THE STATUS OF BANANA POKA IN HAWAI'I

Anne Marie LaRosa

ABSTRACT

Banana poka (*Passiflora mollissima*), a weedy, perennial liana from the Andean highlands, has invaded many of the major upland wet and mesic koa-'ōhi'a (*Acacia koa-Metrosideros polymorpha*) forests on the islands of Hawai'i and Kaua'i. Small, isolated populations have also been found on Maui. Infestations range from scattered individuals with low cover to areas of 100% cover, the latter often inhibiting growth and reproduction of native forest species. According to recent assessments of distribution and abundance in Hawai'i, approximately 200 mi^2 (520 km^2) are infested with this species. As with many tropical lianas, banana poka exhibits an efficient pattern of resource allocation, including staggered germination, rapid growth rates, early reproductive maturity, continuous growth and reproduction, and high seed output. These adaptations and effective dissemination through a number of alien mammals and birds that eat the fruit and seeds have led to the rapid spread of the species in Hawai'i. Annual rainfall in excess of 177-200 in. (4,500-5,100 mm), extremes of elevation, and intensive agriculture appear to limit the distribution of banana poka; very low light levels may check the rate of spread and extent of cover. Establishment and proliferation of the species in low light areas is accomplished through the mechanism of "gap-phase" replacement. Control efforts must address biological and sociopolitical factors. Although banana poka has no known economic value and is a noxious plant in Hawai'i, its close relationship to the edible passion fruit, *P. edulis*, has led to resistance by certain local groups to its control. Control of introduced mammals (especially the feral pig, *Sus scrofa*) and birds that disseminate seeds and often increase the rates of spread and establishment is a necessary adjunct to banana poka control. Deliberate practices that open up closed-canopy forests should also be discouraged, as spread of this climber is tied to disturbance.

INTRODUCTION

Banana poka (*Passiflora mollissima*) is a perennial, fleshy-fruited climber native to the Andean highlands. It occurs over an extensive altitudinal and latitudinal range, from 6,560 to 11,800 ft (2,000-3,600 m) elevation and from Venezuela to Bolivia (Killip 1938; Escobar 1980). The climate of this area may be characterized as a cool, moist, tropical montane environment. Although banana poka is a wide-ranging species that is extensively cultivated throughout the Andes, natural populations are infrequent and limited in size (Pemberton 1982). Natural habitats may be described generally as evergreen, woody formations of relatively low stature containing an abundance of ferns, mosses, and epiphytes (Weberbauer 1936; Cuatrecasas 1953; Escobar 1980). Banana poka also occurs along river courses in the drier inter-Andean valleys, perhaps only where it has escaped from cultivation.

Dispersal by humans has been largely responsible for the widespread distribution of banana poka. Because of its edible fruit and attractive flowers, specimens were introduced into numerous tropical and subtropical areas, including Mexico, California, New Zealand, Australia, Hawai'i, New Guinea, the Kermadec Islands, India, Ceylon, and East Africa (Killip 1938; Martin and Nakasone 1970; Green 1972; deWilde 1975; Sykes 1977; Escobar 1980). Most recently (1987), it was discovered in South Africa (MacDonald 1987). Most information from these areas deals only with banana poka cultivation. Escape from cultivation has been reported in several places, but only in Hawai'i is poka considered a serious pest (Hawaii Volcanoes National Park 1986). Varying land use philosophies within countries may contribute more to the perceived status of the plant than does the biology of the species.

Banana poka was introduced to the Pu'uwa'awa'a area of Hawai'i in the early 20th century (Pung 1971) and has subsequently spread via humans and various birds and mammals. As of 1986 it occupied 200 mi^2 (520 km^2) on the islands of Hawai'i, Kaua'i, and Maui (Fig. 1). Populations occur from 1,640 to 8,200 ft (500-2,500 m) elevation, in areas of 49 to 200 in. (1,250-5,000 mm) annual rainfall and average annual temperatures of 50 to 75 F (11-24 C) (Warshauer *et al.* 1983; Jacobi and Warshauer, this volume).

Only nine of 32 taxa of *Passiflora* introduced into the Hawaiian Islands have naturalized. Only two species, banana poka and sweet granadilla (*P. ligularis*), are known to cause severe impacts to native vegetation (Warshauer *et al.* 1983). Densities of banana poka reported for Hawai'i are often far in excess of those reported for South America (Warshauer *et al.* 1983). The widespread distribution and destructive impact of banana poka in Hawai'i is largely due to several environmental and biological factors, including: favorable environmental conditions similar to those found in the native range, abundance of disturbed habitats suitable for colonization, numerous native and alien dispersal agents, wide degree of environmental tolerance, lack of damaging predators and pathogens, and general plant vigor (LaRosa 1984). The successful pattern of resource allocation, including rapid growth rates, early reproductive

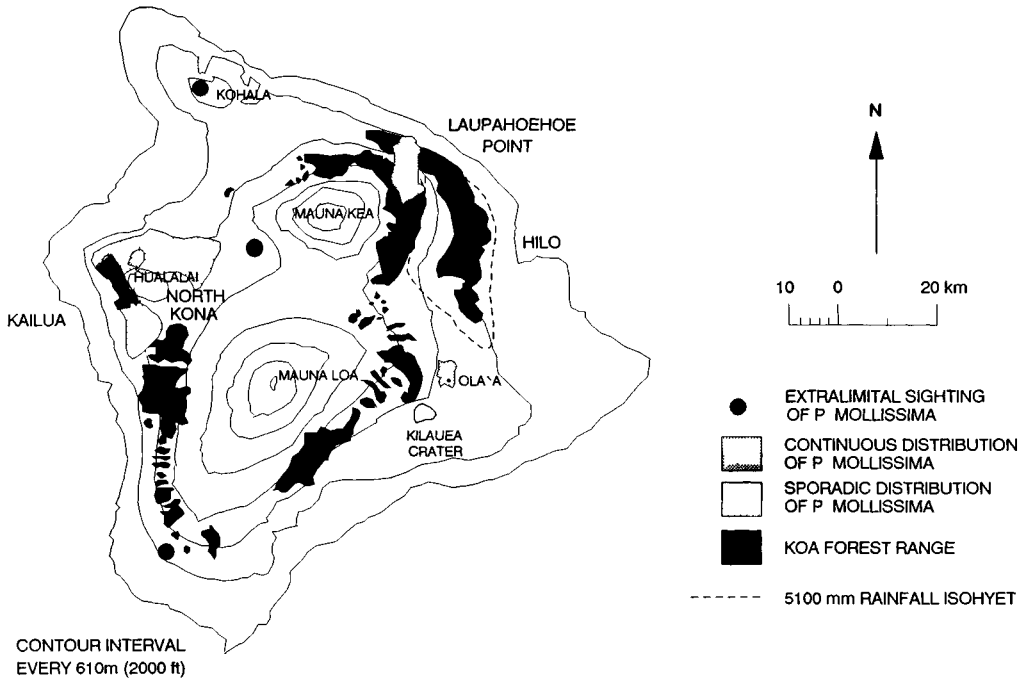

Figure 1a. Distribution of banana poka on the island of Hawai'i.

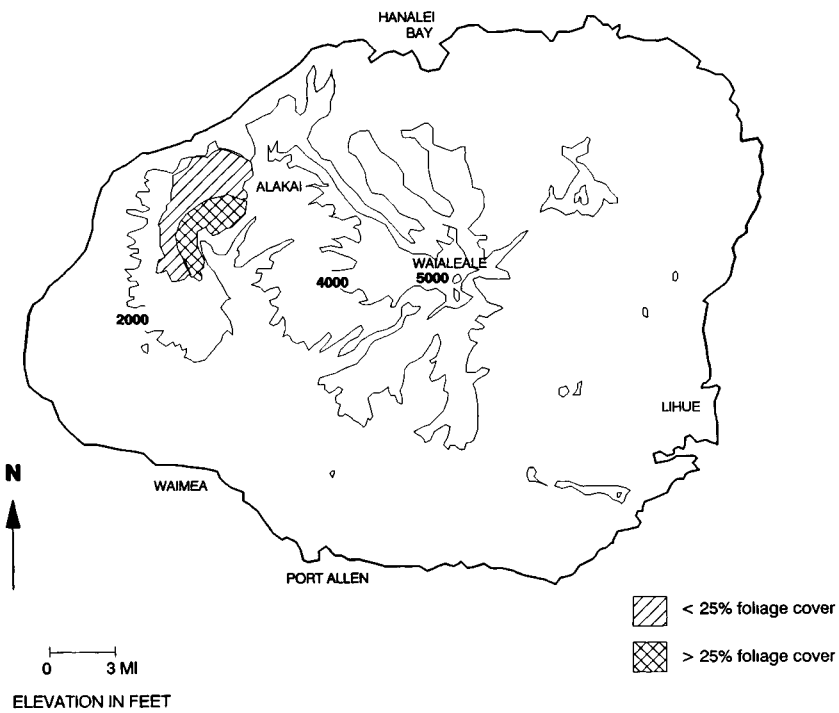

Figure 1b. Distribution of banana poka on the island of Kaua'i.

maturity, continuous reproduction, and high seed output, accompany the favorable environmental conditions. The success of banana poka generally precludes widespread control via mechanical and/or chemical means.

Jacobi and Warshauer (this volume) have demonstrated the potential invasiveness of banana poka in Hawai'i and the immediate need for an effective control program. The impact of the species populations on the koa *(Acacia koa)* logging industry was documented in the late 1970s (Skolmen 1979). An interagency effort to develop an effective biological control program is proceeding. Information on the taxonomy, biology, ecology, and distribution of banana poka, its impacts on Hawaiian ecosystems, and current and past control strategies is available from various sources (Warshauer *et al.* 1983; LaRosa 1984; Jacobi and Warshauer, this volume). This paper summarizes all available information on the subject and formulates management recommendations based on the available information.

