The Phenology of the Dryland Forest of Mauna Kea, Hawaii, and the Impact of Recent Environmental Perturbations

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ABSTRACT

The forest of Mauna Kea, Hawaii, was studied from 1973 through 1975 in order to define composition and phenology patterns of the two dominant tree species, and to determine the influence of man and feral mammals upon the ecosystem. There was a significant change in tree species composition across a 150 m elevational gradient; soil characteristics, drainage conditions, past disturbances by man, and browsing pressure by feral mammals are suggested as possible reasons. Although species composition varied with elevation, the tree density did not change. The phenological patterns of *Sophora chrysophylla* were found more closely tied to the weather pattern than were those of *Myoporum sandwicense*. Methods of pollination and seed dispersal were different between *Sophora* and *Myoporum*, and the spread of the latter is thought to be related to increased seed dispersal by recently introduced avian species, in conjunction with the limitation of *Sophora* reproduction due to browsing pressure by feral sheep. Because of the changes that are affecting the ecological organization of this community, the forest and its associated fauna need to be carefully examined in terms of present management policies.

ONE OF THE LAST REMAINING NATIVE DRYFOREST ECOSYSTEMS in Hawaii is composed of 12,000 hectares of high mountain savanna on the southwestern slope of Mauna Kea. *Sophora chrysophylla* (Leguminosae) and *Myoporum sandwicense* (Myoporaceae) are the most abundant trees, with scattered stands of *Euphorbia olowaluana* (Euphorbiaceae), *Santalum ellipticum* (Santalaceae), *Dubautia arborea* (Compositae), and two small plantings of introduced pine, eucalyptus, and cedar. Shrub and ground-cover species are considered elsewhere. No one has described the phenology of this forest although Hartt and Neal (1940) gave a species account of the vegetation on the eastern slope of Mauna Kea.

This ecosystem has been greatly influenced by the activities of man and introduced animals for the last 100 years (Warner 1960). Until the 1950's Parker Ranch grazed horses and cut *Sophora* for fence posts. Since the 1820's herds of feral sheep have roamed these volcanic slopes eliminating much of the *Sophora* reproduction by destroying the younger trees (Giffin 1976). Because of these perturbations, information was desperately needed on the present condition of the forest. This study was undertaken from April 1973 through August 1975 to compare forest composition and reproductive strategies of the two primary tree species (*Sophora* and *Myoporum*) in an effort to understand ecological interactions and influences on the forest as it exists today.

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METHODS

Study sites were selected on the southwestern slope of Mauna Kea at elevations of 1980, 2130, and 2290 m along the jeep road from Kilohana to Puu Laau (fig. 1). The 1980 and 2130 m sites were open to grazing by feral sheep, while the 2290 m study site was fenced on all sides. Five contiguous 30 x 30 m relevés, arranged in the shape of a T, were arbitrarily established near the center of each study site. All trees taller than 2 m (the height when *Sophora* and *Myoporum* first flower) were numbered, tagged, and, with the aid of a grid system, recorded on a map. Circumference at breast height (CBH) measured 1.4 m above the ground, was determined with a tape measure, and total tree height was measured with a clinometer.

Canopy density, flowering, and fruiting were measured monthly (see Lamoureux 1973, Frankie *et al.* 1974). Canopy density was determined by standing under each tree and recording the percentage of open sky observed. Flowering and fruiting were measured by estimating the number of available terminal branches on each tree, and recording the percentage of those that possessed fully opened flowers or mature ripe fruit. To offset the phenomenon of trees in one area being in heavy flower while 500 m away others lacked blossoms, every month I systematically walked across each study area outside the relevés, measuring the nearest tree each 30 m until 50 trees had been considered. These data were then added to those obtained from the relevés.

With the density of trees and intensity of flowering known, it was possible to extrapolate the yearly

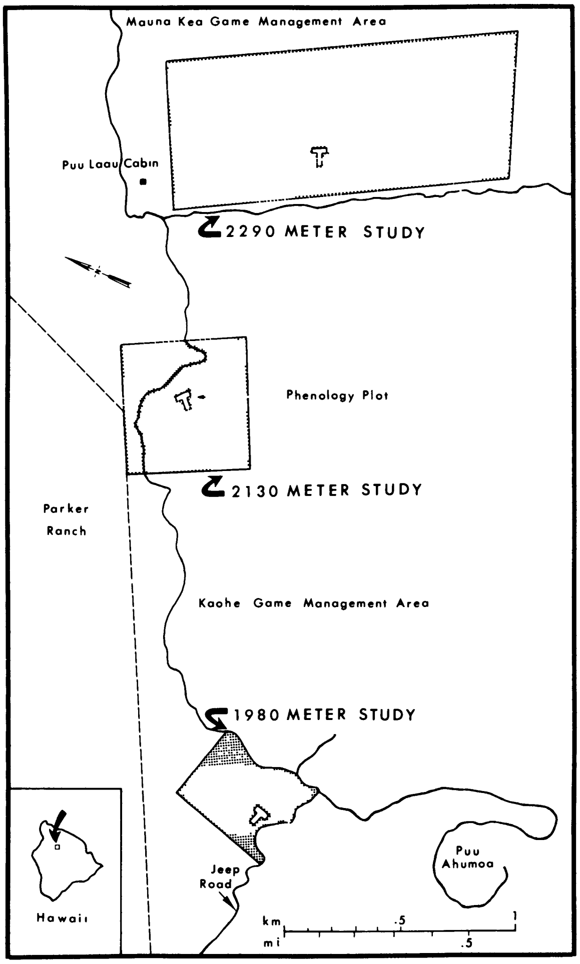

FIGURE 1. Map showing location of study area on the island of Hawaii, the study sites at 1980 m, 2130 m, and 2290 m, and the phenology relevés.

