PLANT INVASION INTO AN 'ŌHI'A-TREE FERN RAIN FOREST FOLLOWING EXPERIMENTAL CANOPY OPENING

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INTRODUCTION

An investigation was initiated in March 1979 to determine the light requirements of 'ōhi'a (Metrosideros polymorpha Gaud.) seedlings and to monitor their invasion and growth following different degrees of canopy removal (Burton 1980). This experiment was carried out with the cooperation of the National Park Service in 'Ōla'a Forest Tract on the island of Hawai'i. This is an area of deep ash and cinder soils, with high rainfall (about 2880 mm/year), high humidity, and prevalent dense cloud cover. The area is well suited to a canopy thinning experiment because canopy density can be easily manipulated by removal of hāpu'u or tree fern (Cibotium spp., especially C. glaucum (Sm.) Hk. & Arn.) fronds, without destroying trees or permanently damaging the canopy.

Concurrent with the measurement of tagged 'ōhi'a seedlings in these experimental plots every two months, percentage cover estimates were made of plants invading the plots subsequent to canopy disturbance. The persistent encroachment of exotic plant species into native Hawaiian forests, causing the displacement of indigenous plant and animal species, needs to be documented and its causes understood before suitable methods can be developed to ward off this threat. In particular, the species composition, the rate of spread, and extent of spread of adventive plants invading a disturbed 'ōhi'a-tree fern forest need to be known before intelligent recommendations can be made with regard to the impact and advisability of hāpu'u harvesting in the native forest (Environmental Communications, Inc. 1978). It is suspected that canopy opening, substrate disturbance, and propagule transport by man and animals are the major factors responsible for the spread of exotics into the rain forest. This investigation documents the effects of canopy opening and thinning.

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METHODS

Twenty 10 m by 10 m contiguous plots were marked out approximately 1 km NE of the first bend in Wright Road, in a tree fern-dominated forest with scattered emergent 'ōhi'a trees. Between 7 April and 12 July 1979, different proportions of the tree fern fronds were cut off and removed from the plots in order to create different light intensities on the forest floor. Treatments, each replicated in four plots, were of 25%, 50%, 75%, and 100% frond removal, plus controls with no canopy disturbance. The desired fraction of cover to be removed was approximated by cutting off that proportion of tree fern fronds, i.e., every fourth frond was removed to open the canopy by 25%, every second frond was removed to open the canopy by 50%, and so on. The desired openness was maintained by periodic removal of the appropriate proportion of fiddleheads which appeared after the first clearing was completed. The location of the experimental site and the layout of canopy removal plots are illustrated in Burton (1980).

The natural forest undergrowth varied from a sparse to moderate covering of ferns, especially *Asplenium* spp., *Athyrium* spp., and *Dryopteris* spp., with scattered occurrences of *Peperomia* spp. and the sedge *Uncinia uncinata* L. f. Kuek. No herbaceous or undergrowth species were disturbed.

A 200 m^2 area consisting of one of the 100% removal plots and one of the control plots was fenced off by National Park Service personnel. This was completed on 1 August 1979. The purpose of this exclosure was to determine the effect of feral pigs (*Sus scrofa* L.) on the establishment of 'ōhi'a seedlings and the establishment and spread of exotic weeds.

Estimates were made every two months of the percentage cover of invading plant species in the herbaceous layer. Cover here refers to the area encompassed by the vertical projection of plant shoots (Mueller-Dombois & Ellenberg 1974). Cover estimates were facilitated by the particular plot size used, such that a 1 m^2 area denoted 1% cover. Newly appearing 'ōhi'a germinants were also counted.

The effect of canopy thinning on the microclimate near the forest floor was documented. Simultaneous measurements of temperature and relative humidity were made in treatment and control plots using two hygrothermographs. In addition, air temperature and soil temperature were measured at noon for a number of days using mercury and thermistor thermometers, respectively; relative humidity was measured using a sling psychrometer. Daily water loss from Piche evaporimeters was also monitored under the different canopy removal treatments. These environmental parameters are representative only of summer conditions, having been determined between 2 July and 3 September 1979. Four replicate sets of light measurements were made at the sites of all 'ōhi'a seedlings throughout the 20 plots at different times of the year, using a LI-COR quantum flux meter. These readings (approx. 50/plot) were expressed as percentages of the light available above the canopy, which was measured at the same time.

Regression analysis of the environmental factors versus weed cover and 'ōhi'a germinant responses was carried out using the curve-fitting "CURVE.P600" program on the HP-2000 computer at the University of Hawaii at Manoa.

The nomenclature and presumed origin of plant species recorded follows St. John (1973).

EXPERIMENTAL RESULTS AND DISCUSSION

The removal of tree fern fronds increased the irradiance near the forest floor from about 10% full light to about 43% full light in the open plots (Table 1). Light levels in the 100% removal plots were still not as high as in the open or above the canopy, due to the shade cast by the surrounding vegetation.

Air and soil temperatures and relative humidity were also altered by canopy removal (Table 1). The relative humidity tended to be 12% lower in the open plots. Mean temperatures rose by at least 2.5°C, and temperature extremes in both air and soil exhibited a wider range once the canopy was no longer there to moderate insolation during the day and reradiation during the night.