TAXONOMY

Some uncertainty and disagreement has existed regarding the identity of the taxon commonly known in Hawai'i as banana poka. It has been variously referred to as *Passiflora mollissima, P. mixta,* and as an introgressive hybrid between banana poka and some unknown species (Fosberg 1975; Mueller-Dombois 1975; Mueller-Dombois *et al.* 1980; LaRosa 1985). Its morphological similarity to *P. tripartita* has also been noted (LaRosa 1985). In its native range, populations of banana poka are morphologically variable and frequently hybridize with other members of the subgenus *Tacsonia*. Introgressive hybrids are common (Escobar 1980).

Hawaiian populations of banana poka exhibit some variability, but little compared with that in native South American populations. The atypical morphology characteristic of Hawaiian populations falls within the range of variation reported for *P. mollissima* (LaRosa 1985). The possibility that this taxon represents an introgressive hybrid has not been ruled out, however. The atypical morphotype of banana poka found in Hawai'i is also found in several other Pacific areas where it has been introduced, suggesting a common ancestry with the Hawaiian introduction (Green 1972; deWilde 1975; Sykes 1977).

BIOLOGY

Information on the biology of banana poka comes principally from measurements and observations of three populations ('Ōla'a Tract, Kaloko-Hualālai, and Laupāhoehoe-Keanakolu) on the island of Hawai'i (LaRosa 1984). For the purposes of the following discussion, the life stages are defined as follows: seedlings -- individuals <3 ft (1 m) in height and having at least one pair of true leaves; juveniles -- non-reproductive individuals >3 ft (1 m) tall; adults -- reproductive individuals of any size.

Life History

Populations of banana poka are density dependent (LaRosa 1984). Although the density of germinants varied by several orders of magnitude, that of established individuals (>4 in. (0.1 m) in height) remained relatively constant (Table 1). High densities of germinants at most sites indicate that site conditions do not generally limit germination. Highest densities occurred near parent vines and in areas of sparse canopy cover and high feral pig (*Sus scrofa*) activity. In areas with little disturbance and greater canopy cover, densities were significantly lower (Table 1).

Seedling (germinant) survival was highly variable and negatively correlated with initial germinant density (Table 1). Most surviving seedlings were vigorous and free of pests, except in wetter areas, where soil-borne organisms (*e.g.*, damping-off fungi) and predators (*e.g.*, slugs) were more common. Growth rates of seedlings were variable but averaged 10 in./yr (25 cm/yr) (Table 2). Many seedlings remain quiescent following germination, forming a seedling bank that can be released under favorable conditions, *e.g.*, when a canopy gap occurs (LaRosa 1984).

The juvenile stage in the life cycle was characterized by fairly high survival (60% survive to reproductive maturity) (Fig. 2) and rapid growth rates (Table 2). Density of juveniles was relatively constant (Table 1). Growth rates in this phase averaged 3 ft (1 m) per year but occasionally exceeded 10 ft (3 m) per year (Table 2), allowing individuals to quickly reach the full sun of the canopy. These growth rates are within the range of rates of other tropical climbers (Bailey 1944; Janzen 1971; Choudhury 1972).

Adults of banana poka are typically climbing but may remain shrubby or become trailing when supports are lacking. Short-term survival records (18 mo) suggest that mortality of adults is low, averaging less than 5% (LaRosa 1984) (Fig. 2). The estimated life span of vines is 15 to 20 years (Schoniger 1969; LaRosa 1984). Growth rates of shoots on adult plants were variable (Table 2) but were composed of two discrete phases: rapidly-growing flushing shoots and slow-growing, non-flushing shoots (LaRosa 1984). Enhanced reproduction usually accompanied the rapid growth of flushing shoots, which were more common in areas of high light intensity, such as the canopy. Plants may reproduce within a single year in areas of full sun or large canopy gaps within closed-canopy forests (Burton 1980; LaRosa 1984).

Reproductive Biology

The reproductive pattern of banana poka combines outcrossing (pollination) early in anthesis (flower opening) with selfing at a later stage (Escobar 1980; LaRosa 1984), ensuring that isolated individuals can produce viable populations from a single colonizer. The natural incidence of selfing observed was low (4.3% fruit set), but a high incidence of fruit set in hand-selfed (pollinated) flowers indicates that flowers of banana poka are potentially highly self-compatible (LaRosa 1984).

Table 1. Estimate of the density (number/hectare) and percent survival of banana poka at seven sites on the island of Hawai'i (LaRosa 1984). Based on population structure analysis, estimates of survival rates can exceed 100%.

	Density (no./ha)				Survival Rate (%)	
	Height classes					
Site	Germinant (< 0.1 m)	Establishment (0.1-1.0 m)	Established (> 1.0 m)	Total	Germinant to Establishment	Establishment to Established
Kaloko 1	3,640	4,610	1,116	9,410	127	24
Kaloko 2	121,600	3,700	1,590	126,890	3	43
Laupāhoehoe 1	4,707	393	387	5,487	8	98
Laupāhoehoe 2	554,000	1,700	775	556,475	0.3	46
Laupāhoehoe 3	267,879	750	458	269,078	0.3	61
'Ōla'a Tract 1	638	625	500	1,763	97	80
'Ōla'a Tract 2	2,957	1,200	700	4,857	40	58

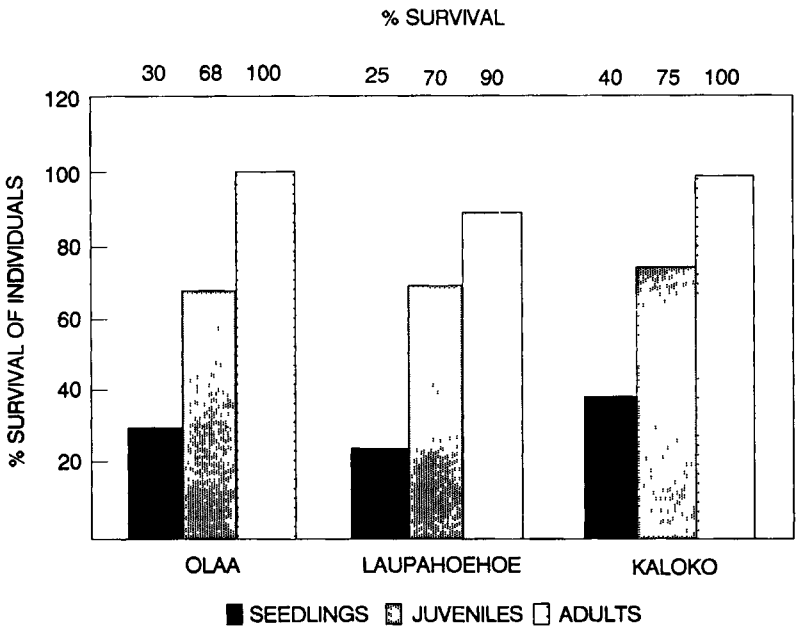

Figure 2. Survival of seedlings, juveniles, and adults of *Passiflora mollissima* over an 18-month period at three sites on the island of Hawai'i.

Table 2. Mean increases in shoot length (cm/yr) at three sites for three ages of banana poka.*

Site	Seedling		Juvenile		Adult	
Kaloko (Hualālai)	14.60	b-2	44.53	c-1	58.77	a-1
Laupāhoehoe (Mauna Kea)	28.83	a-3	101.11	b-1	61.68	a-2
'Ōla'a (Mauna Loa)	33.58	a-2	131.76	a-1	85.04	a-2
Mean	25.55 ± 1.46		91.25 ± 6.20		69.35 ± 5.48	
Overall Range	0 - 80.30		0 - 306.60		0 - 259.15	

*Means in the same column with the same letter are not significantly different by Duncan's Multiple Range Test ($p \leq 0.05$). Means in the same row with the same number are not significantly different ($p \leq 0.05$). Overall means and ranges for all plants measured are also given.

Biotic pollinators played a major role, increasing fruit set in open pollinated flowers to 15.2%. (*Passiflora* pollen is too large and sticky to be wind carried.) Generalist pollinators, including honeybees (*Apis mellifera*) and flower flies (Syrphidae), were the most frequent visitors to flowers in August 1981 (LaRosa 1984). Blowflies (*Calliphora* sp.) and Kamehameha butterflies (*Vanessa tameamea*) were occasional visitors. Pomace flies (*Drosophila* spp.) and thrips (Thysanoptera) were commonly found in flowers but are generally considered too small to be effective pollinators (Nishida 1963). Several species of birds, including the native 'i'iwi *(Vestiaria coccinea)*, 'amakihi *(Hemignathus virens)*, and 'ōma'o *(Myadestes obscurus obscurus)* and the alien Japanese white-eye (*Zosterops japonicus*), regularly visit flowers of banana poka in Hawaiian forests but appear to function principally as nectar robbers (LaRosa 1984). Asexual reproduction contributes little to the overall reproductive rate: apomictic (asexually produced embryos within ovules) fruit set is unknown, and vegetative reproduction is present only rarely, principally in wetter sites.

Banana poka fruits, which ripen in 2.5-3 months, contain an average of 180 seeds and may remain on the vine from several weeks to more than a month. Most ripe fruits are found during the wet months of December to March (LaRosa 1984). Fruit set in Hawai'i is greater than that noted for South America (Escobar 1980; LaRosa 1984). Fruit are reportedly much more abundant in Hawai'i than in most wild populations of banana poka in South America (Pemberton 1982).

Several fungal pathogens, including *Alternaria passiflorae* and *Colletotrichum* sp., attack fruit but generally do not limit fruit production in Hawai'i (LaRosa 1984). Pathogens may also be partially responsible for a condition known as "fruit split" or "fruit crack," which resulted in poor fruit development and abortion of 40% of all fruit in the 'Ōla'a Tract during an 18-month period (LaRosa 1984). Fruit split may also be a result of physiological factors associated with drought and results in significant crop losses of banana poka in South America (Anonymous 1962; Schoninger 1969).

