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THE DISTRIBUTION, IMPACT AND POTENTIAL MANAGEMENT OF THE INTRODUCED VINE *Passiflora mollissima* (PASSIFLORACEAE) IN HAWAI'I

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ABSTRACT

Passiflora mollissima, a weedy vine introduced to Hawai`i, infests significant portions of two of the major islands, Hawai`i and Kaua`i. It grows between 600 and 2200 m elevation in areas where the rainfall does not exceed 5100 mm. The vine is distributed continuously over a total of 190 km^2 and in more widely scattered populations over an additional 330 km^2. Man has been the principle agent of introduction for this species. However, intermediate-distance dispersal may be affected by introduced gallincaeous birds and cattle. Locally feral pigs are the major dispersal agent.

Passiflora mollissima inhabits many of the major upland vegetation types in Hawaii but is most successful in mesic *Acacia koa* - *Metrosideros polymorpha* forests. Although over much of its current range its foliage cover is less than 25%, in some areas it is so dense that it smothers large tracts of native forest. Potential impacts of the infestation on depleted and endangered endemic organisms are also discussed.

It is concluded that *P. mollissima* has become too widespread for successful mechanical or chemical control except in areas of recent local introduction. Prospects for biological control of this species are discussed in the context of current research efforts and practical problems related to a commercially grown congener.

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INTRODUCTION

Passiflora mollissima (HBK.) Bailey (Figure 1) is one of 32 listed taxa of *Passiflora* (Passifloraceae) which have been introduced into Hawai`i (St. John 1973). This species, called "banana poka" in Hawai`i, is the most aggressive of the nine or more of these vines which have escaped cultivation and become naturalized in native plant communities. Specimens of *P. mollissima* have been taxonomically confused with *P. mixta* L. in Hawai`i and elsewhere and may represent variable, hybrid, or introgressed forms (Green 1972; Stephen Tillett, in litt. to Jack Fujii, 8 June 1976; La Rosa 1983a).

P. mollissima is naturally uncommon in its native habitat in the Andes Mountains but is widely cultivated in the Andean highlands from Venezuela to Bolivia (Escobar 1980). In their native habitats, populations of *Passiflora* species are generally sparsely distributed with about 2-3 plants per hectare (Gilbert 1976, 1980). Wild *Passiflora* plants are seldom found with flower or fruit because they are intensively fed upon by numerous species of co-evolved insects (Gilbert 1975, 1980).

The Hawaiian Islands have neither native Passifloraceae nor native insects which are known to attack *Passiflora* species. The only insect which seriously restricts the distribution of any *Passiflora* species in Hawai`i is the recently introduced heliconiine butterfly *Agraulis vanillae* L. (J. Beardsley, pers. comm.). However, *A. vanillae* has not been observed to damage *P. mollissima* even where their distributions overlap (Bianchi 1979).

As a result of the large degree of environmental tolerance displayed by *P. mollissima* in Hawai`i, the abundance of dispersal agents, and the release from the biological constraints operating in its native range (Beardsley 1978), this species of vine has been able to become established in approximately 500 km^2 of forest and woodland since its initial introduction in the early 1900's. In over a third of its distributional area in Hawai`i, *P. mollissima* is found at densities far in excess of what has been reported for wild-growing species of *Passiflora* in their native habitats. *P. mollissima* quickly grows up through the understory vegetation and proliferates in the well-lighted canopy, eventually displacing native vegetation components and disrupting entire communities (Figure 2).

The plant is considered noxious in Hawai`i (National Park Service 1982), but to date there has been no effective control method implemented. Wesley Wong, Jr. and Ernest

Pung, Hawai`i State Forestry personnel, mapped the 1971 distribution of *P. mollissima* on Hawai`i to be 143 km^2. Wong (1971) described this distribution and the deleterious effects of the *Passiflora* infestation in a departmental report. The lack of published information on its distribution and impact has prompted the present paper.

METHODS

Information on the distribution and abundance of *P. mollissima* on the island of Hawai`i was gathered primarily along a series of transects established during the U.S. Fish and Wildlife Service's Hawai`i Forest Bird Survey (HFBS) from 1976-1981 (Scott et al. 1981). These data were augmented by additional ground observations on Kaua`i and Hawai`i in areas not covered by the HFBS transect grid, and by a series of helicopter surveys of the `Ola`a and Mauna Kea areas on the island of Hawai`i in 1980, and of the Koke`e region on Kaua`i in 1981.

During the HFBS the native forest habitats above 500 m on the island of Hawai`i were systematically surveyed along 1027 km of transects established perpendicular to the elevational contours and spaced 3.2 km apart. Information on *P. mollissima* was collected along the transects from over 7800 sampling intervals 134 m in length, and subsequently located on 1:24,000-scale quadrangle maps. The island of Maui and portions of La-na`i, Moloka`i, and Kaua`i were also traversed by 179 km of transects, but *P. mollissima* was not detected during this survey.

Observations of *P. mollissima* were recorded in foliage cover categories as follows: *low* : less than 5% cover; *medium* : 5 - 25% cover; *high* : 25 - 75% cover; and very high: greater than 75% cover. Additionally, sporadic or infrequent occurrences of individual or clustered plants, either seedling or mature, were noted.

Helicopter surveys of `Ola`a, Mauna Kea, and Koke`e also proved to be a very effective, rapid and relatively inexpensive means of determining the current extent of the continuous distribution of *P. mollissima* in an area. Viewing from a low-flying helicopter permitted us to detect mature vines in lower densities than we could on the ground and to adjust ground determined boundaries in low density areas and between transects. The distribution map of this species on Kaua`i was based primarily on a helicopter survey conducted in May 1981. The aerial surveys of `Ola`a and Mauna Kea in December 1981 allowed an update of the distribution of *P. mollissima* in these areas since the 1977 ground survey.

Finally, we attempted to identify areas with *P. mollissima* on several different sets of aerial photographs. Although it appears that this method could be useful in detecting large concentrations of the vine in the canopy using large-scale, true color or infra-red photographs (1:12,000 or larger), the cost of obtaining photographic coverage for potential areas of distribution was considered to be prohibitive.

On Hawai`i the combination of systematic ground coverage and helicopter reconnaissance allowed us to map the three known sizeable and dense populations of *P. mollissima* and to identify two adjacent areas of sporadic distribution plus three disjunct occurrences. The populations were further described in terms of foliage cover classes by examining the mapped aerial extents (determined by digital planimeter) or observed frequencies (by transect intervals) for each category.

Except for disjunct occurrences, the extent of the systematic ground coverage on Hawai`i permitted us to determine the absence as well as presence of sizeable *P. mollissima* populations within the transect grid with a reasonable degree of accuracy. Also, a region of sporadic distribution was identified where sightings of the vine were widely scattered. The intensity of sampling in the western portion of Hawai`i (2850 transect intervals along 380 km of transect) provided enough scattered observations of *P. mollissima* (46) to conservatively delineate approximate boundaries of a region of sporadic distribution in North Kona. Smoothed boundaries were drawn to enclose the minimum area between the highest elevation sighting and the lowest on each transect or transect portion where infrequent observations of *Passiflora* were made. Utilizing a modification of a method used by Scott et al. (in prep.), the frequencies of *P. mollissima* occurrence were combined with the sampling intensity and the small area per transect interval where detection was assumed certain in order to determine an approximate estimate of the density of plants within the area of sporadic distribution.

RESULTS

Extensive populations of *P. mollissima* were encountered on the islands of Hawai`i (Figure 3) and Kaua`i (Figure 4). During our surveys, no plants were located on the islands of La-na`i, Moloka`i and Maui. However, small numbers of *P. mollissima* have been reported in a very localized area on west Hale-a-ka-la, Maui, but have been reduced and contained by ongoing control measures (Wesley Wong, Jr., pers. comm.). O`ahu was not surveyed, but no sightings have been reported from that island despite extensive coverage by numerous biologists. No plants have been reported from the remaining inaccessible islands of Ni'ihau and Kaho'olawe, and none are suspected because of remote dispersal possibilities, arid lowland conditions, and substantial ungulate populations.

Our data permitted fairly detailed mapping of the three known populations on the island of Hawai`i: 1) northeast Mauna Kea (Figure 5), 2) east Mauna Loa (`Ola`a area, Figure 6), and 3) on Hualalai and northwest Mauna Loa (North Kona district, Figure 7). In each population, we found a core region of continuous distribution where P. mollissima was observed at least once in every transect interval (100% frequency of occurrence). The total area of continuous distribution on Hawai`i was determined to be about 157 km^2 (60.8 mi^2). The foliage cover of P. mollissima within this continuous distribution region ranged from less than 1% to nearly 100%.

A region of sporadic distribution was found outside each of the major populations. Within this region, P. mollissima occurred with less than 5% frequency as both immature and reproductive plants and as individuals or in small localized groups. The foliage cover of such plants was negligible. Sufficient data were collected to delineate the extent of sporadically distributed P. mollissima only for the North Kona population (334 km^2, or 129 mi^2). A density range for that area was calculated to be 5-25 plants/km^2 (13-65 plants/mi^2).