The more direct insolation and its resulting higher temperatures during the day caused greater evaporation in the plots subject to canopy removal. Moisture stress was evident at various times throughout the year. Many of the moss and liverwort mats covering fallen logs dried up and died within a few months of the disturbances. Much of the existing herbaceous cover, such as Asplenium spp., Athyrium spp., Peperomia spp., and Uncinia uncinata, became chlorotic and exhibited poor growth in the plots subject to the more extreme canopy opening; however, very few died. Changes in herbaceous cover were due almost exclusively to the invasion of weeds and other colonizing species, and to the expansion of any pre-existing colonies of such species.

The extent of colonizing plant invasion under the five cover removal treatments during the period of one year is illustrated in Figure 1. Only 100% canopy removal has resulted in weeds forming more than 7% of the ground cover, but such complete canopy opening has resulted in weed populations exploding to form 19% of the cover. The comparatively minor invasion of plant cover following 75% canopy removal indicates that any level of shade inhibits weed establishment to an important degree.

The extent of weedy plant invasion seems to be a function of the irradiance of potential habitats on the forest floor. Weed cover after one year plotted against the average relative light intensity found in the plots is shown in Figure 2A. Weed cover shows a near-exponential increase with increasing light, characteristic of any growth process in response to the removal of a limiting factor.

Light intensity is correlated with the other environmental factors which denote increased incoming solar radiation. Weed invasion may be responding to any or all of these factors (air temperature, soil temperature, relative humidity, evaporation rate, and the diurnal ranges in all of these parameters), as indicated by the very high correlation coefficients obtained between weed cover and all of these variables (Table 2). Some of these relationships are illustrated in Figure 2.

After one year, some of the plots subject to 100% removal achieved only 15% colonizing plant cover instead of the 23% cover found in others. This appears to be attributable to the season during which the canopy was disturbed. Those plots cleared in mid-summer are less overrun with weeds than those plots cleared in April (Fig. 3); this difference is significant only for the 100% removal plots. Moister soils and more humid conditions prevailing in the spring may facilitate greater germination and establishment of plants from the soil's seed bank, when the required conditions of temperature and light are also met. If such is the case, we may yet expect to see a profusion of weeds in the July-cleared plots following the next rainy season. This indeed seems to be true, as indicated by the upturning curve representing plots cleared in summer, shown in Figure 3.

Thirty invading species were encountered in the experimental plots (Appendix A) of which only four--'ena'ena (<u>Gnaphalium sandwicensium</u> Gaud.); 'ōhi'a; Hawaiian pokeweed (<u>Phytolacca sandwicensis</u> Endl.); and mamaki (<u>Pipturus albidus</u> (H. & A.) Gray in Mann)--are native. Most of the species are represented by only scattered individuals, often with insignificant cover. The buildup of the 12 most prevalent species is shown in Figures 4a and 4b. Most species, such as hino hana (<u>Erechtites valerianaefolia</u> (Wolf) DC.), mamaki, and yellow raspberry (<u>Rubus ellipticus</u> Sm.), show a steady increase over the course of a year. Others such as Hilo pamakani (<u>Eupatorium riparium</u> Regel) and black nightshade (<u>Solanum nigrum</u> L.) show marked drops in cover after reaching a peak. This may represent their decline and replacement by other species in a successional sequence, or it may merely signify a seasonal or phenological change in foliage area and prominence.

Even the control plots, with no canopy removal, exhibited a small but consistent increase in weed cover (Fig. 1). This is probably an artifact of the experimental design, resulting from weed buildup in areas adjacent to the disturbed plots. On the other hand, such invasions into the control plots may be due to the activities of the investigator, or they may represent the ongoing dynamics of weed dispersal in the undisturbed rain forest. Dispersal agents such as wind and birds were beyond the control and scope of this investigation.

Feral pigs are another important factor in the dispersal of weedy species into the rain forest. Their rooting behavior destroys undergrowth and makes the soil more suitable for weed establishment. The seeds of plants such as <u>Uncinia</u> are carried on their coarse hair, and seedlings of banana poka (<u>Passiflora</u>

mollissima (HBK.) Bailey) and pohā (Physalis peruviana L.) are commonly found germinating from their feces. However, analysis of changes in weed cover over 12 months has shown no significant difference between plots with and without pigs. Pig activity tends to be concentrated in low-lying areas, and did not appear to be highly evident in the immediate vicinity of the pig exclosure referred to in this study.

Another consideration when examining cover buildup is the size of original weed populations before the canopy was disturbed. Although no visible trend was found when plotting the maximum weed cover observed in a plot against the original weed cover, it is nevertheless likely that the existing cover of pioneer or weedy species will increase following canopy opening, and at a faster rate, if individuals are already established and can reproduce vegetatively (e.g., as do drymaria [Drymaria cordata (L.) Willd. ex R. & S.] and many grasses).

Finally, in addition to the invasion of adventive species, most of which are exotics, let us consider the response of some indigenous forest species. Mamaki has become prevalent as rapidly growing seedlings which occupy considerable area in disturbed plots (Fig. 4b). The number of newly germinated 'ōhi'a seedlings also seems to increase with increasing light and the associated factors of increasing temperature and evaporation and decreasing humidity (Table 2; Fig. 5). These seedlings still form only negligible cover after one year.