Phenology

Populations of banana poka exhibit continuous growth and reproduction, a common feature of plants growing in the humid tropics (Daubenmire 1972; Wycherly 1973; Stiles 1977; Opler *et al.* 1980) (Fig. 3). Seasonal differences in phenological activity of banana poka in Hawai'i were principally quantititive (changes in magnitude of activity). Some annual variability occurred in phenological activity patterns (LaRosa 1984), but this type of variability is common in tropical species (Richards 1952; Daubenmire 1972; Croat 1975; Walter *et al.* 1975; Opler *et al.* 1980).

All phases of flowering normally exhibited peak activity in the drier months of April to September. Highest levels of fruiting were concentrated in the wetter months of December to March. Variability in phenological patterns occurred among populations, but peak levels of anthesis (flowering opening) and fruiting were fairly synchronous (within 30 days) (LaRosa

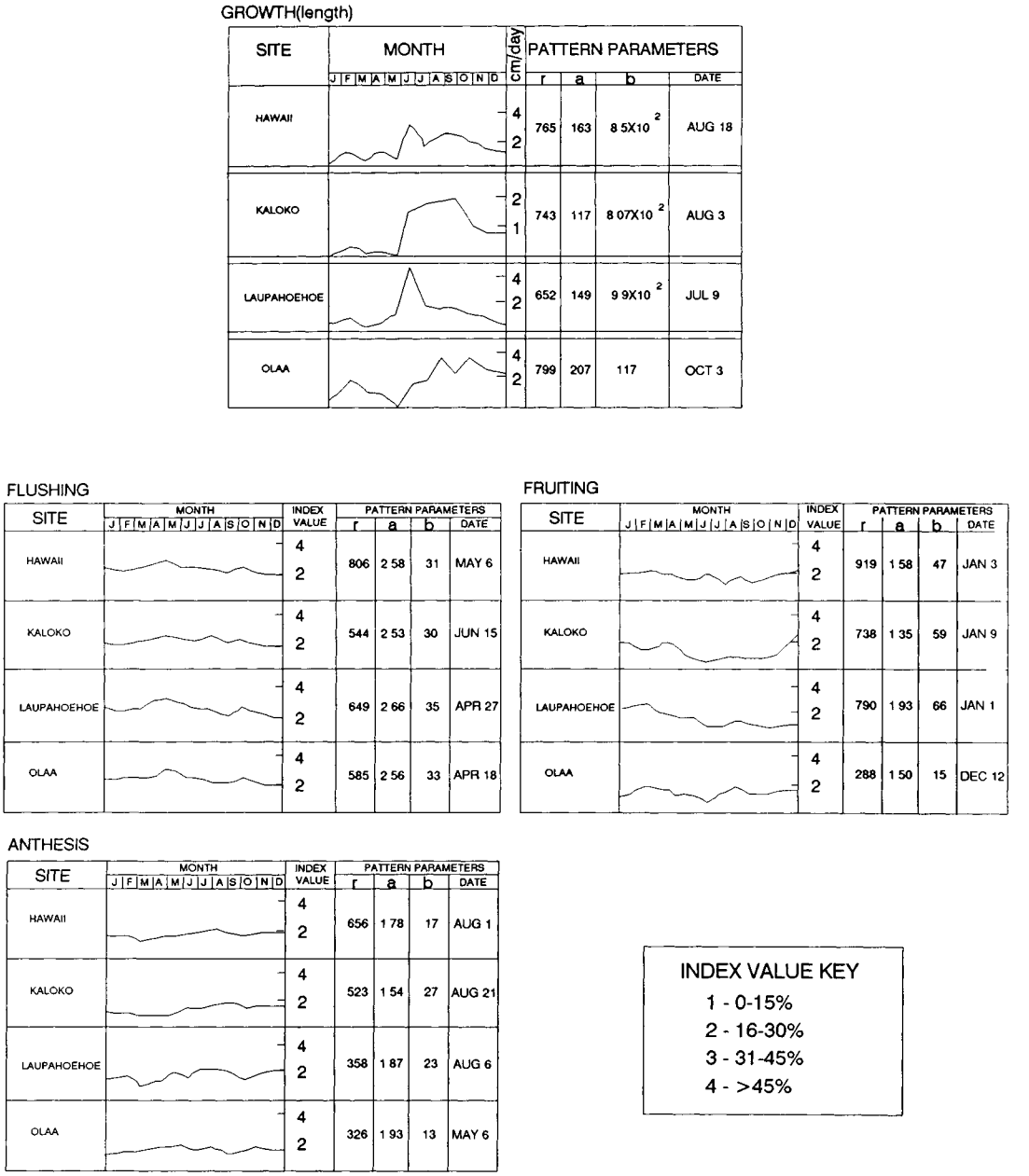

Figure 3. Phenology of banana poka at three sites on the island of Hawai'i: Kaloko (Hualālai), Laupāhoehoe-Keanakolu (Mauna Kea), and 'Ōla'a Tract (Mauna Loa), and all sites combined. Observed values are fitted to a least-squared regression analysis utilizing a sine-based function (Bridges *et al.* 1981). This function examines the annual periodicity of data based on a single peak activity period. r = monthly mean value; b = annual amplitude; c = predicted maximum value. Index values represent percent individuals in a particular phenological state.

1984). Bud initiation (flushing) and growth showed less synchronization among sites (LaRosa 1984).

Growth rates showed greater seasonal fluctuations. Highest levels of shoot growth occurred during the warmer summer months (the highest value in May coinciding with the peak in flushing) at all sites and may be a function of higher summer temperatures. A significant depression in growth occurred from December to April.

Data on climate and seasonality of reproductive activity for Laupāhoehoe, a mesic Hawaiian site, agree well with those for Quito, Ecuador, a site in the range of native populations (Fig. 4) (Herklots 1976; Escobar 1980). At both sites, heightened reproduction occurred during the dry season. A close association exists between seasonality of flowering and pollinator activity for several species, including *Passiflora* spp., in seasonal tropical environments (Janzen 1967, 1968; Gentry 1974; Frankie 1975; Stiles 1977). If this is also true for banana poka, which is largely dependent upon pollinators and occurs in some seasonal habitats in Hawai'i, then the timing of heightened reproduction may be a factor in the relative success of populations. In contrast, reproductive success may be negatively affected by heavy rains, which reduce pollen viability and/or physically damage flowers.

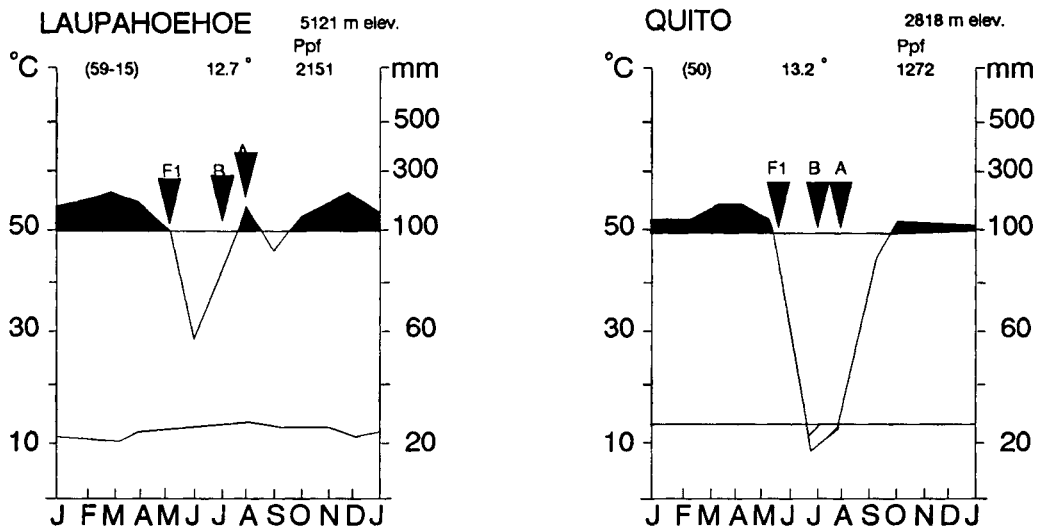

Figure 4. Relationships of climate to phenological activity of banana poka in Laupāhoehoe, Hawai'i, and Quito, Ecuador, South America. Climate diagrams illustrate climatic relationships between mean monthly temperature and rainfall (after Walter *et al.* 1975). Rainfall and temperature data for Hawaii are longtime averages from nearby stations (State of Hawaii 1970) and for South America from the U.S. Department of Commerce (1959, 1966). Arrows indicate peak periods of flushing (Fl), budding (B), and anthesis (A) at each site. Phenological data for Hawaiian site from LaRosa (1984); for South America, from Herklots (1976) and Escobar (1980).

DISPERSAL AND SPREAD

The fleshy fruits of banana poka are well adapted for dispersal by birds and mammals. Hard, impervious seed coats allow adequate seed survival following animal ingestion. While only one-half dozen or so species of birds and mammals are documented dispersal agents in Hawai'i, as many as 20 may disperse seeds of banana poka (Warshauer *et al.* 1983). These dispersal agents may be found in most habitats containing banana poka; therefore, much of the potential habitat is threatened with invasion if these animals colonize new areas (Warshauer *et al.* 1983). Humans may assist in this colonization directly via transplanting or indirectly via the movement of animals (*e.g.*, cattle, *Bos taurus*) from one range or island to another (Warshauer *et al.* 1983).

Two types of dispersal events (short distance and long distance), each having a very different outcome, are important in the spread of banana poka in Hawai'i (Warshauer *et al.* 1983). Most dispersal is over relatively short distances and augments existing populations (*e.g.*, the 'Ōla'a Tract population). Long-distance dispersal is an infrequent event and, when germination and establishment are successful, generally results in the establishment of a new population. Such populations are not subject to the intense intraspecific competition found in dense populations and therefore may expand rapidly if interspecific competition is not too severe. This greatly increases the difficulty of control of outlying populations (Woodall 1981; Mack, this volume); this situation is exemplified in the Kula area of Maui Island, where 15 distinct populations occur within an area of 200 acres (81 ha).

