

Characteristics of the *Psidium cattleianum* (Myrtaceae) Seed Bank in Hawaiian Lowland Wet Forests¹

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Abstract: *Psidium cattleianum* Sabine (strawberry guava) is one of Hawai'i's most disruptive alien plants. Dense stands can suppress growth and establishment of native species, support high populations of crop-damaging fruit flies, and preclude restoration or management of native forests. Our research investigated factors affecting persistence of *P. cattleianum* seeds in lowland wet forest soils. We collected soil cores from four forested sites immediately after fruit fall and 6.5 months later. We found abundant germination of *P. cattleianum* seeds immediately after fruit drop. Soil collected under mature *P. cattleianum* clumps yielded 761 viable seeds/m². We found no viable seeds 6.5 months after fruit drop. We evaluated seed longevity using seed bags buried below the litter layer that we retrieved after 28, 56, 196, and 365 days. Seeds either germinated or deteriorated rapidly after fruit drop; after 28 days, 22.3% of the buried seeds were viable and there were no viable seeds at 196 days. Predator effects were assessed using trays with a known number of seeds with and without predator exclosures. After 28 days, 37% of the seeds in the open trays were damaged by predators. The lack of a persistent seed bank likely is due to a combination of rapid, high germination rates, postdispersal seed predation, and seed mortality. We suggest that chemical or mechanical control efforts would be most efficient and effective if conducted at least 3 months after the fruiting season, when the vast majority of seeds have either germinated or died.

Psidium cattleianum SABINE (Myrtaceae), also known as strawberry guava, is considered one of Hawai'i's most severe invasive weeds (Smith 1985, Wagner et al. 1999, Motooka et al. 2003). *Psidium cattleianum* is common on all the major Hawaiian islands and throughout the Pacific where it continues to increase in density and impact. Rapid growth rates (J.S.D. and A.L.U., unpubl. data), prolific fruit production, and high rates of suckering produce dense stands quickly from small populations (Huenneke and Vitousek 1990). *Psidium cattleianum* is a serious threat to native forest ecosystems in Hawai'i and

elsewhere in the Pacific due to its ability to invade even relatively undisturbed wet forests and form dense thickets (Smith 1985, Huenneke and Vitousek 1990). The fruits of *P. cattleianum* support high populations of fruit flies (e.g., *Dacus dorsalis* Hendel) that are considered one of the most important agricultural pests in Hawai'i (Vargas et al. 1990). The efficacy of any control method for *P. cattleianum* is influenced by the characteristics of its seed bank, because a persistent seed bank contributes to high population growth rates and reduces the likelihood of local eradication. We investigated longevity of seeds of *Psidium cattleianum* in Hawaiian soils, the characteristics of the seed bank, and factors affecting the duration of seeds in lowland wet forest soils in Hawai'i.

MATERIALS AND METHODS

Species Description

Psidium cattleianum has invaded native Hawaiian ecosystems ranging from moist to very

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wet conditions from 15 to 1,300 m elevation (Jacobi and Warshauer 1992, Wagner et al. 1999). All forms of *P. cattleianum* grow as shrubs or small trees, typically 2–6 m tall in mesic to wet forests in Hawai'i (Wagner et al. 1999). We used seeds from the common round, yellow-fruited form (*P. cattleianum* f. *lucidum* Degener) in this study. Fruits contain 15–70 angular seeds (Diong 1982, Huenneke and Vitousek 1990) of 2.5–5 mm in length (Morton 1987, Wagner et al. 1999). Peak fruit fall typically occurs between June and December (Diong 1982, Huenneke and Vitousek 1990). *Psidium cattleianum* seeds are readily spread by humans and feral pigs (*Sus scrofa*) (Diong 1982, Jacobi and Warshauer 1992) as well as by a variety of birds (Me-deiros 2004).