relative amount of flowering or productivity of each study location using the following formula:

$$P_j = I_j \cdot T_j \cdot M_j \cdot D_j \qquad (1)$$

where, $P =$ relative yearly flower production; $j =$ elevation location; $I =$ mean monthly percentage of flowering; $T =$ total number of mature trees in all relevés; $M =$ percentage of *Sophora* or *Myoporum* trees; and $D =$ relative canopy size. Total fruit production (S) for each elevation was calculated in the same manner except that percent fruiting (F) was substituted for percent flowering (I), giving the equation

$$S_j = F_j \cdot T_j \cdot M_j \cdot D_j \qquad (2)$$

To take into account the variability in size among *Sophora* trees at each elevation, their mean circumferences were compared to that for trees at 1980 m; CBH at 2130 m was 1.3 times as great and 2290 m was 2.0 times as great. This conversion was not necessary for *Myoporum* as the CBH was similar at all study sites. Weather data were collected at 2290 m; monthly temperatures were recorded with two maximum-minimum thermometers and rainfall with a National Weather Service rainfall gauge.

RESULTS

WEATHER.—The daily weather pattern was usually predictable, with clear mornings and clouds forming about 1530 h. Temperature fluctuations between day and night were approximately 20°C, and although monthly high-low temperatures were similar throughout the year, there was a slight warming trend from June through October (fig. 2). Cloud cover during 1973 was sparse, and the range of recorded temperatures was larger than in 1974 or 1975.

The southwestern slope of Mauna Kea is in a rain shadow, and all the study sites were above the inversion layer. This meant there was much less rainfall, and lower humidity, than in other areas on the mountain. The average yearly precipitation from 1932 through 1972 was 51.1 ± 18.3 cm; generally there was a pattern of high precipitation in December-January and in April, but yearly variances were great (fig. 3). The wet season usually extended from November to April and the dry season from May to October, although there was an unusual drought during 1973.

FOREST COMPOSITION.—Relative composition of the woods studied varied among the three study sites (fig. 4). At 1980 m *Sophora* comprised 48.2 percent of the forest and *Myoporum* 51.5 percent, at 2130 m *Sophora* abundance decreased to 26 percent and *Myoporum* made up the rest, and at 2290 m the forest consisted primarily of *Sophora* (91.5%) with *Myoporum* contributing only 8.2 percent. Because original numbers were percentages which varied extensively, I used an arc-sin transformation of the data (Snedecor and Cochran 1972); these differences at each elevation were significant (analysis of variance, $P < 0.05$).

TREE DENSITY.—The number of *Sophora* and *Myoporum* trees at each elevation is given in table 1. The highest mean tree density (5.5 trees/100 m^2) occurred at 1980 m; at 2130 m and 2290 m it was 4.0 and 2.5 trees per 100 m^2, respectively. There was no significant difference in the density of trees (both species pooled) between elevations (one-way analysis of variance, $P = 0.34$).

TREE HEIGHT AND CIRCUMFERENCE.—There was a significant increase in tree height of *Sophora* at higher elevations, the trees averaging 1.7 m taller at 2290 m than at 1980 m (one-way analysis of variance, $P < 0.01$). The circumference at breast height of *Sophora* also increased with elevation ($P < 0.05$), showing a mean difference of 48.5 cm between 1980 and 2290 m (table 3). *Myoporum* increased only 1 m from the lower to the upper study site (table 2),

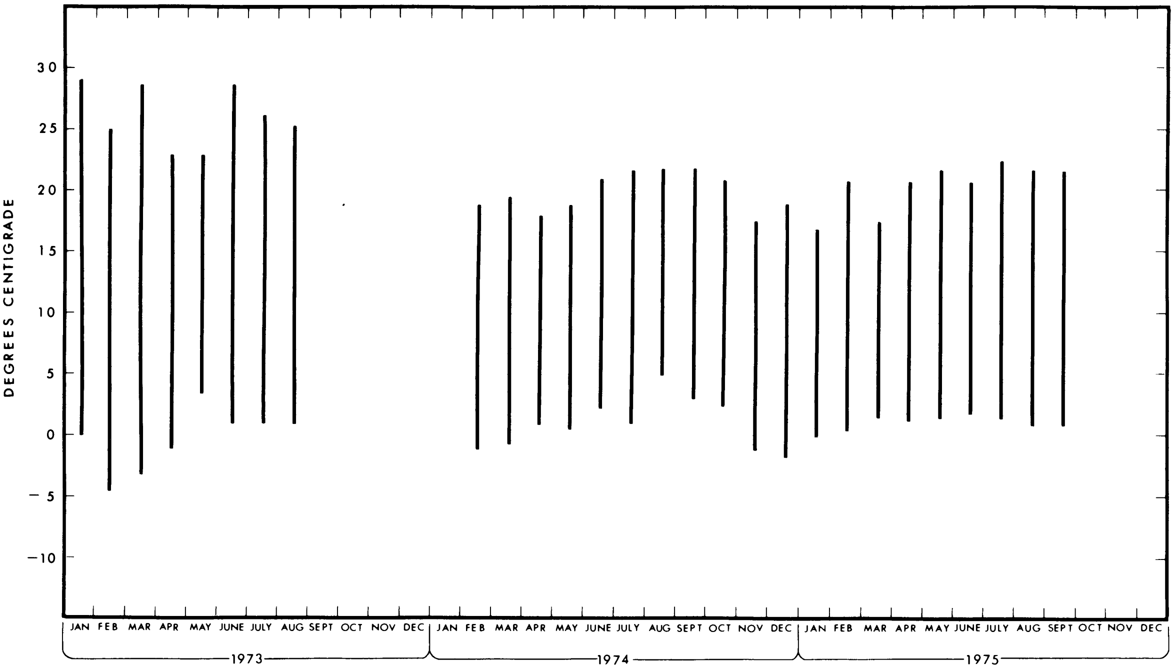

FIGURE 2. Monthly temperature ranges at 2290 m on Mauna Kea, Hawaii.

