Role of Decaying Logs and Other Organic Seedbeds in Natural Regeneration of Hawaiian Forest Species on Abandoned Montane Pasture[1]

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Abstract: Natural regeneration is one mechanism by which native mixed-species forests become reestablished on abandoned pasture. This study was done to determine patterns of and requirement for natural regeneration of native species in an open woodland after removal of cattle. Ten 50- by 50-m quadrats were randomly selected within a 16-ha exclosure located at 1,700-m elevation inside the Hakalau Forest National Wildlife Refuge on the island of Hawaii. In 1989 and 1991, data were collected for all regeneration in the quadrats, including species, height, and seedbed type. More than 2,000 individuals were found in 1989, two years after the cattle were excluded. By 1991, the number had doubled to more than 4,000 individuals. Ohia was the most abundant species both years. Mineral soil accounted for about 97 percent of the potential seedbed area inside the exclosure, but less than 25 percent of all regeneration was rooted there in 1989 and less than 33 percent in 1991. In contrast, decaying logs made up less than 2 percent of the potential seedbed area, but they supported about 70 percent of all regeneration in 1989 and 53 percent in 1991. The data indicated that organic seedbeds are preferred sites for recruitment, establishment, and early growth of olapa, kawau, and ohelo. Ohia's preference for organic seedbed was less pronounced. Tree fern showed a strong preference for mineral soil. Koa was nondiscriminatory.

During the past 10 years, interest has grown in developing technology for restoring native mixed-species forests to deforested and degraded forest lands of Hawaii. Concern for the recovery of endangered species has been a key motivating factor for this interest. Federal and State forest landowners are mandated by law to protect and restore endangered species. Much of the effort to accomplish those goals is focused on habitat protection and restoration.

The Forest Service has no National Forest land in Hawaii, and hence it has no management responsibilities in the State. However, the Forest Service maintains an active forest research program in Hawaii to help other Federal, State, and private forest owners develop technology for better management. Part of that research program is focused on reforestation.

A 16-ha exclosure, hereafter called the woodland exclosure, was built by the Hakalau Forest National Wildlife Refuge in 1987 to provide a cattle-free area for conducting reforestation experiments (Conrad and others 1988). Two years after the fence was erected, I observed that native woody species were regenerating naturally, but almost always in association with fallen, decaying logs or other organic seedbeds. This study was done to determine if organic seedbeds were as important to natural regeneration of native species as cursory observations suggested. Specifically I wanted to (1) determine the abundance of native regeneration, by species and seedbed type, and (2) determine the areal extent of each seedbed type. The findings, if confirmed by similar studies elsewhere, could have application in evaluating the potential for natural regeneration of open pasture where organic seedbeds no longer exist.

Methods

The tropical montane study site was on the east flank of Mauna Kea, island of Hawaii, at about 1,700 m elevation inside the Hakalau Forest National Wildlife Refuge. The climate is cool and moist year around. Mean daily air temperatures average less than 15°C, with an annual variation of only 5°C. Diurnal variation in temperature averages less than 10°C throughout the year. During winters frost is common. Rainfall averages about 2,500 mm per year, with greater amounts falling during winter months. Tradewind-generated clouds often shroud the refuge in mist in the afternoon.

The study area supported an open woodland dominated by Hawaii's two principal native overstory tree species, koa *(Acacia koa)* and ohia *(Metrosideros polymorpha)*. Grazed by cattle for 50 to 100 years, the native forest understory was destroyed and replaced by introduced grasses and forbs. Kikuyu grass *(Pennisetum clandestinum)*, sweet vernal grass *(Anthoxanthum odoratum)*, and velvet grass *(Holcus lanatus)* dominated the ground vegetation.

We divided the woodland exclosure into 50- by 50-m quadrats. I selected ten of these at random using a random number generator. In 1989 and again in 1991 a crew of 3 to 4 persons carefully and thoroughly searched each quadrat for natural regeneration. The grass cover was dense, and I know we must have missed some hidden regeneration that was rooted in mineral soil. However, we found that mineral soil seedbeds with natural regeneration had a certain characteristic that helped us in our search. The banks of cattle tracks and erosion scars often supported regeneration, so we examined especially these areas. Organic seedbeds were generally easy to see or find. I do not think we missed any regeneration rooted in organic material.

