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The Galapagos Giant Tortoise (*Geochelone elephantopus*) and the Spread of Invasive Plants

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**THE GALAPAGOS GIANT TORTOISE (*GEOCHELONE*
ELEPHANTOPUS) AND THE SPREAD OF
INVASIVE PLANTS**

by

ANNE D. SCHULTZ

B.A., Anthropology, Indiana University 1990

THESIS

Submitted in Partial Fulfillment of the
Requirements for the Degree of

**Master of Science
Biology**

The University of New Mexico
Albuquerque, New Mexico

August, 2003

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Finally, I would like to honor the memories of my grandparents, particularly my grandfather Ernie Darlington. He was my first guide to the natural world, and he nurtured and encouraged a city girl's passion for nature.

**THE GALAPAGOS GIANT TORTOISE (*GEOCHELONE*
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ABSTRACT OF THESIS

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ABSTRACT

Island ecosystems are commonly thought to be more vulnerable to the effects of invasive species than mainland systems. In recent decades, the number of exotic plants known to be present in the Galápagos archipelago has increased exponentially. Several of these plants are aggressive invaders that pose a threat to the biodiversity of the islands. Two of these plant species, *Passiflora edulis* Sims and *Psidium guajava* L. were introduced to Santa Cruz Island during the 20th century. Both pose a threat to the floristic diversity of the National Park land on Santa Cruz Island.

This paper explores the role played by the endemic Galápagos tortoise (*Geochelone elephantopus*) in the dispersal of *P. edulis* and *P. guajava*. Tortoises are able to spread viable seed of both species; germination percentages for *P. edulis* indicate that passage through an animal's gut promotes seed germination. The germination percentages for *P. guajava* decrease after ingestion, but ingested seeds still germinate readily. Native animals can be an important factor in the spread of exotic plant species and should be taken into account when designing eradication and control strategies.

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Chapter One – Introduction

Island ecosystems are commonly thought to be more vulnerable to the effects of introduced species than mainland systems (Loope et al. 1988, Loope and Mueller-Dombois 1989, Mauchamp 1997, Mauchamp et al. 1998, Pimm 1987, Schofield 1989, Simberloff 1995). Island systems, particularly oceanic island chains like Hawaii and the Galápagos archipelago, have relatively low levels of biodiversity in comparison to continental areas in the same latitude but relatively high rates of endemism (Loope and Mueller-Dombois 1989, Mauchamp 1997). Vulnerability of island communities to the effects of non-native species is at least in part attributable to the absence of certain taxonomic groups such as carnivorous mammals or nitrogen-fixing plant species (Mauchamp 1998, Simberloff 1995). The severity of the effects of exotic species in island systems is also related to the rapid rate of anthropogenic introductions – the response of native species is forced to take place on a human time scale rather than an evolutionary scale (Sadler 1999). Species which are not able to adapt rapidly to new pressures and changing environmental conditions may be pushed towards extinction.

The Galápagos Islands provide a unique opportunity for the study of invasive species. Unlike other Pacific islands, the Galápagos were not home to a pre-Columbian human population, but they have been impacted by human activity throughout the recent historical past. The deliberate and accidental introductions of several vertebrate species such as goats, cats, and rats have affected both the vegetation and native animals of the Galápagos through heavy grazing and direct predation (Jackson 1997, Schofield 1989). The effects of alien vertebrate species can be dramatic and severe. It is important to remember that exotic plants can also become aggressive invaders that have at least

equally, if not more disastrous, ecological effects by outcompeting native plants and, in some cases, altering ecosystem processes (Huenneke and Vitousek 1990, Vitousek et al. 1997). My research in the Galápagos has focused on aspects of the seed dispersal ecology of two highly invasive plant species: *Passiflora edulis* Sims (passionfruit), and *Psidium guajava* L. (guava).

Non-native plants were deliberately introduced into the Galápagos in the early nineteenth century by temporary settlers, mainly for food (Schofield 1973). The first recorded introduced plants were cultivated by an Irish castaway, Patrick Watkins, on Floreana Island around 1807 (Porter 1822). The rate of introduction of alien plants appeared to proceed relatively slowly until the 1960s, which may be due in part to an artifact of botanical surveying (Mauchamp 1997, Mauchamp et al. 1998, Tye 2001b). The past forty years, however, have seen a dramatic increase in the number of introduced plant species recorded in Galápagos. By 2002, the number of non-native plants known for Galápagos exceeded the number of native species: the total flora is comprised of 500 native and endemic species, sixty species of uncertain origin which may be either native or introduced, and now at least 550 non-native species (Tye 2001a). The majority of these plants were brought by the growing resident human population in Galápagos for agricultural use or as ornamentals; some were accidentally introduced as weeds. At least forty-two percent of the known introduced species known in 1997 now persist outside of cultivated areas (Mauchamp 1997). Up to 10% of these naturalized aliens are already aggressive invaders which pose a threat to native plant and animal communities through direct competition for resources, spread of pests or pathogens, or alteration of the native community composition (Mauchamp 1997, Tye 2001b).

