

Technical Report No. 51

COMPOSITION AND PHENOLOGY OF THE DRY FOREST
ON MAUNA KEA, HAWAII, AS RELATED TO THE
ANNUAL CYCLE OF THE AMAKIHI (LOXOPS VIRENS)
AND PALILA (PSITTIROSTRA BAILLEUI)

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ABSTRACT

An intensive 19-month phenological study was carried out on the southwestern slope of Mauna Kea, Hawaii, from March 1973 through October 1974. This study was part of a larger six year project on the breeding ecology of two native birds in the region, and is only a preliminary report.

Study areas were established at approximately 6,500, 7,000, and 7,500 feet elevation; five 100 x 100 feet (30.5 m x 30.5 m) phenology plots were measured within each study area and all the trees were tagged and measured. Percentage of canopy cover, flowering, and fruit production were measured monthly; index values were established for each phenophase so that they could be expressed graphically as well as analyzed statistically.

The forest on this slope of Mauna Kea is composed almost entirely of mamane (Sophora chrysophylla) and naio (Myoporum sandwicense). Each of the three elevations studied has a significantly different composition of tree species; the birds present at each elevation appear to reflect the composition of the forest. The Palila (Psittirostra bailleui) and Akiapolaau (Hemignathus wilsoni) seem to be confined to the higher elevations where mamane is dominant (7,400 to 8,400 feet).

Tree height and circumference at breast height (CBH) increase with elevation, although not significantly. Tree density in phenology plots decreases with higher elevation. Decreased density and the location of seedlings only in open areas suggest that water may be a limiting factor. Reproduction of mamane is severely curtailed in areas of high sheep-grazing pressure, but shows good regeneration in enclosed areas.

Phenological data from Mauna Kea are similar to those from Mauna Loa. There appears to be seasonality in flowering, fruiting, and leaf fall in both mamane and naio, but seasonality is more difficult to interpret in the latter. Phenophases start gradually and are protracted; flushing and flowering show an inverse relationship. Precipitation peaks coincide with flowering peaks and may trigger this phenophase. Heavy rain may cause a decrease in flowering and an almost total loss of the pod crop in mamane.

Behavioral patterns of both the Amakihi (Loxops v. virens) and Palila seem to be influenced by phenological patterns on Mauna Kea. The extended bloom period of mamane correlates with the protracted nesting season of the Amakihi. Canopy cover is at its maximum density when nesting starts, and remains fairly dense throughout the breeding cycle of the Amakihi. Surplus Amakihi leave an area when mamane bloom ceases, leaving only a few permanent residents; naio blossom visitation increases

at this time. Palila nest throughout the period of peak pod production. When mamane pods are not present the Palila was found to utilize mamane flowers, young leaves, and naio berries.

Phenological aspects of mamane appear to be much more important to the birds on Mauna Kea than those of naio. It would appear that naio serves only as a supplemental food source; naio berries are taken by Palila, House Finch (Carpodacus mexicanus frontalis), and Turkey (Meleagris gallopavo) in dry periods.

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INTRODUCTION

Several phenological studies have been conducted in tropical regions (e.g., Richards 1964; Daubenmire 1972), but little attention has been paid to this biological event in Hawaii. Lanner (1966) and Neal (1965) studied the phenology of introduced plants in Hawaii; four studies have been reported on native species.

The pioneer work on phenology of native plant species in Hawaii is that of Baldwin (1953) who studied the flowering of Sophora chrysophylla and Metrosideros collina in relationship to the annual cycle in four species of Hawaiian honeycreepers. Lanner (1965) studied Acacia koa on Mauna Loa and Porter (1973) reported phenological data of Metrosideros on Oahu and Hawaii (Mauna Loa). The most intensive work on native species is that of Lamoureux (1973) in the Mauna Loa area; his study on the phenology of 12 native tree species at nine different locations is still in progress.

All of these workers found that phenological phenomena are more sharply defined and more easily observed in temperate regions than in tropical areas where the climate is more uniform throughout the year. Blumenstock and Price (1967) noted that daily temperature fluctuations in an area usually are greater than the annual fluctuation in mean monthly temperature for that region in Hawaii. Average monthly rainfall throughout the year, however, does vary enough on Mauna Kea to be inhibitory to plant growth during certain periods.

In Hawaii any particular phenological phenomenon is often relatively drawn out, and, as a result, it is unnecessary to make daily observations which often are required in temperate regions. Lamoureux (1973) found that observations at monthly intervals are satisfactory in most instances. He also has demonstrated that phenophases may differ from year to year in the same species; therefore, observations must be made over periods of several years before valid conclusions can be drawn. This paper covers only a 19-month period and must therefore be considered only a preliminary report.

The study reported here was undertaken to assemble basic information on phenological phenomena so that it could be applied to the annual cycle of Loxops v. virens and Psittirostra bailleui on Mauna Kea, Hawaii. Measurements were made with the following purposes in mind:

- (1) to determine the density and percentage of different tree species at three separate elevations.
- (2) to determine if there is a significant size difference of trees at varied elevations.
- (3) to estimate the reproductive success of the different tree species.

- (4) to compare the phenology of individual species at different elevations.
- (5) to estimate the role of Sophora chrysophylla and Myoporum sandwicense phenology in the ecosystem.

METHODS

The study area is situated on the southwestern slope of Mauna Kea in the Kaohe Game Management Area (Fig. 1). This area has the last remaining major mamane-naio forest in the State of Hawaii (Fig. 2). The area was chosen because both Loxops virens and Psittirostra bailleui inhabit this region. Hunting roads, constructed by the Hawaii Division of Fish and Game, are found throughout the region and thus many areas become accessible by 4-wheel drive vehicle.

Mauna Kea is the highest insular peak on earth. The top is 30 miles across and studded with cinder cones; most of the cones were built on rifts extending eastward, southward, and westward from the summit area. The lower slope of the mountain around the study has been blanketed with layers of fine tan-colored ash deposits. Most of the material is the fine-grained firefountain debris that was wafted from the numerous cinder cones. On the windward side the streams have cut deep canyons, but on the drier westward slope there has been little major erosion.

Stearns (1966) divides the volcanics of Mauna Kea into two series. The older Hamakua series forms the major part of the mountain and is chiefly primitive olivine basalts with picrite-basalts carrying olivine and augite phenocrysts and a few andesites in its upper part. It usually carries and shows a blanket of tan-colored vitric Pāhala ash four to 15 feet thick and is separated from the overlying Laupahoehoe volcanic series by the presence of the ash blanket and the porphyritic picrite-basalts. Interbedded with the Hamakua lavas near the summit are several beds of lithic-vitric explosion breccias reaching 90 feet in thickness. The Laupahoehoe volcanic series is predominantly andesine andesites, but olivine basalts are also present. The lavas of this series form a thin veneer over the upper part of the cone, reaching a maximum thickness at the summit. They are characterized by many short flows and bulky cinder cones. The top of the mountain above 11,000 feet is a plateau and may have been caused by the later Laupahoehoe volcanic series filling an older caldera of the Hamakua series. Flows overlying glacial drift at the summit indicate that Mauna Kea has become dormant in recent times.

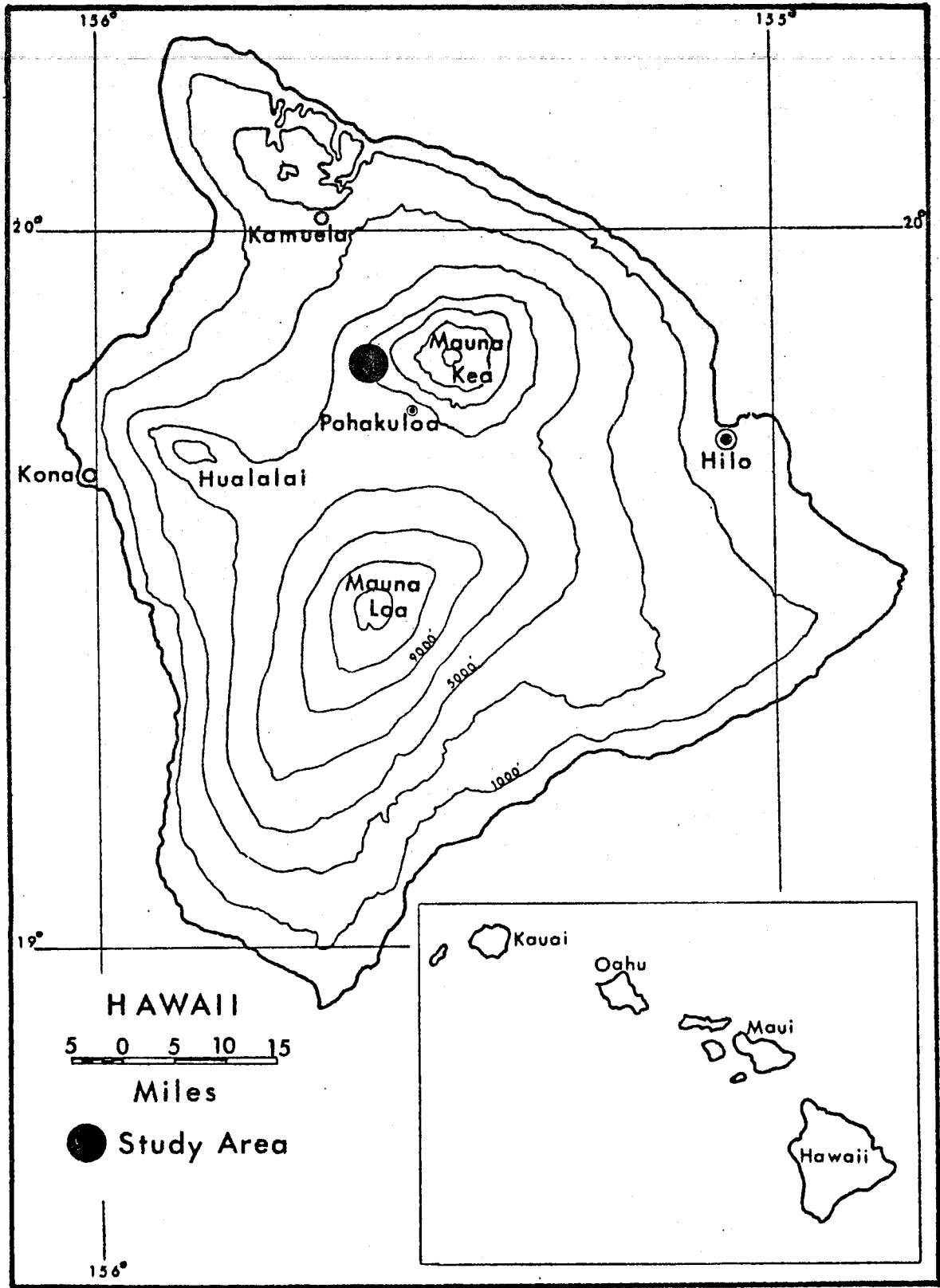


FIG. 1. Orientation map of the Hawaiian Islands, with the island of Hawaii showing study area location.



FIG. 2. Puu Laau on the slopes of Mauna Kea at an elevation of $7,300 \pm$ feet.

Study plots were selected at elevations of approximately 6,500-feet, 7,000-feet and 7,500-feet along the road from the Kilohana check station to the summit (Fig. 3). The 6,500-foot and 7,000-foot plots are open areas subject to feral sheep grazing pressure. The 7,500-foot study site is bounded on all sides by fence; this was, at one time, a 300-acre holding pen for mouflon sheep.