Study Area

Study sites were established within the Upper Waiākea Forest Reserve (19° 35' N, 155° 12' W), the Pu'ū Maka'ala Natural Area Reserve (19° 34' N, 155° 12' W), the 'Ōla'a Forest Reserve (19° 27' N, 155° 11' W), and the Kahauale'a Natural Area Reserve (19° 26' N, 155° 10' W) on the island of Hawai'i. All sites are on windward Hawai'i Island at approximately 900 m elevation. Estimated annual rainfall is 3,000–4,000 mm at 'Ōla'a and Kahauale'a and 4,000–5,000 mm at Upper Waiākea and Pu'ū Maka'ala (Giambelluca et al. 1986). Projected mean annual temperature based on adiabatic lapse rates is 17–17.5°C for the elevation range of the four study sites (Giambelluca and Schroeder 1998). All of the study sites are on relatively young tholeiitic basalt lava flows that formed 200–1,500 yr B.P. (Wolfe and Morris 1996). The soils at Upper Waiākea and Pu'ū Maka'ala are deep and well drained (Typic Udifolists, U.S. Department of Agriculture Natural Resource Conservation Service [USDA-NRCS], unpubl. data) over weathered 'a'a lava. The soils at Kahauale'a (Lithic Hapludands, USDA-NRCS, unpubl. data) and 'Ōla'a (Lithic Udifolists, USDA-NRCS, unpubl. data) are very shallow to shallow, moderately well-drained soils formed in volcanic ash deposited over *pāboeboe* lava bedrock. The forests are classified as native lowland wet forests with

an 'ōhi'a (*Metrosideros polymorpha* Gaud.) lowland wet forest community type (Gagné and Cuddihy 1999).

Seed Longevity

Seed longevity of *P. cattleianum* in soil was assessed by tracking the fates of known numbers of seeds placed in bags and inserted under the litter at each of the four study sites. Fully ripened and intact *P. cattleianum* fruits were collected from and beneath trees in October and pooled from multiple *P. cattleianum* groups across 'Ōla'a Forest Reserve. Seeds were immediately cleaned, air dried, and stored for 1 week in an air-conditioned environment. Percentage seed viability was assessed on a subsample of the pooled seeds (10 replicates of 50 seeds each) 1 week after the seeds were collected and on the same day the seed bags were placed in the field. At each study site, one set of four seed bags was placed under each of five groups of large *P. cattleianum* trees. Each sealed bag (6 by 7.5 cm, 86-mesh silkscreen fabric) contained 20 seeds and 5 g of sieved, autoclaved soil. The bags were placed beneath the litter layer (generally 2.5–5 cm deep) in contact with the soil surface and were placed in the field during the fruiting season in late October. One seed bag from each of the five sets of bags placed at each site was retrieved after 28, 56, 196, and 365 days. When the buried bags were retrieved, the seeds were evaluated and seeds that had germinated or decayed were separated from those that were intact. Intact seeds were tested for viability by planting in sterile growing medium in a greenhouse under irrigation and approximately 53% sun. Germination of seeds was monitored over a 16-week period.

The buried bags provided information on changes in the numbers of viable, persistent seeds and seed decay and senescence over time. We modeled the decline in numbers of viable seeds as an exponential decay function (SigmaPlot 8.02 [SPSS Inc. 1986–2001]):

$$y = y_0 e^{-kt}$$

in which y is the number of the original seeds remaining and persisting as viable seeds in the

soil at time t , y_0 is the number of seeds at time 0, t is the elapsed time in days, and k is the decay constant. The mean residence time (MRT) is calculated:

$$\text{MRT} = 1/k$$

The seed bags excluded mammalian and many invertebrate predators from access to the seeds but did not prevent infestation by soil fungi; therefore, k and mean residence time represent longevity of the seeds in the soil in the absence of predators.

Seed Bank

We collected four soil cores (500 cm³, to 5 cm deep) from beneath each of five clusters of mature *P. cattleianum* trees from each of the four study sites on each collection date. We selected *P. cattleianum* tree clusters with canopies exposed to full sun to maximize the probability of sampling where trees had generated dense seed shadows. Soils were collected twice: immediately after fruit fall (late November) and approximately 6.5 months after fruit fall (early June). The soil from each core was spread to a depth of 1 cm over sterile medium and placed in the greenhouse under irrigation and approximately 53% sun. *Psidium cattleianum* germinants were counted and removed weekly over a 16-week period.