Spread of potentially invasive plants is facilitated by natural dispersal mechanisms as well as direct human action (Mack and Lonsdale 2001). Wind, water, and animal dispersal may widely distribute viable seed, allowing invaders the opportunity to become established at some distance from the parent plant (Howe and Smallwood 1982). Clearing native vegetation for agriculture, roads, or homes provides opportunity for exotic plants to become established.

Herbivores often serve as dispersal agents, particularly when seeds are enclosed by fleshy fruit (Howe and Smallwood 1982, Stiles 1989). Galápagos landbirds, particularly the finches, are known to act as both seed predators and seed dispersal agents (Jackson 1997). There are no native grazing ungulates in the archipelago, and the dominant native quadrupedal herbivore in the islands is the giant tortoise, *Geochelone elephantopus*. Both *Psidium guajava* and *Passiflora edulis* were introduced for cultivation and have large fleshy fruits desirable to people but also suitable for animal consumption and subsequent seed dispersal. Both are naturalized invaders present in the National Park areas on inhabited islands. Guava is known to be an aggressive invader which has established itself in large thickets on the settled islands (Eckhardt 1972, Porter 1973, Schofield 1989). Passionfruit is a relatively recent invader that is becoming a serious threat to the islands (Mauchamp 1997, Moll 1990).

My research in the Galápagos National Park has focused on three questions. Do tortoises consume the fruits of *P. edulis* and *P. guajava*? Can they pass viable seed through their guts? Can they disperse seed to sites suitable for the establishment of seedlings?

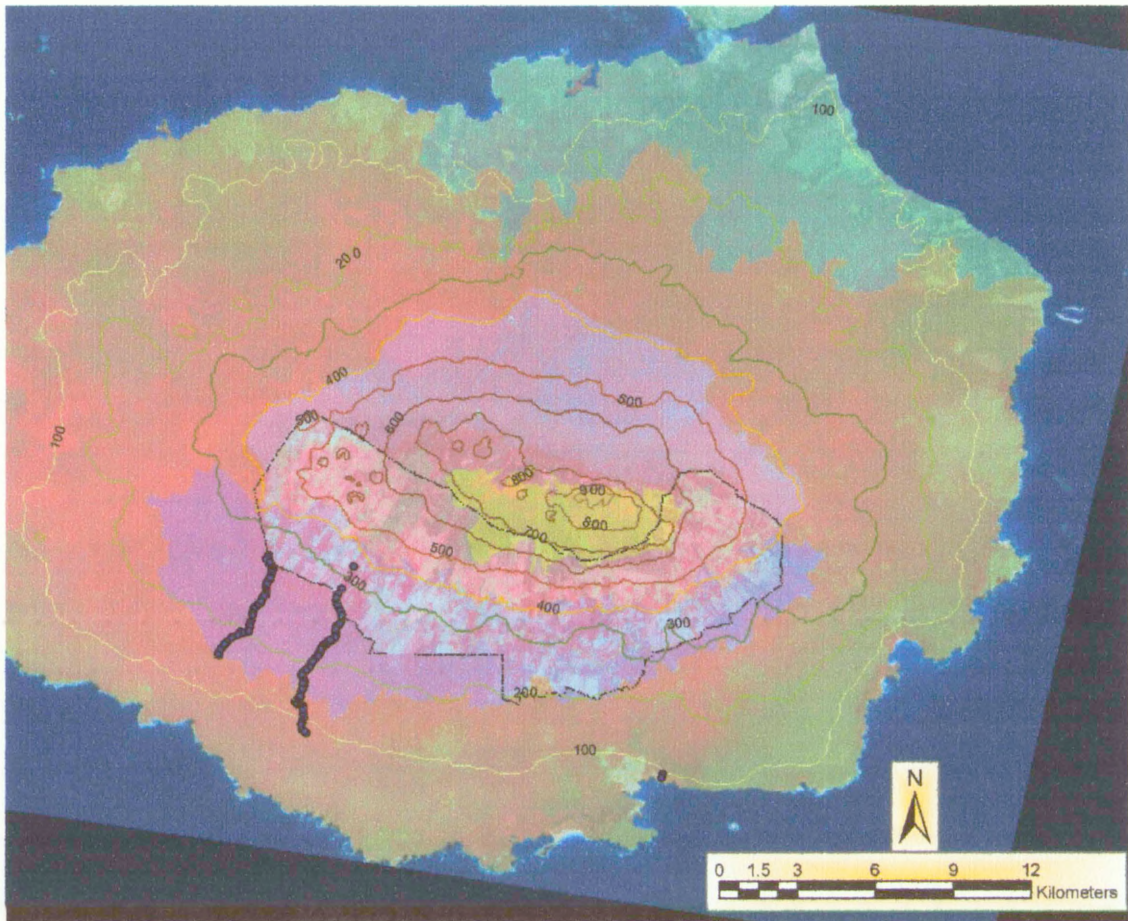


Figure 1: Santa Cruz Island, with the transects at El Chato (to the left) and the Caseta (right) marked in black. The agricultural zone is outlined in the center of the island.