A point was chosen at random and tree sites were established within each study plot. Five 100 x 100 foot (30.5 m x 30.5 m) squares were marked off in the shape of a T. Figure 4 shows how the tree sites are situated within the 7,000-foot study area. The base of the T was designated plot number 1 and the top site number 3; plots 4 and 5 were measured at the inception of the study, but have since been deleted from the phenological aspect of this study.

Each 10,000-square foot (930.25 m^2) area was mapped and each tree was recorded by number (Figs. 5, 6 and 7) and tagged with aluminum tree bands. Circumference at breast height (CBH) and total height were measured; a tape measure was used for CBH and a clinometer for tree height.

While working in the area during previous years, I noticed that microblooms occur around the mountain at the same elevation. The trees in one area might be in full bloom or have fruit, whereas 200 meters away the trees would be barren of blossoms or of usable fruit (usable fruit is defined as only mature green pods). In order to obtain a better picture of the extent of such microblooms, I supplemented the tree-plot data by a "random walk."

I took "random walks" outside of the tree-plot sites, but within the boundary of each study area. Every 100 feet (30.5 m) I measured the nearest tree to my right: I measured 50 trees during such a walk. These data were then added to those of the tree plots.

Percentage estimates of flowering, fruiting, and canopy cover are recorded monthly for each tree within the plots and for each of the 50 trees recorded on the "random walks." An index value of 5 is assigned when 1% to 5% of the total tree is flowering or fruiting, a value of 10 when it is 5% to 25%, and an index of 15 when more than 25% of the tree is blooming or has fruit. Canopy cover is recorded as 5 for few leaves, 10 for medium cover, and 15 for a dense foliage. Each phenophase then has a population index value every month that can range between 0 and 15. Index values were established for each of the three phenophases in order to have numerical data which could be presented graphically as well as be analyzed statistically.

When estimating the percentage of each phenophase, I considered the entire tree.

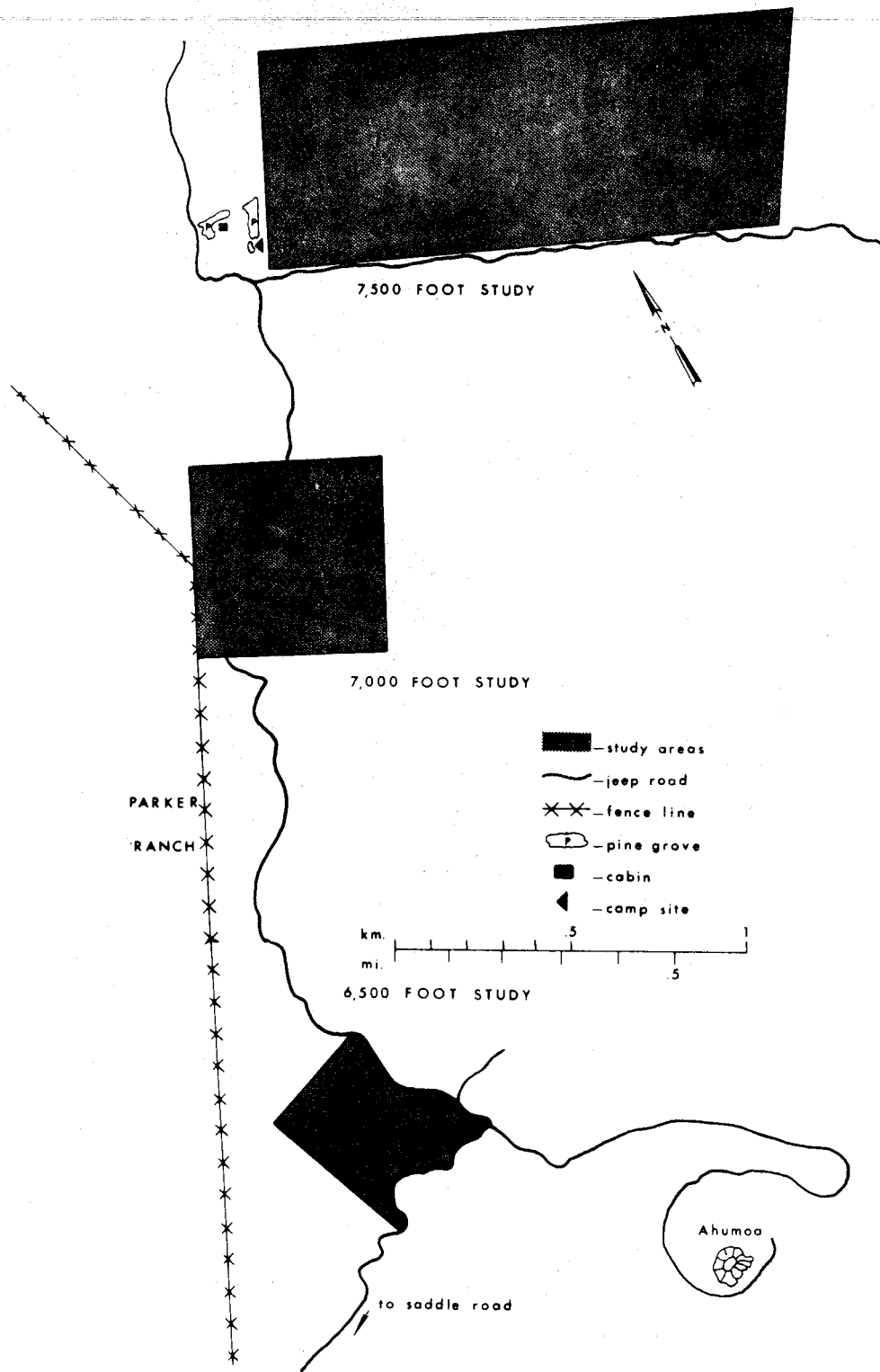


FIG. 3. The three study areas on the southwestern slope of Mauna Kea, Hawaii.

7,000-FOOT STUDY

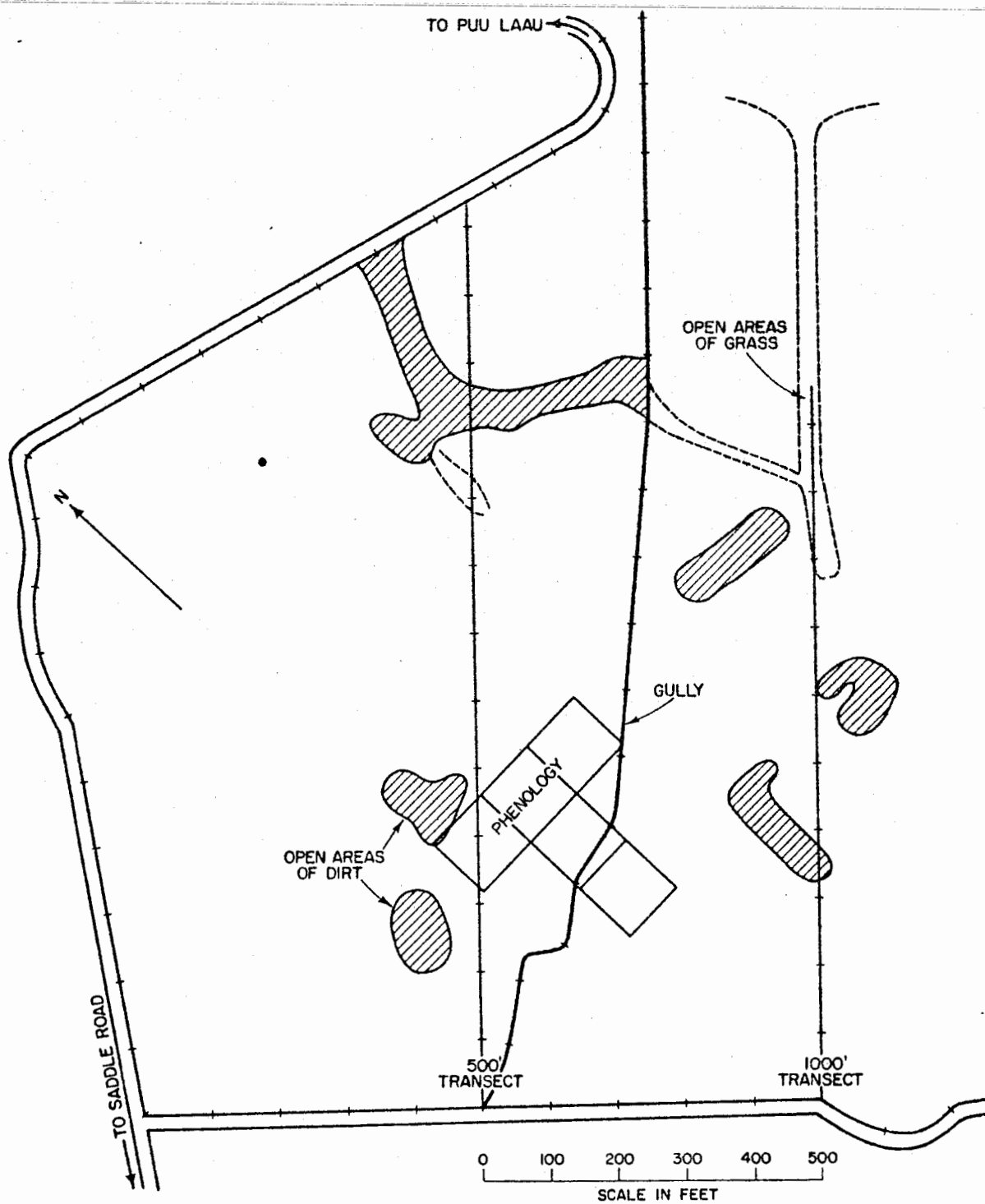


FIG. 4. Map of the 7,000-foot study area showing location of the phenology plot.