We made two extralimital sightings along HFBS transects. These consisted of a single plant in southwest Kohala and a clump of plants at Manuka on the southwest slope of Mauna Loa (Figure 3). A third isolated sighting was made between Hualalai and Mauna Kea volcanoes, outside our transect grid but adjacent to the North Kona region of sporadic distribution; thus, it may actually be part of the latter population. Several very restricted occurrences have also been reported from portions of the north slope of Mauna Kea (Skolmen 1979; Charles Wakida, pers. comm.).

We divided the distribution of P. mollissima on Kaua`i into a large zone of alternating segments of low and medium cover values on the drier west and north sides of a smaller zone of high cover (Figure 4). Interdigitation of adjacent cover levels follows the pattern of alternating drier ridges and moist gulches on this heavily dissected island. There was a lack of homogeneity of P. mollissima cover within zones that appears to correspond, at least in part, to past disturbance to areas of forest by feral cattle and more recently by road and land clearing.

DISCUSSION

Physical Characteristics of Distributional Areas

Passiflora mollissima was found to occur in Hawai`i under a broad range of environmental conditions. The lowest elevation it was encountered at was approximately 600 m (1974 ft) at the lower margin of Manowaiale'e Forest Reserve on northwest Mauna Kea. The range in annual rainfall over which mature individuals were observed extends from approximately 400-500 mm (15-20 in) to between 4500 and 5100 mm (175 - 200 in). Mean annual temperatures for this area range from about 11-25 C (50-72 F) (State of Hawai`i 1970).

Passiflora mollissima was found rooted in several different soil types. On Kaua`i, the soils in its distributional area are all highly weathered derivatives of basalt lava and ash representing three soil orders and four great groups (Foote et al. 1972). Inceptisols (Dystrandepts), Oxisols (Acrohumox and Acrorthox), and Ultisols (Tropohumults).

On the island of Hawai`i, most of the areas P. mollissima is found in lie on weathered ash soils (Inceptisols: Dystrandepts and Hydrandepts), and the remaining distributional area is on organically derived soils on `a`a and pahoehoe lava flows (Histosols: Tropofolists) (Sato et al. 1973).

Habitats Harboring P. mollissima

Our study areas encompassed dry, mesic, and wet habitats. As most of the HFBS transects ran perpendicular to rainfall gradients, many of the transects passed through each type of habitat.

All of the `Ola`a population was found within the wet forest, precluding habitat comparisons for this area. In both the North Kona and Mauna Kea populations, more than half of all the transect intervals containing P. mollissima were in mesic habitat as were three-fourths of the high cover areas. Nearly all of the areas of high Passiflora cover in the Kaua`i population were also found in mesic habitat. Additionally, most populations had some areas of high cover in wet and/or dry habitats. While P. mollissima appears to reach highest cover values in mesic habitats, heavy infestations are not limited to mesic conditions.

Vegetation Types Harboring P. mollissima

Passiflora mollissima was observed as mature, reproducing individuals in a wide variety of vegetation types. However, heavy infestations are presently limited to a few major vegetation types, most notably the mesic koa-`ohi`a (Acacia koa Gray - Metrosideros polymorpha Gaud.) forest (Figure 8).

There is considerable variety in structural complexity, stature, and floristic composition of the vegetation in the region occupied by the North Kona population. This variation reflects a range in moisture conditions and successional development of the vegetation. Early successional vegetation types contained populations with low cover values of P. mollissima and generally a relatively low frequency of occurrence. All of the high cover ratings were limited to the more mature forests, such as characterized by mixtures of koa with `ohi`a or mamane (Sophora chrysophylla) (Salisb. Seem.).

On Mauna Kea nearly all the infested area was found in wet and mesic koa-`ohi`a forest. The few exceptions were in wet and mesic `ohi`a forest and planted stands of introduced trees. The vegetation of the infested `Ola`a area consists predominantly of wet `ohi`a and `ohi`a-treefern (Cibotium spp.) forests. While this area's floristic composition is relatively uniform, structural dominance ranges from the canopy trees to subcanopy treeferns. The small patch of wet koa-`ohi`a forest in the `Ola`a area is infested throughout. On Kaua`i, most of the P. mollissima occurs in diverse mesic koa-`ohi`a forests with only a small amount found in wet `ohi`a forest.

Degree of Infestation

The four major populations of P. mollissima in Hawai`i have their own distribution of abundance classes (Figure 9). Comparisons of these areas allows for some discussion of the process of infestation in the islands.

Judging by the amount of area in the high and very high cover classes (49%), the Mauna Kea population shows the most advanced or severe infestation Approximately half of the remaining areas in low and medium classes were in forests presently grazed by cattle. The remaining areas are along the margins of the infestation farthest from the origin and closest to the very high rainfall zone.

The Kaua`i population is the next most severe infestation having about 30% of the total area in the high cover class. Since our ground survey on Kaua`i was limited, the low and medium cover areas were not separated. Like the Mauna Kea population, the area of highest cover was found in mesic koa forest.

The North Kona population has only 21% of its area in the high cover class and little, if any, of that is grazed. However, parts of the low and medium class areas are grazed. *Passiflora mollissima* appears to be still spreading into favorable habitats in this area, and is likely to continue increasing in foliage cover. Although the North Kona population was established shortly before the Mauna Kea population, the degree of infestation on Mauna Kea is markedly greater. A possible explanation for this difference is that in North Kona the habitats most favorable to *P. mollissima* have a patchy distribution due to their geologic and successional youth, and many portions of the forest have been converted to cattle pasture. Another possible contributing factor is the lower density of feral pigs in Kona. Pigs are considered to be a major short-distance dispersal agent for this species.

The relatively young `Ola`a population currently lacks any areas of high foliage cover except for the limited interfaces with cleared pasture and vegetable farms to the southwest and localized patches in forest gaps. The considerable increase in extent and amount of *P. mollissima* cover in this area between the 1977 transect survey and the 1981 aerial assessment provides evidence that the infestation is intensifying.

Dispersal of P. mollissima in Hawai`i

The dispersal of plant species such as *P. mollissima* is best discussed as two different kinds of events: long-distance and short-distance transport. The lower frequency, long-distance events lead to the development of new populations of the plant in areas clearly distant from existing populations. In Hawai`i, a minimum of eight successful long-distance transport events are believed to have led to the development of the seven confirmed populations of *P. mollissima* (Figures 1 and 2). (The North Kona population represents the merging of populations originating from separate introductions at Pu`u Wa`awa`a and Honua`ula).

High frequency, short distance transport leads to filling-in of the distributions already occupied by established plant populations. The increase in abundance and peripheral range expansion of each of the four major populations of *P. mollissima* has been fostered by sustained short-distance events.

A recurring combination of both long and short-distance transport has created a large region of sporadically distributed _Passiflora_ in North Kona and smaller areas around the other populations. In North Kona such saltatory dispersal has promoted relatively rapid and distant (up to 13 km) spread of _P. mollissima_ away from the continuously distributed infestations. This extensive spread across sub-optimal habitats will allow the plant ready access to isolated patches of more optimal habitats over a large portion of the Island.

The dispersal of _P. mollissima_ in Hawai`i can be ascribed to two major means: direct planting by man, and internally through the digestive systems of various birds and mammals. Man is considered to be the most important long-distance transport agent for _P. mollissima_ both in Hawai`i and in South America.

P. mollissima was first reported in Hawai`i in 1921 by forester W. Bryan from Pu`u Wa`awa`a Ranch on northeast Hualalai. In 1930 it was planted at Honua`ula on southwest Hualalai and at Ke-ana-kolu on northeastern Mauna Kea (Pung 1971). The Kaua`i population was reportedly started by a planting in 1923 (Wenkam 1967). The `Ola`a population is derived from plantings made along Wright Road in 1958 shortly after portions of the forest were cleared for farm lots and pasture (Wong 1971).

The seeds of _P. mollissima_ are 4 - 6 mm in length surrounded by succulent arils. Mature fruit are yellow in color, 10 cm long, and 6.5 cm in diameter (Figure 1). Up to 180 seeds can be found within a mature fruit (Wong 1971). The fruit is locally utilized by a wide variety of birds and mammals as a food source. Additionally, seeds from rotted fruit appear to be attractive to gallinaceous birds as food or grit (V. Lewin, pers. comm.). Although peak fruiting for this species in Hawai`i occurs from December through March, flowers and fruit can be found on the vines throughout the year (La Rosa 1983a).

At least 20 species of birds and mammals in Hawai`i, nearly all introduced, are either known or suspected of being able to ingest and transport _Passiflora_ seeds in their digestive tracts (Table 1). In any given portion of the larger Hawaiian Islands there can be found at least a few of these species, resulting in a considerable local distribution potential for _Passiflora_ . In a detailed habitat correlate analysis, Scott et al. (in prep.) found a high degree of correspondence between many of the bird species listed in this table and areas containing _P. mollissima_ .

In most cases seeds taken into the digestive tract are passed through small animals very quickly, and result in only short-distance transport events. However, livestock which feed on P. mollissima fruits in one area may travel across or between pastures before seeds are passed out of their system. This means of transmission may also be particularly important when cattle or horses are moved between different ranches in the islands.