For each plant found in 1989, we recorded species, height, and seedbed type. I expanded the data set in 1991 to also include crown diameter, elevation of root collar above the soil surface, seedbed characteristics (such as degree of decomposition, grass covered, etc.), and projected area of each seedbed. Space considerations prevent discussion of all of these data in this paper.

Differences in mean plant height among the various seedbed types were examined using one-way ANOVA and Tukey's method of multiple comparisons. Sample size was 10 in all cases. Because sampling was from a finite population (i.e., 54, 50- by 50-m quadrats), all standard errors of the means shown in this paper were adjusted using the finite population correction factor (0.911 in the present study). Plant density refers to number of individuals per hectare of exclosure, not per hectare of seedbed type.

[1]An abbreviated version of this paper was presented at the Session on Tropical Forestry for People of the Pacific, XVII Pacific Science Congress, May 27-28, 1991, Honolulu, Hawaii.

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Results

Abundance of Natural Regeneration

We found 2,024 individual plants in 1989 within our sample quadrats *(table 1)*. Most of these plants (1756) were ohia seedlings. Ohelo *(Vaccinium reticulatum)*, olapa *(Cheirodendron trigynum)*, kawau *(Ilex anomala)*, and pukiawe *(Styphelia tameiameiae)* were the other native species tallied. No natural koa regeneration occurred within our sample, but we saw what we assumed were root sprouts growing elsewhere in the woodland exclosure.

Two years later, in 1991, we found 4,140 individuals, more than double the number tallied in 1989 *(table 1)*. Every species except pukiawe increased in abundance during the 2-year interval. Once again, the most abundant species was ohia, with 3,557 individuals. In addition to the species encountered in 1989, we tallied three new species—koa, kolea *(Myrsine lessertiana)*, and tree fern *(Cibotium glaucum)*. Much to our surprise, there were 150 young tree fern in the sample quadrats. We did not expect tree fern to invade the grass-dominated site so soon, especially considering the total absence of adult tree fern. There were 31 koa and one kolea.

Seedbed Area

We counted 110 live and standing dead trees in our sample quadrats, or an average of 44 trees per hectare (std. err. = 12). These stems occupied 58 sq. m of basal area, or about 0.2 percent of the sample area. Because these areas were already occupied, they were usually unavailable for seedling recruitment.

Mineral soil accounted for an average of 97 percent of the potential seedbed area in the woodland exclosure *(fig. 1)*. Fallen trees in various stages of decay accounted for about 2 percent of the seedbed area. Moss-covered root mats, pockets of organic matter perched in fissures and hollows of live trees, and exposed, decaying wood of live trees each made up less than 0.5 percent of the potential seedbed area.

Table 1—*Total count of natural regeneration of native species in sampled areas of the woodland exclosure, Hakalau Forest National Wildlife Refuge, by seedbed class and year.*

	1989		1991	
Species	Mineral soil	Organic beds	Mineral soil	Organic beds
Ohia	443	1,313	1,214	2,343
Ohelo	18	199	22	312
Olapa	1	43	2	55
Kawau	1	1	0	6
Pukiawe	1	4	1	3
Koa	0	0	14	17
Tree fern	0	0	126	24
Kolea	0	0	1	0
All species	**464**	**1560**	**1380**	**2760**

Seedbed Preferences

Analysis of the data confirmed our initial hypothesis that organic seedbeds are important sites for recruitment of native species. In 1989, more than 75 percent of the natural regeneration was found growing on organic material of one type or another *(table 1)*. In 1991, 67 percent was found on organic seedbeds.