Continuous, prolific fruiting of banana poka provides abundant food for many mammals, particularly feral pigs. Indeed, pig densities are often highest in areas of dense banana poka (Wong 1971; Giffin 1972; Baker 1975). Feral pigs are fairly short-distance dispersal agents. Seed dispersal is limited by their short residence time in the pig's digestive tract (LaRosa 1984) and relatively small home ranges (several miles or less) (Giffin 1972; Baker 1975; Anderson and Stone, in press). Cattle also occasionally disperse seeds over relatively short distances (Warshauer *et al.* 1983). Seed digestion by feral pigs does not enhance germination but provides a fertile medium for germination and seedling growth (LaRosa 1984). Plant establishment is further aided by rooting activities of pigs, which create an environment of low competition.

Several native and alien birds are also important dispersal agents. Seeds of banana poka are used as grit by gallinaceous birds, including wild turkeys (*Meleagris gallopavo*) and Kalij pheasants (*Lophura leucomelana*) (Wong 1971; Warshauer *et al.* 1983). Seeds that pass unharmed through pheasants can germinate (V. Lewin, pers. comm. 1984). Kalij pheasants may be increasingly important dispersers of poka, as they are undergoing rapid range expansion and intensification and are currently found in all mid- and high-elevation forests and forest clearings on Hawai'i except in the Kohala district on Hawai'i Island (V. Lewin, pers. comm. 1982; J. Jacobi, pers. comm. 1987). Songbirds also disperse seeds of banana poka. The common myna (*Acridotheres tristis*) and the Japanese

white-eye, wide-ranging alien species, have not been observed eating fruit in the wild but readily ate banana poka fruit in captivity. Seeds passed through the mynas unharmed and successfully germinated, but no germination of the seeds from the white-eyes occurred (LaRosa *et al.* 1985). Fruits of banana poka are also a regular part of the diet of the endangered Hawaiian crow or 'alalā *(Corvus hawaiiensis)* (Giffin 1978, 1980).

Seeds are also passively dispersed along watercourses. This appears to be significant in range expansion in the Kula area on Maui.

Association with Forest Disturbance

Banana poka tolerates both high and low light levels, allowing individuals to colonize small forest gaps as well as open, disturbed areas. Seeds, shed in a dormant state, require a short period of after-ripening. Seed germination is staggered: once dormancy is broken, most seeds within a cohort germinate fairly rapidly (within eight weeks). Others are delayed for eight months or possibly longer, extending the potential for colonization when suitable conditions arise (LaRosa 1984).

Growth and establishment of banana poka increase proportionately to increasing light intensity and associated high temperatures, conditions found in most disturbed areas. Growth rates increase rapidly with increasing light intensity, and optimal growth occurs in full sunlight (LaRosa 1984). This can readily be observed in openings and at forest margins, which generally support the densest infestations of banana poka.

Germinants do not tolerate dense shade, but shade tolerance increases in older seedlings. In low light levels, individuals sacrifice biomass accumulation and leaf expansion for height growth, giving them a competitive advantage in a multi-tiered forest (LaRosa 1984). The ability to remain in the understory as shade-tolerant seedlings yet respond quickly to canopy gaps with rapid growth has allowed this species to persist and proliferate under varying disturbance regimes.

Most small-scale disturbances are naturally caused (including windstorms and the collapse of dead and dying trees) and result in spatial changes in the existing vegetation mosaic. These small gaps are readily colonized by banana poka, as evidenced by the patchwork pattern of its distribution in 'Ōla'a Tract and its response to experimental canopy opening (Burton 1980; LaRosa 1983, 1984). The spread of banana poka via gap invasion is tied to widespread dispersal of propagules by animals. Effective dispersal by animals is evident in the presence of widely scattered seedlings in remote sections of 'Ōla'a Tract where the canopy has not been disturbed.

Within very small gaps, low light levels may limit the success of banana poka, as growth rates may be insufficient for individuals to reach the canopy before gap closure occurs (Burton 1980; LaRosa 1983, 1984). Following canopy closure, growth and flowering of banana poka are largely restricted to the canopy. Few leaves are supported in the dense shade of the understory, and the death of apical shoots is common (LaRosa 1984). Reduced vigor of plants suggests that shade tolerance may be lost with increasing plant age. In larger openings, rapid growth allows individuals

to reach the canopy and reproduce before gap closure (Burton 1980; LaRosa 1983). In these situations, the competitive position of banana poka is enhanced, as growth rates of banana poka seedlings exceed those of the dominant forest tree, 'ōhi'a *(Metrosideros polymorpha)* (Burton and Mueller-Dombois 1984). Once the canopy is reached, individuals are no longer inhibited by shade and can proliferate, frequently spreading laterally.

Widespread canopy disturbances often follow large windstorms, which can occur as often as once every three to four years (Blumenstock 1967). The proliferation of banana poka in recent years in the 'Ōla'a Tract on Hawai'i and in the Kula area of Maui is largely a result of a single severe windstorm in January of 1980. 'Ōhi'a dieback (Mueller-Dombois *et al.* 1980) is another naturally occurring, large-scale disturbance that allows for proliferation of banana poka. For example, an area affected by canopy dieback in the Ōla'a Tract was initially colonized by a single (surviving) individual of banana poka. A slow establishment phase and a lag in population expansion closely followed the course of dieback (LaRosa 1984), and the area is now heavily infested with banana poka. The Hawai'i Forest Bird Survey undertaken by the U.S. Fish and Wildlife Service in 1977 recorded the highest density and cover of banana poka in areas of 'ōhi'a dieback in 'Ōla'a Tract (Warshauer *et al.* 1983). Banana poka, however, is currently absent from most areas with extensive dieback, probably indicative of lack of dispersal to many of these areas. Large-scale anthropogenic disturbances, including logging, tree fern (*Cibotium* spp.) harvesting, forest clearing, and cattle ranching, also increase the likelihood of banana poka infestations.

Disturbance of native or alien ground vegetation, particularly by feral pigs, increases colonization and establishment of banana poka (LaRosa 1984). Disturbed areas exhibit much higher seedling densities than surrounding areas where seedlings often occur only as scattered individuals (LaRosa 1984). This is particularly evident where introduced grasses form a dense ground cover. In most areas, ground cover of native species seldom reaches 100%, and these areas are more susceptible to invasion by banana poka than those with high alien species ground cover. Mid-level tree fern canopies can also be heavily disturbed by feral pigs, allowing more light to reach the ground and encouraging banana poka. Increased establishment is not directly related to later survival, however, as populations are density dependent.

Limits to Spread

Banana poka is excluded from few areas in Hawai'i, but several conditions may limit plant vigor and population size and thereby reduce its competitive ability and rate of spread. Dense shade and extremes of rainfall, elevation, and temperature all appear to reduce success (Warshauer *et al.* 1983).

Upper and lower elevational limits have been noted in both Hawai'i and South America (Escobar 1980; LaRosa 1984), but the limiting factors are unknown. Extremes of temperature may be at least partly responsible. High temperatures affect the growth, vigor, and reproduction of banana poka;

cultivation has been unsuccessful at lower elevations in the tropics (Hooker 1845; Paxton 1846; Martin and Nakasone 1970; Howell 1976; Escobar 1980). Markin (pers. comm. 1986) reported that banana poka at elevations under 182 ft (600 m) in Hawai'i shows greater susceptibility to attack by pathogens and nematodes. Increased susceptibility to disease may indicate increased stress. Low temperature (frost) limits the upper elevational spread in South America (Jaramillo 1957; Anonymous 1962; Martin and Nakasone 1970) and may be a factor in some areas of Hawai'i as well.

Extremely wet areas appear to be free of banana poka. A sharp demarcation in the distribution of banana poka in Laupāhoehoe coincides with the 200-in. (5,100-mm) rainfall isohyet and cannot be explained by elevation, temperature, or vegetational changes (Warshauer *et al.* 1983). In Kōke'e on Kaua'i Island, the infestation is concentrated in the more mesic koa forest: no individuals have been seen in the adjacent Alaka'i Swamp. Poor soil drainage may partly explain the distribution patterns noted above.

The occurrence of pests, pathogens and associated damage, shoot abortion, and high seedling mortality was generally higher in wet than in dry sites in Hawai'i (LaRosa 1984). Factors contributing to lowered reproductive success also occur more frequently in wetter areas, including lower pollinator activity and success, loss of pollen viability, physical damage to flowers, and increase in abortion. Conversely, lower growth rates, plant vigor, and population densities occurred at very dry sites, such as the recent, relatively unweathered lava flows of Hualālai (LaRosa 1984). In South America, cultivated crops of banana poka are regularly irrigated in dry areas (Jaramillo 1957).

Light is seldom a limiting factor in the spread of banana poka in Hawai'i. Seedlings reach their light compensation point near 2% of full sun (LaRosa 1984), but light is generally greater than this under relatively sparse canopies in most Hawaiian forests (Burton and Mueller-Dombois 1984). Low light levels found in tree fern forests limit population sizes but, because of frequent disturbances to both the canopy and understory layers, rarely exclude banana poka from an area (Burton and Mueller-Dombois 1984; LaRosa 1984). Dense shade occurs under introduced tree plantations of tsugi pine (*Cryptomeria japonica*) and tropical ash (*Fraxinus uhdei*). On Mauna Kea on Hawai'i Island, these plantations contained few or no individuals of banana poka, while surrounding areas of more open forest supported the most dense populations recorded (LaRosa 1984).

DISTRIBUTION AND STATUS OF BANANA POKA IN HAWAII

Banana poka has successfully invaded areas of diverse climate and vegetation. Colonization has occurred in 28 vegetation types (as defined by Jacobi and Warshauer, this volume) ranging from dry lava flows with sparse, open naio (*Myoporum*) scrub communities to dense, montane 'ōhi'a-tree fern rain forests. Within these communities there is

considerable diversity in forest stature, structure, and species composition that reflects variations in moisture conditions and successional states (Warshauer *et al.* 1983). The most heavily impacted vegetation type is the disturbed mesic koa-'ōhi'a forest. Other vegetation types with a high incidence of banana poka are the relatively intact wet 'ōhi'a forest and the wet 'ōhi'a-koa forest with a tree fern subcanopy and native species understory (Jacobi and Warshauer, this volume).