The feral pig, which occurs in a wide range of densities throughout the range of P. mollissima , is the primary agent for short-distance transport in Hawai`i. Giffin (1972) reported that P. mollissima constituted 32% (by volume) of the diet of pigs in the Lau-pahoehoe area (northwest Mauna Kea) on Hawai`i on a year-round basis. He also observed that pigs actively moved into areas with high concentrations of P. mollissima to take advantage of the seasonal abundance of its fruits. While it is not possible to conclude whether the very high cover values of P. mollissima in the central portion of the Mauna Kea population are a cause or a result of the very high densities of feral pigs in the area (an average of 63 pigs/km^2, the highest recorded densities in Hawai`i; Giffin 1972), the connection between the two is very real.

The larger gallinaceous birds may also be important agents for both short and long distance transport of P. mollissima . V. Lewin (pers. comm.) found that Kalij Pheasants retained P. mollissima seeds to be used as grit in their gizzards. He found that 82% of 44 crops and/or gizzards of this species which he collected from North and South Kona contained P. mollissima seeds. This grit material may be retained for a long enough time that the bird may travel well away from the area where it picked up the seeds. When worn seeds pass through the gut, or when the birds die, it is possible that some seeds will be viable and germinate potentially resulting in the establishment of a new population of the plant.

The Kalij Pheasant, first introduced in Hawai`i at Pu`u Wa`awa`a in 1962 (Lewin 1971), appears to have very recently experienced a rapid population and range expansion on the Island and now occurs in most of the areas occupied by P. mollissima (V. Lewin, pers. comm.; Scott et al. in prep.). As a result, the Kalij Pheasant may be becoming much more important as a dispersal agent for P. mollissima .

Limits to Range

Only high rainfall, extremes of elevation, and intensive agriculture appear to be possible barriers to an expanding P. mollisima population in Hawai`i. In addition, browsing by cattle and deep shade under dense vegetation may also serve to limit the vine's cover and slow its rate of spread.

Annual rainfall in excess of 4500-5100 mm (175-200 inches) appears to act as a barrier to range extension of continuously distributed P. mollissima , at least in the environmental conditions found on east and northeast Mauna Kea. The area of continuous distribution terminates fairly abruptly along a line paralleling the 5100 mm (200 inch) isohyet (Figure 3). Both the continuous P. mollissima distribution and the 5100 mm (200 inch) isohyet extend from about 1525 m (5000 feet) down to 760 m (2500 feet) elevation. We were unable to associate The truncated P. mollissima distribution in this area cannot be associated with elevation, temperature or vegetation differences.

A variety of vegetation types are found within the range of P. mollissima in Hawai`i, but the vine has reached epidemic proportions in only a few. Deep shade under a continuously dense cover of vegetation limits its total amount of cover and may retard its spread (La Rosa, 1983b). However, these conditions do not appear to be a long-term barrier as continuously distributed, mature P. mollissima co-occurs with closed canopy vegetation in all of the major populations but primarily in gaps.

Intensive agriculture such as sugar cane cultivation appears to also prevent the distribution of P. mollissima from the adjoining forest on northeast Mauna Kea. Additionally, some introduced tree plantations support less extensive cover of the vine than do adjacent native forests, but they are by no means a barrier. Very dense and shady stands of certain planted exotic trees appear to prevent the establishment of P. mollissima except in gaps and along the margins.

Intensive grazing, with associated forest removal, usually acts to prevent the continuous distribution of P. mollissima . However, this condition does not appear to be limiting to the plant's sporadic occurrence, particularly in North Kona where rough surface features of lava flows locally reduce or restrict access of cattle. Such a low-density, sporadic distribution of P. mollissima exists even in areas of North Kona having high enough densities of feral sheep and goats to seriously restrict the amount and diversity of the understory and ground cover vegetation. Less intensive grazing appears to severely limit the amount of P. mollissima cover while still allowing continuous distribution of the vine, particularly in areas having considerable tree canopy.

Only high rainfall, extremes of elevation, and intensive agriculture appear to be possible barriers to an expanding *P. mollissima* population in Hawai`i. In addition, browsing by cattle and deep shade under dense vegetation may also serve to limit the vine's cover and slow its rate of spread.

Colonization of Disturbed Native Vegetation

The forest borders next to artificially opened areas bear greater foliage cover of the vine than does the forest immediately within each of the observed large populations of P. mollissima. In areas of very dense vegetative cover, dispersed *P. mollissima* seeds appear to be limited in their establishment by the shaded conditions provided by the vegetation. Natural and artificial sources of disturbance to the vegetation such as tree falls, canopy defoliation from "`ohi`a dieback" (Mueller-Dombois 1980), large windstorms, logging, treefern harvesting, forest bulldozing, and feral cattle and pigs allow increased establishment of *P. mollissima* . Such sources of disturbance are widespread in many forested areas in Hawai`i.

Even a small scale, infrequent tree fall event can lead to the occasional establishment of *Passiflora* in areas normally too shaded for the vine's growth. A recent study in `Ola`a by Burton (1980) indirectly simulated the effect of tree falls. The dense treefern subcanopy was artificially opened in small plots, and the growth of pre-existing and colonizing plants was monitored. *Passiflora mollissima* was among the plants that became well-established only where the subcanopy had been opened. Burton (pers. comm.) also found that *P. mollissima* in the disturbed plots could flower within 12 months (La Rosa 1983b).

More important to the epidemic expansion of *P. mollissima* into relatively intact native ecosystems are the larger scale disturbances in communities otherwise resistant to *Passiflora* invasion by virtue of their structural integrity. When the HFBS transects through the `Ola`a area were traversed in 1977, *P. mollissima* was recorded with the greatest regularity and cover in areas where the `ohi`a canopy had been previously defoliated from "`ohi`a dieback" and where a combination of fallen snags and concentrated foraging by feral pigs had considerably opened the understory of treeferns and ground cover ferns. In January 1980, an unusually severe windstorm caused substantial opening of the dense treefern subcanopy over a large portion of the `Ola`a area. We flew over the region 23 months later (December 1981) and saw an extensive tract of *P. mollissima* . Over most of this area the vine was present only sporadically or was absent when the three HFBS transects through the area were traversed in 1977, even though the ground cover of small native ferns was maintained in a partially disrupted state by feral pigs (Warshauer et al., in prep.) It is quite probable that the extensive opening of the dense subcanopy caused by the windstorm admitted enough extra light into the disturbed understory to promote the large-scale establishment of previously-dispersed seeds and seedlings.

There have also been large areas of considerable disturbance to the native forest over the last ten years in the North Kona and Mauna Kea areas. In both of these regions, one of the major disturbances has been an increase in forest opening caused by and for cattle. While the impact of cattle on the native forest is decidedly negative, their browsing on P. mollissima has resulted in the reduction of the vine's foliage cover over considerable acreages. Such a reduction should not be viewed as a favorable sign for P. mollissima control, as it is simply a passing of one form of forest destruction to another.

Recent Changes in Distribution

The information available on the distribution of P. mollissima permits only a limited assessment of its change in abundance and spread. The primary sources for comparison were 1) the Island of Hawai`i distribution maps prepared by Wesley Wong, Jr. and Ernest Pung (Wong 1971), 2) the HFBS ground survey in 1977-1979 , and 3) aerial surveys over `Ola`a and Mauna Kea in December 1981 Table 2). While minor differences in abundance and distribution of P. mollissima for these sampling times can be attributed to a matter of definition of boundary lines and class limits, the larger differences appear to be indicative of population trends and/or responses to outside influences.

The most dramatic increase was the 18-fold change in distributional area for the `Ola`a population from 1971 to 1981. The major part of this increase occurred following, and probably as a result of, the severe windstorm in January 1980. The North Kona population also increased both in area (22%) and cover in the 7 years between the time it was mapped by Wong and Pung in 1971 and by the HFBS in 1978.

Although the 1977-81 distribution map of P. mollissima in the Mauna Kea area shows some localized increases and decreases in both area and cover from the 1971 maps, the overall area of continuous distribution has remained approximately the same. The area occupied by the combined high and very high cover classes has also remained about the same between the two map dates; however, the very high class has declined proportionally since 1971. For both Mauna Kea and North Kona the medium class coverage has also declined in proportion, most of the differences being accounted for by proportional increases in the low abundance class. As mentioned earlier, gross disturbance from logging and increased access by cattle are postulated as causing the decrease in *P. mollissima* cover.

Only the data for North Kona were sufficient for mapping the regions of sporadic distribution outside the major populations on the island of Hawai`i. The 1977 field survey of the `Ola`a population identified several sporadic occurrences, but by 1981 all were included within the enlarging area of continuous distribution. Wong and Pung mapped a 1934 ha area of sporadic distribution ("light spotting", 5-25 plants/km^2) contiguous to the northeast portion of the Mauna Kea population (Wong 1971). No plants were seen in the 1977 field survey and only one plant in the 1981 helicopter overflight. This raises the possibility that there may be only very limited long term survival of *P. mollissima* in that "light spotting" region, most of which receives more than 5100 mm (200 inches) of rainfall annually (Figure 5). Several other sporadic occurrences were noted in 1977, all within the heavily grazed, much-opened koa forest to the west of the main population (Figure 5).

