

"RESPONSE OF PASSIFLORA MOLLISSIMA (HBK.) BAILEY TO EXPERIMENTAL CANOPY REMOVAL:  
A SIMULATION OF NATURAL GAP FORMATION IN A CLOSED-CANOPY CIBOTIUM SPP. FOREST  
IN OLA'A TRACT, HAWAI'I"

Anne Marie LaRosa  
Department of Botany

University of Hawaii at Manoa

Honolulu, Hawaii 96822

Abstract

In 1980, an opportunity arose to study the effects of experimental canopy removal on the success of the exotic vine Passiflora mollissima in a closed-canopy treefern (Cibotium spp.) forest in Hawai'i. Results generally supported the hypothesis that P. mollissima increases in cover, density and biomass following canopy disturbance and that this increase is proportional to levels of canopy disturbance and associated light intensities within study plots. Colonization of plots was rapid and fairly synchronous. Under conditions of 100% frond removal, individuals of P. mollissima reached reproductive maturity and a position in the canopy within one year.

Passiflora mollissima, or banana poka, is a species of wide ecological amplitude functioning as a "gap-phase opportunist" in the closed-canopy Cibotium forests of Hawai'i. In the absence of disturbance, limited populations are maintained as shade tolerant seedlings yet individuals are able to rapidly exploit the higher light intensities associated with canopy disturbance. From this information, it is concluded that, although closed-canopy forests in Hawai'i are not optimal habitats for P. mollissima, they are nevertheless susceptible to invasion and infestation by P. mollissima following a disturbance to the canopy.

## INTRODUCTION

Heliophytic vines commonly exhibit rapid growth following canopy disturbance resulting in a dense tangle of vegetation which smothers undergrowth (Jackson 1956; Foggie 1960; Nicholson 1965; Ogawa et. al. 1965; Fox 1968; Meijer 1970). This problem is most prominent in tropical regions where vines are a significant component of many vegetation types (Richards 1952; Ogawa et. al. 1965). Several studies of native forest communities in Hawai'i have indicated that spread and dominance of Passiflora mollissima (H.B.K.) Bailey, an exotic vine, is aided by factors which tend to disturb the overstory and understory vegetation (Jacobi & Warshauer 1975; Scowcroft & Nelson 1976; Mueller-Dombois et. al. 1977; Burton 1980a).

Passiflora mollissima, locally known as banana poka, is a perennial climber from 2,000 to 3,200m in the Andes Mountains. Introduced to Hawai'i in the early twentieth century, it has spread rapidly and occupies approximately 500 km<sup>2</sup> on Hawai'i and Kaua'i; an increase of more than 300 percent in ten years (Warshauer et. al. in press). A survey of probable dispersal agents indicates at least twenty-five species of birds and mammals known or capable of dispersing seeds or fruit of P. mollissima. Of these, two are native to Hawai'i: the Hawaiian crow, or 'Alala, Corvus tropicus and the Hawaiian thrush or 'Oma'o, Phaeornis obscuris (Warshauer et. al. in press).

Banana poka is a species of wide ecological amplitude, occurring in a variety of climate, soil and vegetation types. Although present in both open and closed forests, densest populations of P. mollissima are presently found only in open forests, often with a history of disturbance. The Ola'a Tract section of Hawai'i Volcanoes National Park contains large areas of closed canopy treefern (Cibotium spp.) forests with emergent 'ohia (Metrosideros polymorpha). Banana poka was planted in the Volcano area in 1958 (Wong 1971) and was soon common along Wright Road but spread slowly into the adjacent forest. In 1971, a survey of Passiflora mollissima in Hawai'i noted low cover and density of banana poka in the Volcano area (Wong 1971). Following the 1977 Hawai'i Forest Bird Survey, Jacobi and Warshauer called attention to the increase in cover of P. mollissima and its potential for spread within the Ola'a Tract (Jacobi & Warshauer 1975). By 1981 the situation had changed drastically. An aerial survey of the Ola'a Tract, in connection with an updated distribution map of P. mollissima, noted an 18-fold increase in cover since 1971 (Warshauer et. al. in press). A severe wind-storm in January 1980, resulting in heavy disturbance to the emergent and treefern canopies, is thought to be the single most important factor responsible for the increase in P. mollissima cover in the Ola'a Tract.

At the conclusion of a study on responses of exotic plant species and Metrosideros polymorpha to experimental canopy opening in Ola'a Tract (Burton 1980a,b), Hawai'i Volcanoes National Park requested eradication of all potentially dangerous exotics, including Passiflora mollissima, within the study area. This provided an opportunity to study the effects of canopy removal, which closely simulates natural gap formation, on the population dynamics of P. mollissima.

## METHODS

The methods of canopy removal are as follows, from Burton 1980a. "Twenty 10 by 10m contiguous plots were marked out approximately 1 km NE of the first bend in Wrightroad, in a treefern dominated forest with scattered emergent 'ohia trees. Between April 7 and July 12 1979, different proportions of the treefern 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 openness was maintained by periodic removal of the appropriate proportion of fiddleheads which appeared after the first clearing. A 200m<sup>2</sup> area consisting of one 100% removal plot and one control plot was fenced off to prevent the entry of feral pigs. No herbaceous or undergrowth species were deliberately disturbed.