Organic seedbeds contained a disproportionate number of plants relative to their surface area. Although mineral soil accounted for 97 percent of the available seedbed area, only one-

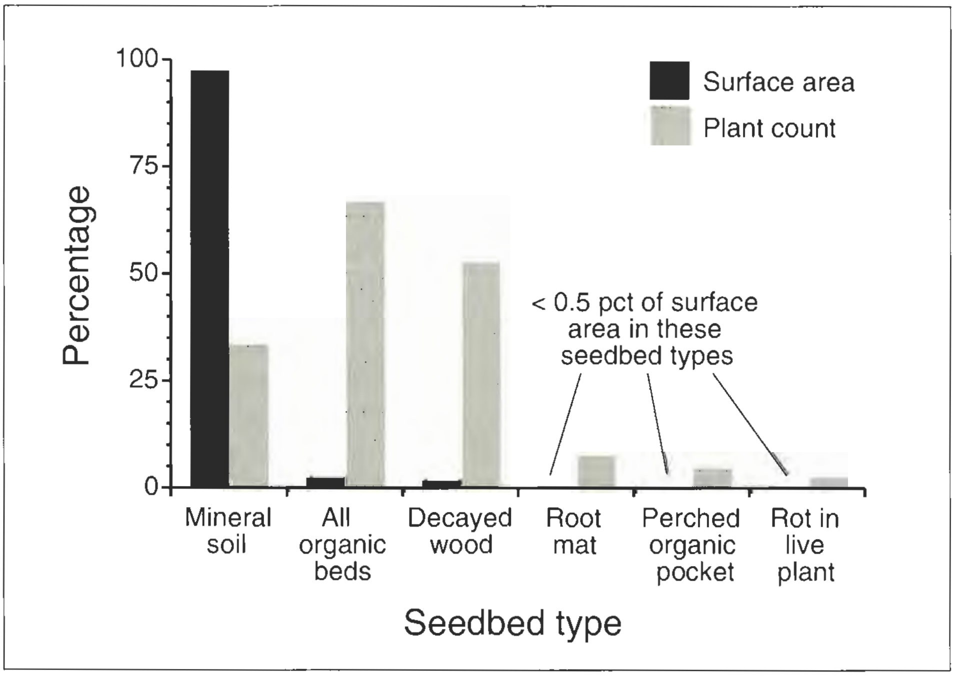

Figure 1—Average proportion of each type of seedbed in the woodland exclosure (surface area) and the average percentage of natural regeneration found growing on each type of seedbed (plant count) in 1991. Sample size (n) was 10.

third of the regeneration was found growing there in 1991 (*fig. 1*). In comparison, decaying logs and limbs made up less than 2 percent of the seedbed area, but they supported more than one-half of the regeneration. Moss-covered root mats, which appear to be important microsites for growth of some native species, supported 7 percent of the regeneration, but represented only 0.3 percent of the available seedbed area.

Seedbed preferences were already evident in 1989 (*table 2*). Ohia showed a moderately-strong preference for organic seedbeds—an average of 524 ohia were rooted in organic material compared to 177 rooted in mineral soil. Ohelo and olapa showed a strong preference for organic seedbeds; more than 90 percent of the regeneration of each of these species was rooted in organic material. The greatest densities of ohia, ohelo, and olapa were found on decaying wood. Too few kawau and pukiawe seedlings were sampled to determine their seedbed preferences.

The seedbed preferences expressed in the 1989 data were confirmed by the 1991 data (*fig. 2*). Natural regeneration of ohia continued to show a moderately-strong preference for organic seedbeds—about 65 percent occurrence in 1991. Decaying logs and other large woody debris were the favored organic site for recruitment of ohia seedlings. An average of 800 ohia per hectare (std. err. = 233) were found on decaying wood.

Natural regeneration of ohelo and olapa also continued to show a strong preference for organic seedbeds (*fig. 2*). Ninety-three percent of the ohelo and 96 percent of the olapa were growing on organic beds in 1991. Decaying logs and large organic debris were less important as safe sites for recruitment of ohelo and olapa than for recruitment of ohia. The largest percentage of olapa occurred on pockets of organic matter perched in crevices and hollows along the surface of living trees. An average of 10 olapa per hectare (std. err. = 5) were growing in such organic pockets.