Direct Effects of *P. mollissima* on Native Forests

Preliminary analyses have shown that wherever *P. mollissima* is found in an advanced stage of infestation, the structural integrity and species composition of the native vegetation has been drastically reduced (Jacobi et al., in prep.). This disturbance of the vegetation also affects its dependant animal cohabitants, particularly the bird communities (Scott et al., in prep.). In these areas, the vine covers much of the foliage of canopy trees, occluding sunlight. Large, dense curtains of *P. mollissima* extend to the ground from canopy branches sometimes causing branch breakage and toppling of trees during storms (Wong 1971). Where the canopy has been opened, dense mats of vines also mantle understory trees and shrubs and cover the ground.

While most of the area presently occupied by *P. mollissima* in Hawai`i is not yet at the advanced stage of infestation, much of the area where it is found to be continuously distributed has this potential. Over 30% of these areas already have more than 25% foliage cover of the vine.

SUMMARY AND CONCLUSIONS

The introduction of *P. mollissima* to Hawai`i has turned into an ecological catastrophe. The impacts of the epidemic invasion were in evidence even before Wong quantified its distribution and described its effects in 1971. During our surveys, we found *P. mollissima* in three main populations on the island of Hawai`i and one on Kaua`i. Additional areas with scattered plants are known from these islands and Maui. The total area occupied by a continuous distribution of *P. mollissima* is over 190 km^2. The most extensive population is in North Kona, where *P. mollissima* is continuously distributed over 62 km^2 and is additionally found scattered (5-25 plants/km^2) over 330 km^2, extending out to 15 km from the more densely distributed part of the population.

Several introduced and native animals have been identified as either known or potential dispersal agents of *P. mollissima* . This dispersal potential plus the continuing range expansion suggest that much of the remaining suitable habitat has a high probability of becoming infested.

Passiflora mollissima attains its highest cover in mesic and wet forests with a wide range of vegetation structure and composition. One of the forest types most commonly occurring in such habitats is the koa-`ohi`a forest. Within this forest type the vine has spread very rapidly and attained the greatest densities. The distribution of the koa forests on the island of Hawai`i indicates where the greatest future spread of this species may occur (Figure 8).

Structural disturbance of forests by *P. mollissima* can be associated with the highest densities of this species (both as cause and effect) and with the greatest rate of spread, which may help to explain the degree of infestation within koa-`ohi`a forests. Once well-established in a native forest, the vine proliferates its foliage cover in the canopy contributing to physical and photosynthetic disruption by its sheer mass and eventually to a marked reduction in the structural and compositional diversity of the forest.

Ultimately, one of the groups of native organisms which could be seriously affected by an increase of *P. mollissima* is the endemic forest birds, particularly those which are already considered to be endangered (Figure 10). The many depleted endemic plants and arthropods which are restricted to areas already infested with *P. mollissima* face more immediate jeopardy.

Potential for Control of P. Mollissima in Hawai`i

Since the 1970's, there have been a series of attempts by the State of Hawai`i, and to a limited extent by the National Park Service, to control the plant by physical and chemical means. Ironically, the mechanisms which have brought about the greatest extent of temporary Passiflora foliage reduction, access by cattle and logging, are in themselves two of the greatest threats to the remaining native koa-`ohi`a forest in Hawai`i.

It is now evident that the only realistic hope for control of P. mollissima in Hawai`i is through biological control methods, utilizing some of the same host-specific biological agents which keep the vine in check in its native habitat (Beardsley 1978). The principal organisms which feed on P. mollissima, heliconiine butterflies and, secondarily, chrysomelid beetles (Gilbert 1980), may display the same sort of population irruption in Hawai`i as has their host once released from their own biotic controls.

Even though co-evolutionary relationships of Passiflora and heliconiines are relatively well known (Gilbert 1975; Waage et al. 1981), the amount of information not yet applied to biological control is substantial. Extensive field searches for candidates are needed, as well as cooperative utilization of information and research facilities already established for studying insects feeding on Passifloraceae (Gilbert 1980).

An important factor which has stood in the way of initiating any biological control attempts on P. mollissima is the presence in Hawai`i of approximately 80 ha of commercially grown "passion fruit" ( P. edulis Sims). Although the distribution of P. mollissima does not overlap that of commercially cultivated P. edulis in Hawai`i (the fields are in the lowlands of O`ahu), there is the possibility that a biological control organism could travel between islands, as did the introduced butterfly Agraulis vanillae, and that it would feed upon P. edulis, as has A. vanillae (Jack Fujii, pers.comm.)

In consideration of this specific problem, Waage et al. (1981) proposed a thoughtful and well-substantiated program for screening members of the genus Heliconius for use as biological control agents. They identified three major components of host selection and tested each with a number of species of Heliconius and Passiflora. The researchers demonstrated that Heliconius adults show strong specific behavioral selection for both habitat and oviposition host species but only a limited degree of host-specificity as feeding larvae. Heliconius species which will find, oviposit on and consume P. mollissima and, additionally, avoid P. edulis in at least two tests of discrimination might be considered safe candidates for introduction as biological control agents.

If potential biological control candidate species are eliminated primarily on the basis of larval feeding abilities, the tests could well be unnecessarily restrictive, since ecological requirements of the control species strongly determine their feeding habits. Instead, the screening of candidate species should emphasize their selection and avoidance of habitats and hosts, and perhaps evasion of parasitism and predation as well. Clearly, ecological and behavioral studies in candidate species' native habitats, in addition to insectary studies, are necessary to fully assess their potential threat to cultivated P. edulis as well as their possible performance on P. mollissima .

It would be prudent to select a pool of candidate species before any introductions are made, as more than one species (or genus) is likely to be required to affect biological control of P. mollissima . As one can never be certain how organisms will distribute themselves in a set of foreign environments, the degree of pressure exerted and habitat utilization achieved by any one introduced agent may not be sufficient to subdue P. mollissima . Additionally, the mortality induced by parasites may limit the effectiveness of control agents. There are already introduced and established in Hawai`i a large number of generalist hymenopteran parasitoids, a legacy from unfettered trials in rudimentary biological control begun in the first years of this century. The one introduced heliconiine, Agraulis vanillae , has been observed to be attacked by at least two introduced hymenopteran parasitoids (Bianchi 1979).

In addition to host specificity, other biological characteristics of heliconiines could be useful to readily reduce any threat by biological control agents to cultivated plants. Heliconius species roost gregariously at the same sites each night and travel the same routes for foraging and egg-laying (Gilbert 1975). Both behaviors could make them quite vulnerable to localized control efforts, if so desired. Gilbert (1977) proposed a scenario in which a Heliconius attracted to the vicinity of P. edulis fields could be utilized to attract parasites to destroy progeny of any errant butterflies of other heliconiine genera. If prevention of serious attack on P. edulis should fail, then the farmer could spray his fields against the insect, as is already practiced in control of other arthropods.

It is encouraging that the State of Hawai`i, in conjunction with the U.S. Forest Service, and the National Park Service has started a field search for potential control organisms of P. mollissima . The weed is so widespread in distribution and habitats that effective control may require several vigorous and vagile control agents, possibly including other heliconiines, chrysomelids and/or other phytophagous insects that show control potential.

Future Outlook

While the biological control aspects of *P. mollissima* have their economic considerations, the *Passiflora* infestation itself has yet to be generally viewed as important to the economic interests of Hawai`i. Few of the residents have been to the upland forests where the problem is so visibly evident, and the intensive agriculture and grazing surrounding the infestation are unaffected by it. The small koa timber industry is likely to feel the threat in the future more than presently. The available timber supply is nearly exhausted, and future cutting will be increasingly dependent upon stands of koa now beginning to be planted. The biggest problem to a koa silviculture program has been identified as the *P. mollissima* infestation (Skolmen 1979).

Another little recognized economic threat posed by the *Passiflora* problem is its role in the large-scale degradation of watershed forests in Hawai`i. Considering the conflicting trends inherent in the increasing consumption of water for development and the continued reduction in watershed forest due to forest conversion, the *P. mollissima* infestation may take on new significance as more concern is paid to the integrity and continued viability of Hawai`i's remaining native watershed forests.

Even though it can be hoped that effective control of *P. mollissima* is forthcoming, it would be wise to continue measures to limit the spread of the plant in Hawai`i. By means of education and increased regulation, the considerable potential for continued human-induced long-distance transport needs to be curtailed. In addition to intentional dissemination, it is conceivable that *P. mollissima* could be carried to other Hawaiian islands internally in trans-shipped livestock or gamebirds originating from infested regions. The Kalij Pheasant, a recent (1962), privately implemented introduction to Hawai`i (Lewin 1971), is a likely candidate.

Newly established inter-island or isolated intra-island populations of *P. mollissima* may be controlled by chemical and physical means if they are detected in time. In 1971 a group of three mature plants was reported from a farmlot at Kula, Maui. Sustained removal efforts since then have contained the problem to periodic appearances of seedlings (Wesley Wong,Jr., pers. comm.) Clearly, prevention rather than treatment is the easier and more rational approach.

There is a grave need to expand protective concepts in

Hawai`i, as elsewhere, to include preventing the introduction of species potentially deleterious to the composition and stability of the native biota. Lewin (1971) pointed out that "more plants and animals have been introduced into the State of Hawai`i than in any area of comparable size on earth." The importation of non-native species has not abated, as each year numerous species are legally introduced by horticulturists, botanical gardens, and pet shops, or smuggled in by individuals. Limited monitoring and partial regulation has not been effective in preventing the periodic naturalization of some of these species, and there is need for additional efforts in identifying and eradicating the incipient problems. The risk of introducing more troublesome species, which is inherent in maintaining the ongoing flood of ornamental organisms, far outweighs the benefits of increasing the range of choice in Hawai`i's gardens and pet shops.