Chapter Two – Methods

Study Sites

The Galápagos archipelago is made up of thirteen major islands and 108 smaller islets (Jackson 1997, Snell et al. 1995). Four of the larger islands and one smaller island have inhabited areas. Santa Cruz Island has the largest resident population and a large number of tourist visitors annually. The island is 986 km² with a maximum elevation of 864 m at Cerro Crocker. The Charles Darwin Research Station (CDRS) and the Galápagos National Park Service (GNPS) are based here in the coastal town of Puerto Ayora. With the exception of Puerto Ayora and an agricultural zone in the higher elevations that contains other small settled areas, the island is protected as a National Park.

My study sites (Figure 1) are located within the tortoise reserve in the southwestern section of the island. The reserve extends from the coast up to an elevation of about 200m, where the agricultural zone begins. The first site is an area used by the GNPS and CDRS personnel for access to the reserve and is locally known as the Caseta. The second site is known as El Chato, and is the entry point for tourist groups into the reserve. El Chato is about 4 km to the northwest of the Caseta. Both sites begin near the agricultural zone border and extend about 6 km down towards the coast.

The vegetation in southwestern Santa Cruz can be categorized as four distinctly identifiable zones (Bowman 1961, Cayot 1987, Itow 1965, Jackson 1997, McMullen 1999, Reeder and Riechert 1975, Stewart 1915). The littoral zone, or coastal zone, is dominated by plants with a high tolerance for salt water, such as red mangroves (*Rhizophora mangle* L.) and saltbush (*Cryptocarpus pyriformis* Kunth) (Jackson 1997,

McMullen 1999). The arid zone, which extends up to an altitude of about 80 - 100 m, is a mixture of fairly open stands of *Opuntia echios* Howell and dense thickets of the small tree *Croton scouleri* Hook. f. (Reeder and Riechert 1975). The most diverse zone is the transition zone, which ranges from an altitude of 80 m to 180 or 200 m. There are no dominant plant species that characterize the entire zone, but rather several subdominants, some of which appear to be influenced by the altitudinal gradient and others which have a patchy distribution not tied to altitude (Reeder and Riechert 1975). The Scalesia zone, which begins at the elevations above the transition zone, is covered by mist during the cool season months of May through November and is dominated by forests of the endemic tree *Scalesia pedunculata* Hook. f. (Cayot 1987, Jackson 1997, McMullen 1999, Reeder and Riechert 1975). Most of the agricultural zone falls within the Scalesia zone. Tortoises move throughout the area, ranging from the arid zone up to the Scalesia zone and can cross freely under the fence line into the agricultural zone. They are opportunistic and fairly indiscriminant grazers and feed upon a variety of native and non-native plants (Cayot 1987, Fowler de Neira and Johnson 1985, Rodhouse et al. 1975, Thornton 1971).

Study Species

Passionfruit (*Passiflora edulis* Sims.) was probably introduced as a cultivated plant sometime before 1977 (Lawesson et al. 1987, Moll 1990). It is not listed in the comprehensive 1971 Galápagos flora (Wiggins and Porter 1971). *P. edulis* is a vine, climbing over trees and shrubs, and is widespread in the agricultural zone and in the island's towns. Guava (*Psidium guajava* L.), a tree found throughout the agricultural

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zone, has been present in the Galápagos since at least the 1920s (Kastadalen 1982, Roosevelt 1930). Both species were deliberately introduced for agricultural purposes and have spread past the agricultural zone boundary into the National Park (Moll 1990).

Consumption of Seeds

In order to determine whether tortoises eat the seeds of the species in question, tortoise scat was collected in the field at both El Chato and the Caseta. Scats are readily identifiable along the tortoise paths, and in many cases, I was able to observe a tortoise defecating and then collect its scat. Eighteen samples were collected in the field. The scats were sun dried for a period of 5 to 7 days at the Charles Darwin Research Station (CDRS). After drying, each sample was washed through mesh sieves. Whole plant matter was discarded, and seeds of the two invasive species were identified and collected.

Seed Germination

Seed germination trials were conducted at the Charles Darwin Research Station and in Albuquerque, NM. Ingested seeds were compared with seeds retrieved from ripe fruit collected at the study sites. The first trial ran for 21 days at the CDRS and involved only *Passiflora edulis*. The second trial, conducted in Albuquerque, tested seeds from both species. In both experiments, seeds were kept moist in Petri dishes. They received approximately twelve hours of natural light each day in the Galápagos, and this condition was replicated in New Mexico by the use of fluorescent plant lights.

The third seed germination trial conducted in Albuquerque was done in the University of New Mexico's research greenhouse. Seeds of both species were planted in four inch pots in a mixture of sand and potting soil and watered daily.