In contrast to the woody species described above, tree fern regeneration showed a strong preference for mineral soil in 1991 (*fig. 2*). Out of 150 plants, 84 percent were rooted in mineral

Table 2—*Mean density[1] of natural regeneration of native woody species 1989, by species and seedbed type*

Species	Mineral soil	Decaying wood	Root mat	Organic pocket	Rot in tree
	plants per hectare				
Ohia	177	478	42	3	1
	(23)[2]	(183)	(28)	(2)	(1)
Ohelo	7	72	8	0	0
	(4)	(36)	(4)	(0)	(0)
Olapa	<1	10	5	2	0
	(<1)	(5)	(4)	(1)	(0)
Kawau	<1	0	<1	0	0
	(<1)	(0)	(<1)	(0)	(0)
Pukiawe	<1	0	<1	0	0
	(<1)	(1)	(<1)	(0)	(0)

[1]Mean density = plants per hectare of exclosure; sample size = 10.
[2]Standard error of the mean shown in parentheses.

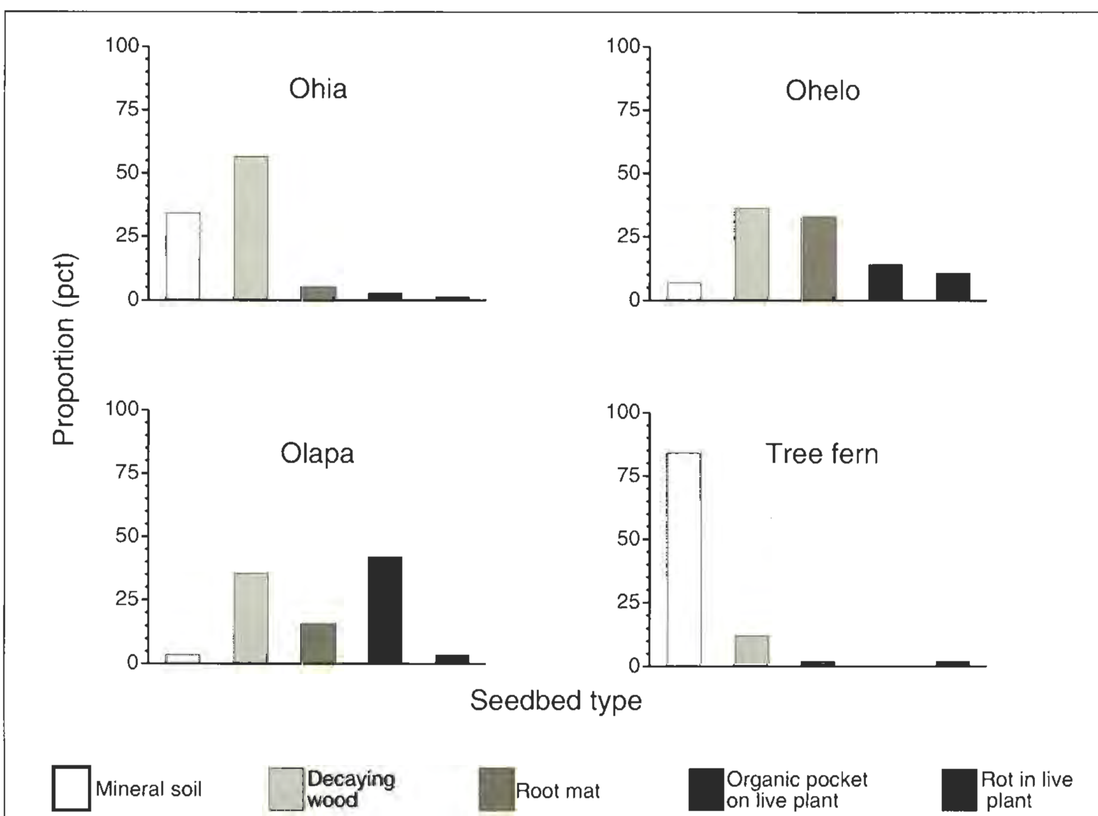

Figure 2—Average proportion of natural regeneration growing in the five different types of seedbeds in 1991, by species. Sample size (n) was 10.

soil. This amounted to an average of 50 ferns per hectare (std. err. = 16). Of the organic seedbeds, decaying logs were the most common sites for establishment of tree fern. But there were only 7 individuals per hectare (std. err. = 3) on decaying logs. No tree fern were observed growing in perched pockets of organic matter.