DISCUSSION OF LONG-TERM TRENDS

The above results document the changes in plant cover over the period of one year where the canopy was maintained in an opened or thinned condition. Of greater importance are the changes occurring following one initial disturbance of the canopy after which the tree fern fronds are allowed to regrow, and the long-term effects of such a disturbance on the prevalence of exotic plants.

Some information is now available on these long-term trends of direct importance to forest management practices. The Hawaii State Division of Forestry (1980) has recently completed an eight-year study which monitored the recovery of vegetation following the harvesting of hāpu'u logs in the Kīlauea Forest Reserve. The vegetation in this area was originally quite similar to that found in the 'Ōla'a Tract, and this area is only 4.1 km west-northwest of the canopy removal experiment site. The vegetational composition was systematically sampled along several transects in areas subject to uncontrolled, controlled, and no logging. Uncontrolled logging resulted in patchy openings with 60% to 100% of the canopy removed and is thus comparable to the 75% and 100% canopy removal plots in this investigation. Controlled logging reportedly removed no upright tree ferns, and opened the canopy by 40% (Environmental Communications, Inc. 1978).

Preliminary data indicate results quite similar to those reported here. Exotic plants were encountered in an average of 1.8% of the frequency frames placed in undisturbed forest. (The results of this study are in terms of the frequency of plant occurrences in several hundred 2 ft by 2 ft [0.61 m by 0.61 m] subplots, but are nevertheless directly comparable to estimates of % plant cover). One year after controlled logging, exotic plants were found 5% of the time. This is similar to the 6.9% value obtained in the 75% canopy removal plots after one year. After five years, this 5% frequency has risen to an average occurrence of 11%, as compared to 43% under uncontrolled logging. This extremely high value of 43% frequency is consistent with expectations based on the experimental results obtained in this study one year after complete canopy opening. Three years later, however, this 43% value has dropped to 27%, and the controlled logging area has likewise dropped from 11% to 9% exotic plant frequency. The statistical significance of these values has not yet been calculated, but a reversal of the colonizing trend by exotics is quite evident.

In interpreting these long-term results, we must recall that the tree fern canopy has gradually recovered and reclosed following the disturbance of harvesting. The Cibotium tree ferns are remarkably adept at maintaining their presence. For example, following the collapse of a large 'ōhi'a snag, a large gap in the tree fern canopy is formed; but the tree fern trunks produce three to six new fronds per year, even when uprooted or broken off. Thus the canopy is frequently restored in one or two years. On the other hand, canopy restoration may take more than five years when numerous tree fern trunks are harvested, and it is during this resultingly more prolonged period of higher light intensities on the forest floor that weedy species become established. So long as a significant proportion of the canopyforming tree ferns remains, the dense shade will probably be restored eventually. Many of the exotic plants then die, most being shade-intolerant ruderal species. That the number of exotic plants will return to predisturbance levels is highly unlikely, and further monitoring is needed to determine at what densities such populations will level off. Interference with the native forest community could be quite severe if the remaining exotics are relatively shade-tolerant, such as firetree (Myrica faya Ait.) and strawberry guava (Psidium cattleianum Sabine), or ramblers and vines such as yellow raspberry and banana poka, which can quite literally suppress the indigenous shrubs and trees.

Exotic plant control or elimination in this forest type cannot be approached with the strategy of controlling propagule dispersal. This study indicates that weed seeds are quite ubiquitous in the area and require only an opening of the canopy to get established. Such invasion occurs in canopy gaps created by the collapse of old trees, by human disturbance, and by destructive winds such as those which occurred in January 1980. Since sunlight is the environmental factor limiting the widespread establishment of exotic plants in the 'ōhi'a-tree fern forest, any activities which disrupt the canopy should be curtailed.

Canopy disturbances made in mid-summer seem to be less deleterious than those made in the early spring, but the significance of this observation and the effect of clearings made in other seasons is not known.

The harvesting of hāpu'u remains a controversial issue. The removal of tree ferns is clearly a canopy-disturbing and shade-removing process. It must be realized that any logging of tree ferns will, therefore, be followed by some invasion of weedy species. The extent of weed invasion can be significantly reduced if enough mature tree ferns are left untouched so as to still form an unbroken canopy. Following recovery of the tree ferns and the return of deeper shade, some of the exotics will be lost. It is still not known how long it takes the forest to return to its pre-disturbance composition, if such a state can be returned to at all.

CONCLUSIONS

Colonizing plant cover in plots subject to complete canopy removal in an 'ōhi'a-tree fern rain forest averaged 19% after 12 months, as compared to 0.4% in the undisturbed plots. As long as one-quarter of the canopy was maintained, weed cover was kept at less than 7%. Asiatic butterfly bush (*Buddleja asiatica* Lour.); hino hana; vaseygrass (*Paspalum urvillei* Steud.); banana poka; yellow raspberry; black nightshade; and oriental hawksbeard (*Youngia japonica* (L.) DC.) were the dominant exotic invaders.

Increased insolation (with associated high light intensities, higher air and soil temperatures, a greater range in temperatures, and higher evaporation rates) resulting from canopy removal is the main factor controlling the invasion of weedy species.

Another study indicates that exotics may continue to invade for five years following canopy disturbance, but their levels have declined eight years after the disturbance, probably due to restoration of a deep shade-producing canopy. It is not known if the density of exotic species will eventually be reduced to pre-disturbance levels.

