, 115–133.

Parrotta, J.A., 1993. Secondary forest regeneration on degraded tropical lands: The role of plantations as 'foster ecosystems.' In: Lieth, H., Lohmann, M. (Eds.), Restoration of Tropical Forest Ecosystems. Kluwer, Dordrecht, The Netherlands, pp. 63–73.

Parsons, W.F., Keller, M., 1995. Controls on nitric oxide emissions from tropical pasture and rain forest soils. Biol. Fert. Soils 20, 151–156.

Piccolo, M.C., Neill, C., Cerri, C.C., 1994. Net nitrogen mineralization and net nitrification along a tropical forest-to-pasture chronosequence. Plant Soil 162, 61–70.

Prasad, P., Basu, S., Behera, N., 1994. A comparative account of the microbiological characteristics of soils under natural forest, grassland, and crop field from Eastern India. Plant Soil 175, 85–91.

Rubenstein, T., 1995. Hakalau Forest National Wildlife Refuge Reforestation Management Plan. U.S. Department of Interior, Fish and Wildlife Service, Hilo, HI, p. 72.

Scowcroft, P.G., 1992. Role of decaying logs and other organic seedbeds in natural regeneration of Hawaiian forest species on abandoned montane pasture. In: Conrad, C.E., Newell, L.A. (Technical Coordinators), Proceedings of the Session on Tropical Forestry for People of the Pacific, XVII Pacific Science Congress, 27–28 May 1991, Honolulu, HI. Gen. Tech. Rep. PSW-GTR-129, Pacific Southwest Research Station, U.S. Department of Agriculture, Forest Service, Albany, CA, pp. 67–73.

Scowcroft, P.G., Conrad, C.E., Goo, D., 1993. 1992 Research Accomplishments: USDA Forest Service at Hakalau Forest National Wildlife Refuge. Annual Report to Hakalau Forest National Wildlife Refuge, typescript, p. 15.

Scott, J.M., Kepler, C.B., van Riper III, C., Fefer, S.I., 1988. Conservation of Hawaii's vanishing avifauna. Bioscience 38, 238–253.

Shuman, G.E., Stanley, M.A., Knudsen, D., 1973. Automated total nitrogen analysis of soil and plant materials. Soil Sci. Soc. Am. Proc. 37, 480–481.

Sullivan, J.H., Teramura, A.H., Ziska, L.H., 1992. Variation in UV-B sensitivity in plants from a 3000 m elevation gradient in Hawaii. Am. J. Bot. 79, 737–743.

TenBruggencate, J., 1991. Hawaii beef feels the heat: Better days ahead, or the beginning of the end? Honolulu Advertiser, sec. A, p. 3.

Veldkamp, E., 1994. Organic carbon turnover in three tropical soils under pasture after deforestation. Soil Sci. Soc. Am. J. 58, 175–180.

Wagner, W.L., Herbst, D.R., Sohmer, S.H., 1990. Manual of the Flowering Plants of Hawaii, vol. 1, Bishop Museum, Honolulu, HI, p. 988.

Whitney, L.D., Hosaka, E.Y., Ripperton, J.C., 1939. Grasses of the Hawaiian ranges. Hawaii Agric. Expt. Stn., University of Hawaii, Bull. 82, p. 148.

Wilen, C.A., Holt, J.S., 1996. Physiological mechanisms for the rapid growth of *Pennisetum clandestinum* in Mediterranean climates. Weed Res. 36, 213–225.

Wood, H.B., 1977. Hydrologic differences between selected forested and agricultural soils in Hawaii. Soil Sci. Soc. Am. J. 41, 132–136.