Height-Seedbed Type Relationships

Mean height of natural regeneration in 1991 was a function of species and seedbed *(fig. 3)*. Ohia seedlings growing in mineral soil averaged 7.8 cm in height (std. err. = 1.2). Those growing in organic seedbeds were more than twice as tall, averaging 20.6 cm (std. err. = 1.0). The difference was statistically significant ($p \leq 0.05$). There was little difference in mean height among the four different types of organic seedbeds.

Olapa seedlings rooted in mineral soil averaged 8.7 cm in height (std. err. = 0.2); those rooted in organic seedbeds averaged 117.3 cm in height (std. err. = 55.8). The difference in height was significant. Moss-covered root mats appeared to be the best seedbed for rapid height growth of olapa seedlings. On that type of seedbed olapa averaged 2.8 m in height. No other species of natural regeneration had attained such tall stature. Variation in height of olapa on root mats was also large (std. err. = 1.7 m).

Height of tree fern was not significantly greater on mineral soil than on organic seedbeds—17.2 cm (std. err. = 1.7) versus 19.6 cm (std. err. = 7.7), respectively *(fig. 3)*. Tree fern, like olapa, was tallest on moss-covered root mats [76.5 cm (std. err. = 42.4)].

The height class distributions for populations rooted in mineral soil were quite different from those rooted in organic seedbeds *(fig. 4)*. I selected ohia, ohelo, and olapa to illustrate this point. For ohia, about an equal number of soil-rooted and organic-rooted seedlings occurred in the smallest height class (0.1 to 9.9 cm). But in all the other classes there were significantly more organic-rooted ohia than soil-rooted ohia. I suspect that recruitment is a continuous process on both types of seedbed, but survival is poor on the mineral soil seedbed because of intense grass competition.

The height class distributions for soil-rooted ohelo were flat *(fig. 4)*. The inverse-J shape common to an actively recruiting, all-age population was absent. There were significantly fewer soil-rooted ohelo than organic-rooted ohelo in all height classes. The distribution for ohelo rooted in organic matter showed active seedling recruitment, and good survival and growth of established plants.

Soil-rooted olapa occurred only in the smallest height class (<9.9 cm). I suspect that recruitment on mineral soil seedbeds occurred slowly, and the seedlings either failed to survive or grew slowly. The distribution for organic seedbeds showed active seedling recruitment, and good survival and growth. I arbitrarily truncated the height class distributions, so those individuals taller than 1.6 m are not shown in *fig. 4*.