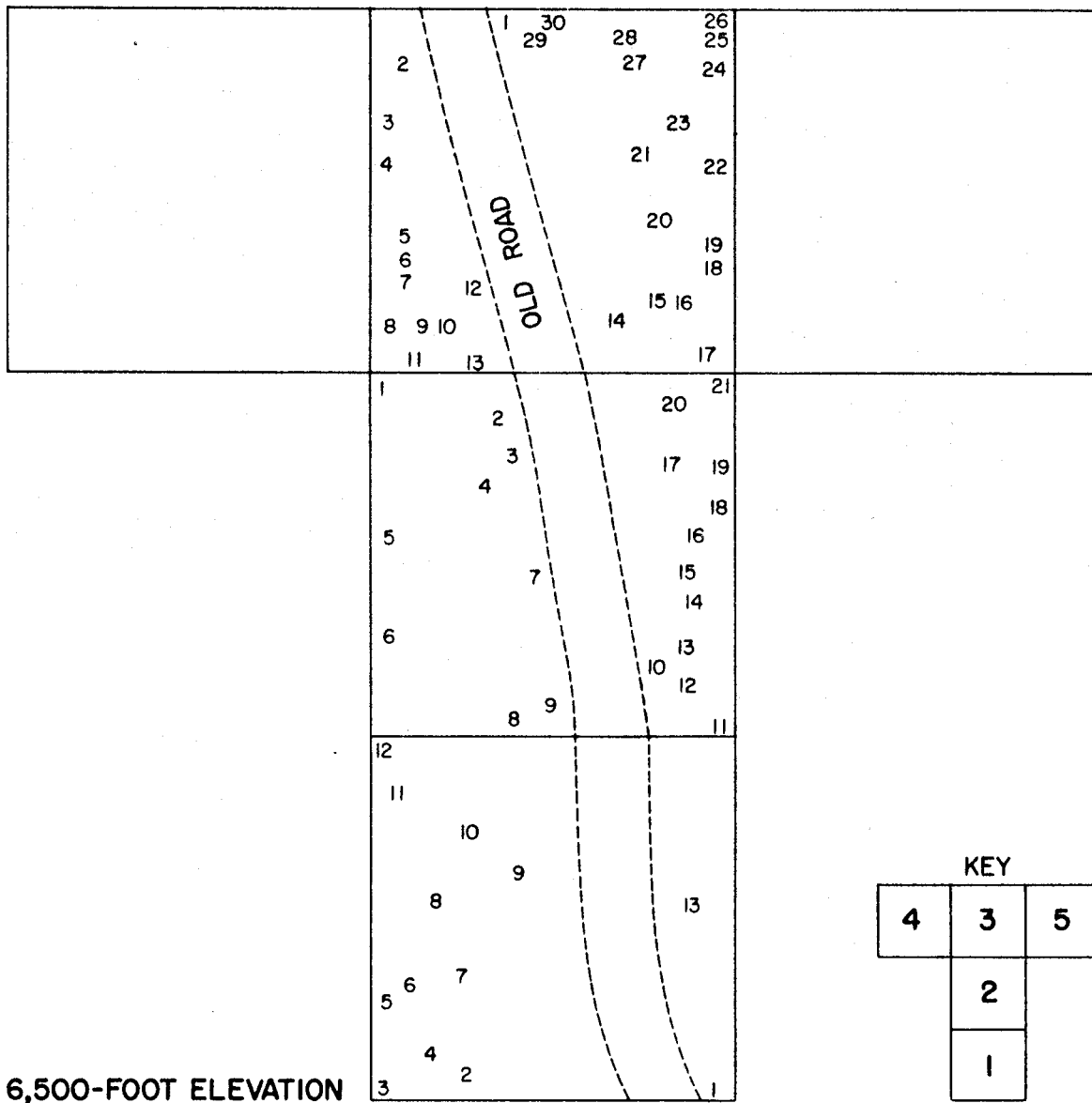


FIG. 5. Map of tagged trees in phenology plots at 6,500 feet elevation on Mauna Kea, Hawaii.

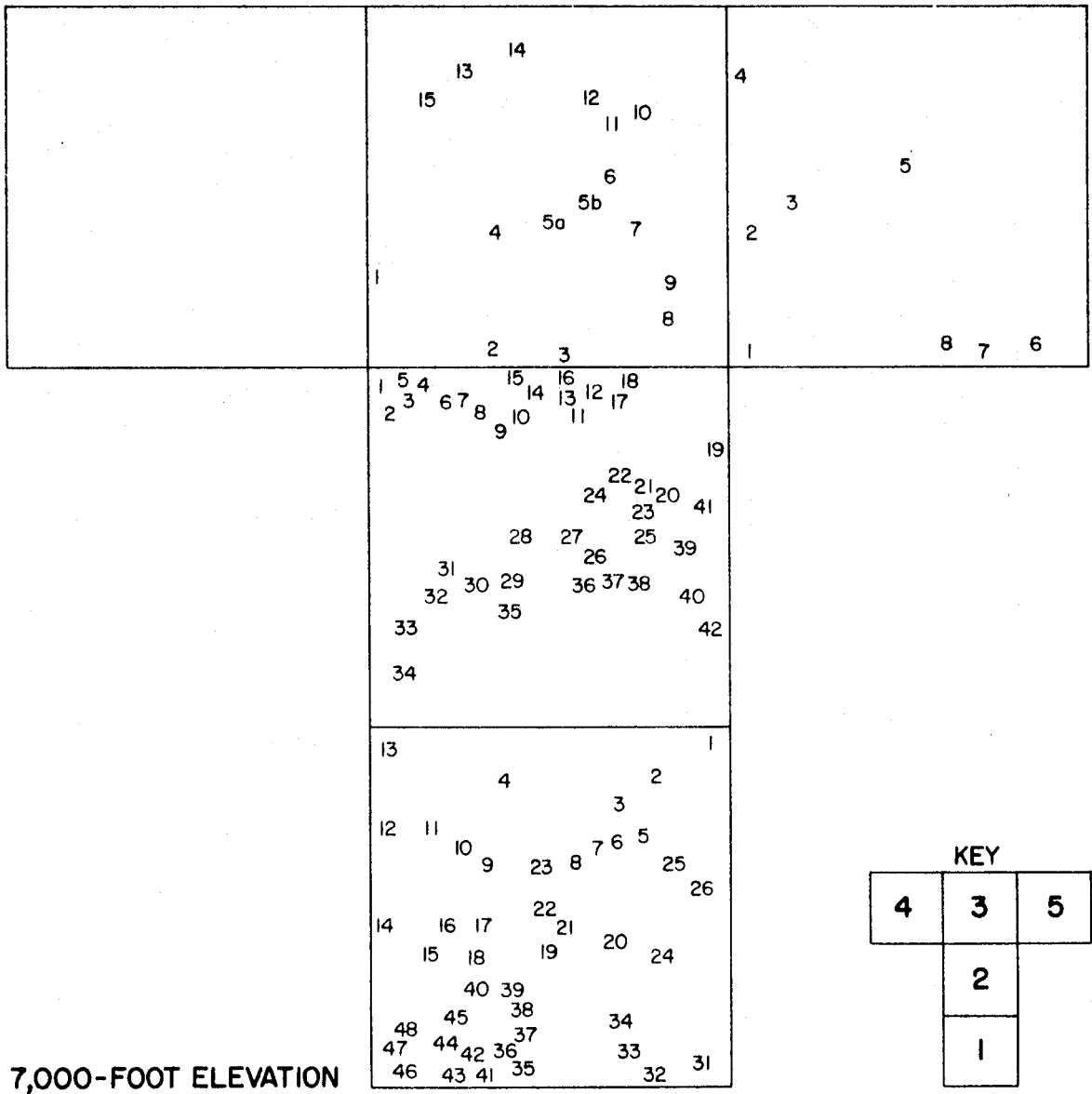


FIG. 6. Map of tagged trees in phenology plots at 7,000 feet elevation on Mauna Kea, Hawaii.

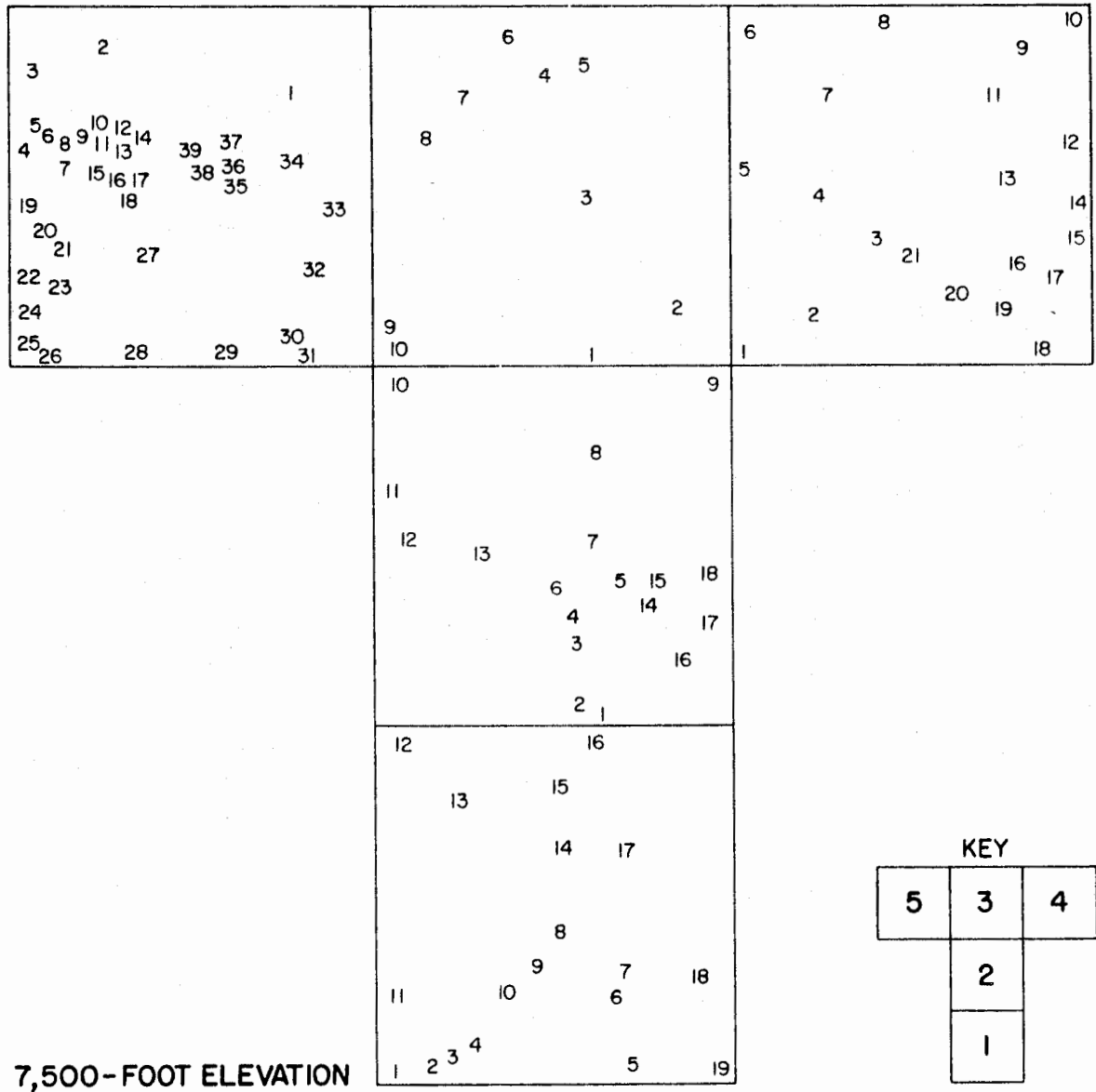


FIG. 7. Map of tagged trees in phenology plots at 7,500 feet elevation on Mauna Kea, Hawaii.

Since I was the only person measuring each month, the data are fairly uniform throughout. Percentages of flowers were recorded as those present and usable by Loxops virens, and fruit as those usable by Psittirostra bailleui; for this reason, very young mamane pods and those that had started to turn brown were not recorded (neither are used as food by Psittirostra).

Weather data included in this report were collected at the 7,500-foot study area. Temperature was recorded with two maximum-minimum thermometers, one under the canopy and one in the open. Humidity readings were taken visually on a hygrometer and recorded three times per day until September 1974, after which hygrothermograph readings were initiated. Rainfall data were obtained from the National Weather Service.

RESULTS

Composition: Mamane (Sophora chrysophylla) and naio (Myoporum sandwicense) are the most abundant tree species of the dry forest on Mauna Kea. There are occasional scattered stands of akoko (Euphorbia olowaluana) with individual trees of sandalwood (Santalum pilgeri) and Dubautia arborea. Aside from two small plantings of pine, eucalyptus, and cedar, these five are the only tree species I have found in the area around my study sites in the past five years of field work.