Three criteria, percent cover, final standing biomass and density, were selected as quantifiable indices of the success of Passiflora mollissima subjected to various degrees of canopy removal for 12 to 14 months. Percent cover was estimated bimonthly by Burton, using the Braun-Blanquet cover-abundance scale. Final standing biomass and density were measured directly. In July of 1981, all individuals of P. mollissima within the study plots were tallied by plot, harvested, dried and weighed. Dry weights were partitioned into leaves, stems, tendrils and reproductive parts and in the case of seedlings and germinants, root were included. All plants were assigned to one of four arbitrary age classes, defined as follows:

- germinants- individuals without true leaves; only cotyledons present
- seedlings - small, non-climbing individuals with true leaves
- juveniles - non-reproductive, climbing individuals or those with well-developed tendrils
- adults - reproductively mature individuals.

For one year following harvesting, no fronds were removed and the canopy within the plots was allowed to recover. At the end of this year, plots were resurveyed for the presence of Passiflora mollissima. Density of each age class and each plot and the height and basal diameter of each plant was recorded.

A one-way analysis of variance was carried out on the data to determine if significant treatment effects existed. Data were also summed by treatment and subjected to a regression analysis using the curve-fitting (CURVE.P600) program on the HP 2000 computer at the University of Hawai'i, Manoa.

## RESULTS

Passiflora mollissima exhibited an increase in density, cover and biomass following artificial canopy disturbance from April 1979 to July 1980 in Ola'a Tract, Hawai'i. Density increased 1.6 to 3.5-fold while cover was 4 to 10 times greater in treated plots than controls. 223 individuals of P. mollissima were harvested from 20 plots, yielding a density of 1115 plants per hectare for all treatments combined. Total cover was estimated at 11.7% (= 11.7m<sup>2</sup>, Burton 1980a) constituting 6.75% of all exotic plant cover within the study area (Table 1). Treated plots with less canopy disturbance had a higher percentage of P. mollissima cover, suggesting a greater degree of shade tolerance when compared with other invading exotics, principally annuals and grasses. Increases in final standing

biomass ranged from 25 to 500 times greater in treated than control plots.

Artificial canopy removal resulted in the alteration of a complex of physical factors (Burton 1980a). Generally, light intensity, air and soil temperatures and the diurnal ranges in temperature and humidity increased while average relative humidity decreased, with increasing canopy removal. Higher solar radiation with accompanying lower relative humidity increased the evaporative power of the atmosphere seven-fold from control to 100% removal plots.

Relative light intensities, as measured by Burton (1980a), do not increase proportionately to predicted levels of canopy removal. This departure from the theoretical values was also noted for actual percent canopy removal (Burton 1980b). The difference between predicted values and actual values were a result of "edge-effects" from adjacent plots and variations within the canopy of vegetation remaining in the treated plots. The irregular distribution of light and shade within the plots more closely simulates natural forest gap formation, with its inherent variability, than the proposed controlled light regimes (Table 2).

An analysis of the final population structure and associated standing biomass within treatments reveals that under low light conditions found in control plots few germinants reached the seedling or juvenile stage and little biomass accumulated after 14 months (Table 3). With increased light intensities, more germinants became established and a growth phase occurred resulting in climbing juveniles and a significant increase in biomass. Increases, however, were not in proportion to greater relative light intensities. Total juvenile biomass of the 50% and 75% removal plots was comparable while in 25% and 100% removal plots, biomass approximately doubled. The reason for the greater final biomass in the 25% removal plots is unclear and in contrast with the cover estimates, but it is interesting to note that Burton (1980a) observed a higher proportion of Metrosideros polymorpha seedlings in these same 25% removal plots.

The rapid, exponential increase in total final standing biomass with 100% frond removal resulted from the presence of two large, climbing adults within the plots. It appears that a rate of assimilation sufficient to result in reproductive maturity within 14 months occurs only under conditions associated with 100% frond removal. The decrease in juvenile density and total lack of seedlings at the time of harvest in the 100% removal plots could be explained as a smaller initial seed bank or, more likely, a higher mortality rate in germinants under extreme environmental conditions associated with extensive canopy disturbance. This latter hypothesis is supported by the results of Jarvis (1964) and Wallace & Dunn (1980) which indicate that shade grown plants are susceptible to photo-bleaching when exposed to high levels of irradiance. Wallace & Dunn (1980) further conclude that only newly-expanding leaves are capable of adapting to extreme changes in light intensity, therefore seedling survival is dependent upon the rate of leaf production following disturbance. Germinants of Passiflora mollissima, with their preformed cotyledons, may be responding to this phenomenon, resulting in a high initial mortality rate in the 100% removal plots. Additionally, germinants and seedlings in these plots may have experienced a period of water stress as a result of increased evaporation rates shortly following the initial disturbance. Those germinants capable of surviving the above conditions established quickly and rapidly reached reproductive maturity, resulting in the large final standing biomass observed.

An analysis of variance provided inconclusive proof of significant treatment effects on cover, density and biomass, with one exception (Table 3). The small sample sizes and large variances within treatments account for the low F-values obtained. These variances were, in part, due to uncontrolled elements including the uneven size of the initial seed banks and the random influx of propagules during the study which could result in variation equal or greater than those due to treatment alone. For this reason, data was summed for each treatment and regression analysis applied to examine any significant trends in the data. Regressions of density, cover and biomass on relative light intensity and levels of canopy removal (theoretical) yielded significant correlations in all cases (Table 4), at least at the 90% confidence level and most often at the 99% level. All factors exhibited positive linear or near-exponential increases in response to greater canopy removal and associated relative light intensities (Figs. 1,2). The high  $r^2$  values obtained, in all cases, for relative light intensity implicates light as the most significant factor determining the success of Passiflora mollissima under conditions of experimental canopy removal.