Vegetation Surveys

In order for effective dispersal to occur, seeds must be spread to ecologically appropriate locations, or safe sites. A safe site is described as a location in which seeds have a high probability of germination and in which seedlings have the necessary environmental conditions to persist and mature to reproductive age (Stiles 1989).

The ecological requirements for establishment of *P. edulis* and *P. guajava*, are not specifically known for the Galápagos ecosystems. Vegetation surveys were conducted to develop a descriptive method of categorizing suitable safe sites. Eighteen species were selected as index species (Appendix 1). The species are a mix of native, endemic, and non-native plants known to occur on Santa Cruz.

At each study site, a long transect was established along the main tortoise path between the agricultural zone boundary and the arid zone, which is the tortoise nesting zone. Park guards and researchers also use these trails. In addition, the trails at both sites have had a history of use by tourists and local residents. The presence and abundance of each of the index species was recorded in paired 2 m by 10 m plots 5 meters off the trail. The paired plots were located at 400 m intervals along the transect.

Statistical Analysis – seed germination

Data from the seed germination trials were analyzed using a failure-time analysis technique. This method accounts for both the amount of time elapsed until an event occurs and the possibility that no event occurred or was observed (Fox 2001). At discrete time intervals, the researcher determines whether the event has occurred. Three outcomes are always possible: the individual is still in its original state because nothing has yet occurred; the event has occurred and the individual is in an altered state; or the event does not occur during the course of the study and no observation is recorded (Fox 2001). In the case of seed germination studies, the event, or “failure”, is germination of an individual seed. Seeds that do not germinate during the course of the trial are considered right-censored data points and are incorporated into the analysis rather than being discarded. This approach has several advantages over the more traditional ANOVA comparison of treatments: it does not require normality of the data; survivorship curves for all failure times can be compared, rather than only those on the same time scale; and censored data can be included (Fox 2001). I used the SAS LIFETEST procedure to test the similarity of survivorship curves for the various germination trials.

Statistical Analysis – vegetation data

Data from the vegetation plots at both the Caseta and El Chato were analyzed using multivariate analysis of variance (MANOVA) and canonical discriminant analysis. The discriminant analysis was used to test the response of the index species to the altitudinal gradient. Canonical discriminant analysis separates transects based upon their

similarity, maximizing the differences between transects while accounting for the variability within transects (Reeder and Riechert 1975).

The distribution of *P. guajava* and *P. edulis* was mapped in the field, recording the location of individual plants with a GPS. I analyzed the difference in abundances of the index species and compared the plots that fell within the mapped range of each of the invasive species with those outside of the ranges.

Chapter Three – Results

Seed Consumption

Do tortoises consume the fruits of *Passiflora edulis* and *Psidium guajava*?

Analysis of tortoise scats provided the answer to this question. Five samples contained plant matter from several forbs and grasses but no seeds. Seven scat samples contained seeds from *P. edulis*, with a mean value of 590 seeds per scat. Six samples contained seeds from *P. guajava*, with a mean value of 483 seeds per scat.

Seed Germination

Can tortoises pass viable seed through their digestive tracts? I conducted three separate germination trials to answer this question. The first trial was conducted in the Galápagos, for *P. edulis*. Germination percentages were higher for tortoise ingested seeds than noningested seeds. Nineteen percent of the ingested seeds in the Galápagos trial germinated in a twenty-one day period. Two percent of the control group germinated in the same time period (Figure 2). The difference between the treatments is significant ($P = 0.0042$ for the log-rank chi-square test and $P = 0.0039$ by the Wilcoxon test).

The second germination trial took place three months later, in Albuquerque. The results for *P. edulis* were consistent with the first experiment. No seeds in the control group germinated, and only six percent of the experimental group germinated during the forty day period (Figure 3). The difference again is statistically significant ($P = 0.0131$ for both the log-rank and Wilcoxon chi-square tests).

Germination percentages for *P. guajava* were tested concurrently with the second trial for *P. edulis*. Eighty percent of the control seeds germinated within 31 days. Forty-two percent of the ingested seeds germinated during the forty day trial period (Figure 4). The difference is significant, with a P-value of $< .0001$ for both the Wilcoxon and log-rank chi-square statistics.

The third germination trial was conducted in the University of New Mexico's research greenhouse at the conclusion of the second trial. Both species were tested. The results of this trial were consistent with the previous two, but were not analyzed, due to the small sample size. There was no germination in the control group for *P. edulis*; only one of the ingested seeds germinated. For *P. guajava*, four of the control seeds germinated, and two of the ingested seeds germinated.