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Table 1. Suspected and confirmed dispersal agents of *Passiflora mollissima* in Hawai'i. Only species which are at least partially sympatric with the vine are listed.

SPECIES	REFERENCE	NOTES
MAMMALS		
Man *Homo sapiens*	Pung 1971; Wenkam 1967; Wong 1971	Primary dispersal agent
Feral pig *Sus scrofa*	Giffin 1972; Wong 1971; authors' observations	6
Cattle *Bos taurus*	Authors' observations	1
Horse *Equus caballus*	No reference, but probable	1
BIRDS		
Black Francolin *Francolinus francolinus*	No reference, but possible	5
Erckel's Francolin *Francolinus erckelii*	No reference, but possible	5
Gray Francolin *Francolinus pondicerianus*	No reference, but possible	5
Kalij Pheasant *Lophura leucomelama*	Victor Lewin (pers. comm.)	Undergoing population irruption; 1, 6
Red Jungle Fowl *Gallus gallus*	Schwartz and Schwartz 1949	4

Table 1, continued

SPECIES	REFERENCE	NOTES
Ring-necked Pheasant *Phasianus colchicus*	Schwartz and Schwartz 1949; Wong 1971	2, 3, 4
Common Pea Fowl *Pavo cristatus*	No reference, but possible	5
Wild Turkey *Meleagris gallopavo*	Wong 1971	3, 4
Spotted Dove *Streptopelia chinensis*	No reference, but possible	3, 4
Hawaiian Crow *Corvus hawaiiensis*	Giffin 1977; H. Sakai (pers. comm.)	Hawai'i only; disperses widely following breeding season; 1, 3, 7
Hawaiian Thrush *Phaeornis obscurus*	No reference, but possible	Common only on Hawai'i; 3, 6, 7
White-rumped Shama *Copsychus malabaricus*	No reference, but possible	Not on Hawai'i; fruit included in diet
Melodius Laughing-Thrush *Garrulax canorus*	No reference, but possible	Fruit included in diet; 6
Red-billed Leiothrix *Leiothrix lutea*	No reference, but possible	3, 6
Common Myna *Acridotheres tristis*	No reference, but possible	1, 3, 6
Japanese White-eye *Zosterops japonicus*	Dina Kageler (pers. comm.)	Seeds passed through gut; 3, 6
House Finch *Carpodacus mexicanus*	No reference, but possible	3, 4

Table 1, continued

NOTES

1 -- Likely to disperses seeds a long distance as well as a short distance.

2 -- Eats Passiflora edulis, which has similar seeds.

3 -- Eats fruit with seeds similar in size to those of P. mollissima.

4 -- Eats seeds similar in size to those of P. mollissima.

5 -- Diet suspected to be similar to that of pheasants.

6 -- Wide ranging in at least some closed forests.

7 -- Endemic to the Hawaiian Islands.

Table 2. Summary of the area coverage and abundance classes[1] for the four major Passiflora mollissima population in Hawai'i, 1971 and 1978-1981.

	OLA'A			NORTH KONA				KAUA'I			MAUNA KEA				
	LOW	MED.	TOTAL	LOW	MED.	HIGH	TOTAL	LOW-MED.	HIGH	TOTAL	LOW	MED.	HIGH	V. HI.	TOTAL
1971[2]															
AREA (ha)	142	---	142	141	3746	262	5150	----	----	----	615	939	2402	1202	7156
PROPORTION	100%[4]	---		2.2%	72.7%	5.1%[5]		----	----	----	8.6%	41.1%	33.6%	16.8%	
1978-1981[3]															
AREA (ha)	2330	242	2572	---	---	---	6263	2350	1050	3400	1946	1497	3156	325	6924
PROPORTION	90.6%	9.4%		53.0%	25.7%	21.3%		69.1%	30.9%		28.1%	21.6%	45.6%	4.7%	
CHANGE IN DISTRIBUTION BY 1978-1981			+1810% (over a 10 year period)				+22% (over a 7 year period)			----					-3.2% (over a 10 year period)

Summary

Total area of continuous distribution of P. mollissima in Hawai'i in 1981 = 19,157 ha = 191.6 sq km.
Approximate total area of sporadic distribution of P. mollissima in Hawai'i in 1978 = + 35,000 ha = +350 sq km.

1 Percent foliage cover for each abundance class, 1971: LOW = < 10%, MED. = 10-30 %, HIGH = 30+%-70%, V.HI. = 70-100%;
1978-1981: LOW = < 5%, MED. = 5-25 %, HIGH = 25-75 %, V.HI = 75-100%

2 Areas for 1971 distribution determined by planimeter from maps by W. Wong, Jr. and E. Pung, Division of Forestry and Wildlife, State of Hawai'i. Their 1934 ha region of "light spotting" (equivalent to our sporadic distribution, 5-25 plants/sq km) is not included.

3 Areas for 1978-1981 distribution determined by planimeter from maps by Hawai'i Forest Bird Survey, U.S. Fish and Wildlife Service.

4 Area for Ola'a in 1971 assumed to be all in LOW class, even though the margins of the forest probably were higher locally.

5 Proportions for North Kona in 1978 taken from ratings on each station along HFBS transects.

Figure 1. Photograph of flowers and fruit of Passiflora mollissima.

Figure 2. Photograph of *Passiflora mollissima* draping native trees.

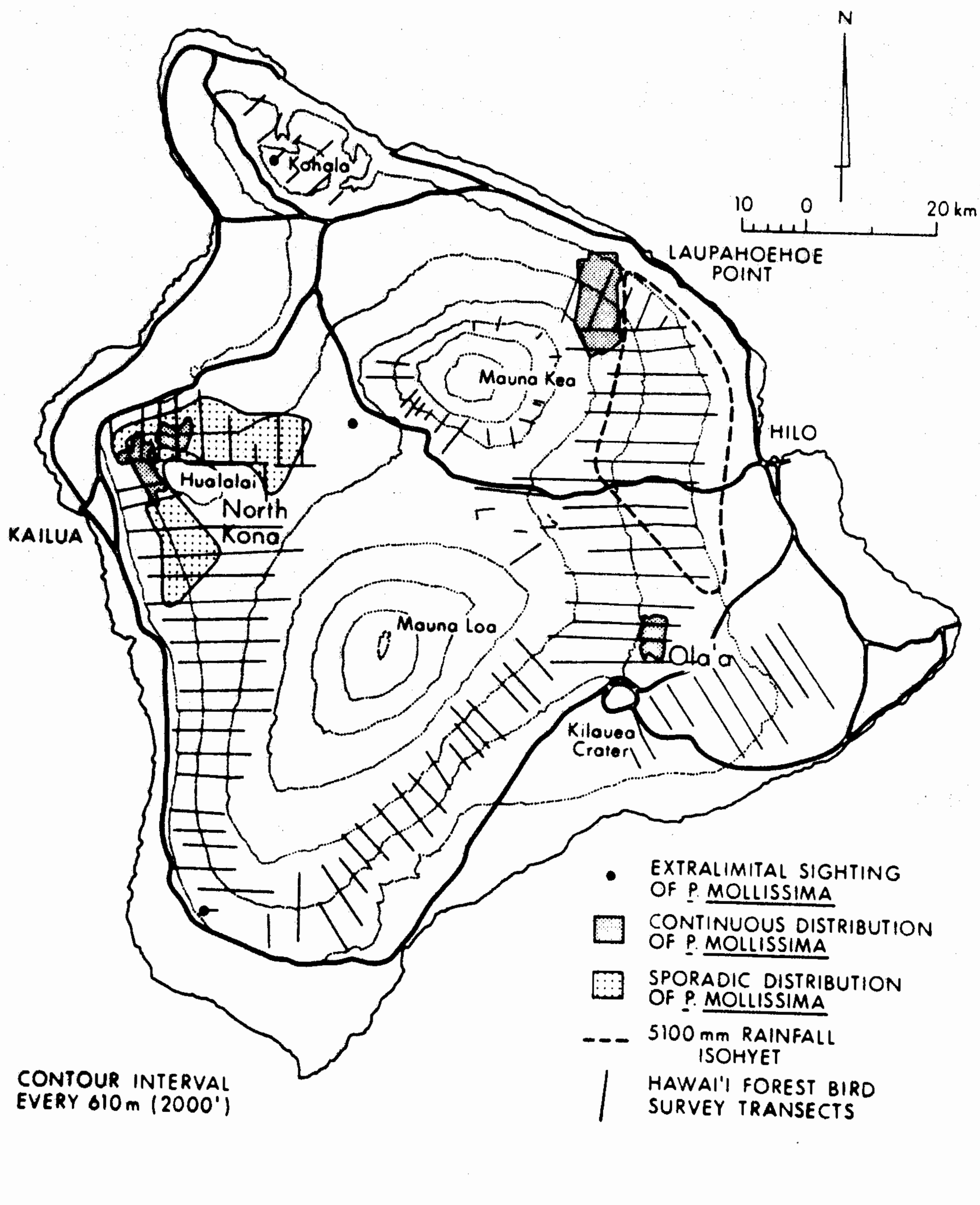

Figure 3. Distribution of Passiflora mollissima on the island of Hawai'i.