Initial colonization of plots was rapid (Fig.3) and accompanied by a period of meager increases in cover. Six months following the initial canopy disturbance, 65% of all plots had been colonized by Passiflora mollissima but only 15% of these had measurable cover; after 14 months, 90% of the plots were colonized and 75% had measurable cover. The rapid and synchronous colonization of plots suggests that germination was due to the release of dormant or quiescent seeds present in the soil at the time of disturbance.

Figure 4 illustrates several distinct patterns of establishment and growth under various disturbance regimes. Increases in cover of Passiflora mollissima over 14 months were used as an index of relative growth; density figures were lacking for a comparable time period. Accepting seedling establishment as the point at which seedlings have "expanded a photosynthetic surface and are theoretically capable of pursuing an independent existence" (Harper 1977) and negligible total germinant-seedling biomass or cover when compared with that of juveniles and adults, negligible cover increases would be expected prior to seedling establishment. Following this period, significant increases in cover may be attributed principally to a growth phase rather than an increase in density.

Increases in cover were negligible in control plots over 14 months indicating little establishment of individuals. 50% and 75% removal plots exhibited an extended establishment phase while this period was condensed under conditions of 25% and 100% frond removal. Cover increases following establishment were nearly linear suggesting the presence of a limiting factor in control and 25% removal plots. 50%, 75% and 100% removal plots all showed exponential increases in cover characteristic of unlimited growth.

Cover in 75% and 100% removal plots exhibited a tendency towards equilibrium, however there is insufficient data to distinguish among a true equilibrium condition, a temporary reduction in growth due to adverse environmental conditions, such as a summer dry period, and competition effects. The initial decrease in cover within the 75% removal plots occurred in the single plot colonized prior to canopy disturbance and may have resulted from a high mortality rate immediately following clearing.

Little data is available on long term trends. When plots were surveyed, in 1981, after one year of canopy recovery, only 10 individuals of Passiflora mollissima

were collected from all study plots compared with 223 found during the year of canopy removal (Table 5). The low number of individuals found in 1981 indicates that a depletion of the seed bank occurred after the initial disturbance and further colonizations are dependent upon seed dispersal into the area. The presence of one four meter tall reproductive individual in a 100% removal plot in 1981 and the high proportion of juveniles (90%), suggests that some time is needed for mitigation of the effects of more extensive disturbances to the canopy. A similar conclusion was reached by Burton (1980a).

## DISCUSSION

From the data obtained in this study and field observations of Passiflora mollissima, it appears that successful regeneration of P. mollissima in the closed-canopy Cibotium spp. forests of Hawai'i is dependent upon the regular formation of gaps or upon regular disturbances to the canopy and that the size of these gaps determines the nature of the ensuing population.

Seed germination and establishment are favored by the higher temperatures and light intensities associated with canopy disturbance. Colonization is rapid and fairly synchronous. Elsewhere in the tropics, similar conditions of increased light and temperature were found to stimulate germination in other secondary tropical forest species (Meijer 1970; Quarterman 1970; Lebron 1979).

In the absence of gap formation, populations are maintained by low numbers of shade tolerant seedlings but several lines of evidence suggest that canopy disturbance must occur for populations to reproduce and regenerate. Within the Ola'a Tract, seedlings of Passiflora mollissima are fairly frequent in undisturbed areas but larger individuals are rare in these same areas. Examination of the growth rates of shaded seedlings (LaRosa, unpublished data), average final standing biomass (Table 6) and the ratio of supporting to dependent biomass (Table 7) indicates that seedlings are existing at or near their compensation point and suggesting that death may eventually occur in the absence of disturbance.

Increased growth rates are encountered with increasing gap size. Within small gaps, the growth rate may be insufficient to allow individuals to reach the treefern canopy before gap closure occurs. With larger gaps, growth exceeds a critical level and individuals can reach the canopy as reproductive adults within one year. If Burton's estimates of treefern regeneration are accurate (Burton 1980a), Passiflora mollissima becomes firmly established in the canopy well before the two to five years necessary for canopy recovery. Little phytomass is maintained by adults in the understory following canopy closure and few flowers or fruit are found. In the canopy, individuals proliferate, forming large blankets of vegetation which spread laterally, overtopping the existing treefern canopy. Production of reproductive structures is abundant. Individuals are not shaded out and replaced following canopy closure but persist until senescent.

Small, isolated gaps form in Ola'a following the collapse of dead or senescent trees and windthrows of shallow-rooted emergents. Disturbance of the treefern subcanopy is associated with the fall of emergents. More direct disturbance to the Cibotium canopy occurs with the rooting activities of feral pigs. Large scale disturbances associated with gap formation include 'ohia dieback (Metrosideros polymorpha) and occasional heavy windstorms such as the January 1980 storm. Storms accompanied by heavy winds may occur in the islands every year and during any season but those with winds in excess of 50mph and capable of uprooting large

trees occur on the order of once every three to four years (Blumenstock 1967). These disturbances have, no doubt, resulted in the drastic increase in cover of Passiflora mollissima observed between 1971 and 1981 in the Ola'a Tract.