Vegetation Analysis

Can tortoises distribute seed to sites suitable for seed germination? The presence and abundance of the index species in all vegetation plots was analyzed along the altitudinal gradient in an attempt to describe "safe sites" for both *P. edulis* and *P. guajava*. The patchy nature of the transition zone makes it difficult to discern individual species distribution patterns, but four species demonstrated an observable relationship to the altitudinal gradient ($P < 0.0001$). The abundance of *Hippomane mancinella* L. (Figure 5), a native tree, and *Sida* spp. (Figure 6), native forbs, decreases as the altitudinal gradient decreases. *Bastardia viscosa* L. (Figure 7), another native herbaceous plant, becomes quite prevalent at distances between 2400 and 5000 meters from the study sites. *P. edulis* (Figure 8) does not show a strictly linear relationship to the altitudinal gradient

but its distribution appears, at this point in time, to be primarily limited to the first 2 –3 kilometers from the agricultural zone border at both El Chato and the Caseta. *P. guajava* did not occur within the study plots with enough frequency to be included in the discriminant analysis.

P. guajava was largely concentrated in groves around the Caseta, at roughly 180 m in altitude. Some species are more likely to occur within the same range as guava than outside that range. *H. mancinella* was strongly correlated with distribution of guava ($P = 0.0008$). *Sida* spp. also showed a relationship to the guava distribution ($P = 0.0191$) as did *P. edulis* ($P = 0.0293$). Given the results of the discriminant analysis, this relationship among species is likely due to the influence of the altitudinal gradient.

The current range of *P. edulis* extends from the agricultural zone to almost 3 km into the tortoise reserve. *Senna occidentalis* L. was found in the same range in more open areas, but rarely at lower altitudes ($P = 0.0262$). *Bastardia viscosa* occurs only towards the lower end of the range of *P. edulis* but is abundant at the lower altitudes closer to the arid zone ($P = 0.0353$).

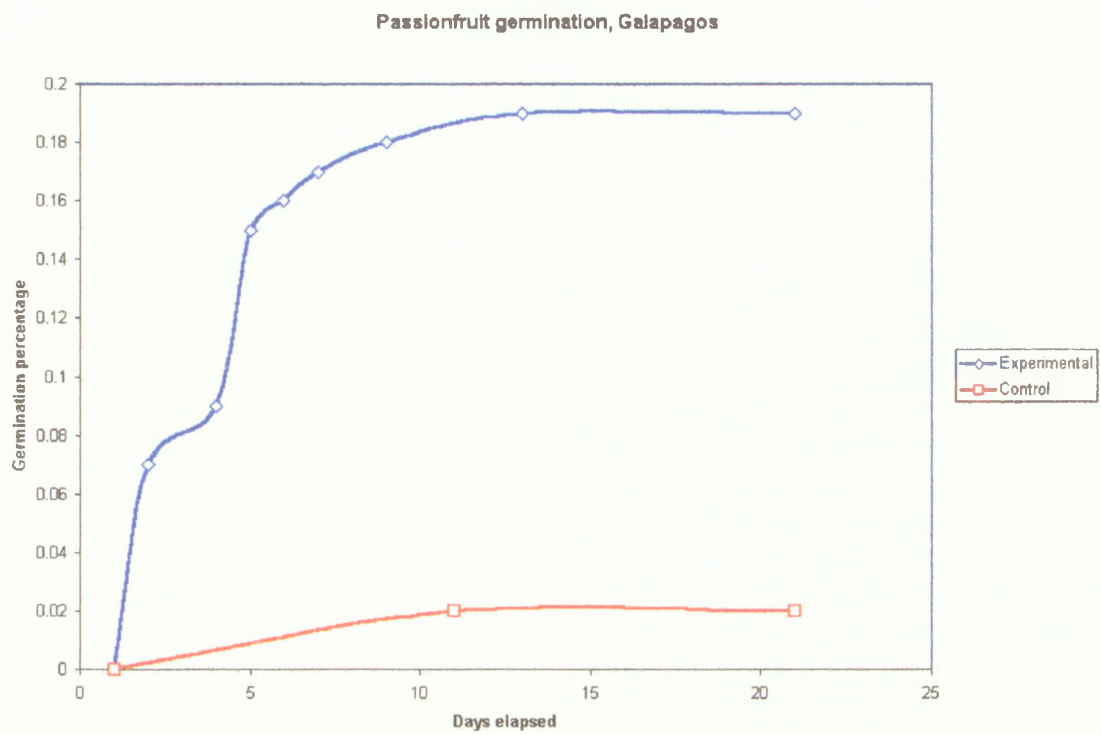


Figure 2, Germination percentage of ingested *P. edulis* seeds (experimental) and control from Galápagos seed germination trial.