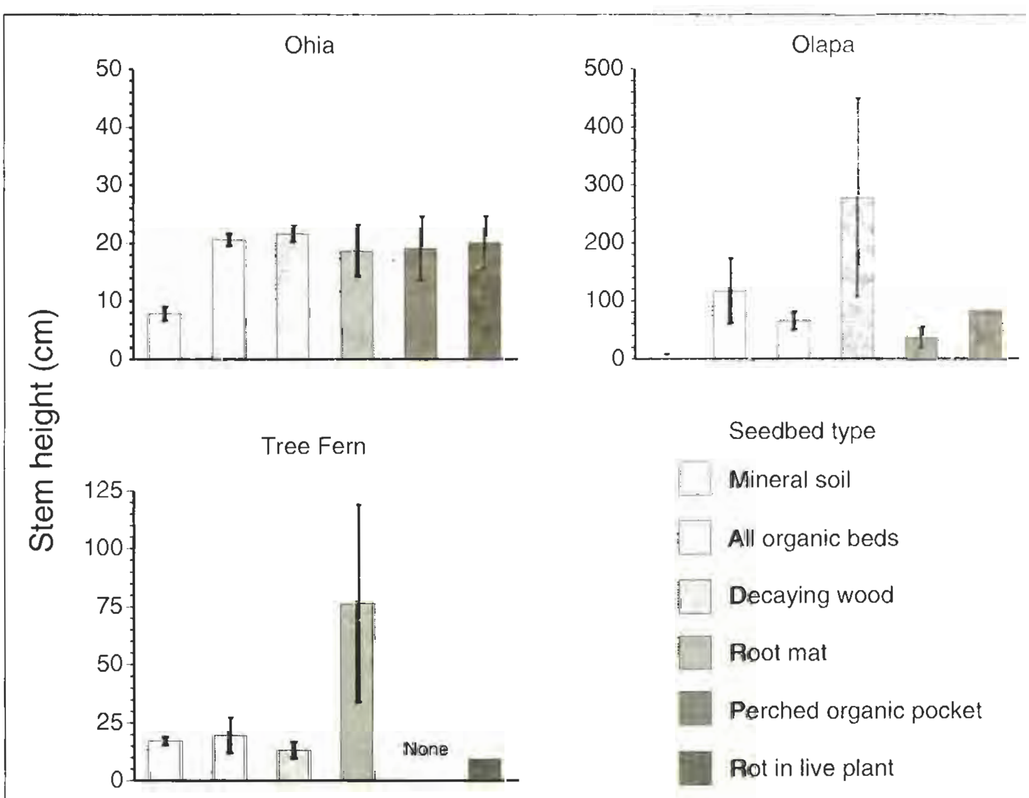

Figure 3—Average height of natural regeneration of ohia, olapa, and tree fern in 1991, by seedbed type. Vertical bars denote standard errors of the mean. Sample size (n) was 10.

Competition and Seedbed Type

A universal feature of mineral soil seedbeds in the woodland exclosure is dense grass cover. Seedlings germinating in the soil would therefore face competition for light, moisture, and nutrients. The grass cover would also affect the soil temperature. Many of the organic seedbeds are free of grass, and hence free of interspecific competition. Whether such competition or the lack of it affects growth and survival of native species in my study site cannot be directly assessed from my data.

Recall the height class distributions for ohia, ohelo, and olapa *(fig. 4)*. Little of the regeneration on mineral soil was growing into larger height classes. In contrast, lots of the regeneration on organic beds was apparently growing into larger classes. *Table 3* shows the percentage of plants, by species, that was growing under a grass overstory. A large proportion of the ohia, ohelo, and olapa rooted in mineral soil were grass covered. A smaller proportion rooted in organic matter were grass covered. Could grass competition account for the differences in height class distributions? Additional research will be needed to satisfactorily answer that question.

Discussion

On the basis of my analyses, I concluded that organic seedbeds were important sites for natural regeneration of several but not all native species in the woodland exclosure. It is possible that site factors are primarily responsible for the preference.

Table 3—***Percent of plants that were growing under an overstory of grass in 1991, by species and seedbed class***

Species	Mineral soil	Organic beds
	percent	
Ohia	95.4	45.4
Ohelo	63.6	22.8
Olapa	50.0	20.0
Kawau	–	0.0
Pukiawe	100.0	0.0
Koa	92.9	81.9
Tree fern	92.9	66.7
Kolea	100.0	

The natural vegetation of the study area has been drastically modified by humans and cattle—only a scattering of the overstory remains, along with a few remnant individuals of shrub and fern species on elevated logs. Throughout the area, introduced grasses covered the ground to a depth of more than 0.5 m. Light, temperature, and moisture regimes of mineral soil at ground level were no doubt much different from those found in a natural forest. Relative to healthy forests at slightly lower elevation, there were few decaying logs and other organic seedbeds.