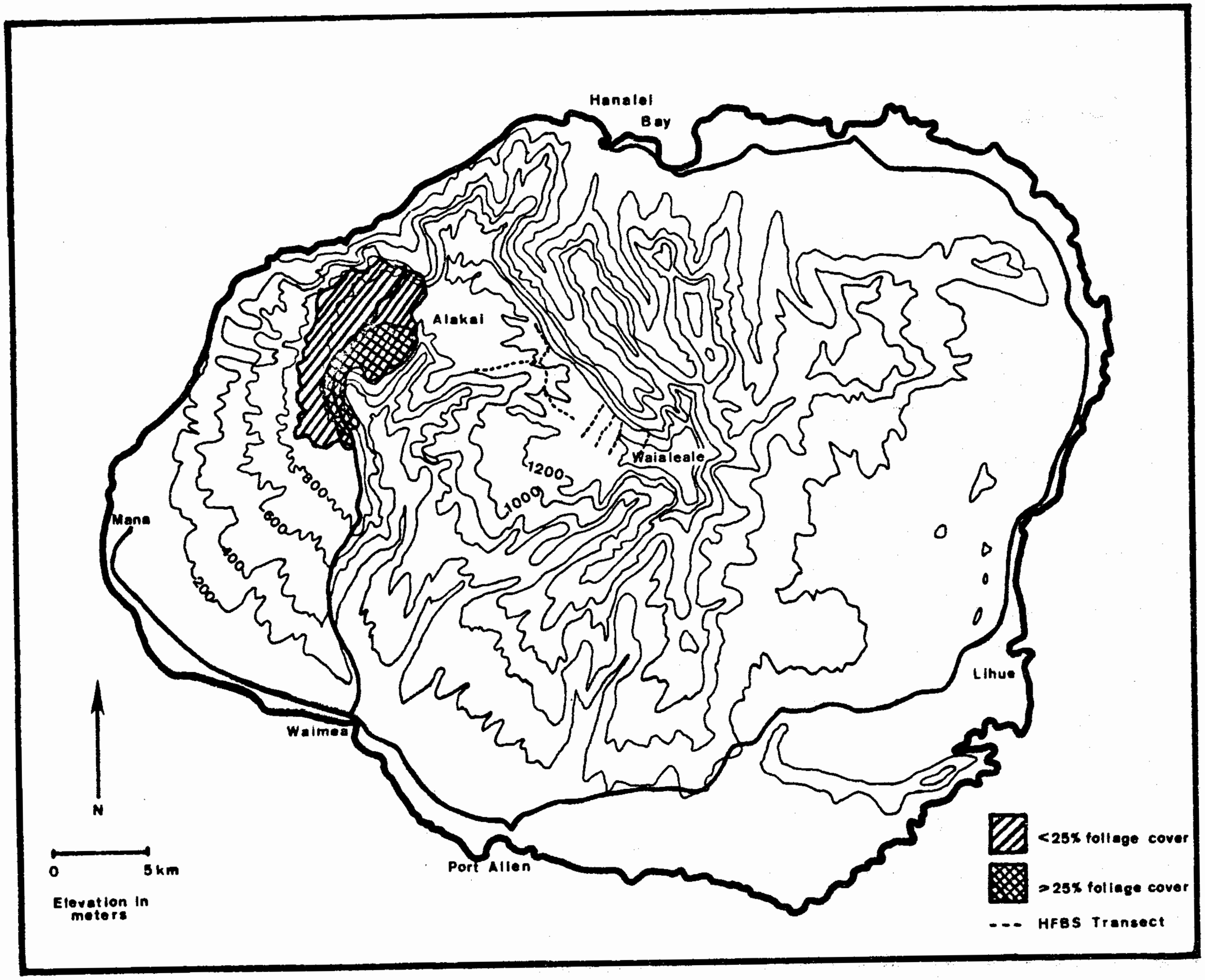

Figure 4. Distribution of Passiflora mollissima on the island of Kaua'i.

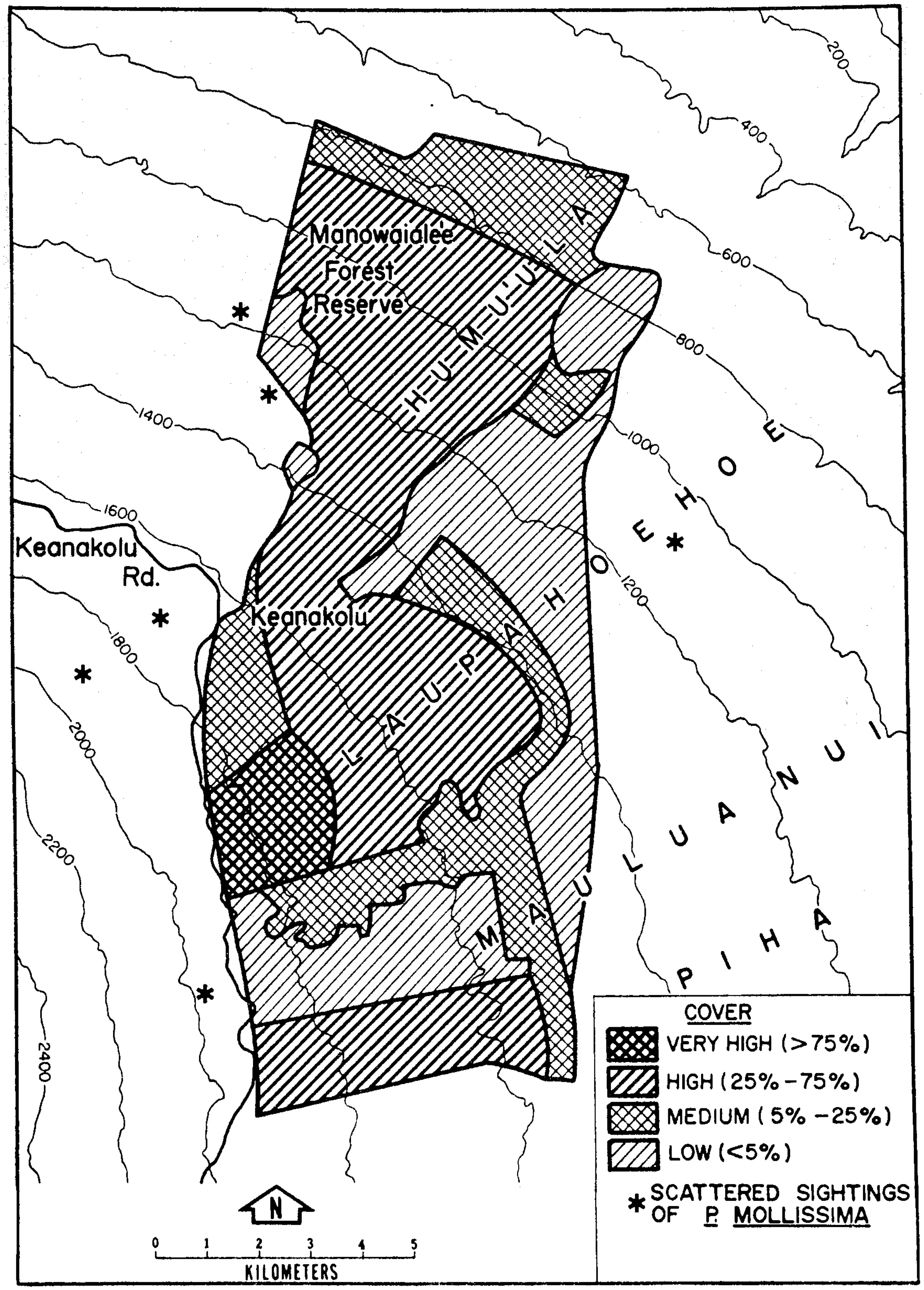

Figure 5. Detailed map of northeast Mauna Kea showing the distribution of Passiflora mollissima in four abundance classes.