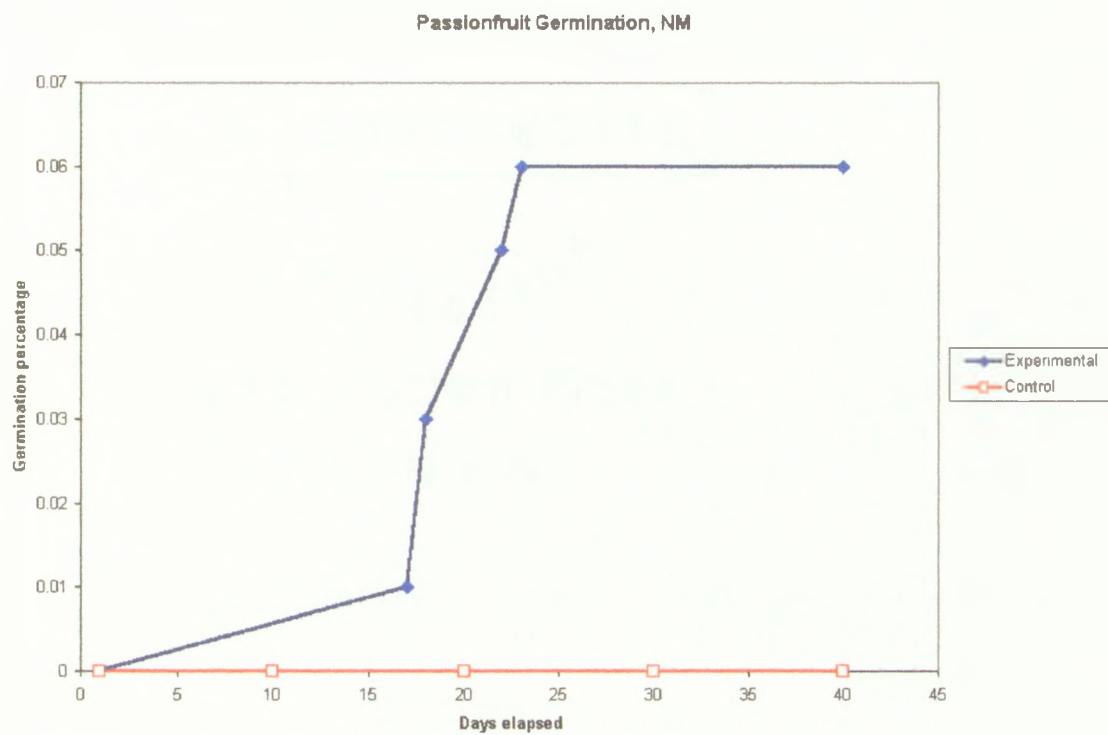


Figure 3, Germination percentage of ingested *P. edulis* seeds (experimental) and control from New Mexico seed germination trial.