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TABLE 1. Plant invasion into an 'Ōhi'a-tree fern rain forest following experimental canopy removal: Environmental variables and colonizing plant cover under different degrees of canopy removal (where values in parentheses indicate samples with less than 10 observations).

Variable	% Canopy Removal 0	25	50	75	100
Light Intensity, % Full	10	17	15	27	43
Noon Air Temperature, °C	18.0	(19.2)	(19.1)	(19.6)	20.5
Diurnal Range in Air Temperature, °C	5.6	(6.8)	(6.1)	-	11.6
Noon Soil Temperature, °C	16.5	(16.8)	(16.6)	(17.5)	19.2
Noon Relative Humidity, %	87	(79)	(86)	(83)	75
Diurnal Range in Relative Humidity, %	13	(28)	(20)	-	37
Evaporation, mg/cm^2/Day	.013	(.057)	(.039)	(.049)	.093
Colonizing Plant Cover After 12 Months, %	0.4	2.5	2.1	6.9	19.0
Number of Exotic Plant Species	4	8	7	9	12
'Ōhi'a Germinants/100 m^2/Year	86	211	169	253	272
Colonizing Plant Cover After 12 Months, in Plots Cleared in April, %	0.2	2.5	1.6	4.4	23.0
Colonizing Plant Cover After 12 Months, in Plots Cleared in July, %	0.8	2.4	2.7	9.4	15.0

TABLE 2. Regressions of colonizing plant cover after 12 months and the occurrence of 'ōhi'a germinants on various environmental factors.

	Factor X	Factor Y	Regression Equation	R^2
A.	Light Intensity	Colonizing Plant Cover	$Y = -7.577 + 0.637X$	0.973
	Air Temperature	"	$Y = -109.279 + 6.025X$	0.601
	Range In Air Temperature	"	$Y = -17.644 + 3.142X$	0.990
	Soil Temperature	"	$Y = -110.329 + 6.726X$	0.995
	Relative Humidity	"	$Y = -94.01 + (8190.53/X)$	0.686
	Range in Relative Humidity	"	$Y = 0.068e^{0.147X}$	0.925
	Evaporation Rate	"	$Y = 1063.62X^{1.844}$	0.871
B.	Light Intensity	'Ōhi'a Germinants	$Y = 351.837 - (2688.36/X)$	0.951
	Air Temperature	"	$Y = 1706.69 - (29032.2/X)$	0.920
	Range in Air Temperature	"	$Y = 437.616 - (1758.45/X)$	0.834
	Soil Temperature	"	$Y = 1153.25 - (16489.3/X)$	0.615
	Relative Humidity	"	$Y = 1164.16 - 11.78X$	0.629
	Range in Relative Humidity	"	$Y = -355.008 + 172.589 \log X$	0.991
	Evaporation Rate	"	$Y = 1272.89X^{0.61}$	0.975