The following discussion of the distribution and status of populations of banana poka in Hawai'i is largely a summary of information presented in Warshauer *et al.* (1983). To determine changes in distribution and abundance, the authors compared information from a 1971 ground survey and map prepared by Pung and Wong (Wong 1971; on file at the Hawaii Division of Forestry Office, Honolulu) with data from ground surveys made between 1976 and 1981 by the U.S. Fish and Wildlife Service Hawai'i Forest Bird Survey (Scott *et al.* 1981), from 1981 aerial surveys of the 'Ōla'a Tract and Mauna Kea populations, and from examination of aerial photographs. Information on survey methods and detailed distribution maps of each major population of banana poka may be found in Warshauer *et al.* (1983). Information gathered during a demographic study from 1979 to 1983 (LaRosa 1984) and incidental observations (R. Hobdy, pers. comm. 1986, 1987) are used to augment the discussion.

In 1986, banana poka inhabited approximately 134,425 a (54,400 ha) on three major islands in Hawai'i (Table 3). Populations are characterized by a core of continuously distributed individuals surrounded by an area of sporadic distribution. The five major populations -- 'Ōla'a Tract, Mauna Kea (Laupāhoehoe), and North Kona (Kaloko), on Hawai'i; Kōke'e on Kaua'i; and Kula on Maui -- all originated from deliberate plantings by humans. In addition, three small, extralimital populations, consisting of from one to several individuals, occur on Hawai'i Island: Kohala, Manukā State Park (Warshauer *et al.* 1983) and Pōhakuloa (Higashino *et al.* 1977) (Fig. 1). More detailed surveys may yield additional isolated populations.

Following is an assessment of the extent and status of each of the major populations from published accounts. Changes in distribution and abundance from 1971 to 1986 are summarized in Table 3.

'Ōla'a Tract, Hawai'i

The most recent and rapidly expanding population of banana poka on Hawai'i is in the 'Ōla'a Tract of Hawaii Volcanoes National Park; this infestation originated from a transplant from Keanakolu (Mauna Kea) to Volcano in 1958 (Pung 1971). Density was generally low (on the order of 2,025 individuals/a or 5,000 individuals/ha) (LaRosa 1984), as are foliage cover values (generally less than 5%) (Warshauer *et al.* 1983). However, cover was much greater locally along forest margins and in forest openings. Habitats occupied by banana poka include closed-canopy, wet 'ōhi'a-tree fern forests, and more open-canopy, wet ohi'a forests (lacking a dense tree fern subcanopy). A small, relict stand of wet koa-'ōhi'a forest is heavily infested with banana poka (Warshauer *et al.* 1983).

Table 3. Summary of the area of continuous distribution and relative abundance of banana poka in five areas in Hawai'i. Continuous distribution in 1986 = 19,357 ha; sporadic distribution in 1978 = 35,000 ha. (Adapted from Warshauer *et al.* 1983.)

Population/ Island	Year of Survey*	Abundance Class** Low	Medium	High	Very High	Total	No. Years between Surveys	% Change in Area of Distribution (%)	
'Ōla'a Tract,	1971	142***	--	--	--	142			
Hawai'i	1981	2330***	242	--	--	2572	10	+18.11	(1711)
Mauna Kea,	1971	615	2939	2402	1202	7158			
Hawai'i	1981	1946	1947	3156	325	7374	10	+1.03	(3)
North Kona,	1971	141	3746	262	--	4149			
Hawai'i	1978	n/a	n/a	n/a	n/a	6263	7	+1.51	(50)
Koke'e,	1975	n/a	n/a	n/a	n/a	4900			
Kaua'i	1981	---------2350--------		1050	--	3400	6	-1.44	(30)
Kula,	1971	2	--	--	--	2			
Maui	1986	200	--	1.5	70	200+	15	+100.00	
	1988	7		16	77				

* 1971: Kula, Maui: Report by E. Tamura (1978a,b). All others from distribution maps of W. Wong and E. Pung (Wong 1971).
1975: Koke'e, Kaua'i: Report by R. Daehler (1975).
1978: Hawai'i Forest Bird Survey, 1978-81, U.S. Fish and Wildlife Service (Warshauer *et al.* 1983).
1986: Pers. comm., R. Hobdy, Hawaii Div. Forestry.
1988: Memo by R. Hobdy (Dec. 23, 1988) to C.W.S. Lum.

** Percent foliage cover in each abundance class as determined by Warshauer *et al.* (1983):
1971: Low = 10%; Med = 10-30%; High = 30-70%; Very High = 70-100%.
1978: Low = 5%; Med = 5-25%; High = 25-75%; Very High = 75-100%.
n/a: Data for abundance classes not available.

*** Forest margins support greater cover locally.

\+ Main survey detailed acreage actually covered by vines to be 9.05 a (3.6 ha) within a 200-a (81-ha) radius (Hobdy 1988).

The 'Ōla'a Tract population has grown explosively in the last 10 years. The infested area increased 17-fold (1,700%; from 350 to 5,775 a or 142 to 2,338 ha) from 1971 to 1981 (Table 3; Warshauer *et al.* 1983). Most of this increase can be attributed to the severe windstorm of January 1980 (Warshauer *et al.* 1983; LaRosa 1984). Prior to the storm, small seedlings were numerous in the understory, but mature canopy vines were rare. Following the storm, banana poka increased visibly in the many canopy gaps created by the loss of tree fern fronds and canopy trees. Feral pigs played an important role by dispersing seeds throughout the area before and after the disturbance (LaRosa 1984).

Mauna Kea, Hawai'i

Banana poka was introduced to the Keanakolu area of the Laupāhoehoe district in 1928 and spread rapidly. The highest density and cover values (≥202,000 individuals/a or 500,000/ha; 75 to 100% cover) of banana poka occur in the Laupāhoehoe-Keanakolu area of Mauna Kea (Warshauer *et al.* 1983; LaRosa 1984). The heavy infestation may be largely a consequence of historical grazing and subsequent logging. Cattle used the area heavily prior to the introduction of banana poka in 1928 but were removed in the early 1940s (Pung 1971). Following removal, banana poka spread rapidly through the heavily disturbed forest. Areas with less than 30% cover are often grazed by cattle, which reduces most species, including banana poka. Optimal habitats on Mauna Kea include mesic and wet koa-'ōhi'a forests. Rainfall in excess of 175 to 220 in. (4,500-5,100 mm) appears to limit population expansion into wet 'ōhi'a forests on Mauna Kea (Warshauer *et al.* 1983).

Feral pigs, which reach their highest density on Hawai'i on Mauna Kea (Giffin 1972), are now largely responsible for the intensive dispersal of seeds. Other dispersal agents include cattle (feral and escaped livestock), turkeys, gallinaceous birds, and horses (*Equus caballus*).

The Mauna Kea population of banana poka is stable (Warshauer *et al.* 1983): the total area infested by banana poka on Mauna Kea declined 3% between 1971 and 1981 (Table 3). Localized changes in distribution and abundance, however, indicate that population expansion is still occurring within limited areas, but that some population losses have also occurred. For example, the area in the highest cover class declined from 2,970 to 803 a (1,202 to 325 ha). Cattle grazing and the disturbance accompanying koa logging may account for some of the banana poka cover loss.

North Kona, Hawai'i

This infestation is the result of the merging of two populations from separate introductions -- the original introduction to the Hawaiian Islands at Pu'uwa'awa'a in 1921, and a later introduction to Honua'ula in 1928 (Pung 1971). Banana poka is still spreading into favorable habitats in North Kona. The area of continuous distribution increased 51% from 1971 to 1978 (Table 3); 20% of this increase was in the high cover class (30% to 70% cover). In 1981, a 15,565-a (6,300-ha) core area of continuously distributed individuals surrounded a sparsely populated (3-16 individuals/a or 8-40/1,000 ha), 15,565-a (6,300-ha) area with low banana poka cover (Warshauer *et al.* 1983).

While banana poka populations in Kona are as old or older than the Mauna Kea population, the degree of infestation is less. The rate of spread has been slower in Kona, and cover values are less (Warshauer *et al.* 1983). Several factors may explain lower success in Kona, particularly on Hualālai Volcano. Growth of banana poka shoots from Hualālai was slower than for those from 'Ōla'a Tract and Mauna Kea (LaRosa 1984), likely a function of the lower annual rainfall on Hualālai. Other site factors may also be limiting. Hualālai is a composite of geological and plant successional stages, and much of the area is geologically young, with little soil development and early successional vegetation (Warshauer *et al.* 1983). Areas of low-stature 'ōhi'a forest support lower densities and cover of most plants, including banana poka (LaRosa 1984). Areas with banana poka cover in excess of 30% are restricted to more mature forests, such as mesic koa-'ōhi'a or koa-mamane *(Sophora chrysophylla)* (Warshauer *et al.* 1983).

In addition, disturbance factors, including cattle grazing, logging, and forest clearing, have generally been less in Kona than at many areas on Mauna Kea, although disturbance is rapidly increasing. Feral pigs and cattle, Kalij pheasants, and the 'alalā are known to disperse seeds in the Kona area, but dispersal may be less intensive than elsewhere. Coarse lava flows isolate some animal populations, reducing home ranges and resulting in fewer potential sites colonized (Warshauer *et al.* 1983). Also, the density of feral pigs is much lower on Hualālai than on Mauna Kea (Giffin 1972).

Kōke'e, Kaua'i

Banana poka was introduced to the Kōke'e area in 1923 (Wenkham 1967). The infestation currrently extends from 2,790 to 4,265 ft (850-1,300 m) elevation (Daehler 1975; Warshauer *et al.* 1983). Principal habitats invaded include mesic koa-'ōhi'a forests and, to a lesser extent, wet 'ōhi'a forests (Warshauer *et al.* 1983). Alien feral pigs and red jungle fowl (*Gallus gallus*) range throughout the area and, along with passive dispersal of the plant via streams, are largely responsible for its widespread occurrence.