A 500 foot rise in elevation reveals a remarkable change in percentage-composition among the three study sites (Table 1). The ratio of mamane to naio at 6,500 feet is 56% to 44%. A drastic change takes place at 7,000 feet as naio increases to 73.6% of the total trees and mamane drops to only 26.4%. At 7,500 feet a reversal takes place in most areas, with the forest consisting primarily of mamane. I feel that the tree ratio (61.2% mamane, 38.8% naio) at plot 5 in the 7,500-foot site is atypical, and when combined with data from the other plots creates a biased picture of composition. Plot number 5 is located in a dense stand of naio which is uncommon for this elevation. If we eliminate plot 5 data, mamane constitutes 94.2% and naio only 5.8% of the vegetation, which is much more indicative of the true tree composition of the area.

The "random walks" show much the same as the plot data do (Tables 2, 3, 4; Fig. 8). At 6,500 feet mamane is 46.6% of the population, naio totals 53.0%, and akoko, 0.4%. At 7,000 feet the percentages remain remarkably similar: naio, 74.4%, and mamane, 25.6%. The 7,500 feet "random walks" show mamane comprising 92.4% of the forest, naio, 7.2%, and akoko, 0.4%. These data justify omitting plot number 5 from the 7,500-foot compilation.

TABLE 1

TREE SPECIES DISTRIBUTION IN STUDY PLOTS
ON MAUNA KEA, HAWAII

<u>Elevation</u>	<u>Plot Number</u>	<u>Composition</u>
6,500 feet	1	12 mamane 1 naio
	2	17 mamane 4 naio
	3	26 mamane 5 naio
	4	33 mamane 47 naio
	5	56 mamane 56 naio
7,000 feet	1	13 mamane 35 naio
	2	7 mamane 36 naio
	3	14 mamane 6 naio
	4	11 mamane 52 naio
	5	3 mamane 5 naio
7,500 feet	1	20 mamane 0 naio
	2	16 mamane 2 naio
	3	10 mamane 0 naio
	4	19 mamane 2 naio
	5	6 mamane 41 naio

TABLE 2

NUMBER OF EACH TREE SPECIES IN MONTHLY RANDOM WALKS
AT 6,500 FEET ON MAUNA KEA, HAWAII

Date	Number of Mamane	Number of Naio	Number of Akoko
September	22	28	0
October	21	29	0
November	17	33	0
December	21	29	0
January	-	-	-
February	32	17	1
March	22	27	1
April	26	24	0
May	25	25	0
June	24	26	0
July	23	27	0
August	28	22	0
September	30	20	0
October	22	28	0

TABLE 4

NUMBER OF EACH TREE SPECIES IN MONTHLY RANDOM WALKS
AT 7,500 FEET ON MAUNA KEA, HAWAII

Date		Number of Mamane	Number of Naio	Number of Akoko
June		47	3	0
July	1973	-	-	-
August		41	6	0
September		44	5	1
October		47	3	0
November		48	2	0
December		49	1	0
January	1974	-	-	-
February		49	1	0
March		43	6	1
April		48	2	0
May		47	3	0
June		47	3	0
July		40	10	0
August		45	5	0
September		43	7	0
October		46	4	0

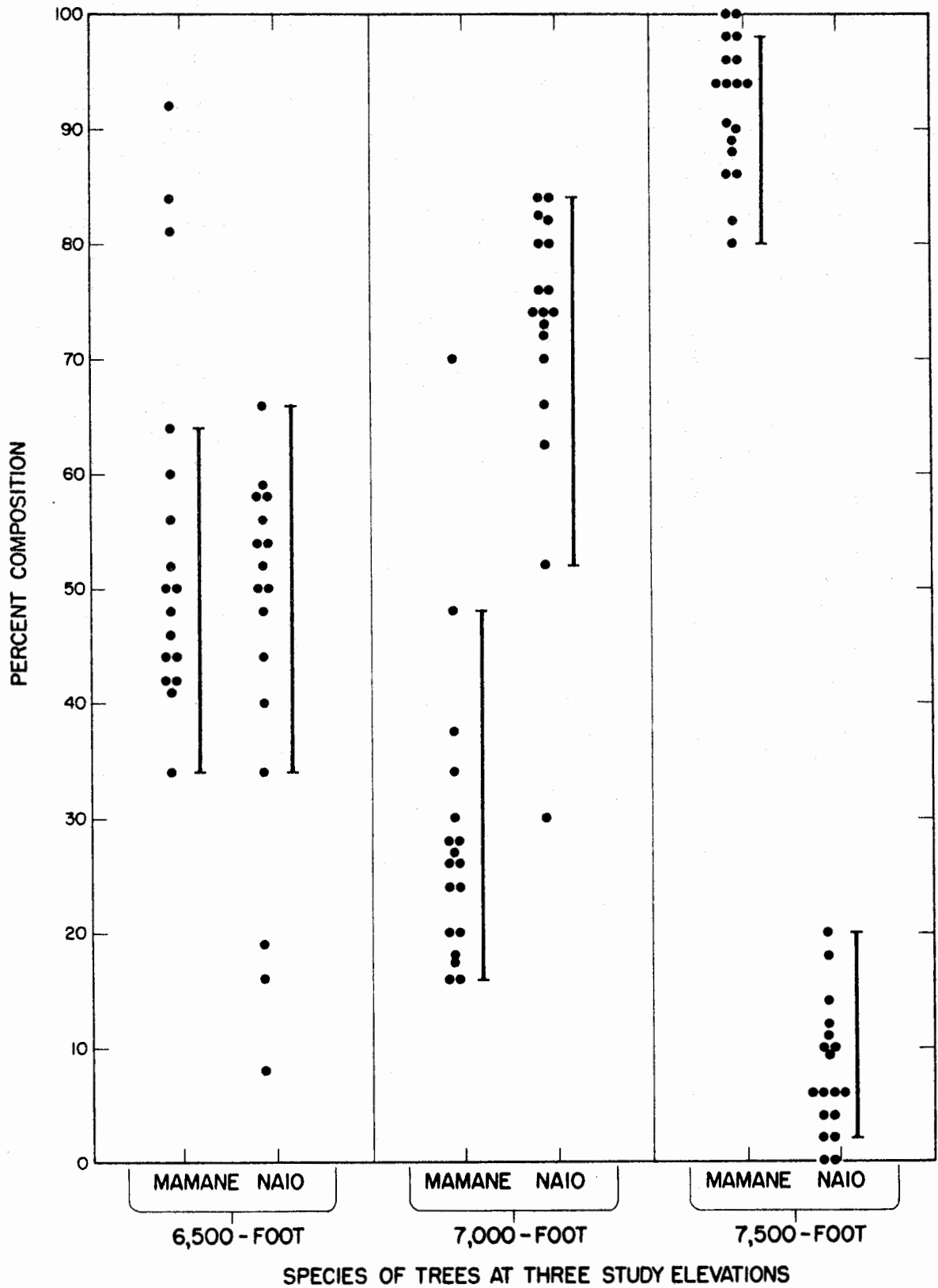


FIG. 8. Percent composition of mamane and naio at the three study areas on Mauna Kea, Hawaii. Each point represents a monthly percentage computed from random walks and plot composition. The bars show variance of monthly computations with the original study-plot data excluded.

Composition

To see if a significant difference in percentage composition existed in species between elevations I conducted a one-way analysis of variance test (Snedecor and Cochran 1967): the test (called anova) had a completely randomized design. The original numbers were percentages from each plot and random walks, and, because they varied extensively, I used an arc-sin transformation on the data: mamane had $F = 111.6$, $m/n = 2/50$, $P = < 0.001$; naio had $F = 112.28$, $m/n = 2/50$, $P = < 0.001$. The large F values for both mamane and naio gave good evidence that differences were present in the means of the various populations.

To test which elevations had significant differences I used the L.S.R. test of Sokal and Rohlf (1969). Elevational differences in mamane were all obviously different except for 6,500-7,000 foot comparison. The calculated L.S.R. was 1.23 with a difference in means of 16.41 (to be significant the difference in means must be equal to or greater than the L.S.R. value). The only other close comparison was 6,500 to 7,000 feet in naio, and here $L.S.R. = 6.12$ with $\bar{X}_1 - \bar{X}_2 = 16.64$. It was surprising to find that each 500-foot rise in elevation showed a very significant difference in composition percentage for both mamane and naio.

Density: The density of trees at each elevation is given in Table 5. The highest tree density occurs at 6,500 feet: 52 trees per 10,000-square feet (930.25 m^2). The density at 7,000 feet is 36.4 trees; at 7,500 it is 23.2 trees per plot. If we consider only trees suitable for nesting (those three meters and over), there are 36.2 trees per 10,000-square feet at 6,500 feet, 29.2 at 7,000 feet elevation, and only 15.6 trees per plot at 7,500 feet.

Density

The density of trees in phenology plots were combined at each elevation and the means tested to see if significant differences existed. I used a one factor anova and found $F = 1.44$, $m/n = 2/12$, and $P = 0.32$, thus showing there was no evidence of rejecting the null hypothesis that densities of trees were the same at all three elevations. Apparently differences in composition between the three study areas has no effect upon the density of the trees.

Tree Height and CBH: On the northwestern slope of Mauna Kea there appears to be an increase in tree height as higher elevations are reached. This holds true for both

TABLE 5

THE NUMBER OF TREES IN EACH PHENOLOGY PLOT
ON MAUNA KEA, HAWAII

Elevation	Plot Number	Total number of trees	Number of mature trees
6,500 Feet	1	13	12
	2	21	18
	3	31	20
	4	81	60
	5	114	71
7,000 Feet	1	48	36
	2	43	29
	3	20	19
	4	63	55
	5	8	7
7,500 Feet	1	20	15
	2	18	12
	3	10	5
	4	21	17
	5	47	29

of the dominant species of tree in the area (Tables 6 and 7). Mamane seems to be more variable with elevation than does naio: the total change in mean height of the former is 5.5 feet (4.8 m), and the latter is only 3.1 feet (0.9 m).

The circumference at breast height (CBH) of mamane increases strikingly with elevation change showing a difference of 19.1 inches (47.5 cm) between 6,500 and 7,500 feet elevation (Table 8). Although the mean height of naio increases with elevation, this was not the case with CBH (Table 9). The largest girth of naio was found at 6,500 feet, dropped sharply at 7,000 feet, and, at 7,500, came back up only 0.8 inches (2 cm).

Tree height and CBH

To determine if there was a significant difference in tree-height increase with elevation, I ran one factor anova tests on the data from Tables 6 and 7. Neither species exhibited a significant difference in height at the different elevations; mamane had $F = 3.00$, $m/n = 2/14$, $P = 0.087$, and naio had $F = 0.87$, $m/n = 2/13$, $P = 0.458$. The large F value for mamane, being almost significant, suggested why there is a visual impression of tree-height increase with an increase in elevation.

The data from Tables 8 and 9 also fit well into an analysis of variance one factor, completely randomized design. The change in CBH of naio at different elevations was not significant: $F = 0.521$, $m/n = 2/10$, $P = 0.624$. Mamane, on the other hand, did show a significant CBH difference: $F = 3.95$, $m/n = 2/12$, $P = 0.049$. The difference existed only between 7,500 and 6,500 feet: L.S.R. = 1.03, $\bar{X}_1 - \bar{X}_2 = 1.18$. L.S.R. tests on the other two possible combinations of elevations gave no evidence of rejecting the null hypothesis: 6,500 vs. 7,000 feet, L.S.R. = 1.098, $\bar{X}_1 - \bar{X}_2 = 0.33$, and 7,000 vs. 7,500 feet, L.S.R. = 0.95, $\bar{X}_1 - \bar{X}_2 = 0.85$.