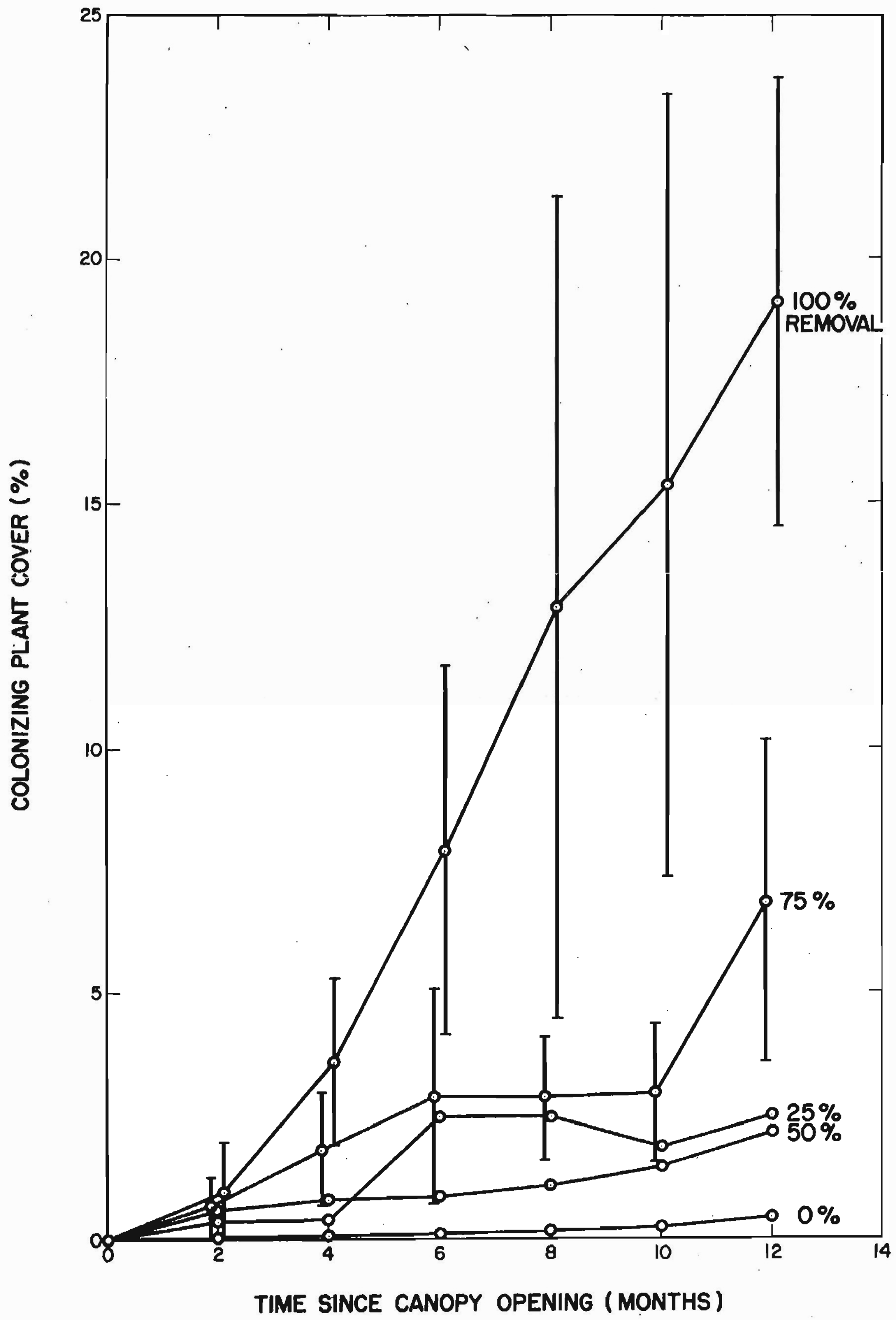

FIGURE 1. Plant invasion during the period of one year following different degrees of canopy removal. Each point represents the average of four plots (± 1 s.d. is indicated for 100% and 75% removal points).

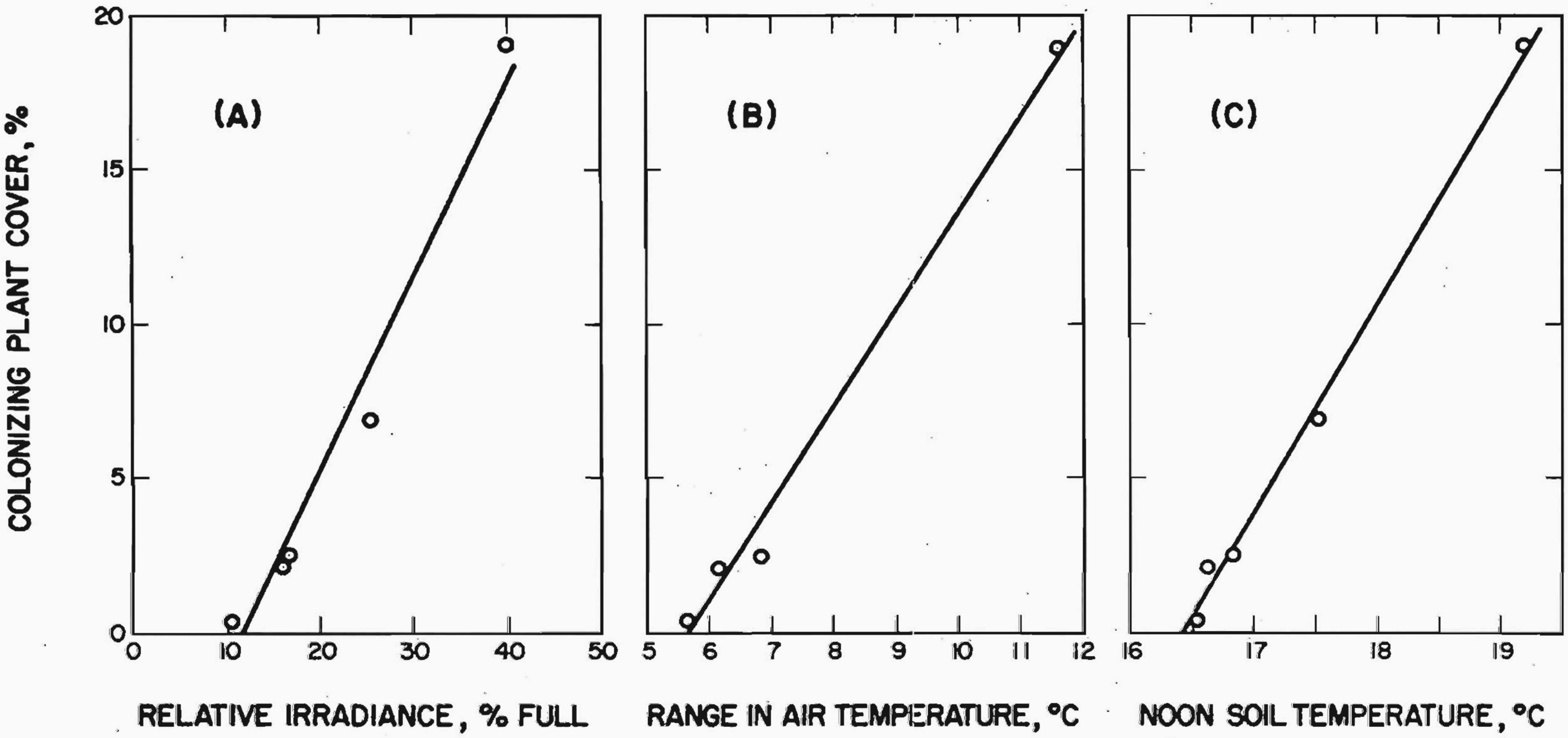

FIGURE 2. The response of colonizing plant cover to some environmental factors: (A) light intensity; (B) diurnal range in air temperature; (C) soil temperature. Fitted lines are described by the equations given in Table 2A.