Little quantitative information is available on the distribution and population dynamics of banana poka on Kaua'i. In 1981, approximately one-third of the infested area had high cover values ($\geq$ 30% banana poka foliage cover). Highest cover values occurred in mesic areas such as gulches, while surrounding drier ridges had lower cover values (Warshauer *et al.* 1983). Banana poka is excluded from the wettest habitats (*e.g.*, Alaka'i Swamp).

Comparison of a 1975 population estimate (Daehler 1975) with a 1981 aerial survey (Warshauer *et al.* 1983) suggests that the population declined 30% (Table 1) in six years, although the estimates may not be comparable due to differences in estimation techniques.

In 1982, Hurricane Iwa severely disturbed the vegetation in the Koke'e area and damaged many canopy trees. While its effects on the banana poka infestation have not been quantitatively assessed, a cursory examination of

the area suggests a proliferation of banana poka in the ground layer. This likely resulted from extensive canopy disturbance, which allowed more light to reach the forest floor. Vines that were in the canopy prior to the storm were displaced to the ground along with supporting trees (and branches). As the forest recovers, banana poka will be carried into the canopy, increasing its cover in the upper strata. A recent study (LaRosa and Floyd 1988) suggested that banana poka may be interfering with the post-hurricane reproduction of the endemic understory species mokihana *(Pelea anisata)* in a heavily disturbed area of Kōke'e.

Kula, Maui

Prior to the early 1970s, the only known specimens of banana poka on Maui were part of a cultural planting at the Hawaii Agricultural Experiment Station (Wong 1973). However, the most recently documented infestation began presumably as an ornamental planting on private property and when "discovered," in 1971, by Hawaii Division of Forestry personnel, consisted of one adult and approximately 250 seedlings (less than 2 a (0.8 ha) in extent) in the Waiakoa (Kula) area. The potential invasiveness and dominance of banana poka was known to Division of Forestry officials at that time, and they immediately alerted the Hawaii Department of Agriculture, which promptly eradicated the population (Wong 1973). They presumed this was so until 1978, when it was again noted in the same area (Tamura 1978a, 1978b). Little attention was paid to the periodic appearance of seedlings until the early 1980s, when banana poka was noticed spreading through a forest of black wattle (*Acacia mearnsii*).

In 1988, the Waiakoa population was mapped, using aerial and ground surveys, by the Hawaii Division of Forestry (Hobdy 1988). Their data represent the most comprehensive information available on this infestation. In 1989, banana poka continuously covered 9 a (3.6 ha) within a 200-a (80.9-ha) radius (Table 3), largely on privately owned agricultural parcels and homesteads in the Waiakoa area. Fifteen different invasion centers have been mapped. Cover ranges from light (<10%) to heavy (>50%), with 77% of the infestation in the heavy class. Outside of developed areas (agriculture, landscaping), vegetation in the area is primarily a mixture of black wattle and *Eucalyptus* sp. Heaviest densities and cover occur in the gulches.

Comparison of the 1971 and 1988 population estimates indicates an explosive population increase (Table 3). Most of this increase appears to be local population enhancement rather than expansion beyond the 200-acre radius and may be largely a result of banana poka invasion following large-scale vegetation disturbance in the area during the January 1980 windstorm. Additionally, some population expansion is occurring downslope, presumably via passive dispersal down watercourses (gulches). Much of the potential expansion of this population will be held in check by rapid development and utilization of the area, but State-owned lands in the Kula Forest Reserve, located at higher elevation than the infestation, are threatened.

The most encouraging note to date has been the continued support and efforts of the local community, particularly the local chapter of the

Sierra Club, to eradicate this pest from the area. Consequently, in 1988, Senate Bill 599 was passed, appropriating State monies for control of this population.

IMPACTS ON HAWAIIAN ECOSYSTEMS

While little specific information is available on the direct effects of banana poka on host trees, lianas are often detrimental to their hosts and may be considered structural parasites. Dense liana foliage covers tree crowns, thus occluding sunlight and reducing photosynthesis, growth, and reproduction of the host tree (Stevens 1987). Substantial reduction in photosynthetic capacity results in eventual tree death. The physical weight of lianas also causes branch breakage, which often facilitates the entrance of pathogens. Lianas also compete directly with their host tree for soil nutrients (Whigham 1984). They are also recognized as major economic forest pests; increasingly, tropical forests are being replaced by liana thickets following large-scale disturbances, particularly logging (Telford and Childers 1947; Dawkins 1961; Kochummen 1966; Fox 1968; Meijer 1970; Thomas 1980; Putz 1984; Nicholson 1985; Stevens 1987). In open forests, the reduction in light intensity at the forest floor under dense liana cover may inhibit the growth and regeneration of understory species and lead to premature succession (Ogawa *et al.* 1965a, 1965b; Mueller-Dombois *et al.* 1980; Friedland and Smith 1982; Putz 1984).

In Hawai'i, infestations of banana poka have resulted in large-scale disturbances and changes in native vegetation, particularly in the Laupāhoehoe-Keanakolu area of Mauna Kea. Banana poka was identified as the most serious problem in koa silviculture (Skolmen 1979). In logged areas, banana poka dominates koa, completely smothering seedlings and saplings within the first four years of koa forest regeneration (Scowcroft and Nelson 1976). In extreme cases, degradation of watersheds can result from such large-scale changes in vegetation.

Infestations of banana poka have additional impacts on native Hawaiian ecosystems. Shallow-rooted trees, including 'ōlapa *(Cheirodendron trigynum)*, koa, and 'ōhi'a, topple more easily with the added weight of vines, forming gaps in closed-canopy forests, which are further invaded by banana poka (Burton 1980; LaRosa 1983). Banana poka may persist after canopy closure and become a permanent component of the vegetation (Burton 1980; LaRosa 1984). Eventually, the loss of structural integrity and a lowered species richness results (Jacobi and Warshauer 1975; Mueller-Dombois *et al.* 1980; LaRosa 1984; Jacobi and Scott 1985).

Degradation and loss of habitat for native fauna occur concurrently, as in the upper elevation koa-'ōhi'a forest on Hawai'i (Warshauer *et al.* 1983; Jacobi and Scott 1985). Only 13.4% of the original acreage of this forest type remains in Hawai'i, and it is habitat for six endangered forest birds and 11 species of endangered plants (Jacobi and Scott 1985). The wet and mesic 'ōhi'a forest and the wet koa-'ōhi'a forest types also support populations of banana poka and are important habitats for endangered birds and plants. The rich native invertebrate fauna is also seriously affected

by alien plants that affect invertebrate host plants (Gagné and Christensen 1985).

HISTORY OF CONTROL EFFORTS

Mechanical, biological, and chemical means of control have all been attempted for banana poka, but to date no comprehensive management strategy exists. In the early 1970s, several small-scale chemical control projects, using picloram (Tordon), 2,4-D (Tordon 22K), a mixture of picloram and 2,4-D (Tordon 212), and Paraquat, were conducted on the island of Hawai'i by the Hawaii Division of Forestry. All herbicides proved effective against banana poka but were nonselective and resulted in undesirable effects on nontarget species (Landgraf 1971; Cusset 1975). The Division of Forestry then looked for biological control agents present in Hawai'i. Several species of the fungus *Alternaria* and a scale insect (*Ceroplastes cerripidiformis*) were identified as potential control agents, but work on these projects was inconclusive (Laemmlen 1971).

In the early 1970s, an alien passion vine butterfly, *Agraulis vanillae*, was introduced to Kōke'e (Kaua'i Island) to control banana poka. Individuals did not readily establish on banana poka and were therefore unsuccessful in its control (Murai 1977; Nakahara 1977; Bianchi 1979). Serious attempts at biological control began in 1981, when the Hawaii State Legislature appropriated funds to begin control work on forest pest plants. This ongoing joint effort of several government agencies is the subject of another paper (Markin *et al.*, this volume).

Hawaii Volcanoes National Park personnel have conducted a herbicide sensitivity test on a small, isolated population of banana poka in the 'Ōla'a Tract (L.W. Cuddihy, pers. comm. 1990). Three herbicides (triclopyr, glyphosate, and a commercial mix of picloram + 2,4-D (Tordon-RTU)) were applied to cut stumps on a very limited basis (three plants per treatment). Early results on the efficacy of herbicide control concur with previous findings: herbicides, and in this case, mechanical means, appear effective in controlling banana poka. More data are needed on nontarget effects, resprouting of vines, and long-term control efficacy.

MANAGEMENT RECOMMENDATIONS

Banana poka has invaded, and is expanding in, a wide range of habitats in Hawai'i. Because of its widespread distribution and dense populations in many areas, overall control of banana poka in Hawai'i can only be achieved by using biological control. But biological control is not a panacea (Howarth 1983), and the potential impacts of introduced control organisms on other native vegetation and the native arthropod fauna must be carefully considered. Follow-up studies will be necessary to monitor the long-term efficacy and effects on the ecosystem.

Because biological control is a long-range goal, if in fact a successful agent (or agents) can be found, it is necessary to weigh the short-term

consequences and costs of no action. Following the principles of weed population expansion set forth by Mack (this volume) and Woodall (1981), we may predict several things. For a dense, mature population such as that at Mauna Kea, there would be little additional consequence in waiting for a successful biological control program to become established. Some population expansion might occur on the perimeter of this population, but this would take place at a relatively slow rate.

For populations of limited extent, efforts should be directed toward timely mechanical and/or chemical control. Delaying control measures could be costly. With the potential for rapid rates of banana poka population growth under favorable conditions, the possibility of later control by these means may be quickly lost forever. Rapid increases have probably occurred very recently for the population at Kula, Maui (R. Hobdy, pers. comm. 1986).