Reproduction: The reproductive rate of both mamane and naio at all study areas is shown in Table 10. These figures were derived by counting all trees less than three meters in height in each phenology plot. These immature trees are used as a general index of reproductive success. The figures in no way reflect the general condition throughout the forest on Mauna Kea. Figure 3 shows that all study areas are located near main roads and, on the whole, these regions receive minimal sheep damage; this is one of the primary reasons that I chose these study sites. The 7,500-foot area is enclosed by fence and, as a result, there is no grazing pressure there at all.

When both species of trees are grouped together, the reproductive success at all

TABLE 6

MEAN TREE HEIGHT OF MAMANE ON MAUNA KEA, HAWAII

	Mean Tree Height m(ft)					
	6,500-foot Study	No. Meas.	7,000-foot Study	No. Meas.	7,500-foot Study	No. Meas.
Plot 1	6.6(21.8)	11	6.2(20.3)	12	7.1(23.2)	15
Plot 2	5.3(17.3)	14	5.8(18.9)	6	7.0(22.9)	10
Plot 3	4.9(16.0)	15	5.4(17.7)	14	6.1(20.1)	5
Plot 4	5.5(17.9)	15	6.3(20.7)	7	7.3(23.9)	15
Plot 5	4.9(16.1)	21	5.0(16.5)	2	- -	-
Random Walk	6.3(20.6)	10	5.2(17.0)	8	7.2(23.6)	47
Ave. Mean Height	5.4(17.8)		5.7(18.7)		7.1(23.3)	

TABLE 7

MEAN TREE HEIGHT OF NAIIO ON MAUNA KEA, HAWAII

	Mean Tree Height m(ft)					
	6,500-foot Study	No. Meas.	7,000-foot Study	No. Meas.	7,500-foot Study	No. Meas.
Plot 1	8.7(28.5)	1	6.4(21.0)	24	none	-
Plot 2	6.6(21.6)	3	6.1(20.1)	20	8.6(28.2)	2
Plot 3	5.9(19.5)	5	5.8(18.9)	6	none	-
Plot 4	5.7(18.6)	44	6.5(21.4)	48	6.2(20.5)	2
Plot 5	5.5(18.0)	53	5.5(18.2)	3	- -	-
Random Walk	7.1(23.3)	6	5.7(18.8)	42	5.7(18.8)	3
Ave. Mean Height	5.7(18.8)		6.2(20.2)		6.7(21.9)	

TABLE 8

MEAN CIRCUMFERENCE AT BREAST HEIGHT OF MAMANE ON MAUNA KEA, HAWAII

	Mean CBH cm(in)					
	6,500-foot Study	No. Meas.	7,000-foot Study	No. Meas.	7,500-foot Study	No. Meas.
Plot 1	60.7(23.9)	10	65.5(25.8)	12	92.7(36.5)	15
Plot 2	40.6(16.0)	15	73.4(28.9)	6	64.0(25.2)	10
Plot 3	48.5(19.1)	15	55.1(21.7)	9	63.5(25.0)	5
Plot 4	- -	-	- -	-	64.0(25.2)	15
Plot 5	- -	-	36.8(14.5)	2	68.1(26.8)	4
Random Walk	46.2(18.2)	10	56.6(22.3)	8	121.2(47.7)	47
Ave. Mean CBH	48.0(18.9)		60.7(23.9)		96.5(38.0)	

TABLE 9

MEAN CIRCUMFERENCE AT BREAST HEIGHT OF NAIIO ON MAUNA KEA, HAWAII

	Mean CBH cm(in)					
	6,500-foot Study	No. Meas.	7,000-foot Study	No. Meas.	7,500-foot Study	No. Meas.
Plot 1	71.1(28.0)	1	40.4(15.9)	24	none	-
Plot 2	52.6(20.7)	3	36.6(14.4)	20	120.7(47.5)	2
Plot 3	46.7(18.4)	5	35.1(13.8)	6	none	-
Plot 4	- -	-	- -	-	43.2(17.0)	2
Plot 5	- -	-	72.9(28.7)	3	41.4(16.2)	24
Random Walk	51.6(20.3)	6	51.3(20.2)	42	49.0(19.3)	3
Ave. Mean CBH	51.6(20.3)		45.2(17.8)		47.2(18.6)	

TABLE 10

NUMBER OF TREES BELOW 3 METERS IN PHENOLOGY PLOTS ON MAUNA KEA, HAWAII

	6,500-foot Study		7,000-foot Study		7,500-foot Study	
	Mamane	Naio	Mamane	Naio	Mamane	Naio
Plot 1	0	2	1	11	5	0
Plot 2	2	1	1	16	6	0
Plot 3	11	0	1	0	5	0
Plot 4	18	2	4	4	4	0
Plot 5	35	3	1	2	2	16

three elevations is remarkably similar. At 6,500 feet the young trees comprise 24.6% of the total population; 23.9% at 7,000 feet, and 33.1% in the 7,500-foot "exclosure."

The percentage of young of each species mirror the composition of mature trees at each elevation. At 7,500 feet, where almost all the trees (92.4%) are mamane, 26.3% of the trees are young of this species and only 6.8% of the trees are young naio. At 7,000 feet elevation, where 74.4% of the forest is naio, 18.3% of all the trees are young naio and only 5.6% are young mamane. The 6,500-foot area has a very high percentage of young mamane (19.6% as compared to 5.0% of naio) because, as shown in Table 2, the phenology plots are located in a fairly dense region of mamane.

Phenology-mamane: Mamane exhibits a definite bimodal flowering pattern at the three elevations on Mauna Kea. Flowering appears to be limited to the winter and spring months of the year; during late summer and fall flowering ceases at all locations except for a ^{few} widely scattered individuals. There appears to be a more profuse bloom at succeeding higher elevations.

During 1973-1974 the heaviest flowering occurred at 7,500 feet (Fig. 9). The flowering started in early October 1973, increased steadily until the first peak in January, dropped off in February, started a second increase to a late April peak, then fell off rapidly until flowering had almost stopped completely by August 1974. The bloom pattern at 7,000 feet was very similar to that of 7,500, with flowering starting in October and increasing until a January peak (Fig. 10). The drop off in flowering at 7,000 feet seems to be slightly more pronounced and prolonged, with a steady decrease until April, when a second blooming occurs, followed by a steady decline until flowering stops in August. The flowering at 6,500 feet follows the same pattern as the above two areas except that it is not as intense and the period of bloom is shortened (Fig. 11).

Pod production in Sophora during 1974 did not exhibit a uniform pattern as flowering did. In analyzing these data it must be remembered that only pods mature enough to be consumed by the Palila were measured, and, as a result, the graphs do not show when fruiting started. It is necessary to extrapolate back one to two months to find when pods first formed.

The production of edible pods followed flowering by a three to four month period (Figs. 9, 10 and 11). The first flowering peak was in January; the production of pods peaked in April. Where flowering exhibited two distinct peaks (7,000 feet), there were also two distinct peaks of pod production (Fig. 10). At 7,500 feet the bimodal aspect of flowering was not as pronounced and pod production reflected this as it

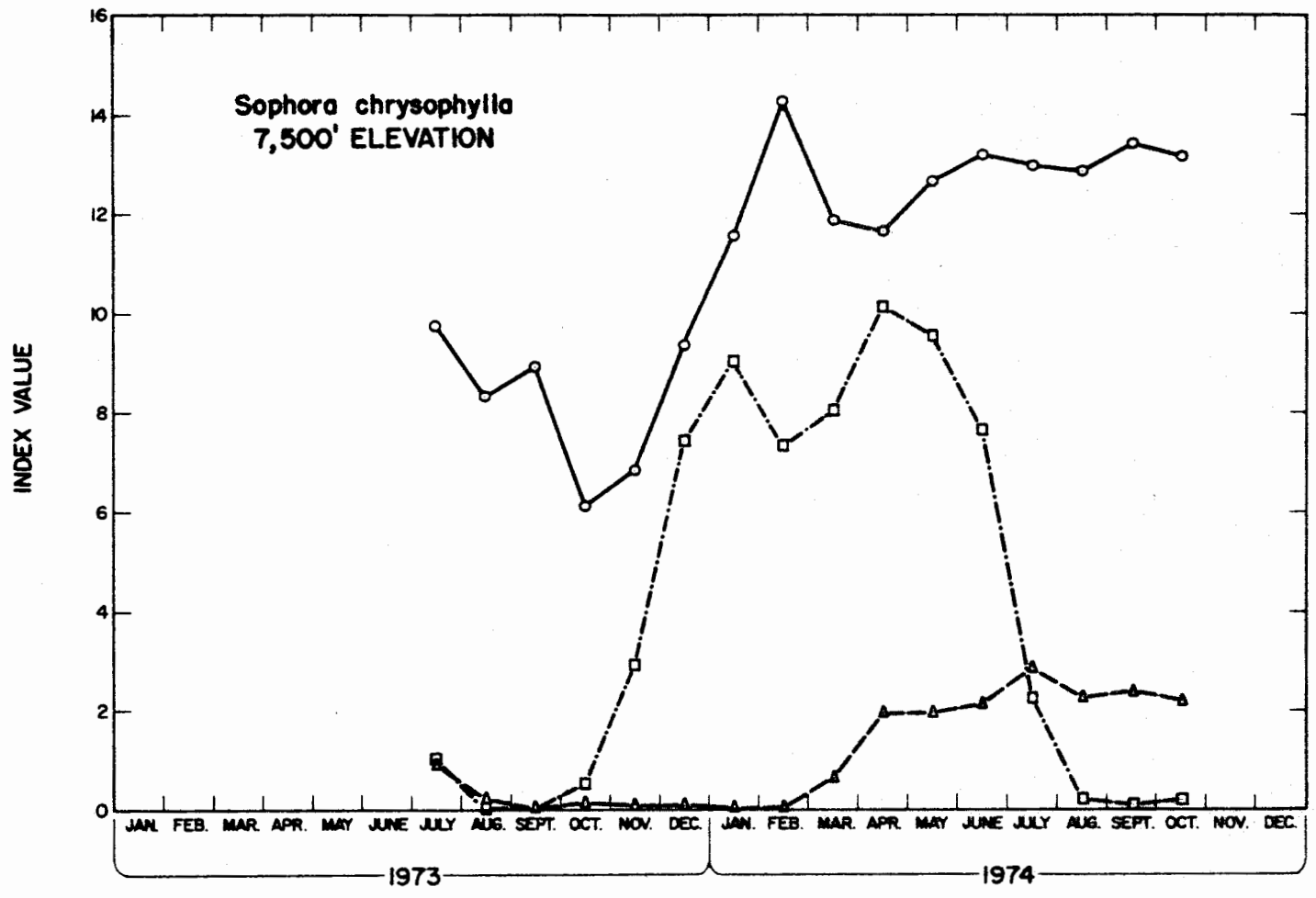


FIG. 9. Phenology graphs of mamane with index values of canopy cover (—), flowering (---), and fruiting (----) for each elevation studied.