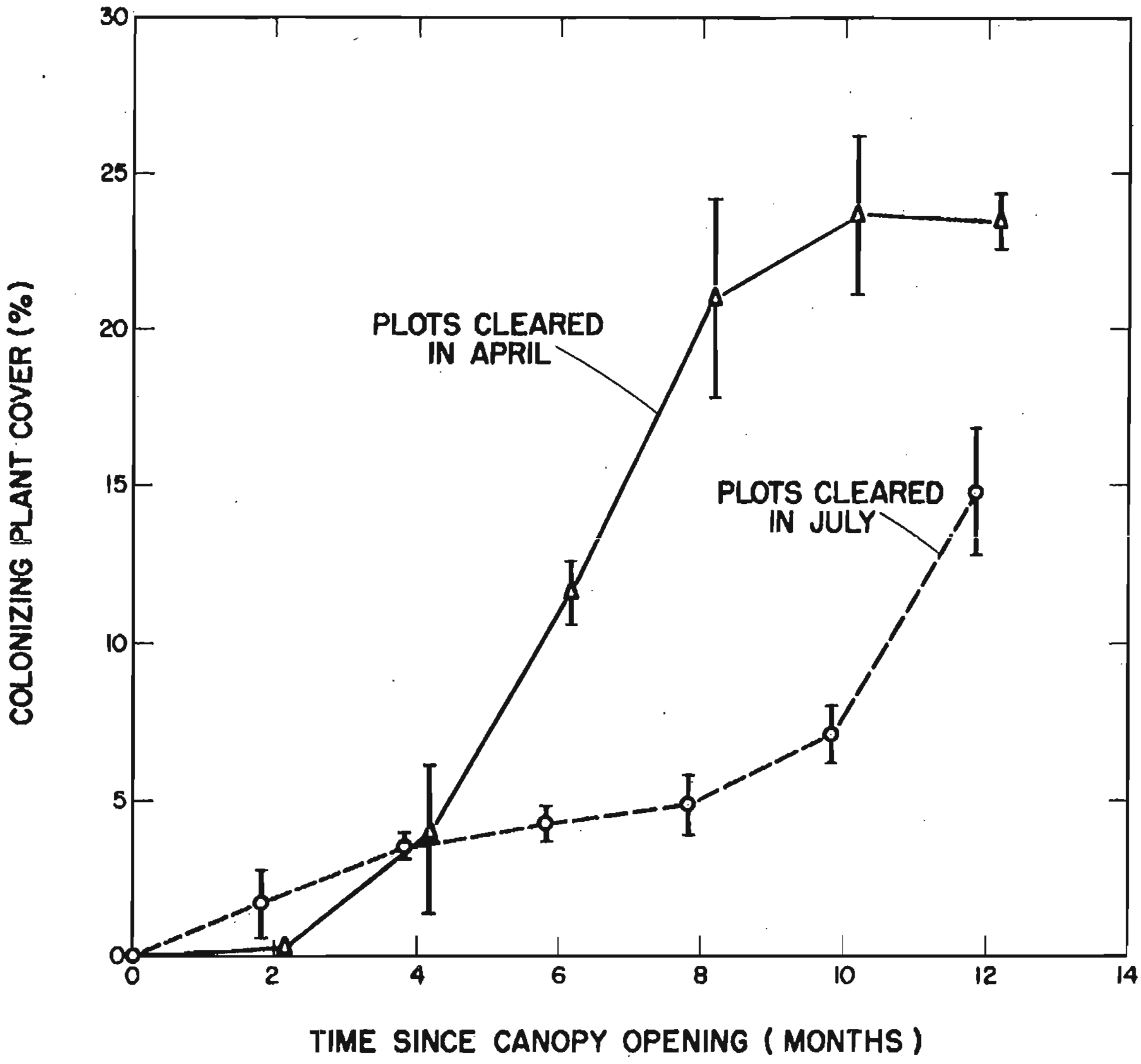

FIGURE 3. Plant invasion in 100% canopy removal plots, showing the effect of the season of disturbance.