Human-induced disturbances, such as hapu'u harvesting (Cibotium spp.), logging and land clearing for alternate use are usually of a much greater magnitude than natural disturbances and would likely result in dense stands of P. mollissima within a short time.

The phenomenon of "gap-phase replacement" exhibited by Passiflora mollissima in the Ola'a Tract is a common regenerative strategy of secondary forest species growing in dense shade in tropical forests where light is a limiting factor. The relative scarcity of dense, closed-canopy forests in the Hawaiian Islands may partially account for the success of P. mollissima in Hawai'i. Indeed, densely shaded exotic plantations of Tropical ash (Fraxinus uhdei) and Sugi pine (Cryptomeria japonica) located within areas of native forest infested with P. mollissima contain few to no individuals of P. mollissima and those present are small seedlings. Further support of this comes from an observation of a small population of P. mollissima, with all age classes represented, in a gap of approximately 100 m<sup>2</sup> in size in a Tropical ash forest at Puulaalau on Mt. Hualalai. The surrounding ash forest contained no individuals of P. mollissima.

#### CONCLUSIONS

Passiflora mollissima is a species of wide ecological amplitude combining characteristics of primary and secondary tropical forest species. Functioning as a "gap-phase opportunist", sensu Baur 1954, in the closed-canopy Cibotium spp. forests of Hawai'i, it is able to maintain small populations of shade tolerant seedlings yet effectively exploit the greater light intensities associated with canopy disturbance and gap formation.

While closed-canopy Cibotium spp. forests are not optimal habitats for Passiflora mollissima they are nevertheless susceptible to invasion and infestation by P. mollissima with the aid of repeated disturbances to the canopy. The ability of P. mollissima to become established in gaps and overtop the existing treefern canopy allows individuals to proliferate in the full light of the canopy, even after gap closure, and precludes a reversal of the colonizing trend which was observed by Burton (1980a) for other exotics invading the treefern forest.

Invasion of new areas in Ola'a is dependent upon the existence of two random types of events: dispersal to an area by feral pigs or birds and gap formation. It appears that both these events occur with sufficient regularity in Ola'a to allow Passiflora mollissima to spread throughout the Ola'a Tract. In the absence of control, the patchwork pattern of distribution now observed will likely become an uninterrupted cover of P. mollissima before long.

#### MANAGEMENT RECOMMENDATIONS

Small scale, localized efforts at eradication of any but the most limited, isolated populations of Passiflora mollissima, such as at Kula, Maui, are labor intensive and counter-productive in the long run. Use of chemical controls is not compatible with areas of native forest ecosystems therefore biological control remains as the only realistic means of control of this forest pest.

In the meantime, efforts to control feral animals responsible for the dispersal of Passiflora mollissima and the control of deliberate disturbances to the canopy would aid in preventing the further spread of this species. Additionally, the public must be educated to the problem banana poka poses in our native forests today. Man has many times been responsible for the spread of this species to new areas. Its attractiveness as an ornamental makes it a prime target for dispersal by man. Considering the rapid transformation of forested areas into subdivisions and the fact that many of these are occupied by newcomers to the islands, this problem could become a serious one before long.