Still, some of the seedbed preferences I observed have been noted by others, albeit in habitats quite different from the one in which I worked. Burton and Mueller-Dombois (1984) reported that ohia seedling preferentially established on moss-covered logs and other bryophyte-covered organic seedbeds in an intact

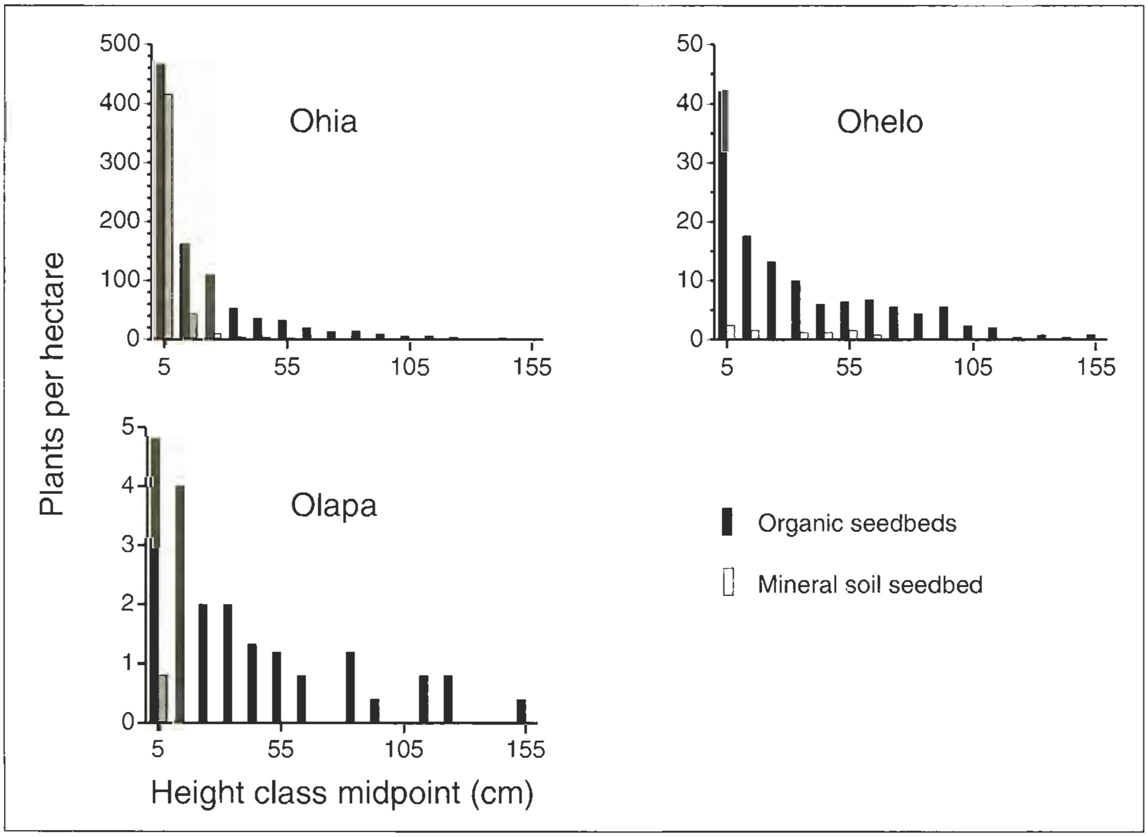

Figure 4—Average number of plants per hectare of exclosure growing in mineral soil and organic seedbeds in 1991, by height class and species. Each height class was 10 cm wide.

wet ohia-tree fern forest. A similar preference was found for other species as well as ohia in an intact mesic ohia-koa forest on Mauna Loa, island of Hawaii (Cooray 1974). There the ratio of log-established trees to soil-established trees was significantly greater ($p \leq 0.01$) than expected on the basis of the ratio of log seedbed area to soil seedbed area, a finding similar to that shown in *fig. 1*.

Two explanations have been offered to account for the preference of some species for organic seedbeds. The explanation heard most often is that logs and other organic seedbeds are elevated out of reach of rooting feral pigs. Such elevated beds thus serve as safe sites for seedling recruitment. There is little doubt that disturbance by pigs is extensive in montane rain forests (Mueller-Dombois and others 1981), and that pig rooting interferes with natural regeneration in general (Diong 1983; Higashino and Stone 1982; Katahira 1980). But studies to date have used unreplicated exclosures, and they have not been designed to test the hypothesis that the preference for organic seedbeds is an artifact of pig rooting in mineral soil seedbeds.