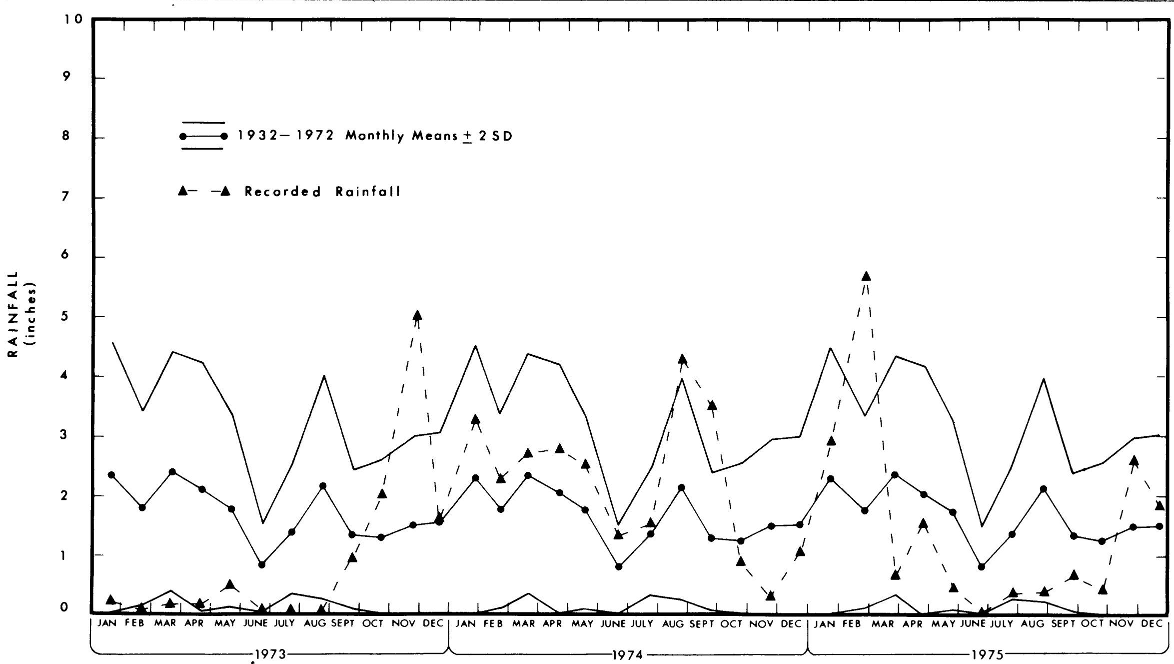

FIGURE 3. Mean precipitation over a 40-year period and recorded rainfall from 1973-1975 at Puu Laau on Mauna Kea, Hawaii.

and the variability in circumference of *Myoporum* among study sites was not significant.

RATIO OF MATURE TO IMMATURE TREES.—The ratio of mature to immature trees for *Sophora* and *Myoporum* was determined for each relevé (table 1). When counting, all trees less than 2 m high were considered immature because they rarely produce