#### ACKNOWLEDGEMENTS

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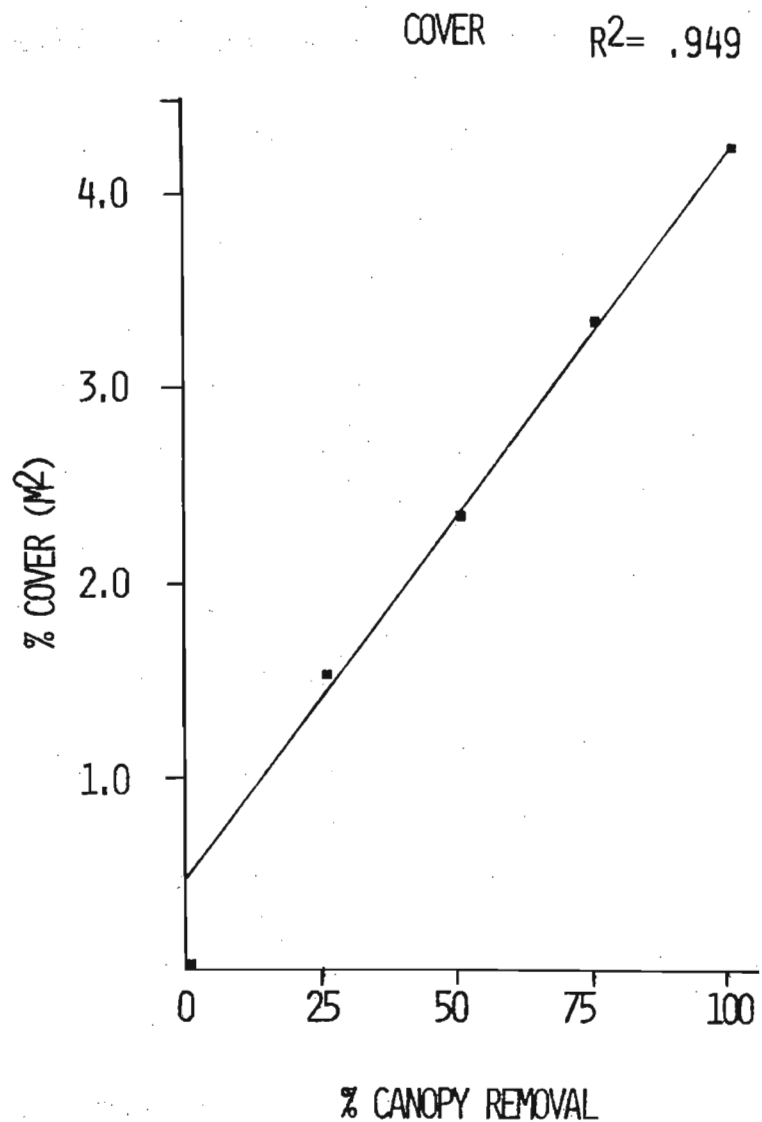
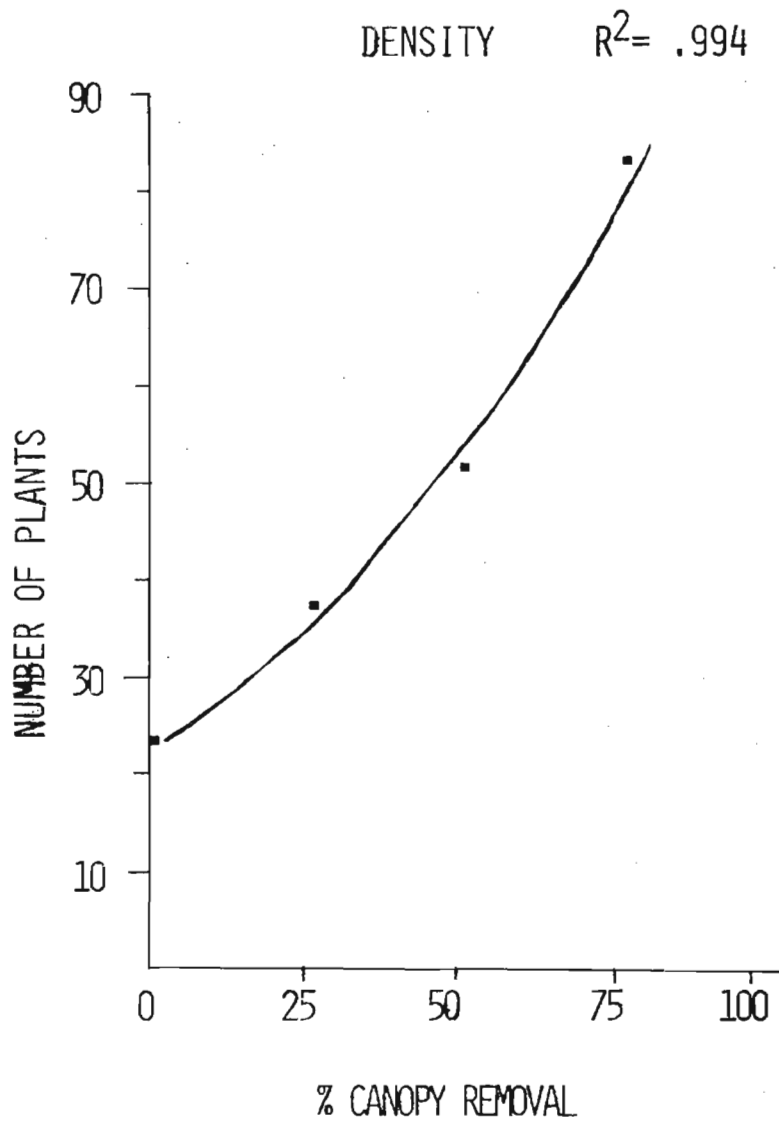
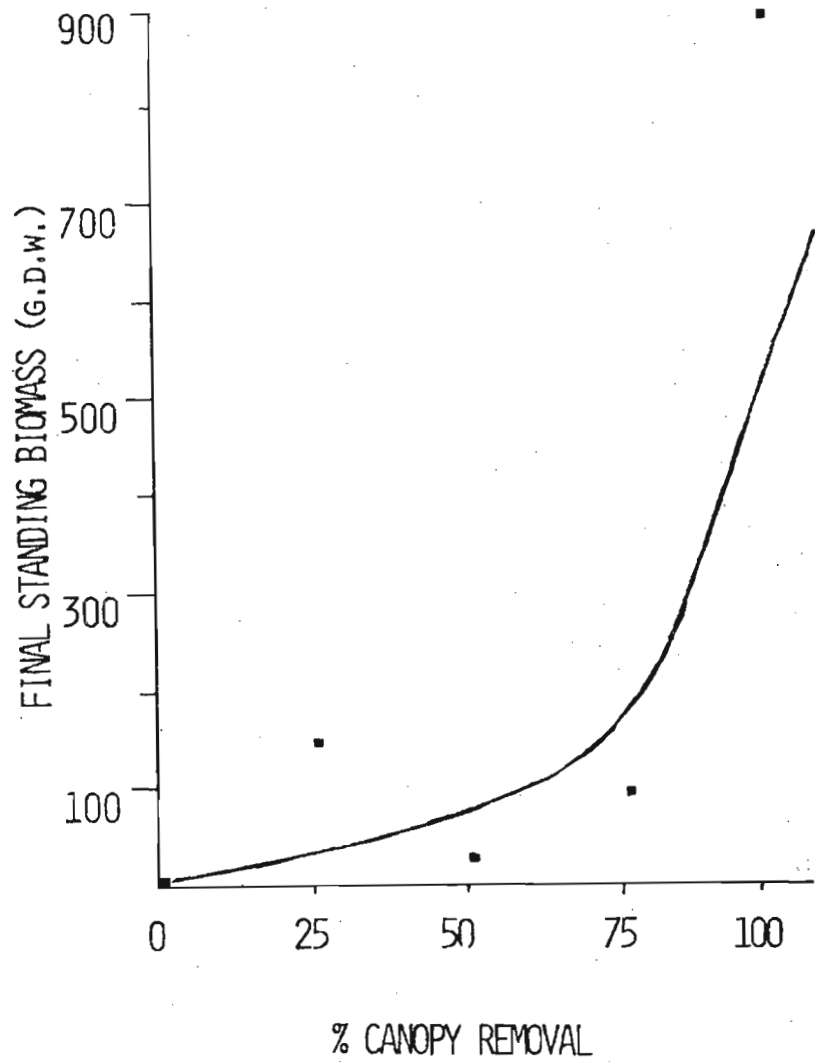