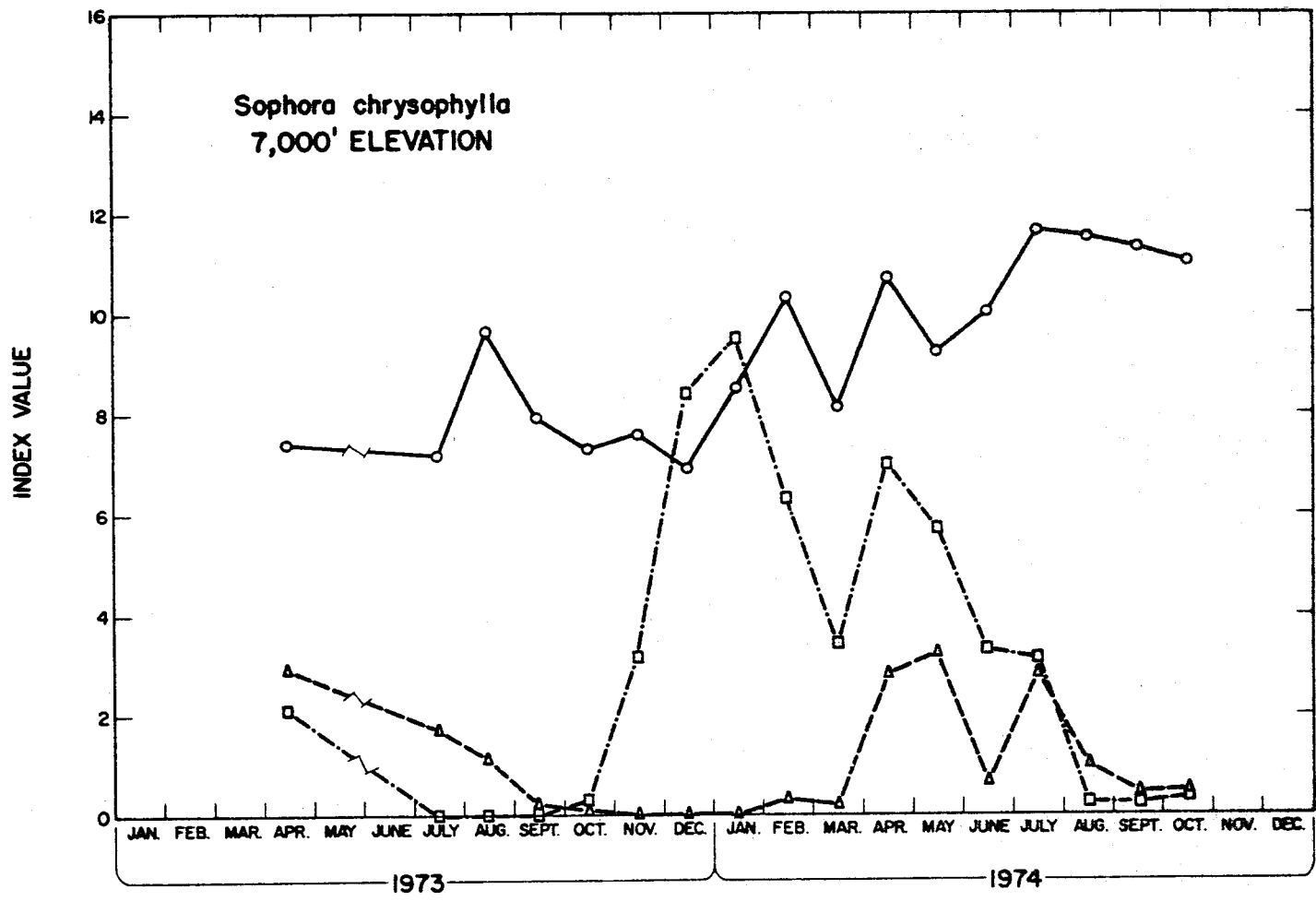


FIG. 10. Phenology graphs of mamane with index values of canopy cover (—○—), flowering (·····□·····), and fruiting (----△----) for each elevation studied.

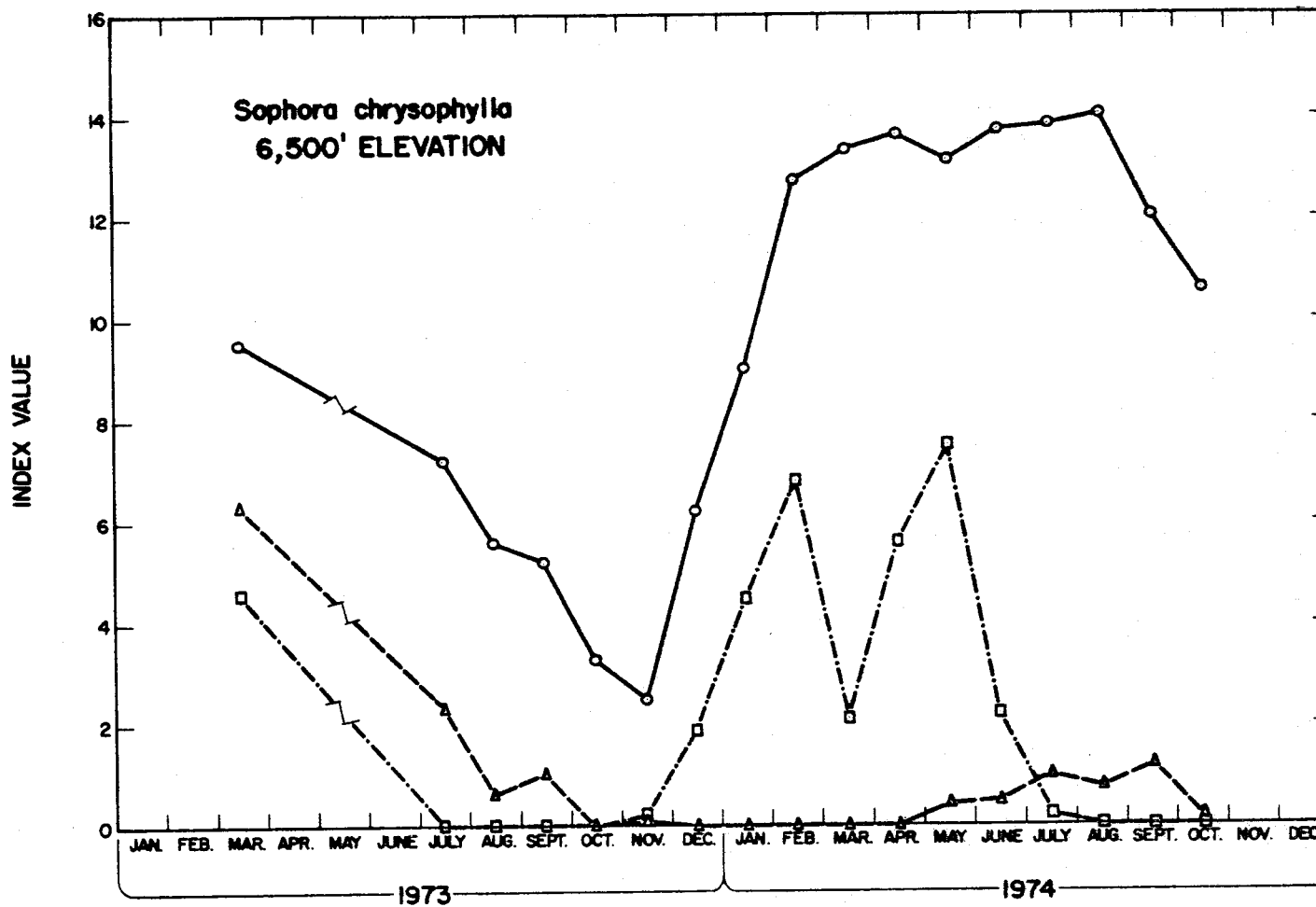


FIG. 11. Phenology graphs of mamane with index values of canopy cover (—○—), flowering (—△—), and fruiting (—□—) for each elevation studied.

remained fairly constant over a six month period from April to September (Fig. 9).

For some reason the pod crop at 6,500 feet was nonexistent in 1974; data from the end of 1973 shows a much heavier fruiting (Fig. 11).

Leaf production and the resulting amount of canopy cover is, at this time, still confusing to interpret (Figs. 9, 10 and 11). During 1974 leaf drop began in summer and continued through late fall; flushing commenced in early winter when heavy rains came to this area. By February the canopy was fairly dense and remained so throughout the following six to seven month period. Loss of canopy was much more pronounced at 6,500 and 7,500 feet than at the 7,000 foot level. The 6,500 foot study area was almost totally denuded of leaves in November of 1973. The general leaf production pattern seems to follow the flowering pattern on Mauna Kea with the canopy becoming more dense as blooming increases.

Phenology-naio: The amount of flowering in naio was much more difficult to measure than mamane, as the flowers are small and inconspicuous. Flowering did occur throughout 1973 and 1974 with major production during the spring and early summer. The bimodal flowering pattern seen in mamane is also present in naio but not as conspicuous. Blooming declined in the fall and the period of minimum flower production was winter (Figs. 12, 13 and 14).

Fruiting occurred throughout the year and thus the pattern is difficult to follow. June was the month of peak production at 6,500 and 7,500 feet, with a gradual increase and decrease for five months on either side. The 7,000 foot area showed exactly the opposite results with a peak in the spring and a low in the summer. It appears that the data collected thus far on the fruiting of naio are not adequate to give any definite pattern.

The naio does not seem to produce pronounced seasonal flushes and therefore canopy cover is not drastically changed throughout the year. The general increase in canopy cover shown by Figs. 12, 13 and 14, I believe, may be due to the heavy rains throughout 1974. If this is not the case, canopy cover would be greatest in late spring, with leaf drop in the fall, but the data are hardly conclusive at this point.