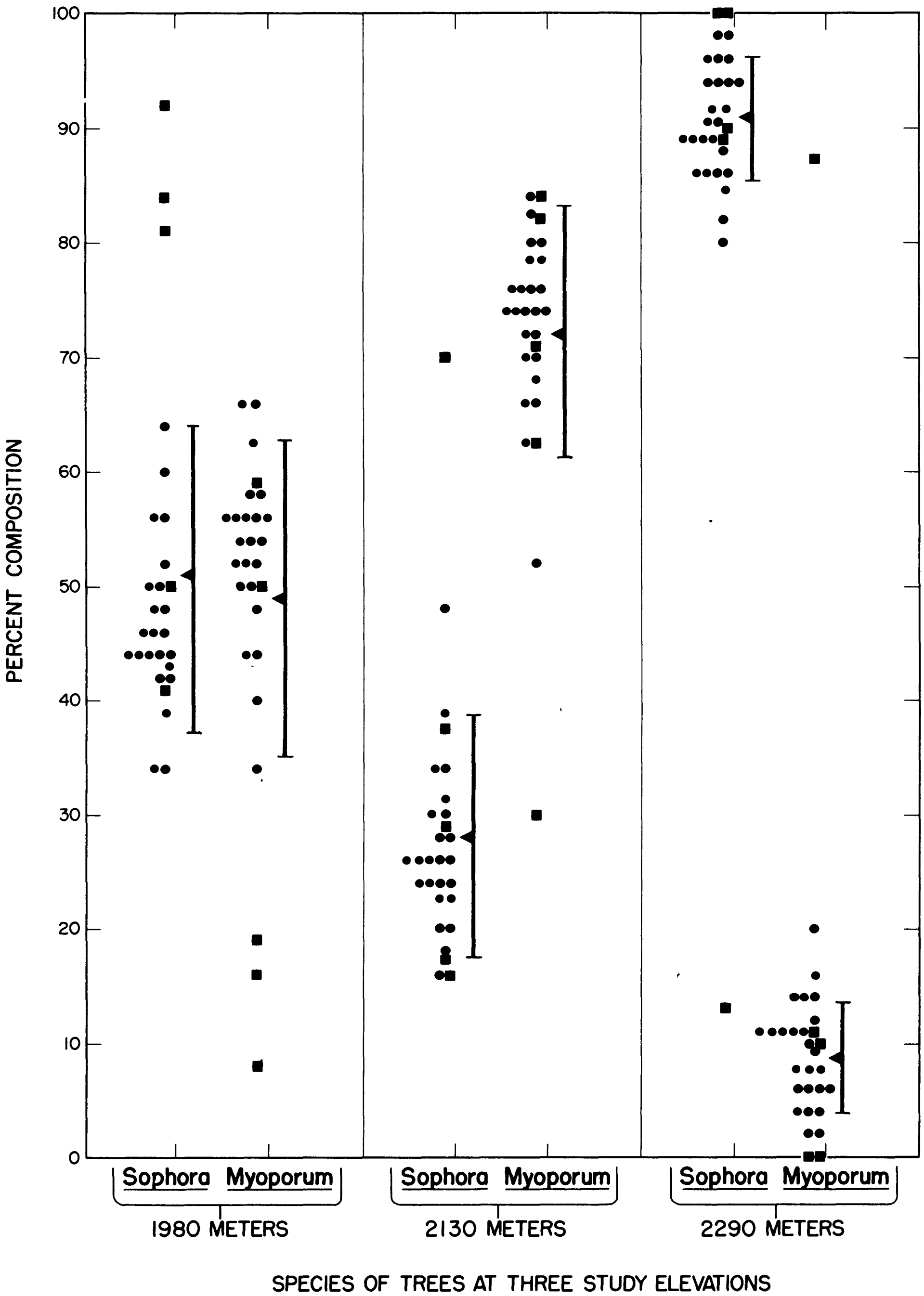

FIGURE 4. The percent forest composition of *Sophora chrysophylla* and *Myoporum sandwicense* at 1980 m, 2130 m, and 2290 m on Mauna Kea, Hawaii. Squares represent quadrat data, circles monthly walks through study sites; triangles are means, lines ± 2 SD.

flowers or fruit. The immature trees comprised 28.8 percent (26.5% *Sophora*; 2.3% *Myoporum*) of the forest at 1980 m, 20 percent (3.8% *Sophora*; 16.2% *Myoporum*) at 2130 m, and 30.2 percent (19% *Sophora*; 11.2% *Myoporum*) at 2290 m.

PHENOLOGY OF *Sophora*.—*Sophora* flowering was limited roughly to November through June, but a few widely scattered individuals with blossoms could be found during any month (fig. 5). Mature *Sophora* fruit followed flowering by three to four months in 1974 and by two to three months in 1975 (fig. 6). Generally, the intensity of flowering affected the amount of pod production: for example, in 1975 a tremendous blossom production at 1980 m gave rise to a large pod crop, while in 1974 at 1980 m a small amount of flowering yielded a small pod crop. Density of canopy or vegetative growth appeared to be influenced more by precipitation than by the time of year (fig. 7).

TABLE 1. *Number of mature* (over 2 m) *and immature* (under 2 m) *trees in relevé.*

		Sophora		*Myoporum*		Total	
Elevation	Quad.	Mat.	Immat.	Mat.	Immat.	Mat.	Immat.
1980 m	1	10	2	1	0	11	2
	2	15	2	3	1	18	3
	3	15	11	5	0	20	11
	4	15	18	45	2	60	20
	5	21	35	53	3	74	38
2130 m	1	13	1	25	10	38	11
	2	7	0	24	14	31	14
	3	13	1	6	0	19	1
	4	7	4	48	4	55	8
	5	2	1	3	2	5	3
2290 m	1	15	5	0	0	15	5
	2	10	6	2	0	12	6
	3	5	5	0	0	5	5
	4	4	2	28	13	32	15
	5	15	4	2	0	17	4

TABLE 2. *Mean tree height* (in m) *of mature* Sophora *and* Myoporum *on Mauna Kea, Hawaii. Parentheses indicate number of trees measured.*

	1980 m		2130 m		2290 m	
Relevé	*Sophora*	*Myoporum*	*Sophora*	*Myoporum*	*Sophora*	*Myoporum*
1	6.6 (10)	8.7 (1)	6.2 (12)	6.4 (24)	7.1 (15)	— (0)
2	5.3 (14)	6.6 (3)	5.8 (6)	6.1 (20)	7.0 (10)	8.6 (2)
3	4.9 (15)	5.9 (5)	5.4 (14)	5.8 (6)	6.1 (5)	— (0)
4[a]	5.5 (15)	5.7 (44)	6.3 (7)	6.5 (48)	(0)	(0)
5	4.9 (21)	5.5 (53)	5.0 (2)	5.5 (3)	7.3 (15)	6.2 (2)
Study Area	6.3 (10)	7.1 (6)	5.2 (8)	5.7 (42)	7.2 (47)	5.7 (3)
Average Mean Height	5.4	5.7	5.7	6.2	7.1	6.7

[a]The tree ratio in relevé four at 2290 m was unusual for the elevation, and when combined with other plot data created a biased composition; for this reason data were eliminated in calculations.

PHENOLOGY OF *Myoporum*.—Flowering occurred throughout most of 1974 with major blossom production during the dry period from April to August (fig. 8). This species fruited from May 1974 throughout May 1975, with very few fruits found during the six-month intervals before and after this period. In each year, inception of fruiting occurred first at either 2290 m or 1980 m (fig. 9). Vegetative growth occurred throughout the first part of the year, with canopy density greatest from May through August (fig. 10).