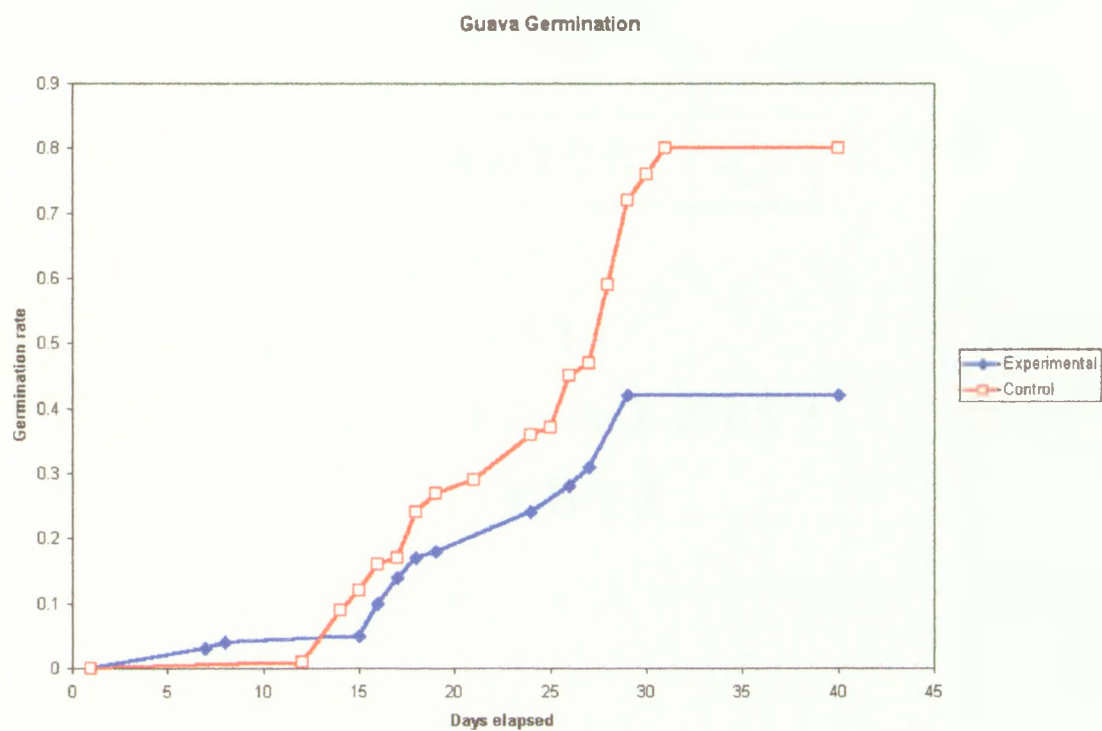
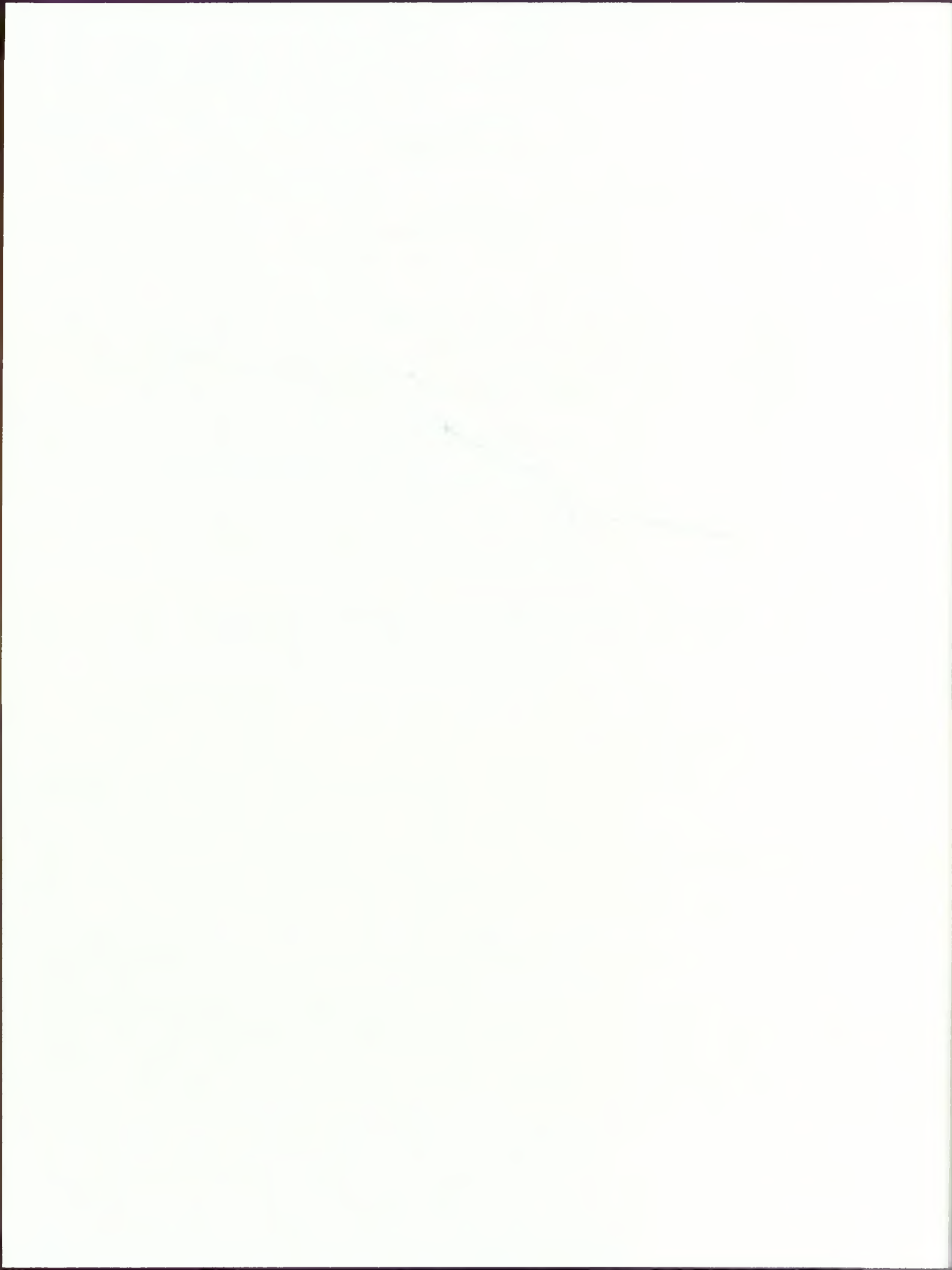


Figure 4, Germination percentages for *P. guajava* seed germination trial.