FIGURE 1. REGRESSIONS OF DENSITY AND COVER ON % CANOPY REMOVAL

BIOMASS  $R^2 = .701$



BIOMASS  $R^2 = .837$

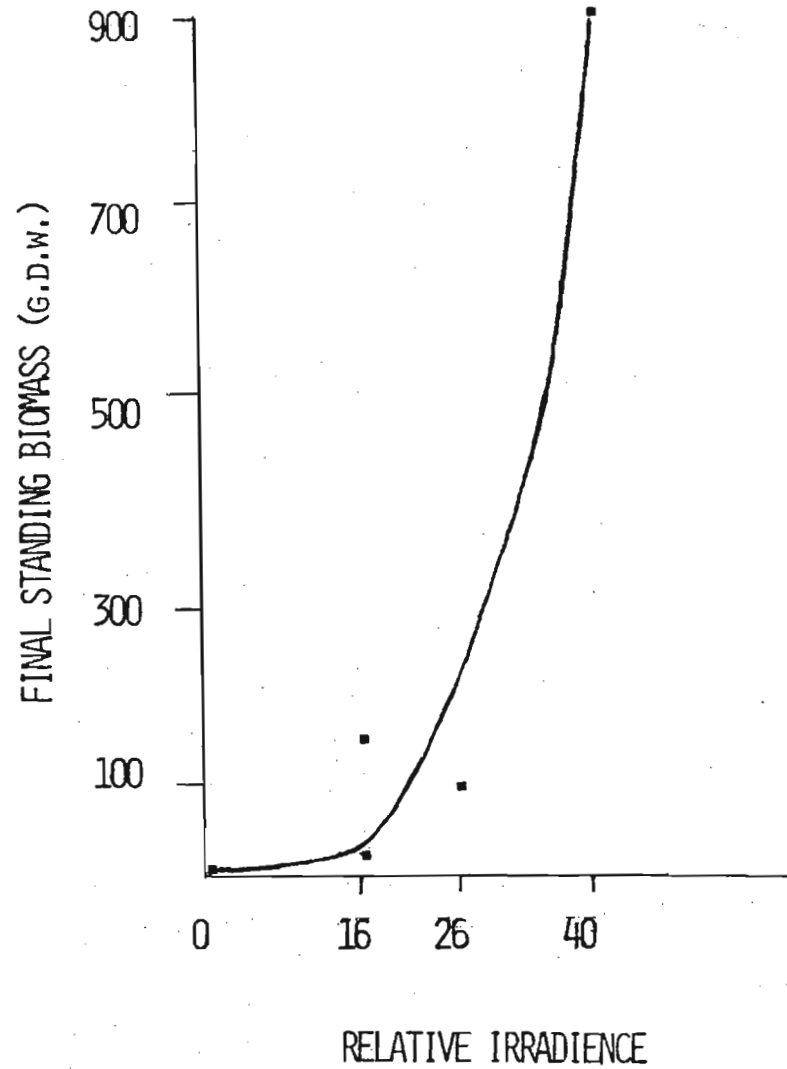


FIGURE 2. REGRESSIONS OF BIOMASS ON % CANOPY REMOVAL AND RELATIVE IRRADIANCE

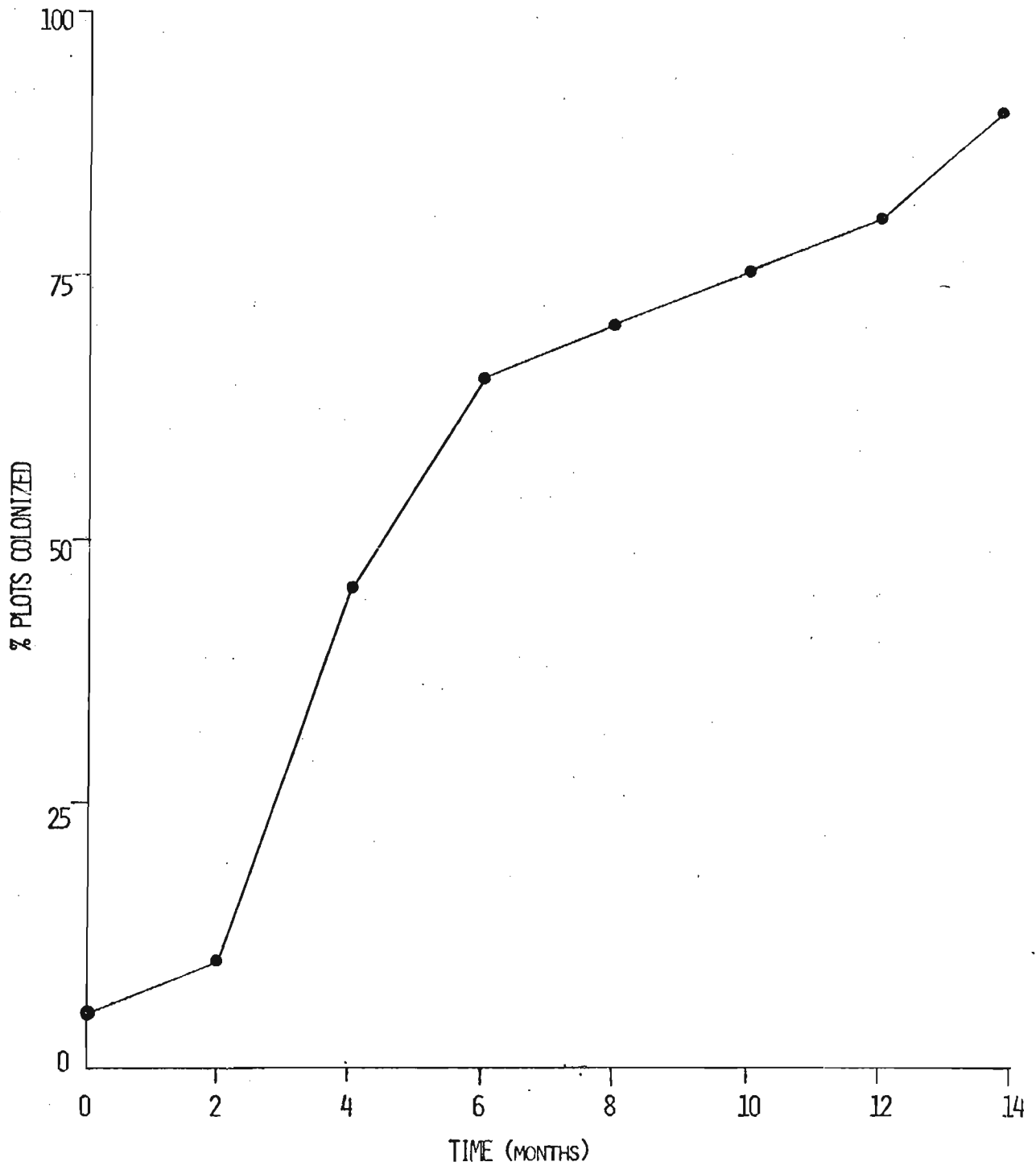


FIGURE 3. RATE OF COLONIZATION BY *PASSIFLORA MOLLISSIMA* UNDER CONDITIONS OF ARTIFICIAL CANOPY DISTURBANCE

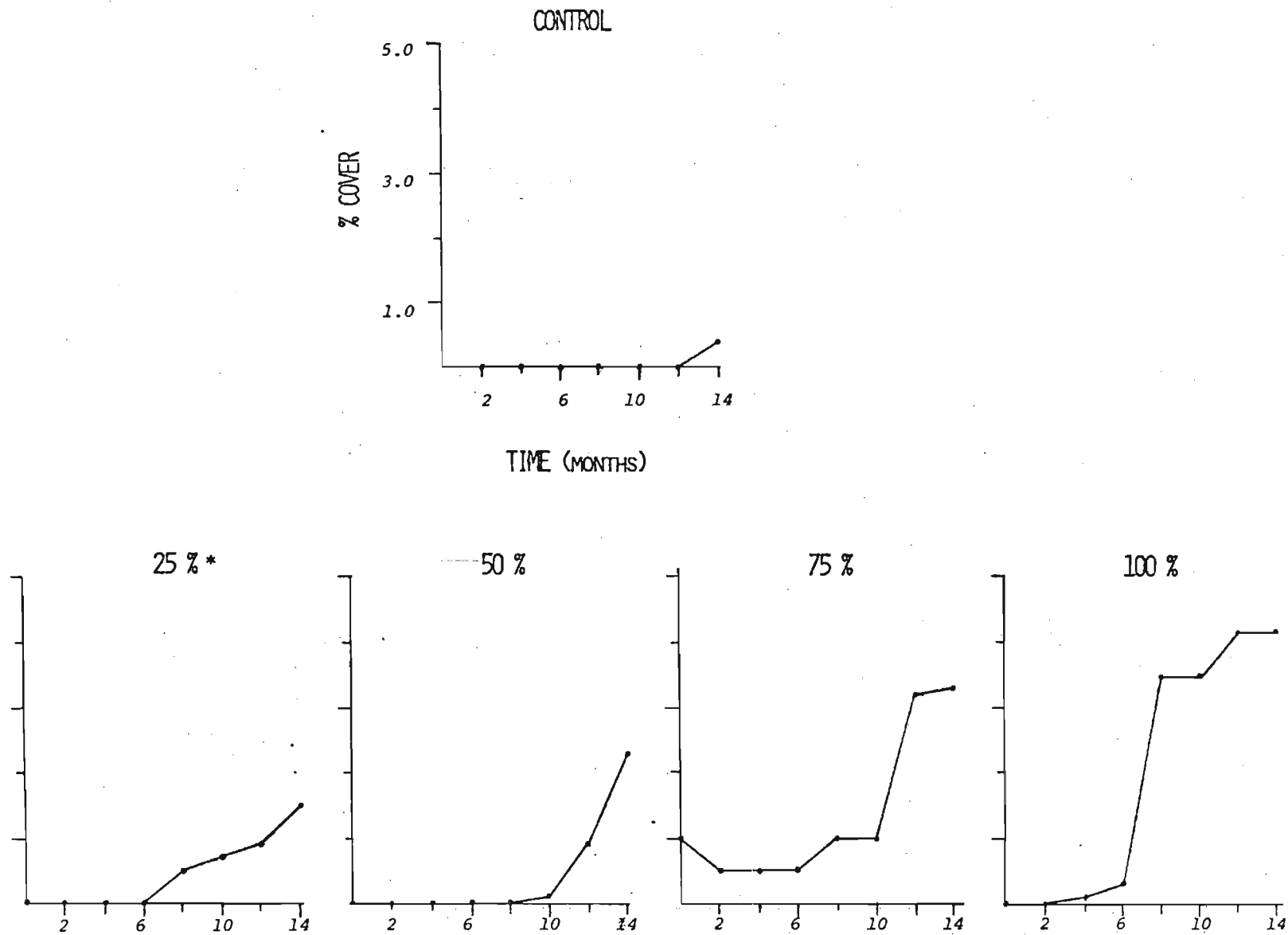


FIGURE 4. RATE OF ESTABLISHMENT AND GROWTH OF *PASSIFLORA MOLLISSIMA* UNDER VARIOUS DISTURBANCE REGIMES BASED ON ESTIMATES OF PERCENT CANOPY COVER

TABLE 1. Average percent cover of Passiflora mollissima and all exotic species after 12 months of canopy disturbance

% canopy removal	0	25	50	75	100	TOTAL
<u>P. mollissima</u> *	0.0	0.25	0.20	0.40	1.25	2.10
exotic spp.**	0.5	2.50	2.20	6.90	19.00	31.10
<u>P. mollissima</u> / exotic spp.	0.0	10.00	9.09	5.80	6.58	6.75

\* UNPUBLISHED DATA P.J. BURTON

\*\* FROM BURTON, P.J. 1980a

TABLE 2. Relationship of theoretical levels of canopy removal to observed levels of canopy removal and relative irradiance

canopy removal theoretical % *	0	25	50	75	100