PRODUCTIVITY.—Productivity at each study site was calculated using formulas (1) and (2) in addition to data from intensity of flowering and fruiting of individual trees (table 4). *Sophora* usually produced about six times as many blossoms as pods. The fruits of *Myoporum* remain on the tree for a much longer

TABLE 3. *Mean circumference at breast height* (in cm) *of mature* Sophora *and* Myoporum *on Mauna Kea, Hawaii. Parentheses indicate number of trees measured.*

	1980 m		2130 m		2290 m	
Relevé	*Sophora*	*Myoporum*	*Sophora*	*Myoporum*	*Sophora*	*Myoporum*
1	60.7 (10)	71.1 (1)	65.5 (12)	40.4 (24)	92.7 (15)	— (0)
2	40.6 (15)	52.6 (3)	73.4 (6)	26.6 (20)	64.0 (10)	120.7 (2)
3	48.5 (15)	46.7 (5)	55.1 (9)	35.1 (6)	63.5 (5)	— (0)
4	— (0)	— (0)	— (0)	— (0)	68.1 (4)	41.1 (24)
5	— (0)	— (0)	36.8 (2)	72.9 (3)	64.0 (15)	43.2 (2)
Study Area	46.2 (10)	51.5 (6)	56.6 (8)	51.3 (42)	121.2 (47)	49.0 (3)
Average Mean Height	48.0	51.6	60.7	45.2	96.5	47.2

time period than do blossoms, a circumstance which accounts for the higher fruiting value at some locations. However, the closer similarity of *Myoporum* flower and drupe production indicates that this species has a higher seed set than does *Sophora.*

DISCUSSION

The forest today on Mauna Kea is a unique ecosystem with *Sophora* and *Myoporum*, the two dominant tree species, utilizing different mechanisms of reproduction and responding differently to the same environ-

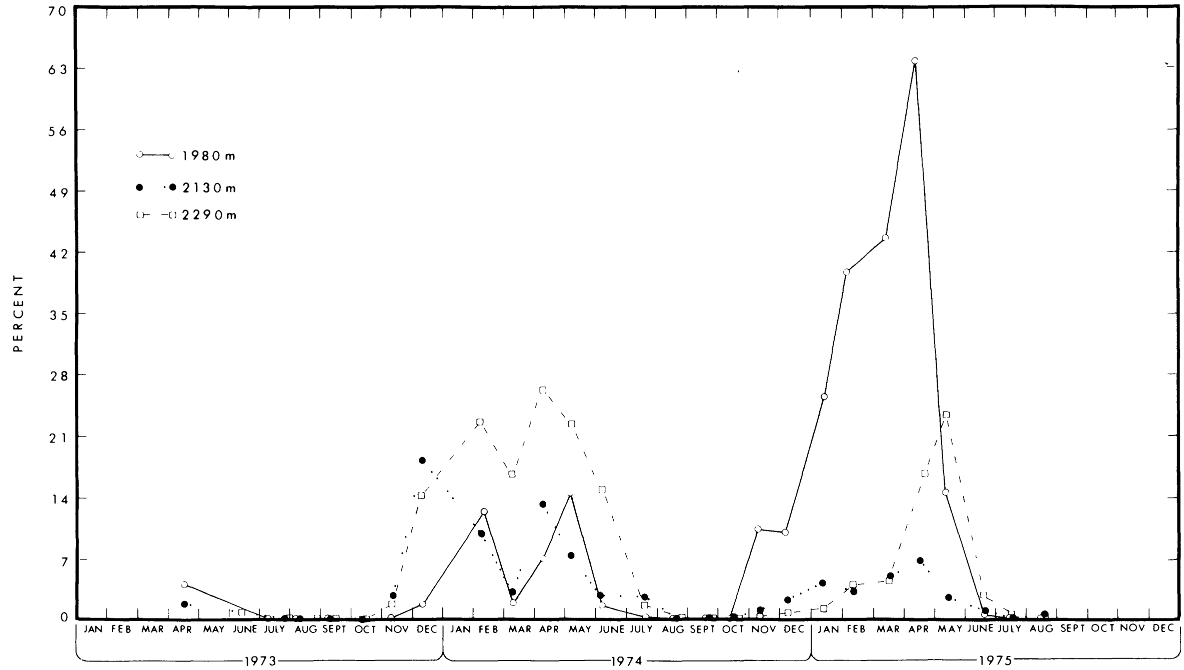

FIGURE 5. Percent of flowering per *Sophora chrysophylla* tree from 1973-1975 in study relevés on Mauna Kea, Hawaii.

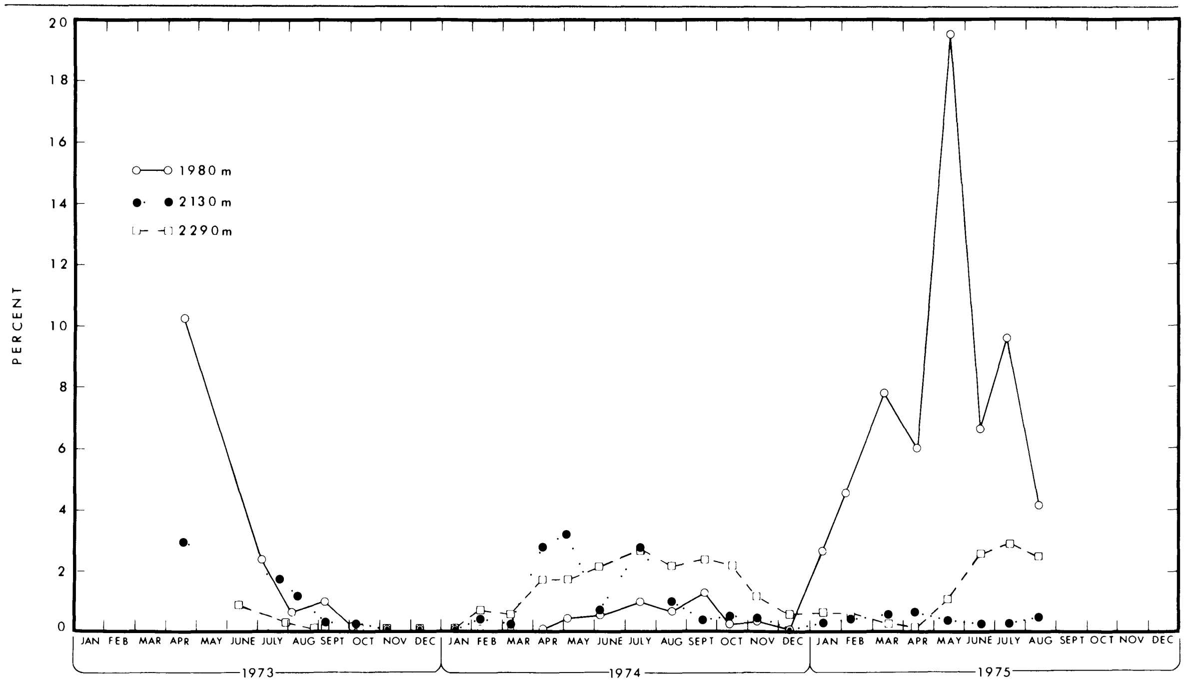

FIGURE 6. Percent of fruiting per *Sophora chrysophylla* tree from 1973-1975 in study relevés on Mauna Kea, Hawaii.