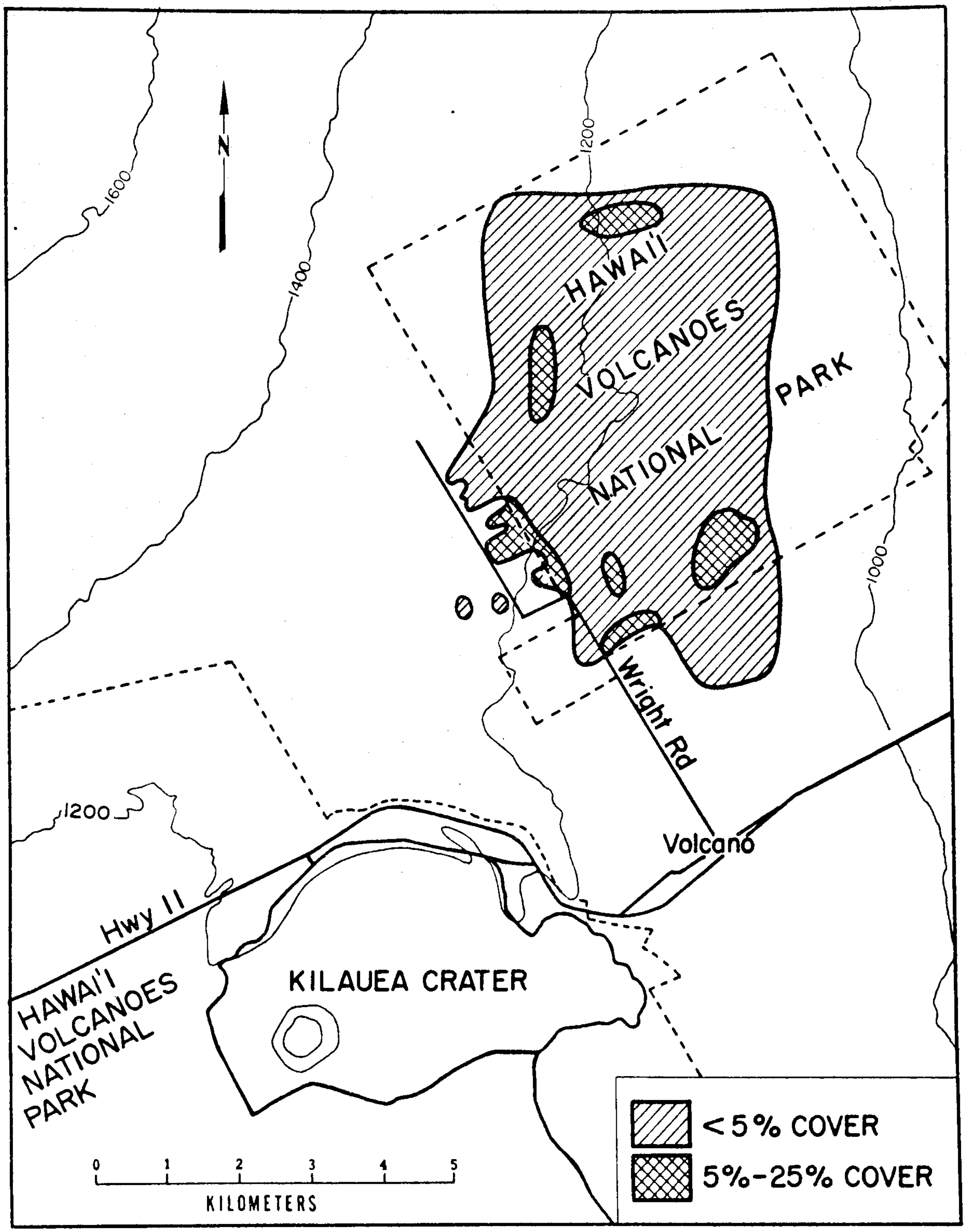

Figure 6. Detailed map of the 'Ola'a area showing the distribution of <u>Passiflora mollissima</u> in two abundance classes.

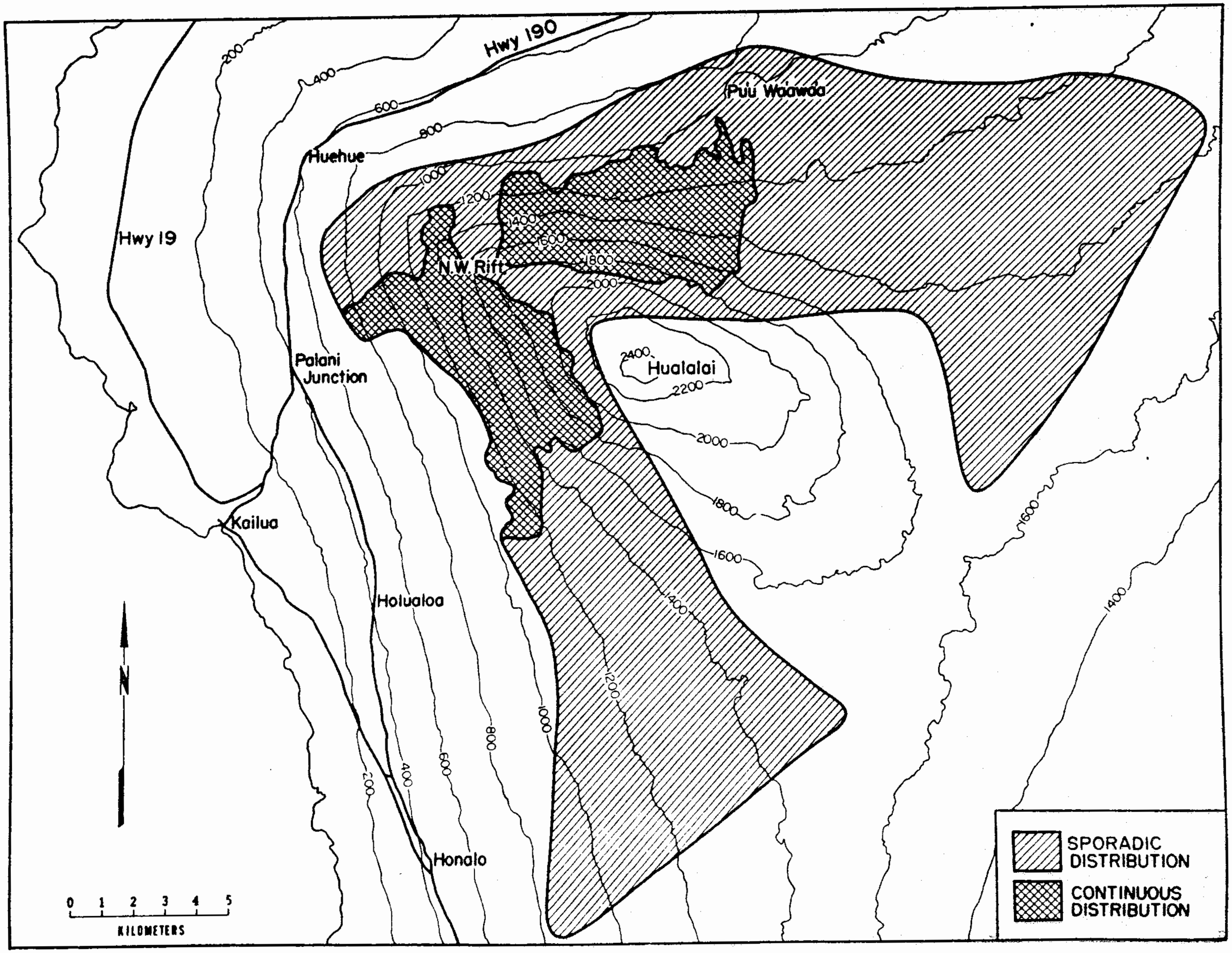

Figure 7. Detailed map of North Kona showing the distribution of Passiflora mollissima.

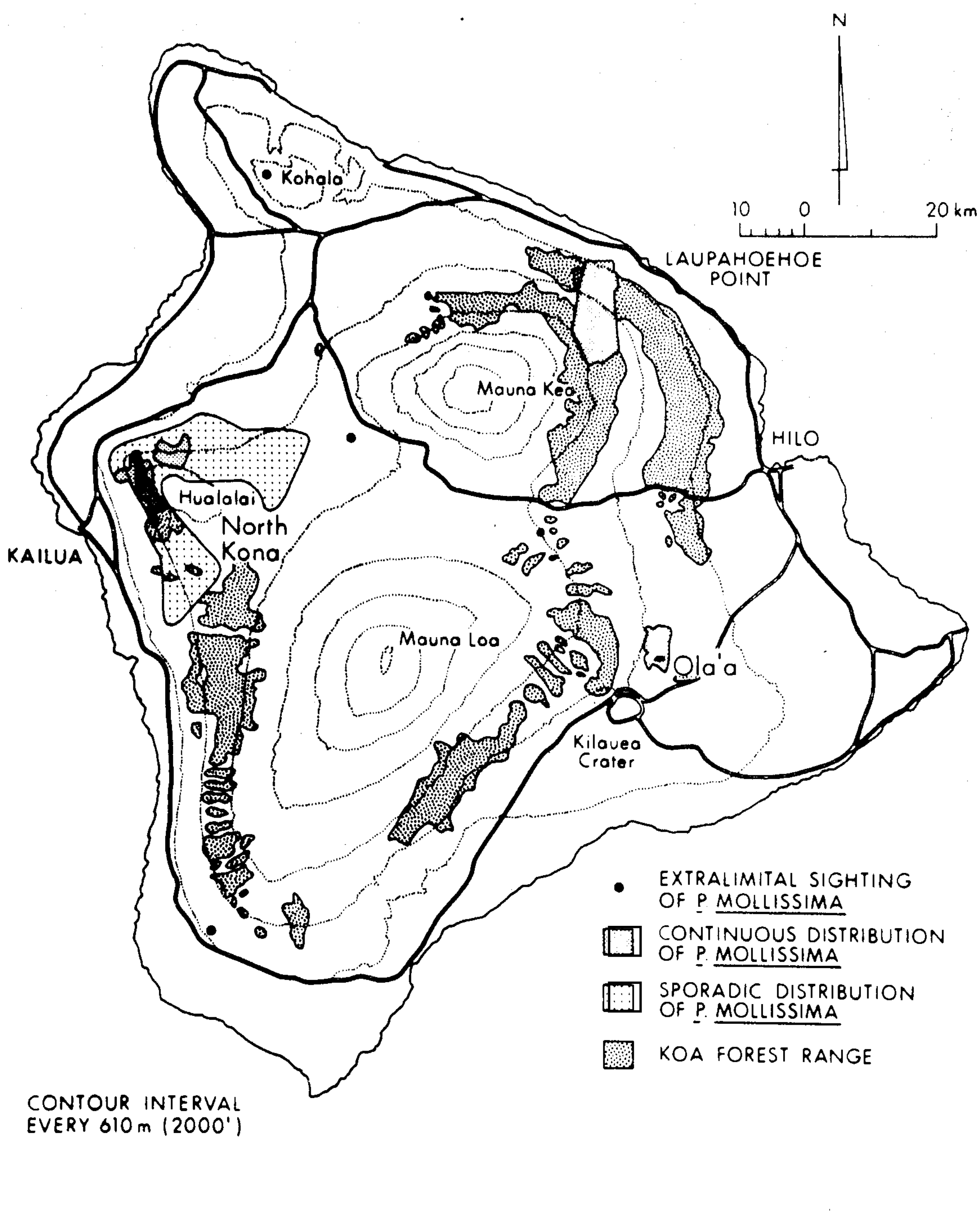

Figure 8. Map of the island of Hawai'i showing the distribution of *Passiflora mollissima* and *Acacia koa* forests.