actual canopy removal **	10	27	33	70	92
actual relative irradiance *	8.2	16	16	26	40

\*BURTON, P.J. 1980a

\*\*BURTON, P.J. 1980b

TABLE 3. Success of *Passiflora mollissima* under various disturbance regimes T= 14 months

criteria for success	0	25	50	75	100	F *	df
GERMINANTS							
density	19	8	8	13	0		
SEEDLINGS							
density	4	6	19	25	0	1.94	4+14
biomass **	2.10	3.75	7.45	6.70	0	2.48	4+11
JUVENILES							
density	1	24	25	44	23	2.11	4+14
biomass	3.20	375.25	105.15	277.30	727.89	1.17	4+11
ADULTS							
density	0	0	0	0	2		
biomass	0	0	0	0	1909.36		
TOTAL							
density	24	38	52	84	25	3.59 <sup>+</sup>	4+14
biomass	5.30	379.00	112.60	284.00	2637.25	3.07	4+10
cover ***	0.40	1.50	2.30	3.30	4.20	3.43	4+10

\* one-way analysis of variance

+ =significant at .01 level

\*\* final standing biomass g.d.w.; biomass of seedlings and germinants combined

\*\*\* data from P.J. Burton 1980a; 1% cover = 1m<sup>2</sup>

TABLE 4. Regressions of various measures of Passiflora mollissima success on the degree of canopy disturbance and relative irradiance

FACTOR X	FACTOR Y	REGRESSION EQUATION	r <sup>2</sup>