mental conditions. What appears most important, however, is the inability of *Sophora* to cope with the browsing pressure exerted by introduced feral sheep (Giffin 1976). To understand the ecology of this area, abiotic as well as biotic factors must be considered in terms of their combined pressure on the forest.

It is evident that forest composition of Mauna Kea has changed dramatically over recent years. At one time the area must have been composed of a

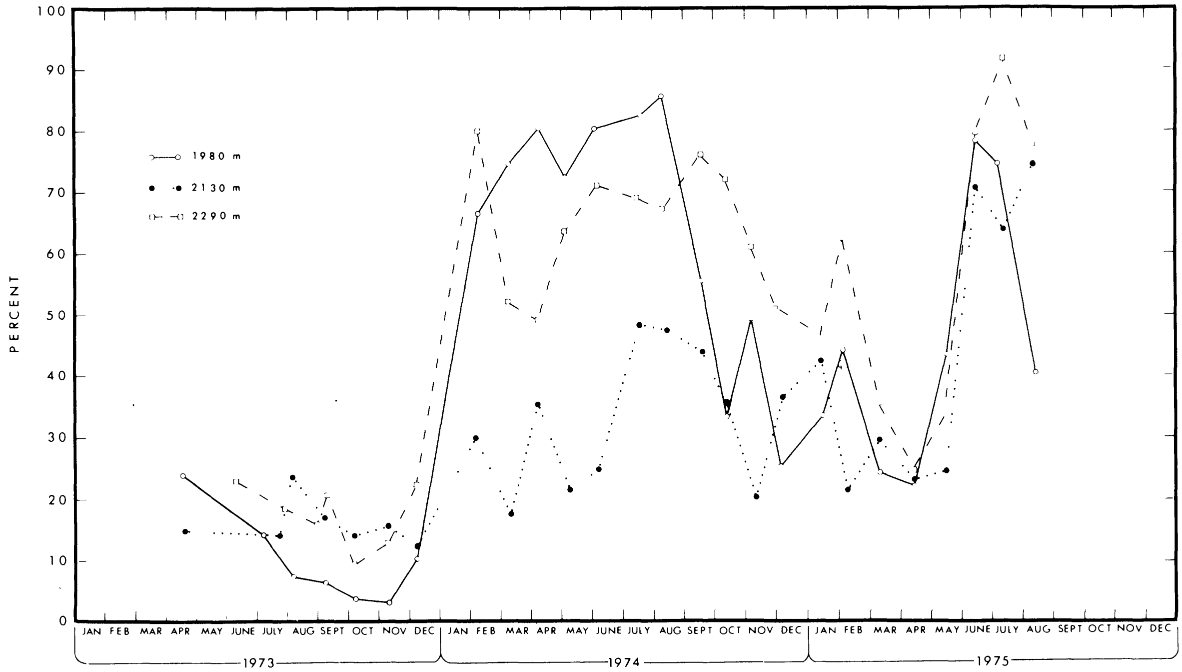

FIGURE 7. Percent of canopy cover per *Sophora chrysophylla* tree from 1973-1975 in study relevés on Mauna Kea, Hawaii.