Weather: The southwestern slope of Mauna Kea is in the rain-shadow of the mountain and, as a result, rainfall appears to be a critical factor in regulating the phenological aspects of the area. The average yearly rainfall over the past nine years was 24.2 ± 4.0 inches (1 standard deviation) at Puu Laau; yearly totals do not reveal any cyclic pattern of precipitation in the area, other than ^{after} an extremely dry year the rainfall almost doubles the following year. For instance, 1973 was extremely dry and the

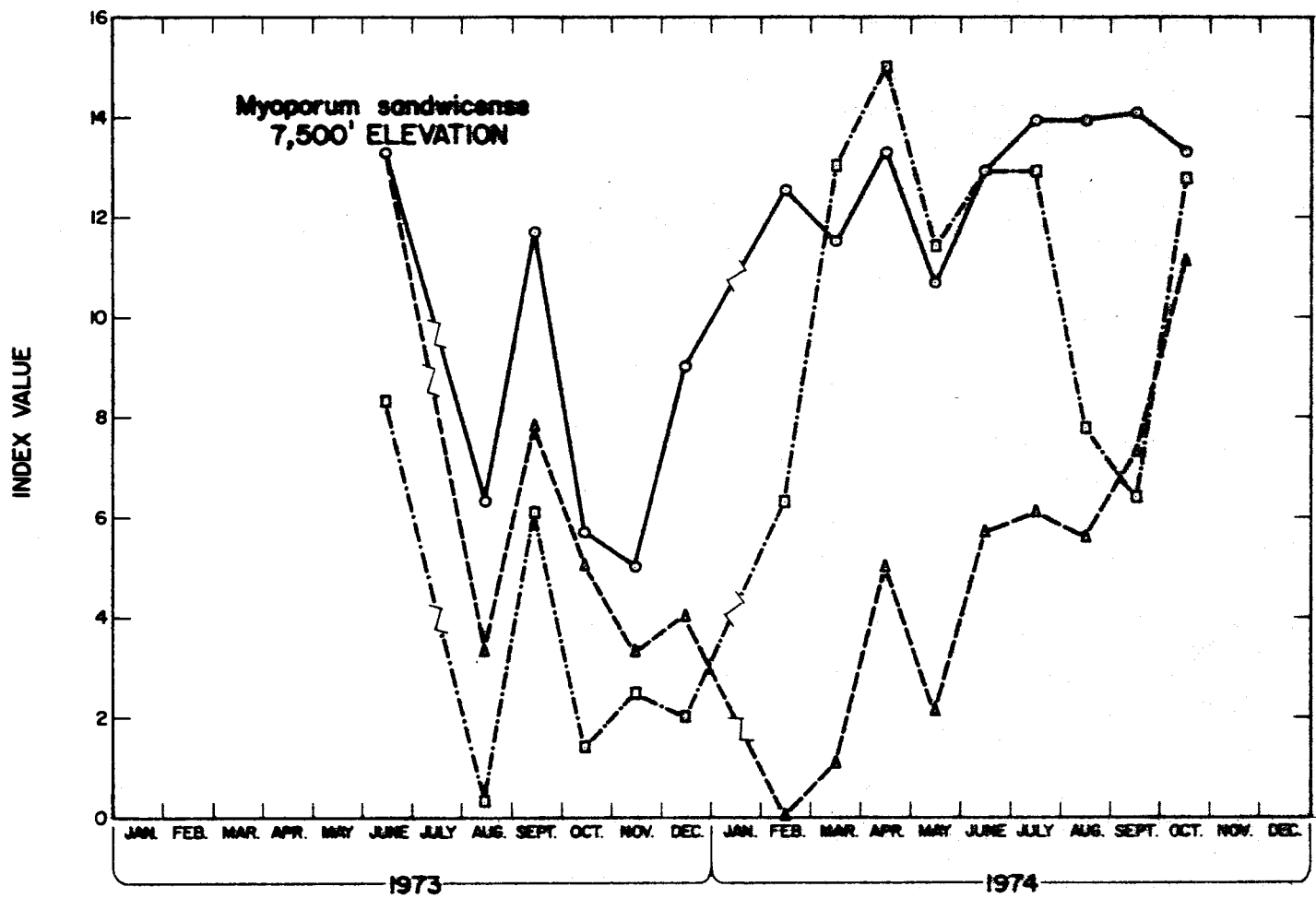


FIG. 12. Phenology graphs of naio with index values of canopy cover (—●—), flowering (—■—), and fruiting (—▲—) for each elevation studied.

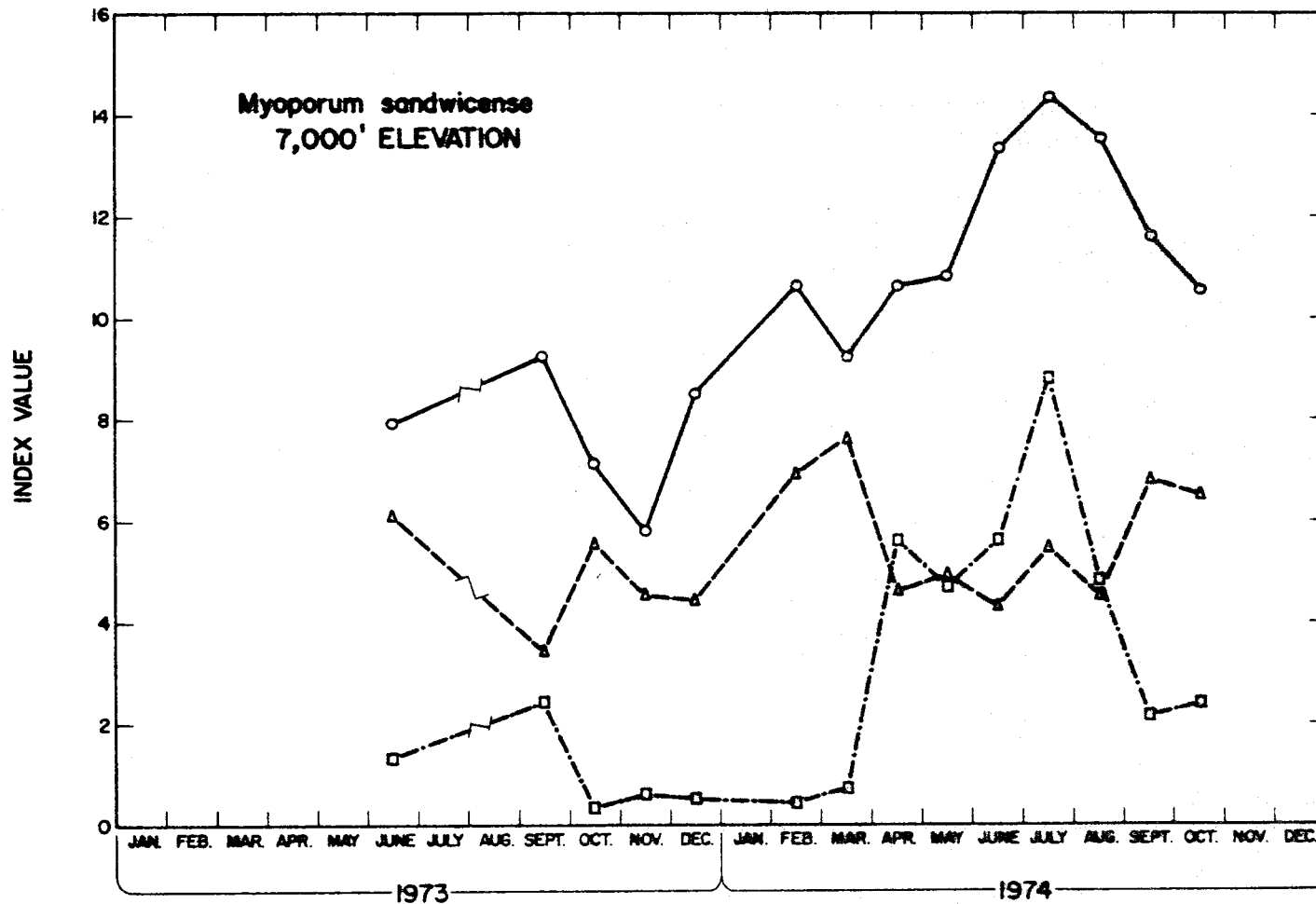


FIG. 13. Phenology graphs of naio with index values of canopy cover (—○—), flowering (---△---), and fruiting (-.-.□.-.) for each elevation studied.

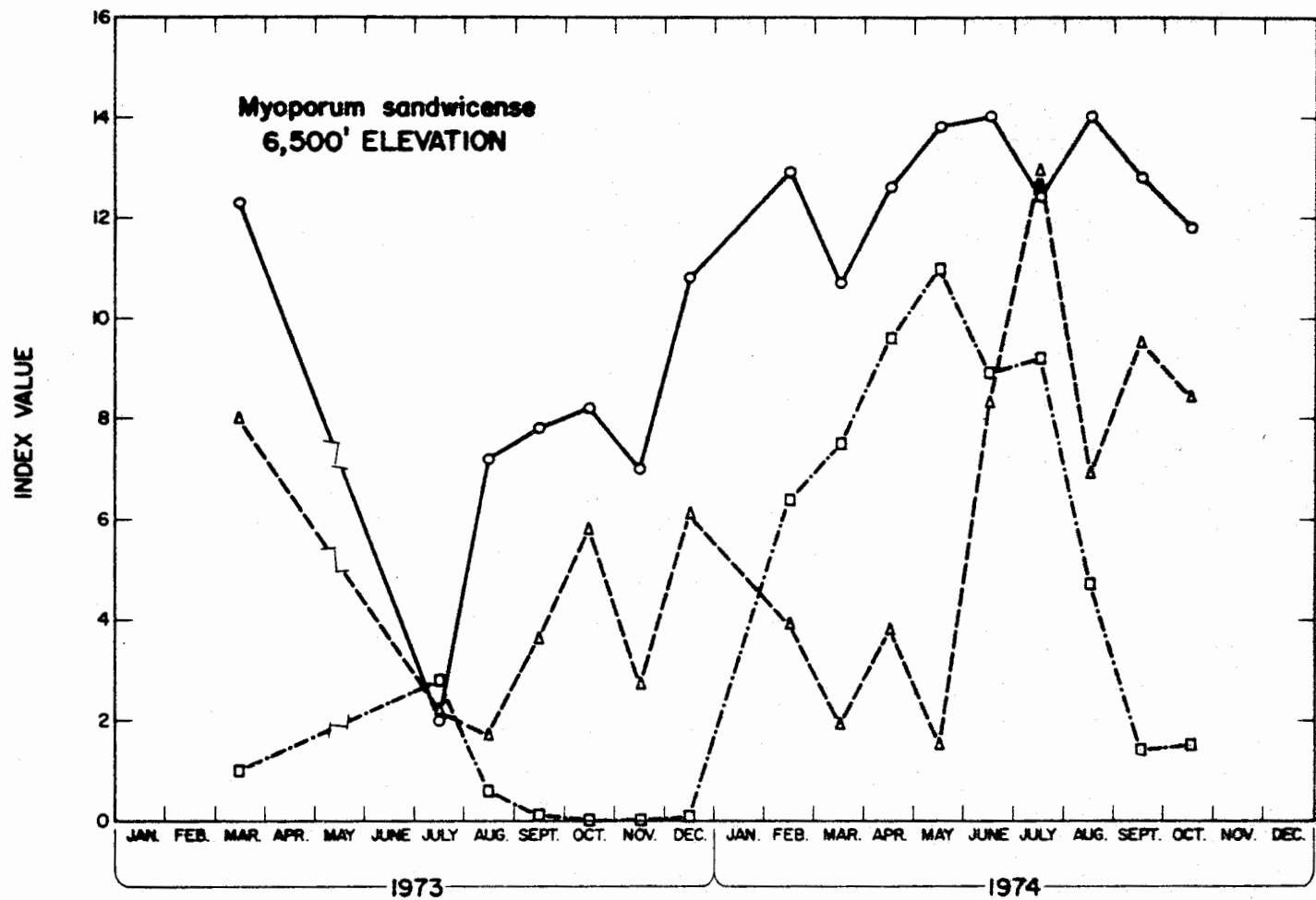


FIG. 14. Phenology graphs of naio with index values of canopy cover (—○—), flowering (---△---), and fruiting (-·-·-□-·-·-) for each elevation studied.

following year more than doubled. Monthly rainfall shows extreme variability with the variance almost as great as the mean each month (Fig. 15).

The daily weather pattern is usually similar with clear mornings and the afternoons clouding over (from 1400 to 1530 hours). During the morning clouds build in the pocket between the Kohala Mountains and Mauna Kea, with the clouds being eventually pushed up to the 7,000 foot area by the constant pressure of the northeast trade winds from below. Only infrequently do clouds ever come around from the Mauna Kea-Mauna Loa saddle area. When clouds come from the southwest, "Kona storms" often occur and are characterized by deluges over short periods of time. April is the most common time for these storms on Mauna Kea as shown by Fig. 15.