When deciding whether to use mechanical or chemical control methods, managers must weigh the success of control efforts against the possible disturbance to the surrounding environment. Herbicide effects on nontarget species and possible drift or leaching of herbicides are especially important. Chemical control can be relatively safe when herbicides are applied carefully, correctly (according to label specifications), and directly to individual target plants. Because stems of banana poka do not readily sprout, mechanical means of control may suffice in selected areas. Some sprouting has occurred on the abaxial cut surface, however (J.T. Tunison, pers. comm. 1986). Careful use of these techniques may be effective for control of small populations in the immediate future.

Following the recommendations of Woodall (1980) and Mack (this volume), current control efforts should be concentrated on outlying populations, as they are the easiest to control and have the greatest potential for spread. Several such populations on the island of Hawai'i were identified by Warshauer *et al.* (1983), including one each in Kohala, Manukā, and Pōhakuloa. Any additional sightings omitted from this most recent distribution survey should be immediately controlled, if possible.

Spread and proliferation of banana poka can also be limited by the control of anthropogenic forest disturbance and introduced animals. The association of banana poka with forest disturbance has been clearly demonstrated. Heavy disturbance has historically occurred in areas where banana poka infestations are presently dense. It is evident from the study of the ecology of this species that control of feral pigs and certain alien birds is necessary to prevent further spread. Studies in pig-free sections of 'Ōla'a Tract support the idea that feral pigs enhance distribution. Studies of the effects of feral pig removal without concommitant treatment (chemical or mechanical) of banana poka on populations in the 'Ōla'a Tract of Hawaii Volcanoes National Park are ongoing (J.T. Tunison, pers. comm. 1989).

Successful biological control programs seldom completely eliminate a pest, but elimination of banana poka from selected areas, such as current efforts in the Special Ecological Areas within Hawaii Volcanoes National

Park (Tunison and Stone, this volume), remains a viable management alternative. Control of banana poka is a long-term problem requiring continued involvement and commitment by government agencies. Coordination is necessary to develop an effective statewide control program, but a single agency needs to take the lead in compiling and updating distribution information and formulating statewide priorities for control of populations. A recent demonstration project to determine the feasibility of chemical/mechanical control solely with the use of volunteers has shown that such an effort, even with the limited population (200 a or 81 ha), requires an intensive, concerted effort preferably coordinated by a governmental agency.

Efforts to predict potential habitat (Jacobi and Warshauer, this volume) are quite helpful in determining future management strategies, and more work should be put into refining the preliminary model. Finally, banana poka can be considered an "attractive nuisance;" increase in public awareness of the problem and proposed solutions are necessary and would decrease chances of intentional introductions to new areas.

ACKNOWLEDGMENTS

This review paper would not have been possible without the assistance and cooperation of the staff of the U.S. Fish and Wildlife Service Hawaii Research Station at Hawaii Volcanoes National Park. In particular, work on the distribution and abundance of banana poka by James D. Jacobi, Fredrick Warshauer, and J. Michael Scott contributed significantly. Data on the distribution and abundance of banana poka were obtained during the U.S. Fish and Wildlife Service Hawai'i Forest Bird Survey.

Research on the biology and ecology of *Passiflora mollissima* fulfilled the requirements for a Master of Science degree by the author and was made possible by grants from the Cooperative National Park Resources Studies Unit at the University of Hawaii (contract CA 8001-2-0001) and the U.S. Forest Service Institute of Pacific Islands Forestry (CPO 40-9231-1-126). Supplemental funding was provided by the Hawaii Division of Forestry, Pacific (now National) Tropical Botanical Garden, and Dr. Dieter Mueller-Dombois at the University of Hawaii Department of Botany. The critical review of an early draft by Dr. Lisa Floyd-Hanna greatly improved the manuscript, and the clerical assistance of Gail Boone and Margie Bouchard was invaluable. The continued support and assistance offered by Dr. Clifford W. Smith is gratefully acknowledged.

Literature Cited

Anderson, S.J., and C.P. Stone. In press. Snaring to control feral pigs (*Sus scrofa*) in a remote Hawaiian rain forest. *Biol. Conserv.*

Anonymous. 1962. Cultivo de la curuba. *Revista Nac. Agric.* 55.

Bailey, R.Y. 1944. Kudzu for erosion control in the Southwest. *USDA Farmers Bull.* 1840.

Baker, J.K. 1975. The feral pig in Hawaii Volcanoes National Park. Pres. Ann. meeting West. Sec. Wildl. Soc. and Calif.-Nevada Chap. Amer. Fisheries Soc., Sacramento. Files, Research Div., Hawaii Volcanoes Natl. Park.

Bianchi, F. 1979. Report to the Bishop Museum, Honolulu. Files, Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit, Honolulu.

Blumenstock, D.I. 1967. *Climates of the states: Hawaii.* Climatography of the United States. Washington D.C.: U.S. Dep. Commerce.

Burton, P.J. 1980. Plant invasion into an 'ohi'a-tree fern rain forest following experimental canopy opening. *Proc. 3rd Conf. Nat. Sci., Hawaii Volcanoes Natl. Park*, 21-39. Honolulu: Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit.

Burton, P.J., and D. Mueller-Dombois. 1984. Response of *Metrosideros polymorpha* seedlings to experimental canopy opening. *Ecology* 65:779-791.

Choudhury, A.K. 1972. Controversial *Mikania* (climber) a threat to the forests and agriculture. *Indian Forester* 98:178-183.

Croat, T.B. 1975. Phenological behavior of habit and habitat classes on Barro Colorado Island (Panama Canal Zone). *Biotropica* 12:42-55.

Cuatrecasas, J. 1953. A sketch of the vegetation of the North-Andean province. *Proc. 8th Pac. Sci. Congr. Pac. Sci. Assn.* Vol. 4, *Botany*, 167-173. Natl. Research Coun. Philippines. Quezon City, Philippines.

Cusset, G. 1975. Correspondence to J. Fujii, Jan. 10. Files, Hawaii Dep. Land Nat. Resour., Div. of For. Honolulu.

Daehler, R.E. 1975. Memorandum to L. Landgraf, June 19. Files, Hawaii Dep. Land Nat. Resour., Div. For. Honolulu.

Daubenmire, R. 1972. Phenology and other characteristics of tropical semi-deciduous forest in northwestern Costa Rica. *J. Ecol.* 60:147-169.

Dawkins, H.C. 1961. New methods of improving stand composition in tropical forests. *Caribbean Forester* 22:12-20.

de Wilde, W.J.J.O. 1975. *Passifloraceae (Flora of tropical East Africa).* London: Whitefriars Pr.

Escobar, L.K. 1980. Interrelationships of the edible species of *Passiflora* centering around *Passiflora mollissima* (HBK.) Bailey subgenus *Tacsonia*. Ph.D. diss., Univ. Texas at Austin.

Fosberg, F.R. 1975. Letter to J. Fujii, April 16. Files, Hawaii Dep. Land Nat. Resour., Div. Forestry. Honolulu.

Fox, J.E. 1968. Logging damage and the influence of climber cutting prior to logging in the lowland dipterocarp forest of Sabah. *Malayan Forester* 31:326-347.

Frankie, G.W. 1975. Tropical forest phenology and pollinator-coevolution. In *Coevolution of animals and plants*, ed. L.E. Gilbert and P.H. Raven, 192-209. Austin: Univ. Texas Pr.

Friedland, A.J., and A.P. Smith. 1982. Effects of vines on successional herbs. *Amer. Midl. Nat.* 108:402-403.

Gagné, W.E., and C.C. Christensen. 1985. Conservation status of native terrestrial invertebrates in Hawai'i. In *Hawai'i's terrestrial ecosystems: preservation and management*, ed. C.P. Stone and J.M. Scott, 105-126. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit. Honolulu: Univ. Hawaii Pr.

Gentry, A.H. 1974. Flowering phenology and diversity in tropical Bignoniaceae. *Biotropica* 6:64-68.

Giffin, J. 1972. *Ecology of the feral pig*. Final Rep. N-15-3. Hawaii Dep. Land Nat. Resour., Div. Fish and Game. Honolulu.

Giffin, J. 1978. *Alala investigation*. Hawaii Dep. Land Nat. Resour., Div. Fish and Game Project #W-18-R-3. Job #R-11-B. Dep. Land Nat. Resour., Div. Fish and Game. Honolulu.

Giffin, J. 1980. *Alala investigation*. Hawaii Dep. Land Nat. Resour., Div. Fish and Game Project #W-18-R-5. Job #R-11-B. Dept. Land Nat. Resour., Div. Fish and Game. Honolulu.

Green, P.S. 1972. *Passiflora* in Australia and the Pacific. *Kew Bull.* 26:539-558.

Hawaii Department of Land and Natural Resources. 1970. *An inventory of basic water resources, island of Hawaii, state of Hawaii*. Div. Water and Land Dev., Dep. Land Nat. Resour. Honolulu.

Hawaii Volcanoes National Park. 1986. Natural resources management plan and environmental assessment, revised January 1986. Hawaii Volcanoes National Park. Mimeo.

Herklots, G. 1976. *Flowering tropical climbers*. Kent, England: Dawson and Sons, Ltd.

Higashino, P.K., C.H. Lamoureux, L.R. Stemmermann, and F.R. Warshauer. 1977. The botanical survey for the installation. Pohakuloa Training Area. Environmental Impact Statement. U.S. Army Support Command, Hawaii. Dep. Army Corps Engineers, Pac. Div., Honolulu. Honolulu: Environmental Impact Study Corp.

Hobdy, R. 1988. Memorandum to C.W.S. Lum, December 23. Files, Hawaii Dep. land. Nat. Resour., Div. For., Maui.

Hooker, W.J. 1845. *Tacsonia mollissima* Curtis. *Bot. Mag. 1* 3rd ser. tab. 4178.

Howarth, F.G. 1983. Classical biocontrol: panacea or Pandora's box. *Proc. Hawn. Entomol. Soc.* 24(2,3):239-244.

Howell, C.W. 1976. Edible fruited *Passiflora* adapted to South Florida growing conditions. *Proc. Florida State Hortic. Soc.* 89:236-238.