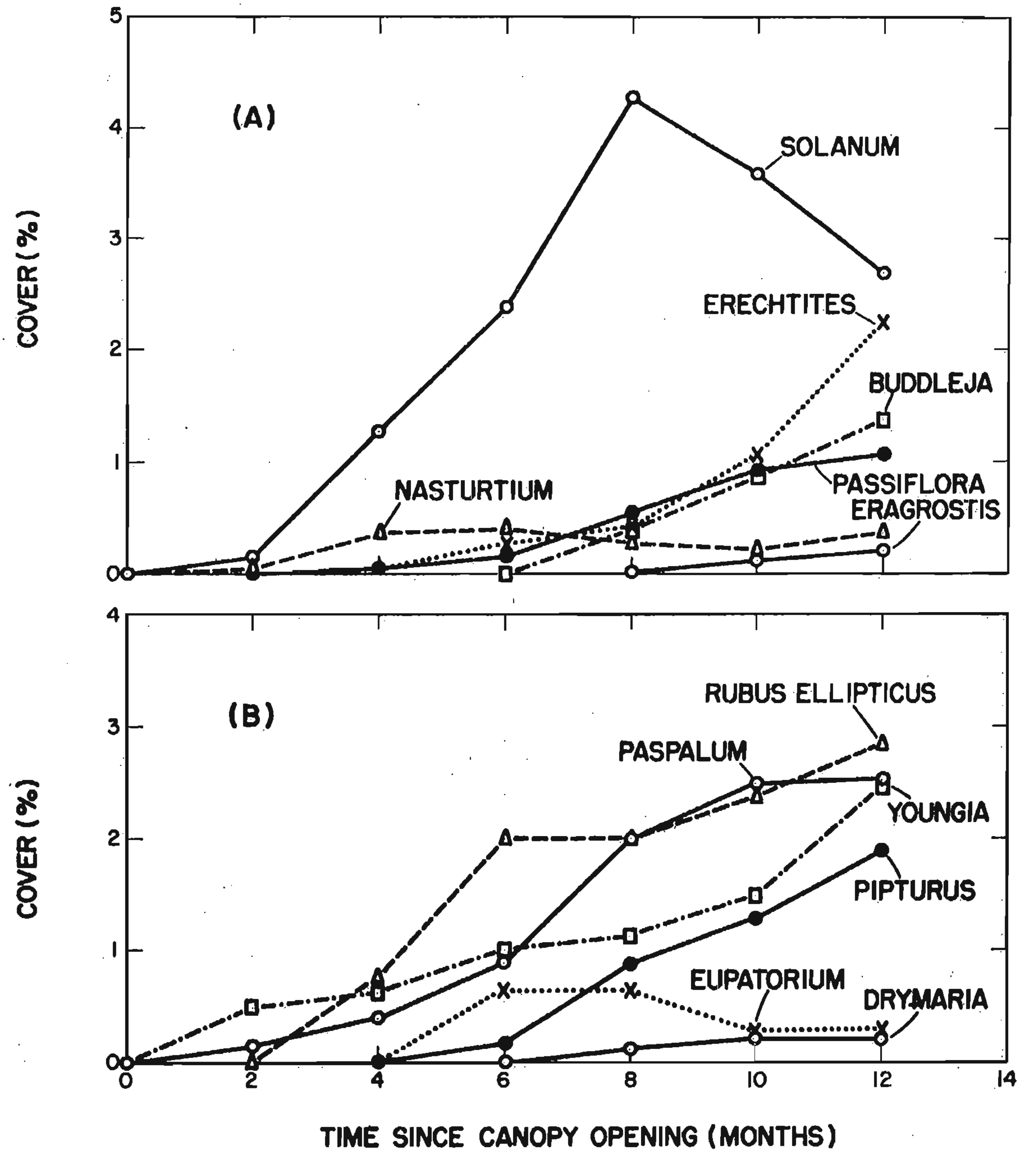

FIGURE 4. Plant invasion in 100% canopy removal plots, by species.