Seed Predation Rates

We compared rates of seed damage to protected and unprotected seeds spread on trays placed in the forest. Twenty trays (43 by 43 by 5 cm deep) containing 50 *P. cattleianum* seeds each were placed at each of the four study sites; half of these trays were covered with hardware cloth (6.35-mm mesh) to exclude large predators and half were left open. Open and protected trays were placed adjacent to one another, but 10 m away from the canopy of *P. cattleianum* trees to avoid additional seed input from fruit fall. The seeds placed in the trays were from the same composite sample of seeds used in the buried seed bags and were cleaned, air dried, and stored for 1 month in an air-conditioned environment until the seeds were placed in the field. Forest floor litter material was placed in the

trays with the seeds, and the trays were lined with 2 mm nylon mesh to prevent washout. Trays were placed in the field in late November at the end of the fruiting season at all study sites. After 28 days, the trays were collected, seeds and litter material were separated, and seeds were counted and evaluated for evidence of predation. We assumed that secondary seed dispersal did not occur and, by extension, that missing seeds had been consumed and not dispersed as viable seeds. Seeds with evidence of animal activity (i.e., teeth marks, seed fragmentation) were considered damaged and were assumed to be nonviable as well. Data from one subsequently overturned tray were excluded.

Data Analysis and Synthesis

We used the data from the seed longevity and seed predation experiments to develop a projection of the fate of *P. cattleianum* seeds 6.5 months after fruit fall. The baseline germination trial was used to estimate the percentage of nonviable seeds in the seed rain. Data from the buried seed bags provided information on persistent, viable seeds in the seed bank. Seeds recovered intact in the seed bags were considered persistent or viable if they subsequently germinated in the greenhouse. Seeds that did not germinate in the seed bags while in the field nor in the greenhouse when removed from the bags were considered to have died. The enclosure experiment provided the rate of predation; we assumed that all predation occurred during the 28-day period following seed dispersal. We assumed that nongerminating seeds from the seed bags included those that were nonviable in the seed rain and that a certain percentage of seeds that subsequently germinated in the seed bags in the field would have been lost to mammalian and invertebrate predators in the first month.

RESULTS

Seed Longevity

Results from the buried seed bags showed that the decrease in viable seeds with time followed an exponential decay curve ($y = 86.41e^{-0.0463t}$, $r^2 = 0.99$, $P = <.0001$) (Figure