Jacobi, J.D., and J.M. Scott. 1985. An assessment of the current status of native upland habitats and associated endangered species on the island of Hawaii. In *Hawai'i's terrestrial ecosystems: preservation and management*, ed. C.P. Stone and J.M. Scott, 3-22. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit. Honolulu: Univ. Hawaii Pr.

Jacobi, J.D., and F.R. Warshauer. 1975. A preliminary bioecological survey of the Ola'a Tract, Hawaii Volcanoes National Park. Prep. for Hawaii Natural Hist. Assn. Hawaii Volcanoes National Park. Hawaii Volcanoes National Park Library.

Jacobi, J.D., and F.R. Warshauer. [this volume] Distribution of six alien plants in upland habitats on the island of Hawai'i.

Janzen, D.H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution* 21:620-637.

Janzen, D.H. 1968. Reproductive behavior in the Passifloraceae and some of its pollinators in Central America. *Behavior* 32:33-48.

Janzen, D.H. 1971. Escape of juvenile *Dioclea megacarpa* (Leguminosae) vines from predators in a deciduous tropical forest. *Amer. Naturalist* 105:97-112.

Jaramillo, A. 1957. Primeros resultados de un ensayo sobre el cultivo de la curuba. *Agric. Trop.* 13:301-308.

Killip, E.P. 1938. *The American species of Passifloraceae*. Bot. Ser. 19. Chicago, Illinois: Field Mus. Nat. Hist.

Kochummen, K.M. 1966. Natural plant succession after farming in S.G. Kroh. *Malayan Forester* 29:170-181.

Laemmlen, F. 1971. Correspondence to W. Wong, May 20. Files, Hawaii Dep. Land Nat. Resour., Div. For. Honolulu.

Landgraf, L. 1971. Memorandum to A. Kawasaki, May 6. Files, Hawaii Dep. Land Nat. Resour., Div. of For. Honolulu.

LaRosa, A.M. 1983. Response of *Passiflora mollissima* (H.B.K.) Bailey to experimental canopy removal: a simulation of natural gap formation in a closed-canopy *Cibotium* spp. forest in Ola'a Tract, Hawaii. *Proc. 4th Conf. Nat. Sci., Hawaii Volcanoes Natl. Park*, 118-134. Honolulu: Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit.

LaRosa, A.M. 1984. The biology and ecology of *Passiflora mollissima* in Hawaii. M.S. thesis, Univ. Hawaii, Honolulu.

LaRosa, A.M. 1985. Note on the identity of the introduced passionflower vine "banana poka" in Hawaii. *Pac. Sci.* 39:369-371.

LaRosa, A.M., and M.E. Floyd. 1988. The effects of Hurricane Iwa on understory regeneration of Koke'e Kauai forests. (Abstract) Pres. Ecol. Soc. Amer. Mtgs., Aug. 1988, Davis, Calif..

LaRosa, A.M., C.W. Smith, and D.E. Gardner. 1985. Role of alien and native birds in the dissemination of firefree (*Myrica faya* Ait. - Myricaceae) and associated plants in Hawaii. *Pac. Sci.* 39:372-378.

MacDonald, I.A.W. 1987. Banana poka in the Knysna forest. *Veld & Flora* 73(4): 133-134.

Mack, R.N. [this volume] Characteristics of invading plant species.

Markin, G.P., P.-Y. Lai, and G.Y. Funasaki. [this volume] Status of biological control of weeds in Hawai'i and implications for managing native ecosystems.

Martin, F.W., and H.Y. Nakasone. 1970. The edible species of *Passiflora*. *Econ. Bot.* 24:333-343.

Meijer, W. 1970. Regeneration of tropical lowland forest in Sabah, Malaysia forty years after logging. *Malayan Forester* 33:204-229.

Mueller-Dombois, D. 1975. Some aspects of island ecosystem analysis. In *Tropical ecological systems -- trends in aquatic and terrestrial research*, ed. F.B. Golley and E. Medina, 353-366. Vol. 11, Ecol. Stud. Ser., Analysis and synthesis. New York: Springer-Verlag.

Mueller-Dombois, D., J.D. Jacobi, R.G. Cooray, and N. Balakrishnan. 1980. *'Ohi'a rain forest study: investigations of the 'ohi'a dieback problem in Hawaii.* Hawaii Agric. Exp. Sta. Misc. Pub. 183. Univ. Hawaii Coll. Trop. Agric. and Human Resour., Honolulu.

Murai, K. 1977. Notes on the life cycle and host range of the passion vine butterfly, *Agraulis vanillae* L. Internal rep., June 24. Files, Hawaii Dep. Agric. Honolulu.

Nakahara, L. 1977. Memorandum to Chief, Entomology Branch, Jan. 17. Files, Hawaii Dep. Land Nat. Resour., Div. For. Honolulu.

Nicholson, D.I. 1985. A review of the natural regeneration in the dipterocarp forests of Sabah. *Malayan Forester* 28:4-25.

Nishida, T. 1963. *Ecology of the pollinators of passion fruit.* Tech. Bull. 55, Hawaii Agric. Exp. Sta., Univ. Hawaii. Honolulu.

Ogawa, H., K. Yoda, K. Ogino, and T. Kira. 1965a. Ecological studies of three main types of forest vegetation in Thailand. II. Plant biomass. *Nat. Life Southeast Asia* 4:49-80.

Ogawa, A., K. Yoda, T. Kira, K. Ogina, T. Shidei, D. Ratanawongse, and C. Apasutaya. 1965b. Comparative ecological studies of three main types of forest vegetation in Thailand. I. Structure and floristic composition. *Nat. Life Southeast Asia* 4:13-48.

Opler, P.A., G.W. Frankie, and H.G. Baker. 1980. Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 68:167-188.

Paxton, J. 1846. *Tacsonia mollissima. Paxton's Mag. Bot.* 13:24-26.

Pemberton, R.W. 1982. Exploration for natural enemies of *Passiflora mollissima* in the Andes. U.S. Dep. Agric. Biol. Contr. Weeds Lab., Albany, Calif. Unpub. rep.

Pung, E. 1971. The diet of the 'i'iwi. *Hawai'i Aloha Aina* 2:3-5.

Putz, F.E. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 68:77-81.

Richards, P.W. 1952. *The tropical rain forest.* Cambridge: Univ. Pr.

Schoniger, G. 1969. El cultivo de la curuba. *Rev. Esso Agric.* 6:4-12.

Scott, J.M., J.D. Jacobi, and F.L. Ramsey. 1981. Avian surveys of large geographical areas: a systematic approach. *Wildl. Soc. Bull.* 9(3):190-200.

Scowcroft, P.G., and R.E. Nelson. 1976. Disturbance during logging stimulates regeneration of koa. Res. Note PSW-306. Pac. Southwest For. Range Exp. Sta., USDA For. Serv. Berkeley, Calif.

Skolmen, R. 1979. Koa timber management. Pres. Hawaii Forestry and Wildlife Conf., Kahului, Maui, Oct. 1, 1979. Files, U.S. Forest Serv. Inst. Pac. Is. For. Honolulu.

Stevens, G.C. 1987. Lianas as structural parasites: the *Bursera simaruba* example. *Ecology* 68:77-81.

Stiles, F.G. 1977. Co-adapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest. *Science* 1177-1178.

Sykes, W.R. 1977. *Kermadec Islands flora: an annotated checklist.* Bull. 219. Wellington, New Zealand: New Zealand Dep. Sci. Industr. Res.

Tamura, E. 1978a. Corres. to Maui County Noxious Weed Advisory Commision, Dec. 7. Files, Hawaii Dep. Land Nat. Resour., Div. For. Honolulu.

Tamura, E. 1978b. Corres. to J. Raynor, Dec. 2. Files, Hawaii Dep. Land Nat. Resour., Div. For. Honolulu.

Telford, E.A., and N.F. Childers. 1947. Tropical kudzu in Puerto Rico. Circ. 27, USDA Fed. Exp. Sta. Puerto Rico.

Thomas, L.K. 1980. Winter growth of Japanese honeysuckle (*Lonicera japonica* (Thunb.) on Theodore Roosevelt Island. *Proc. 2nd Conf. Sci. Res. Natl. Parks,* Nov. 26-30, 1979, 408-418. Washington D.C.: Natl. Park Serv.

Walter, H., E. Harnickell, and D. Mueller-Dombois. 1975. *Climate diagram maps of the individual continents and the ecological climate regions of the earth.* Berlin: Springer-Verlag.

Warshauer, F.R., J.D. Jacobi, A.M. LaRosa, J.M. Scott, and C.W. Smith. 1983. *The distribution, impact and potential management of the introduced vine* Passiflora mollissima *(Passifloraceae) in Hawai'i.* Tech. Rep. 48, Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit. Honolulu.

Weberbauer, A. 1936. Phytogeography of the Peruvian Andes. In *Flora of Peru*, ed. B.E. Dahlgren, Part I, 1-81. Field Mus. Nat. Hist. Bot. Ser. Vol. 13, Pub. 351. Chicago.

Wenkham, R. 1967. *Kauai and the park country of Hawaii.* San Francisco, Calif.: Sierra Club.

Whigham, D. 1984. The influence of vines on the growth of *Liquidambar styraciflua* L. (sweetgum). *Canad. J. For. Res.* 14:37-39.

Wong, W. 1971. The banana poka problem. Pres. 13th Forestry Conf. Hilo, Hawaii May 13. Files, Hawaii Dep. Land Nat. Resour., Div. For. Honolulu.

Wong, W. 1973. Correspondence to E. Tamura, April 17. Files, Hawaii Dep. Land Nat. Resour., Div. For. Honolulu.

Woodall, S.L. 1981. Integrated methods for *Melaleuca* control. *Proc. Meleleuca Symp.*, ed. R.K. Geiger, 135-140. Tallahassee, Florida: Fla. Div. For.

Wycherly, P.R. 1973. The phenology of plants in the humid tropics. *Micronesica* 9:75-96.