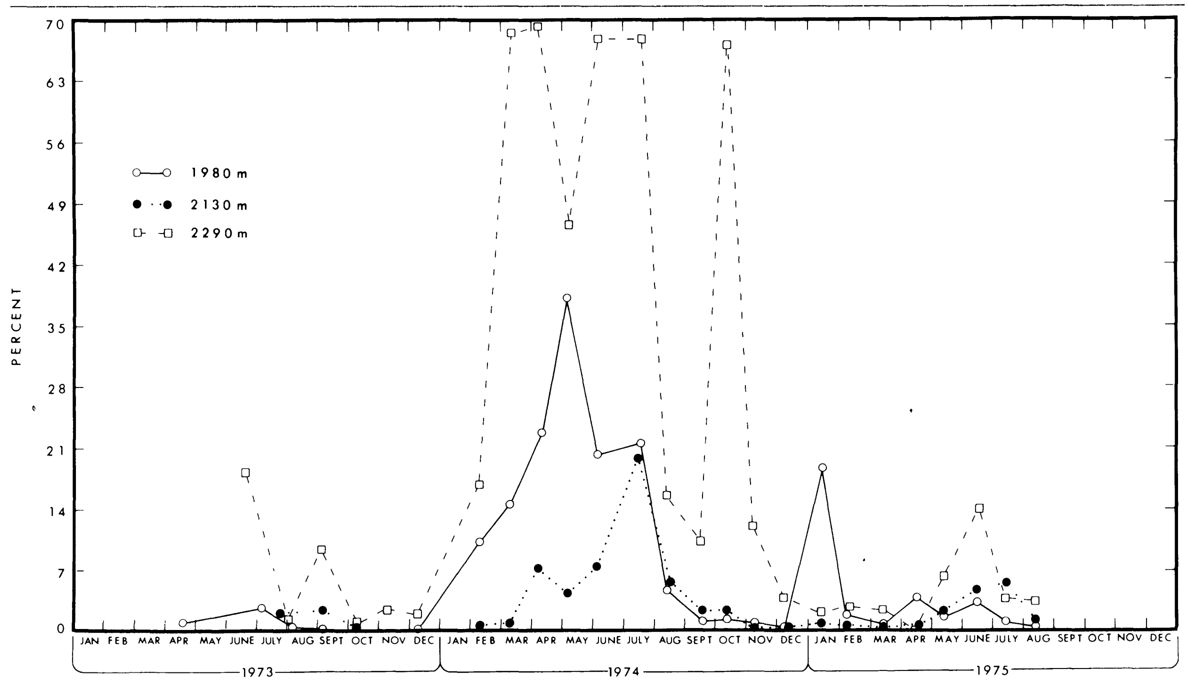

FIGURE 8. Percent of flowering per *Myoporum sandwicense* tree from 1973-1975 in study relevés on Mauna Kea, Hawaii.

variety of trees, as small remnant pockets of these now rare species can be found scattered around the mountain. *Santalum* was cut extensively for export (Rock 1913); *Euphorbia* is restricted to rocky outcrops; and *Dubautia* is found only on the sides of steep gullies, where sheep and cattle cannot reach it. Because *Myoporum* is not a preferred browse species, the trend in the forest today is for the tree to in-

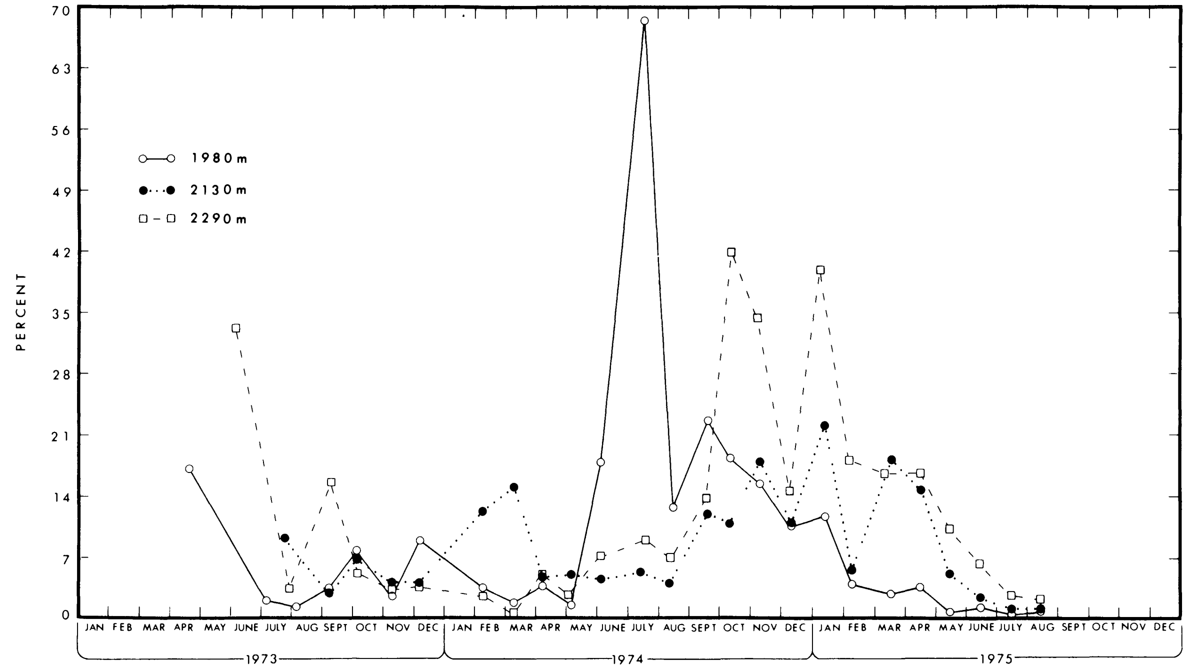

FIGURE 9. Percent of fruiting per *Myoporum sandwicense* tree from 1973-1975 in study relevés on Mauna Kea, Hawaii.