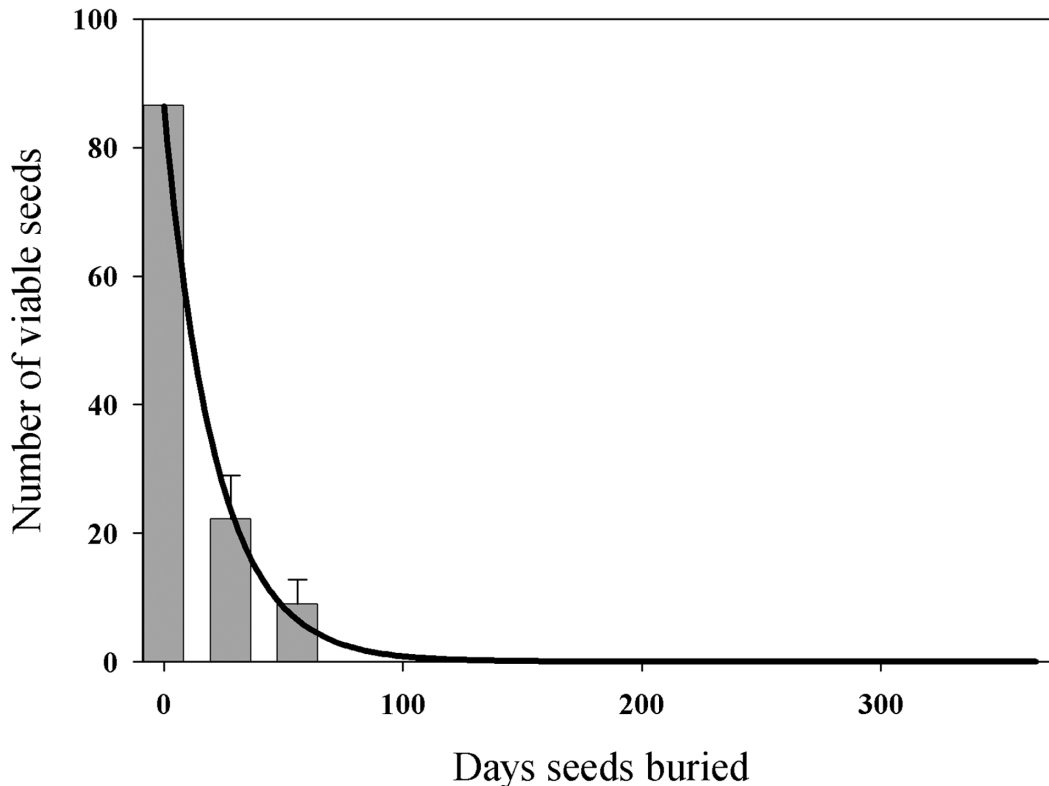


FIGURE 1. Mean number of *P. cattleianum* seeds (per 100 seeds) germinating after being buried in seed bags. Baseline viability was assessed when the bags were buried (day 0), and bags were collected after 28, 56, 196, and 365 days. Error bars represent the standard error among four study sites. There were no viable seeds in the bags collected after 196 and 365 days.

1). Mean residence time for the seeds was 21.6 days. In the absence of predation, 95% of the seeds had either germinated in the field or lost viability in 66 days; 99% of the seeds were nonviable after 96 days.

Seed Bank

High numbers of viable *P. cattleianum* seeds were found in soil collected during fruit fall at our sites (761 viable seeds/m², $n = 4$ sites, SE = 309), yet no viable seeds were found from soil collected 6.5 months after peak fruiting season. Results from the soil samples collected 6.5 months after fruit drop were consistent with results from the seed bags retrieved after 6.5 months; in neither case was there evidence of a persistent seed bank.

Seed Predation Rates

A mean of 36.9% ($n = 4$ sites, SE = 7.1) of the seeds in open trays were missing or damaged by predators after 28 days in the field. The amount of seeds missing or damaged by predators ranged from 0 to 90% in the open trays. Less than 0.1% of seeds ($n = 4$ sites, SE = 0.05) were missing from the protected trays after the same time period.

Seed Fates

Figure 2 summarizes the fates of *P. cattleianum* seeds in lowland wet forests 6.5 months after dispersal. At 196 days, 28 seeds out of 100 placed in the bags were dead when recovered, having failed to germinate when placed

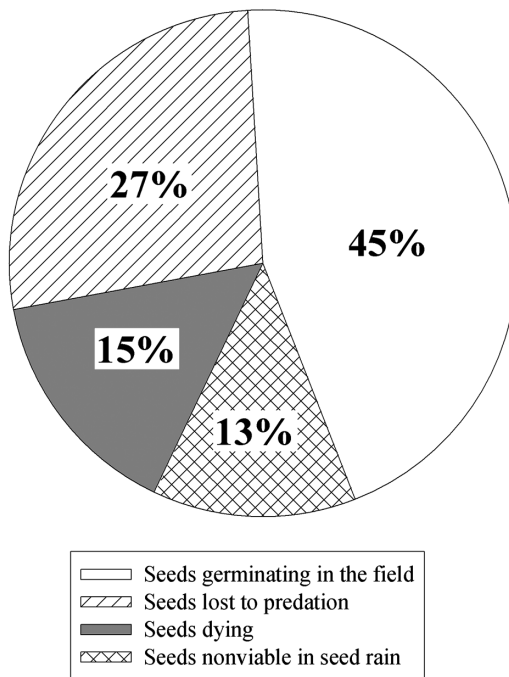


FIGURE 2. Projected fates of *P. cattleianum* seeds 6.5 months after dispersal into lowland Hawaiian forest soils.

in the greenhouse. We assumed that 13 of those seeds had been nonviable in the seed rain and estimated therefore that 15 seeds had died after being placed in the field. The remaining 72 seeds germinated in the field before the bags were recovered. We assumed that 36.9% or 27 of those would have been lost to predation in the first month following dispersal, leaving an estimated 45 seeds germinating in the field. Dead and nonviable seeds also lost to predation (36.9% of 13 nonviable and 15 dead seeds) are not shown in Figure 2. We estimate that most *P. cattleianum* seeds were lost from the seed bank due to predation and germination, with smaller percentages nonviable from pre- or post-dispersal processes. We found no evidence of viable seeds 6.5 months after fruit fall.