Humidity and temperature are quite variable at the higher altitudes on Mauna Kea. Early morning humidity is fairly high (average 60%); mid-day humidity drops to 40%, and in the evening usually rises back to the 90% range. During dry periods the humidity remains between 40% and 60% both day and night (it did this for most of 1973). High temperatures during the day are reached in the late morning and usually lie between 65° and 73°F. At night it cools rapidly and low temperatures range from the 20's in the winter to the low 40's in the summer. Cloud cover has a marked influence on the night-time temperatures; with no cloud cover the temperature drops much lower than if a cover remains through most of the night. The recorded temperatures during 1973 were more variable than 1974 because of the lack of cloud cover for most of 1973.

DISCUSSION

A detailed analysis of relationships between the structure and phenology of the dominant tree species, and the behavior of the avian species will not be attempted until further information is available. However, certain trends are shown with the available data. It is interesting that only a thousand foot change in elevation produces such diverse composition of tree species (Tables 1 through 4). There is no readily available explanation for the drastic change in tree-species composition at the three elevations. It may be that 7,000 feet is an optimum habitat for naio, and at this elevation it outcompetes mamane for limiting resources. Soil depth, drainage, or former grazing pressure (7,400 feet and lower was used by Parker Ranch as pasture for a number of years), may also be factors contributing to these composition differences.

The composition of bird species at different elevations appears to correspond with dominant vegetation. The higher elevations (7,400 feet and above), where mamane is most common, are where I have recorded most Palila and Akiapolaau (Hemignathus wilsoni)

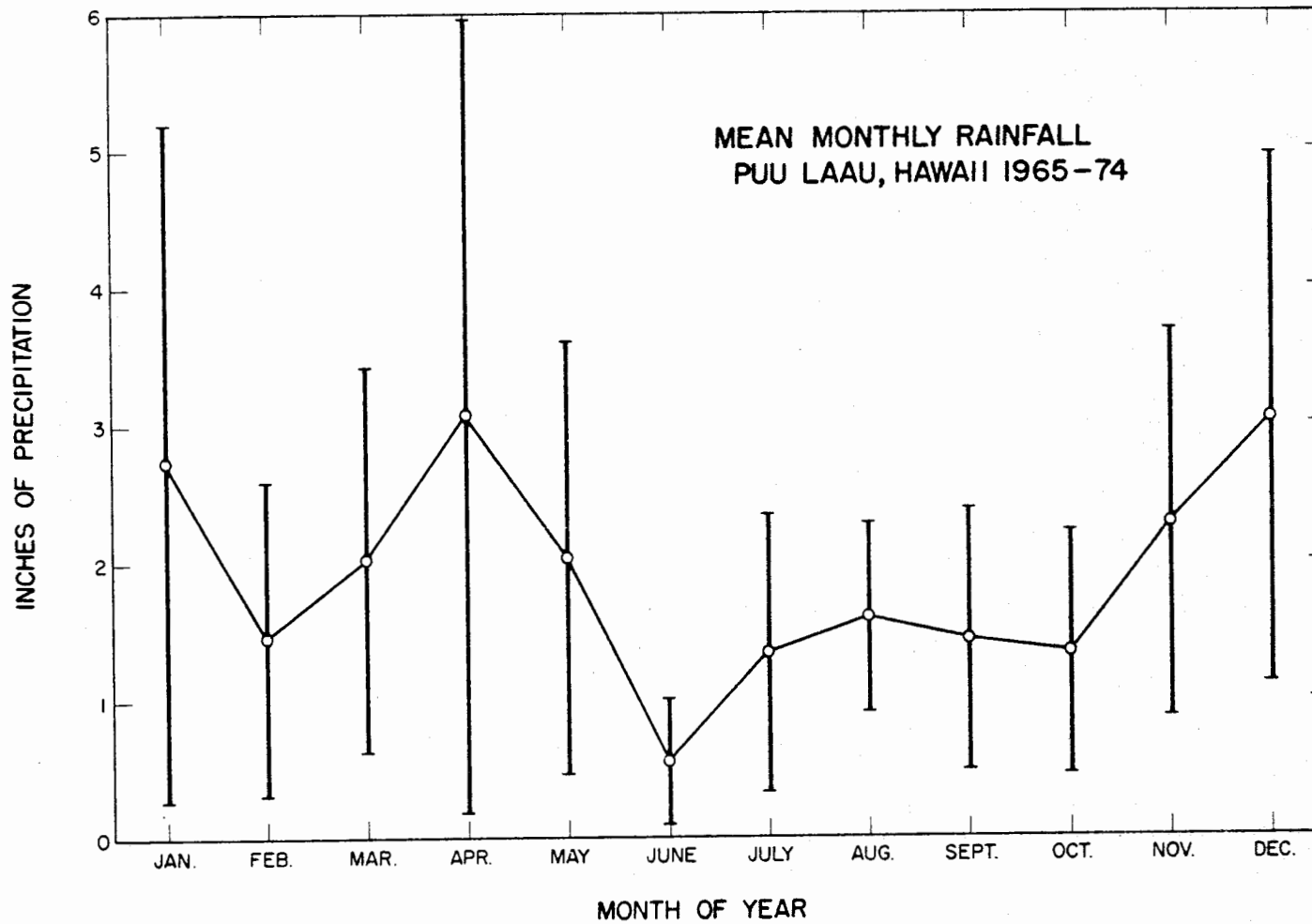


FIG. 15. Mean monthly rainfall in inches at Puu Laau, Hawaii, from January 1965 through April 1974. The lines either side of the mean are one standard deviation.

activity. I have never observed an Akiapolaau below 7,100 feet, and Palila are rarely seen this low. At lower elevations the Elepaio (Chasiempis sandwichensis sandwichensis) is much more common, but this may be due to a change in the insect fauna. The House Finch (Carpodacus mexicanus frontalis) is also very common in the naio belt of this forest (van Riper 1974c). The Amakihi is found abundantly at both higher and lower elevations, but the birds appear to be clustered around stands of mamane whose nectar they use extensively.

Density of mamane and naio decreases as tree height and CBH increase. Characteristic of xerophytic vegetation, this may result because the trees are competing for water. At 7,500 feet and upward the mamane might have developed a much more extensive root system as they are much larger and more widely spaced.

The location of seedlings also suggests that water may be a limiting factor in the environment. Throughout the forest there are natural areas of die-back, usually on the west-facing slopes. When this happens, or when older trees die, the immediate area is sometimes filled with young seedlings; adjacent to this area are scattered old trees with few seedlings present. The loss of the mature tree root systems may enable seedlings to survive due to increased availability of water.

The reproductive success of both mamane and naio at different elevations reflect the amount of sheep-grazing pressure applied to each. The 7,500-foot study area, which is totally enclosed by fence, shows a much higher reproductive rate than do the two study areas which are not enclosed. Areas of the mountain which are inaccessible by jeep have larger concentrations of feral sheep and are completely denuded of vegetation, such as the southwestern and southern slopes at tree line and below. Naio is reproducing in these remote places, but mamane, because it is a preferred browse plant, shows no reproductive success. Unless some immediate measures are taken to control the sheep-grazing pressure, mamane will most likely be completely absent from these sections of the forest in the near future.

My data indicate that the trees on Mauna Kea exhibit seasonality in flowering, fruiting, and leaf fall. Each phenological phase starts gradually and persists over an extended period of time, which is characteristic of many species of trees in tropical regions. There appears to be an inverse relationship between flowering and flushing; it may be that each produces such a drain on the energy reserves of the tree that only one can be carried on at a time. Some trees do, however, flower and flush at the same time. Seeds drop all year long and brown pods have remained up to three years on some of my tagged trees.

The phenological data of Baldwin (1953) and Lamoureux (1973) are similar to mine except for minor differences. Lamoureux records only one flowering peak at lower elevations, whereas all three of my study sites exhibited a bimodal flowering pattern. My spring "flush" at 6,500 feet was not as great as Lamoureux records, although all of my plots do exhibit two annual flushes as his did. My study sites are located at higher elevations than those of Lamoureux, and this may account for difference in our findings, as may variations in rainfall and temperature patterns between Mauna Kea and Mauna Loa.

One of the most striking results of my 1974 phenological data on Mauna Kea is the almost total absence of pods at 6,500 feet. During 1974 precipitation was much higher than normal and came, for the most part, from Kona storms. Because the northwestern slope of Mauna Kea faces Kona, the lower elevations would receive the majority of the rain from these storms. I have recorded many trees that did not bloom all year and others that bloomed profusely but produced no pods. There may be some relationship between the high rainfall and the subsequent rotting of fruit on the trees. The heavy rains might also have inhibited the pollination of the mamane blossoms.

Precipitation correlates well with the flowering period in mamane, and may possibly trigger this phenophase. Table 11 shows that December through January and April are the two times of greatest precipitation; correspondingly, the bimodal flowering asymptotes occur in December-January and April-May. The nesting data I have thus far on the Amakihi show nesting peaks in December and May. Further study may reveal a close relationship between these three events.

At present it does appear that the breeding season of the Amakihi follows closely some of the phenophases in mamane. Mamane is a favored nesting tree in this area (Berger 1969b, 1972; van Riper 1973, 1974a, 1974b, 1974c). Flushing in mamane starts well before the inception of nest building; at the start of nesting, canopy cover is at its maximum and remains fairly dense throughout the nesting cycle. The extended bloom period of this species seems to correspond with the protracted breeding season of the Amakihi. Blooming mamane can be found from November to July, and Berger (1969) reports the breeding season of the Amakihi to be from October to May in this area. I have found that Amakihi nest from October in some years and continuing until August in others; the majority of nesting occurs from December through May. When the bloom in an area ceases, there is an exodus of Amakihi to other areas of microbloom, with only a few residents remaining.

The phenology of mamane is also closely tied to the life cycle of the Palila.

Many authors comment on the predilection for mamane pods by the Palila (Perkins 1903; Rothchild 1893-1900; Henshaw 1902, Munro 1944; Berger 1972). The only published records of active Palila nests are those of Berger (1970), who found a nest with eggs in July and Wilson and Evans (1890-1899) who found an empty nest in mid-June. My phenology data at present show edible pods present from March through August-September, which is the same time of year the Palila nests.

The phenophases of naio do not show a clear pattern for the short amount of time they were studied, and it is therefore hard to determine any relationship between this species of tree and bird activity. I have noticed two phenological phenomena of naio that tie well into behavioral aspects of the bird species on Mauna Kea. The flowering period in naio is later than that of mamane and extends well into the fall. The blossoms are small, and therefore most likely give less nectar than mamane. The "permanent resident" Amakihi rely heavily upon these blossoms after the cessation of mamane bloom in an area. Almost all of the recorded sightings of Amakihi feeding upon naio blossoms have come in the months of minimum mamane bloom.

Fruiting in naio shows no particular pattern at present. Heaviest berry production seems to occur in summer and fall, but ripe fruit can be found on some trees in any month of the year. Although not the major diet of any extant bird, the naio berry becomes extremely important during the drier periods of the year. I have recorded heaviest utilization of this berry by the Palila in the fall and winter months when green mamane pods are absent on Mauna Kea. The House Finch rely heavily upon these berries in the early spring and summer. During the severe drought of 1973, wild turkey (Meleagris gallopavo) consumed a large number of these berries, as the roosts had piles of naio seeds beneath. The flower and fruit of the naio do seem to serve a supplemental food role for some of the birds on Mauna Kea.

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