% Canopy Removal	density <sup>1</sup>	Y= 20.339 + .776X	.950 **
"	cover	Y= .459 + .037X	.998 **
"	biomass <sup>2</sup>	Y= 6.246e <sup>.045X</sup>	.701 +
Relative Irradiance	density	Y= 12.257e <sup>.076X</sup>	.916 **
"	cover	Y= 5.256 + -50.562/X	.945 **
"	biomass	Y= .001X <sup>3.693</sup>	.837 *

+ significant at .01 level  
 \* " " .05 "  
 \*\* " " .001 "

1. excluding 100% removal plots  
 2. adjusted for missing data

TABLE 5. Number of plants appearing in plots following one year of disturbance (1980) and one year of canopy recovery (1981)

% canopy removal	0	25	50	75	100	TOTAL
1980	24	38	52	84	25	223
1981 *	0	2	2	3	3	10

\* by age class: 1 seedling, 8 juveniles, 1 adult budding

TABLE 6. Ratio of above-ground supporting biomass to dependent biomass under various disturbance regimes

% canopy removal	0	25	50	75	100	F	df
germinants + seedlings	0.89	0.88	1.42	1.92	--	6.85*	3+7
juveniles	1.10	0.97	1.47	1.02	1.38	1.67	4+10

\* significant at .01 level

TABLE 7. Average biomass per plant in control and study plots

age class	0	25	50	75	100	F	df
seedlings	0.20	0.30	0.61	0.20	0.00	1.16	4+11
juveniles	3.20	10.99	6.11	5.03	23.78	1.47	4+11