DISCUSSION

Seeds of tropical rain forests may have the shortest ecological longevity of seeds of any plant community (Vasquez-Yanes and

Orozco-Segovia 1993). The absence of persistent seed banks among trees in tropical systems has been attributed to predation (Thompson 1987) and to simultaneous and rapid germination of the seeds immediately after dispersal (Vasquez-Yanes and Orozco-Segovia 1993) or in response to favorable ephemeral conditions (Skoglund 1992). Although many seeds of tropical and subtropical rain forest trees are desiccation tolerant (orthodox) and thus have the potential to form persistent seed banks in the soil (Vasquez-Yanes and Orozco-Segovia 1996, Tweedle et al. 2003, Dalling 2005), most tropical rain forest plants do not do so (Hopkins and Graham 1987, Thompson 1987, Skoglund 1992, Vasquez-Yanes and Orozco-Segovia 1993). *Psidium cattleianum*, with orthodox seeds (Becwar et al. 1983), appears to be typical of most tropical trees. Desiccation tolerance in the laboratory is not necessarily correlated with the persistence of the seeds in the field (Tweedle et al. 2003) because seeds in the natural environment are subject to predation, invertebrate and microbial infection, and conditions conducive to germination. Germination and predation appear to account for the majority of the loss of *P. cattleianum* seeds from soils of Hawaiian lowland wet forests.

Although our study did not identify the seed predator(s), damage was typical of that by rodents. Black rats (*Rattus rattus*), house mice (*Mus musculus*), and Polynesian rats (*Rattus exulans*) are known seed predators in Hawaiian forests and are an important constraint on reproduction of native plants (Tomich 1986, Cuddihy and Stone 1990, Cabin et al. 2000). Rodents have been shown to be effective predators of exotic plant seeds in Hawaiian forests as well (Medeiros 2004), and *P. cattleianum* seeds may be a readily available food source for alien rodents. Predation rates are likely to be spatially variable; a previous study found no evidence of *P. cattleianum* seeds in rodent droppings at another site (Medeiros 2004).

Results from the buried seed bags suggest that even in the absence of predation *P. cattleianum* seeds do not survive burial in natural conditions for an extended period of time.

The persistence of seeds has been shown to increase with an increased depth of burial (Toole and Brown 1946, Lonsdale et al. 1988), and we might have found *P. cattleianum* seeds to have been viable longer if our seeds had been buried more deeply. Despite the many combinations of variables that may have affected the outcome of the buried bag experiment, the lack of any viable seeds in the soil samples we collected 6.5 months after fruit drop suggests that seeds do not naturally persist from one fruiting season to the next in the soil environment. In two other studies where soil cores were collected from forests with mature *P. cattleianum* plants present, viable *P. cattleianum* seeds were not encountered either (Huenneke and Vitousek 1990, Drake 1998).

An understanding of local *P. cattleianum* phenology and the characteristics of the seed bank is of value in the selection and scheduling of control methods for this invasive plant. Because most *P. cattleianum* seeds do not live beyond 3 months in the soil, chemical or mechanical control efforts would be most efficient and effective if conducted at least 3 months after the fruiting season. The biological control agent *Tectococcus ovatus* is currently proposed for the control of *P. cattleianum* in Hawai'i and has been documented to reduce fruit and seed production of plants in Brazil (Johnson 2005). Our results suggest that a biocontrol agent that reduced *P. cattleianum* seed production would also rapidly deplete soil seed stocks, therefore increasing effectiveness of chemical and mechanical control.

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