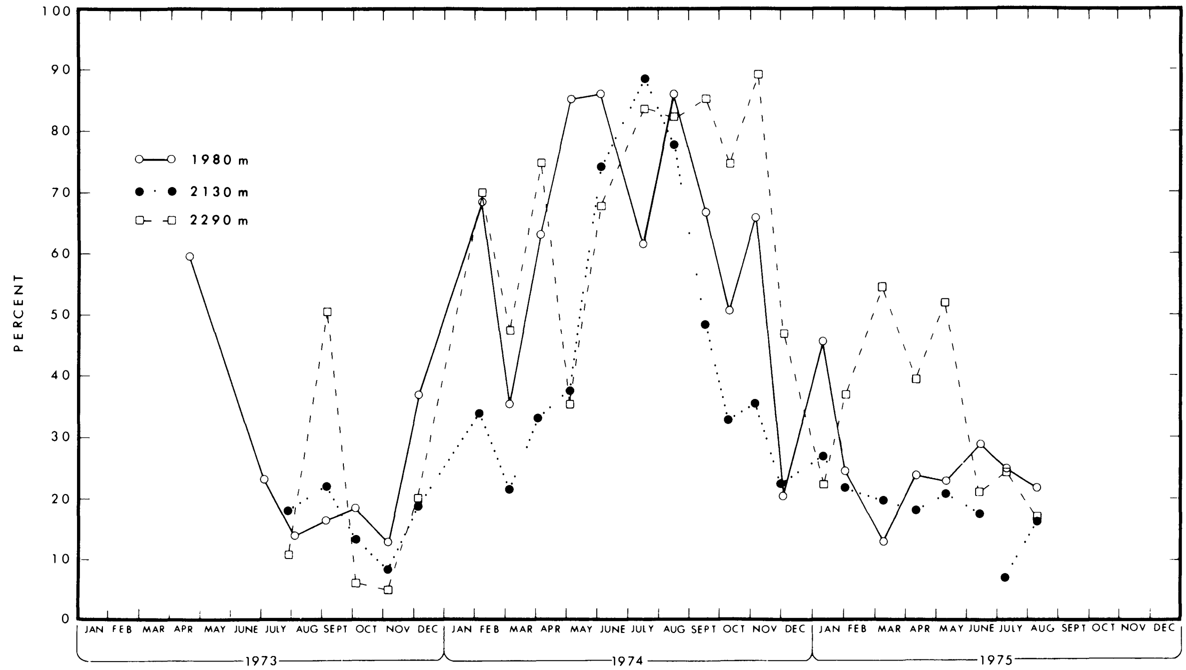

FIGURE 10. Percent of canopy cover per *Myoporum sandwicense* tree from 1973-1975 in study relevés on Mauna Kea, Hawaii.

crease in numbers. This effect is shown by the much higher proportion of *Sophora* in the 2290 m study plot than at higher elevations on the southern slope of Mauna Kea where feral sheep browsing pressure is greater (pers. obs.). Moreover, the 2290 m study area was a fenced enclosure where feral sheep could no longer browse, and it had the highest young-to-adult *Sophora* ratio occurring at that elevation. The remaining two study areas were near roads, and because of hunting pressure sheep flocks visited them infrequently.

TABLE 4. *Productivity index for flowering and fruiting of* Sophora *and* Myoporum *on Mauna Kea, Hawaii.*

Species	Elevation	1974 Flower	1974 Fruit	1975 Flower	1975 Fruit
Sophora	1980	182.3	12.6	786.0	241.0
	2130	153.9	26.1	72.9	10.3
	2290	423.8	72.5	293.0	56.6
Myoporum	1980	549.3	711.0	178.3	164.3
	2130	201.3	408.7	83.8	393.6
	2290	596.6	167.9	62.2	187.7

Taking into account productivity values and the ratio of young to adult trees (tables 1, 4), *Sophora* and *Myoporum* appear to have a similar reproductive potential. Given an environment free of browsing pressure, *Sophora* could compete successfully with *Myoporum*. However, there still remains considerable browsing pressure on Mauna Kea, and Giffin (1976) found that in a region where both tree species were in approximately equal abundance, *Sophora* comprised over 20 percent of the sheeps' diet whereas *Myoporum* comprised only 0.1 percent. This observation may explain why the composition of the forest, especially on the southern slope of the mountain at tree line, has changed so radically. *Myoporum* is a pioneer species (see also the discussion by Cooray 1974); when *Sophora* trees die, *Myoporum* fills the vacant areas rapidly. In a normal sequence of events, *Sophora* would eventually replace *Myoporum*, but with selected browsing pressure against *Sophora, Myoporum* is able to persist and is now the only species that remains in some of these more remote areas.

Aside from the pressures exerted by introduced mammals, the most pervading and proximate influences upon the flora of Mauna Kea are abiotic factors. It is interesting that within only a 300 m elevational rise, tree-species composition changed dramatically within the study sites (fig. 4). Differences in soil characteristics may have accounted for this because the 2130 m site had a larger number of rock outcrops, and the soil is classed as 'stony' (Sato *et al.* 1973); the 1980 and 2290 m study sites had much deeper and less stony soil. *Sophora* numbers were lowest at the 2130 m site as were values for flowering and fruiting productivity. *Sophora* may, therefore, need a greater soil depth in order to maximize reproduction.

Although the percent composition differed among elevations, tree density remained constant. This situation suggests that some controlling factor (e.g., water) limits the number of trees (regardless of species) per unit area of ground. Drainage conditions may also be important, although all three study locations had similar 12 to 20 percent slopes.

Sophora and *Myoporum* responded differently to the yearly weather pattern, but both were well adapted for successful pollination and seed dispersal. *Sophora* has large conspicuous flowers with quantities of nectar; this situation usually indicates that birds are the primary pollinators (Wolf *et al.* 1972). I have observed *Vestiaria coccinea* migrate into the forest during the early flowering period (December-January) and establish feeding territories at flowering *Sophora* trees. The peak bloom period of *Sophora* also occurs when *Loxops virens* populations are at their greatest density (van Riper 1978), and this bird is probably the primary species responsible for pollination. The grey-green foreheads and crowns of juvenile *L. virens* are often so covered with *Sophora* pollen that they appear yellow. *Myoporum,* on the other hand, flowers after *L. virens* populations have dispersed. The blossoms of this tree are small and inconspicuous, and I have rarely observed *L. virens* feeding on them. It appears that this tree relies upon wind or insects for pollination, but this hypothesis remains to be documented.

The physical appearance of *Sophora* and *Myoporum* fruit differs considerably. *Sophora* has a thick outer covering that is very hard when mature, and the seeds are viable over extended periods of time (Akamine 1951). Such a dormancy mechanism may prevent germination in the dry season, during which an adequate root system could not develop. *Sophora* seeds are eaten principally by *Psittirostra bailleui,* and there is evidence that this bird acts as a disperser by carrying partially eaten pods to areas away from the parent tree (van Riper 1980). *Myoporum* fruit, on the other hand, is moist and fleshy, and is taken by a variety of avian species (van Riper 1975). It is a common pattern for dryforest trees to fruit in the dry season (Daubenmire 1972, Hopkins 1970, Richards 1952), with the presumptive advantage that fruit is readily taken by birds for its moisture content.

Presently, a number of birds newly introduced to Hawaii eat *Myoporum* fruits, e.g., Red-billed Leiothrix (*Leiothrix lutea*); House Finch (*Carpodacus mexicanus*); Turkey (*Meleagris gallapavo*). Some of these seed dispersers might be contributing to the recent expansion of *Myoporum.*

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