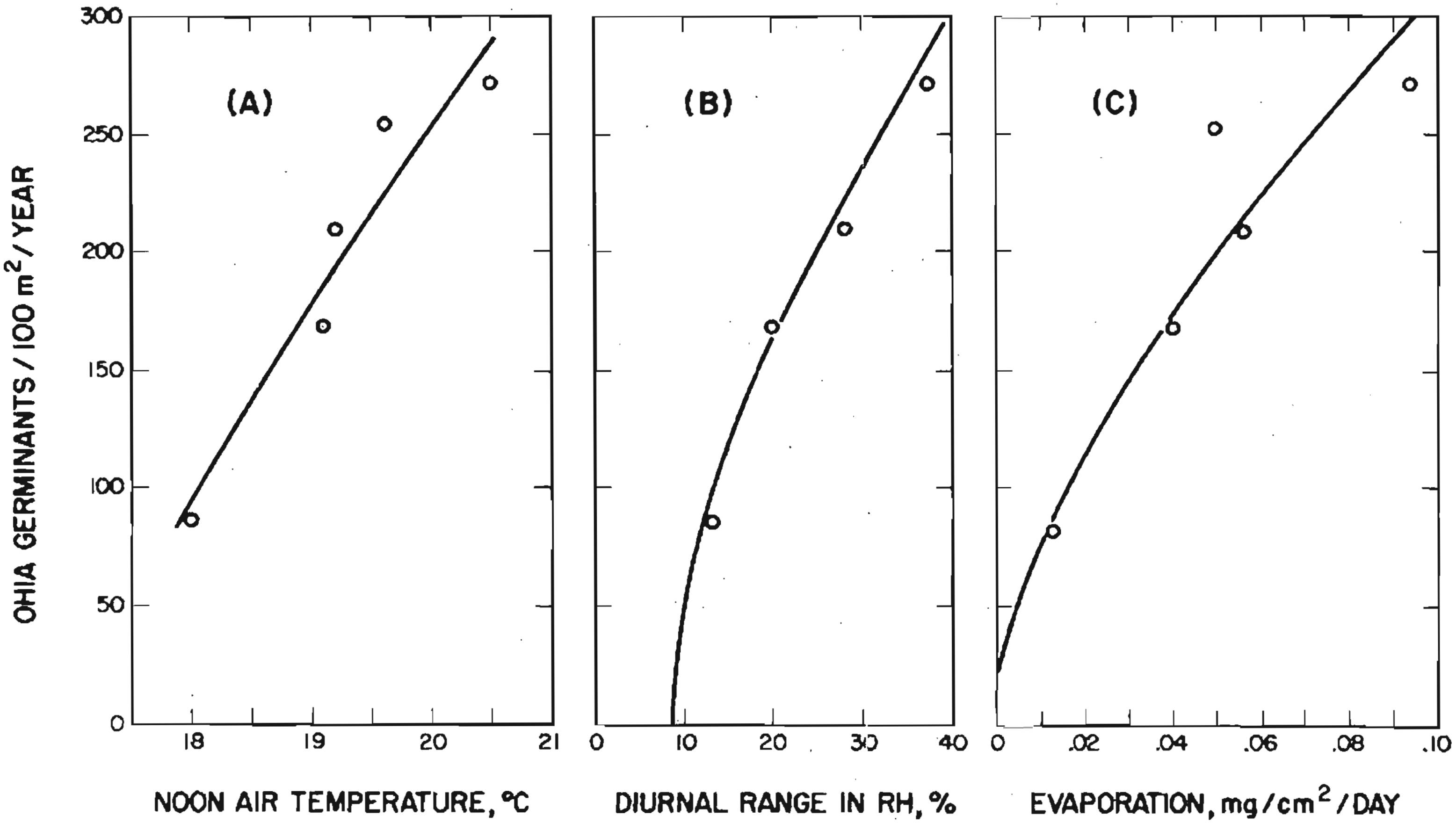

FIGURE 5. The occurrence of 'ōhi'a (Metrosideros polymorpha) germinants in response to some environmental factors: (A) air temperature; (B) diurnal range in relative humidity; (C) rate of evaporation. Fitted lines are described by the equations given in Table 2B.

Appendix A. A checklist of plant species found invading openings in the 'ōh'a-tree fern montane rain forest, 'Ōla'a Tract, Hawai'i.

FAMILY Genus/species	Common/Hawaiian Name	Origin
GRAMINEAE		
Andropogon virginicus L.	Broomsedge	E. U.S.A.
Eragrostis cilianensis (All.) Vignolo-Lutati	Stinkgrass	Europe
Paspalum urvillei Steud.	Vaseygrass	S. America
CYPERACEAE		
Cyperus gracilis R. Br.	McCoy grass	Australia
JUNCACEAE		
Juncus tenuis Willd.		Europe, N. Africa, N. America
URTICACEAE		
Pipturus albidus (H. & A.) Gray in Mann	Mamaki	Hawaiian endemic
POLYGONACEAE		
Polygonum glabrum Willd.	Knotweed, kāmole	India

PHYTOLACCACEAE		
Phytolacca sandwicensis Endl.	Hawaiian pokeweed, pōpolo-ku-mai	Hawaiian endemic
CARYOPHYLLACEAE		
Drymaria cordata (L.) Willd. ex R. & S.	Drymaria, pipili	Tropics
RANUNCULACEAE		
Anemone hupehensis (Lem. & Lem. f.) Lem. & Lem. f.	Hupeh anemone	China
CRUCIFERAE		
Nasturtium sarmentosum (DC.) Schinz & Guillaumin	'Ihi-ku-kēpau, pa'ihi	Polynesian introduction
ROSACEAE		
Rubus ellipticus Sm.	Yellow raspberry	Himalaya
R. penetrans Bailey	Prickly Florida blackberry	(Cultivated, adventive)
R. rosaefolius Sm.	Thimbleberry, 'ākala, 'ākalakala, ola'a	Tropical Asia

Appendix A.--Continued.

FAMILY Genus/species	Common/Hawaiian Name	Origin
GUTTIFERAE		
Hypericum mutilum L.	St. Johnswort	N. America
PASSIFLORACEAE		
Passiflora mollissima (HBK.) Bailey	Banana poka	Trop. or Subtrop. America
LYTHRACEAE		
Cuphea carthagenensis (Jacq.) McBride	Colombian cuphea, puakamole	Trop. America
MYRTACEAE		
Metrosideros polymorpha Gaud.	'Ōhi'a-lehua	Hawaiian endemic
ONAGRACEAE		
Epilobium cinereum A. Rich.	Willow herb, pūkāmole	New Zealand to Java
Ludwigia octivalvis (Jacq.) Raven	Primrose willow, kāmole	Africa, Asia

LOGANIACEAE		
Buddleja asiatica Lour.	Asiatic butterfly bush, huelo-'ilio	India, S.E. Asia
SOLANACEAE		
Physalis peruviana L.	Cape gooseberry, ground cherry, husk tomato, pa'ina, pohā	S. America
Solanum nigrum L.	Black nightshade	Cosmopolitan (possibly indigenous)
COMPOSITAE		
Ageratum conyzoides L.	Ageratum, maile-honohono	Trop. America
Erechtites valerianaefolia (Wolf) DC.	Fireweed, hino hana	Trop. America
Erigeron bonariensis L.	Hairy horseweed, ilioha	Tropics
Eupatorium riparium Regel	Hilo pamakani, spreading mist flower	Mexico
Gnaphalium sandwicensium Gaud.	Hawaiian cudweed, 'ena'ena	Hawaiian endemic
Pluchea odorata (L.) Cass.	Pluchea, shrubby fleabane, sour bush	Trop. America
Youngia japonica (L.) DC.	Oriental hawksbeard	E. Asia