The second explanation is that the temperature and water holding capacity of decaying logs (especially moss-covered ones) and other organic seedbeds are higher than those on mineral soil. These factors are thought to favor seedling establishment on the organic seedbeds (Burton and Mueller-Dombois 1984). Burton (1982) found that as temperature decreased below 20°C, germination of ohia seeds declined sharply. Under low light levels, which are common in closed canopy rain forests, germination ceased at about 12°C.

In the present study, pigs were not a factor. So the first explanation does not apply. The second explanation, however, bears closer examination. Air temperatures in the vicinity of the exclosure are generally below 15°C. At 10 cm depth beneath dense grass, soil temperatures average 17°C. I do not have data for the temperature of the soil surface under a dense stand of grasses, but I suspect it is close to the air temperature. At these temperatures germination could well be inhibited. The surfaces of logs are generally elevated above the grass, and exposed to higher solar radiation than the soil surface. Their surface temperature could be higher than at ground level.

I have no data comparing moisture holding capacity and moisture depletion curves of soil and organic seedbeds. I assume, however, that while the dense stands of grass inhibit evaporation from soil surfaces, they promote soil drying by transpiration. On the other hand, although decaying logs may not undergo large losses of water through transpiration, they are exposed to evaporative losses. The question of water relations of organic versus grass-covered mineral soil needs to be explored.

Light levels at the soil surface under grass are probably very low, perhaps even lower than under a closed canopy native forest. Such low light levels may not inhibit germination, but they could reduce growth and survival. My data showed that ohia less than 10 cm in height were just as abundant in mineral soil as in organic material. But relatively few seedlings on mineral soil grew into the larger height classes. Low light could be a factor, especially if coupled with low temperature and low moisture availability.

Management Implications

Before considering the management implications of these findings, I need to sound a note of caution. This study is unreplicated. No data exist that will allow me to assess variability of natural regeneration over the range of woodland sites present in the Hakalau Forest National Wildlife Refuge, much less extrapolate to other abandoned pasture lands located elsewhere on the island of Hawaii or in the State. This study did not address the issue of regeneration dynamics as a function of proximity of seed sources, means of seed dispersal, or any other factor associated with seed rain and seed storage. Thus, the following comments are subjective and speculative.

What are the implications of these findings for managers faced with the difficult task of restoring native forest to abandoned pasture lands? First, managers should realize that recolonization of sites devoid of organic seedbeds probably will be slow for some species, even assuming that seed rain is not limiting. Extensive areas of open pasture land on Mauna Kea lack organic seedbeds because of natural decay, fire, harvesting, etc. If a manager wants or needs to rely on natural regeneration in such areas, then organic seedbeds will have to be created. Fast-decaying or partially decayed organic matter (logs, hapuu trunks, bagasse, etc.) could be brought on site but would be costly. Furthermore, the probability of success is unknown. No studies have been done to determine if artificially created organic seedbeds would stimulate natural regeneration of the desired species.

Second, given the anticipated high cost of creating organic seedbeds and the uncertainty of success, managers may decide to rely on artificial regeneration to restock sites with species such as olapa. Such a decision has its own set of unknowns. Will the species establish at all in mineral soil, or does it still require organic matter in which to root? How well does it compete with pasture grasses? Does it require shade? What are the costs of getting plants established in the field? These and other questions need to be answered before artificial regeneration can be adopted for widespread use.

Third, these findings should remind managers that logs and other coarse woody debris are not undesirable waste or trash to be disposed of quickly and efficiently. Not only are they important as sites for natural plant regeneration, but they also perform other ecosystem level roles—nutrient reservoirs, energy sources for microorganisms, water reservoirs, homes for forest invertebrates, and soil-stabilizing structures. Thus, whether managers are trying to rehabilitate degraded forest land or to manage intact forests, coarse organic material needs to be recognized as an important component of ecosystem structure and function.

Acknowledgments

I thank Janis Haraguchi, Donovan Goo, Alan Urakami, and Shane Eversfield for their diligence in collecting the field data; Michael Buck, Niels DeHoop, and James Baldwin for critical review of an earlier draft of this manuscript.

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