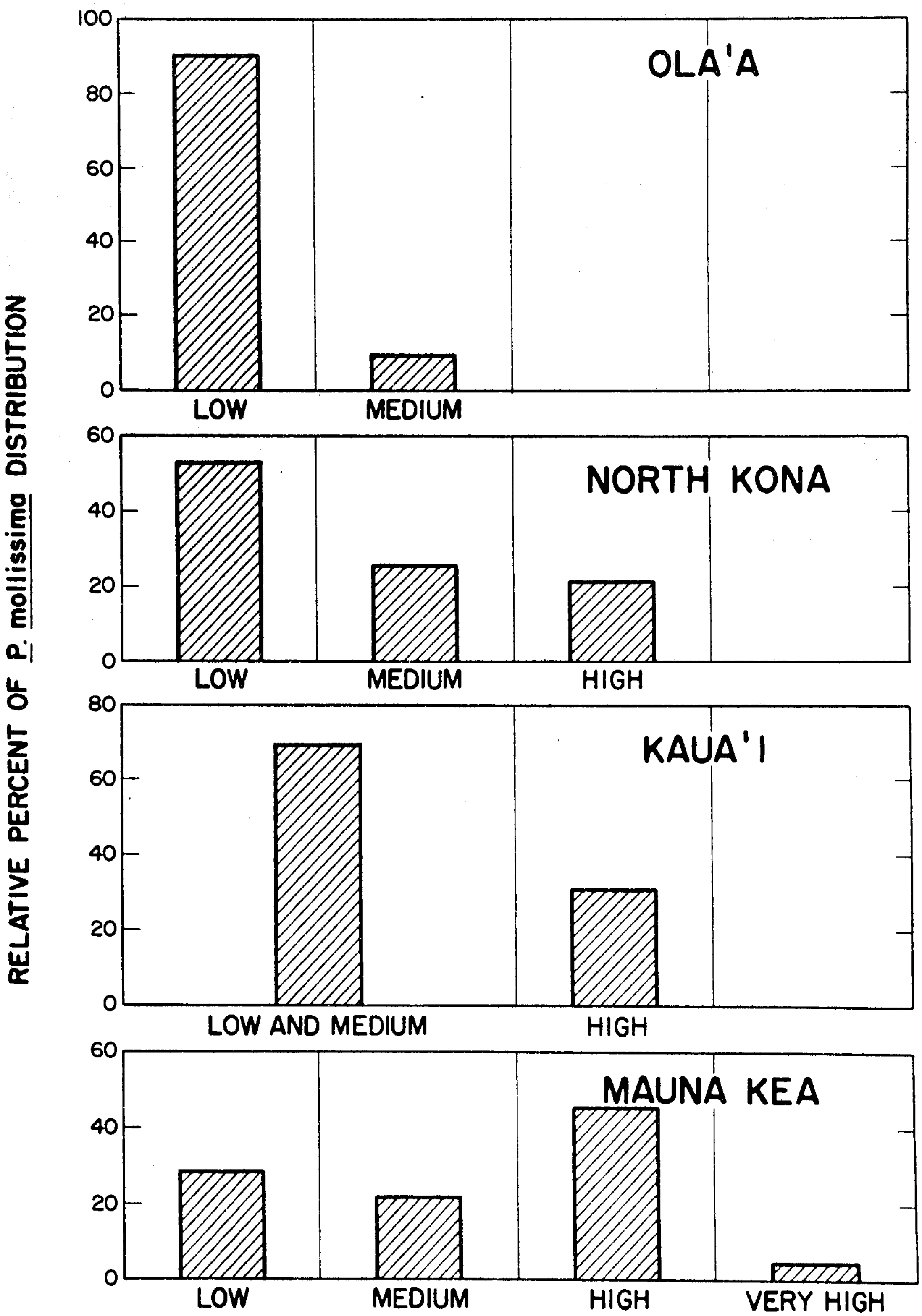

Figure 9. Arrays of abundance classes in the four major Passiflora mollissima populations in Hawai'i, based on information gathered during 1978 - 1981.

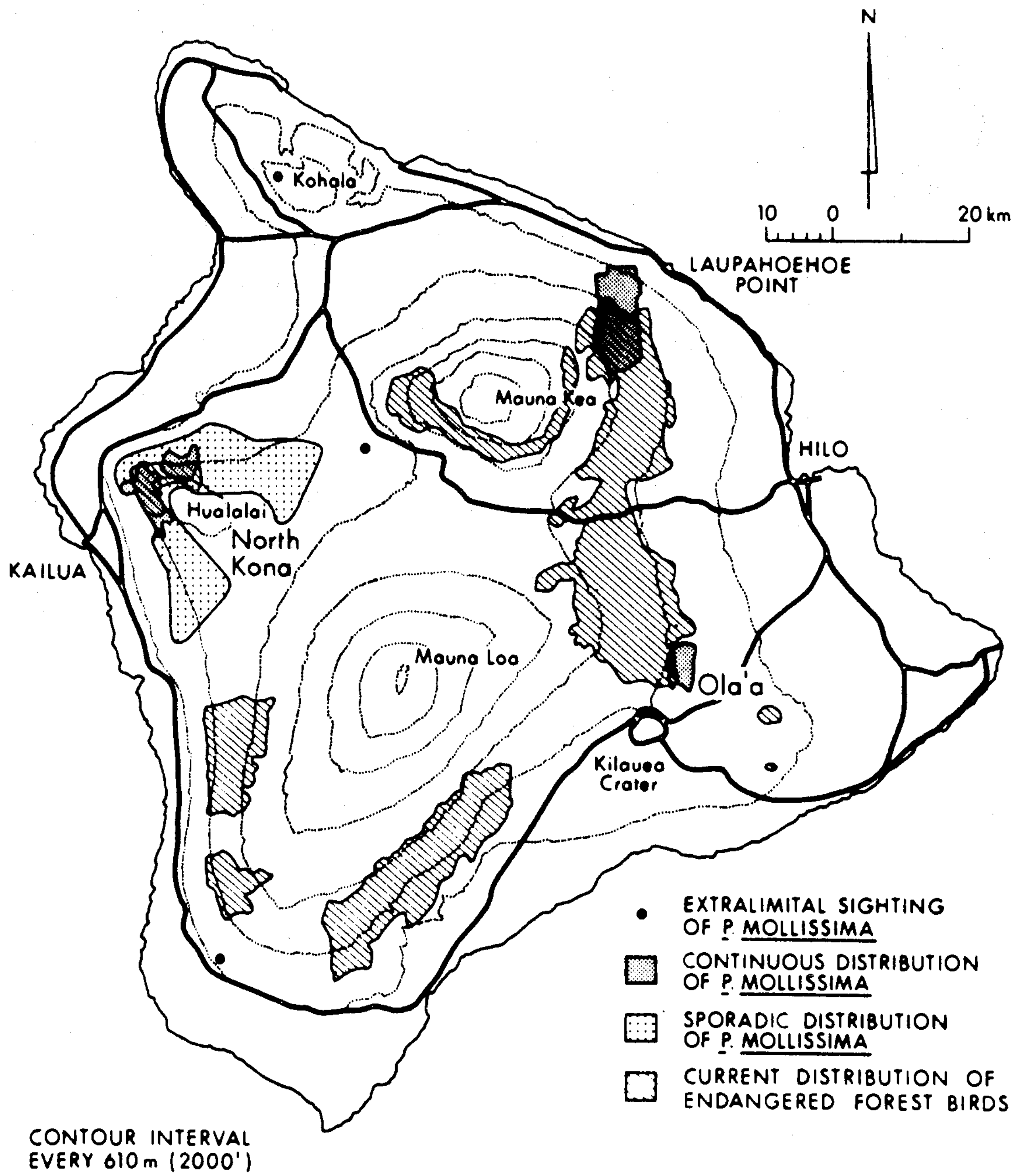

Figure 10. Map of the island of Hawai'i showing the distribution of <u>Passiflora mollissima</u> and endangered forest birds.