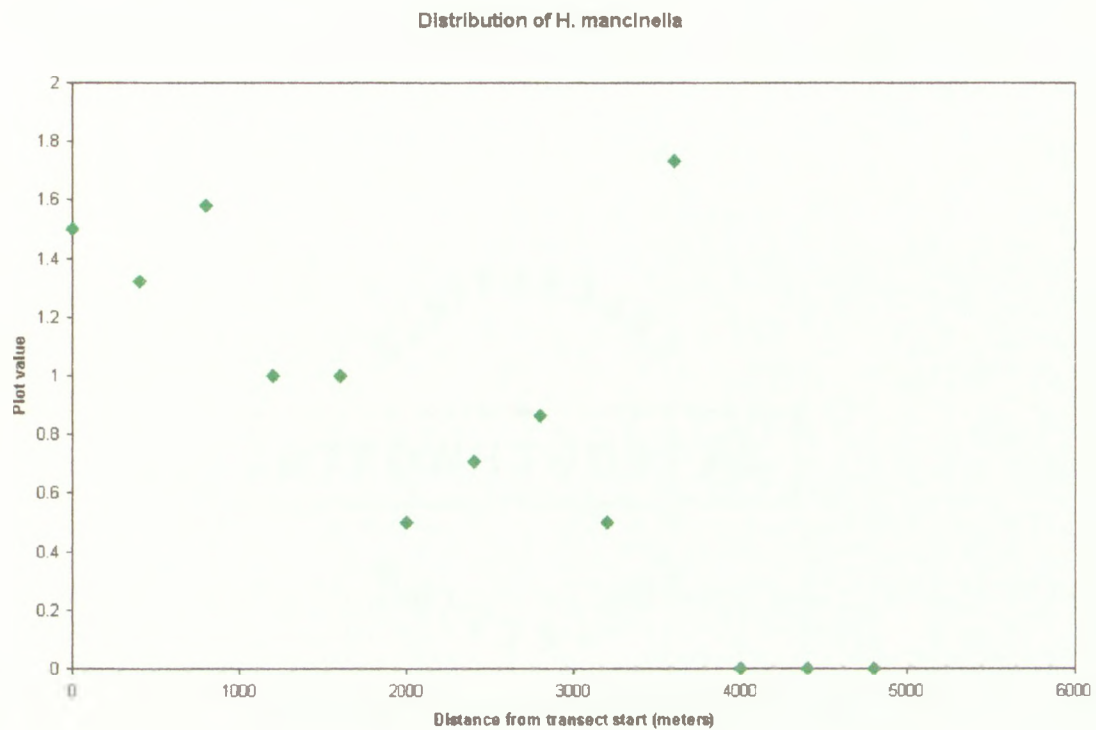


Figure 5. Distribution of *H. mancinella* along the altitudinal gradient on Santa Cruz. All plot values were obtained by averaging the number of individuals in each plot at a given distance and then taking the square root of that value. The distance in meters for figures 5 – 8 extends from the start of the transect (high altitude) towards the coast (low altitude).



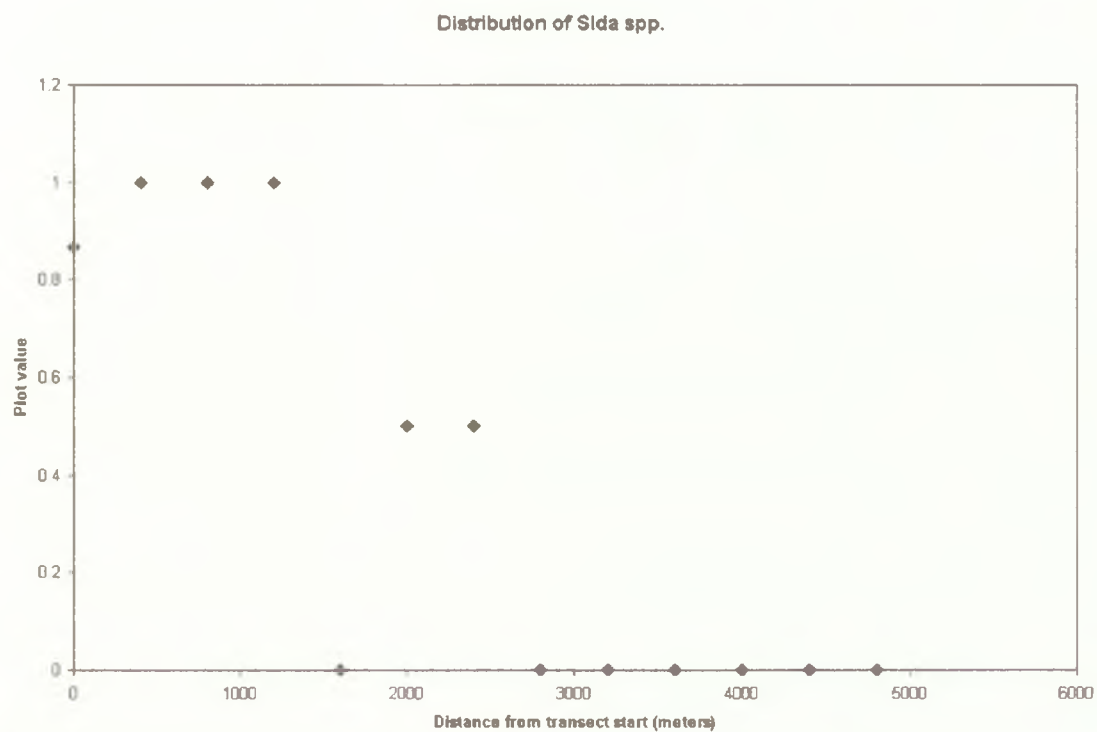


Figure 6. Distribution of *Sida* spp. along the altitudinal gradient on Santa Cruz.

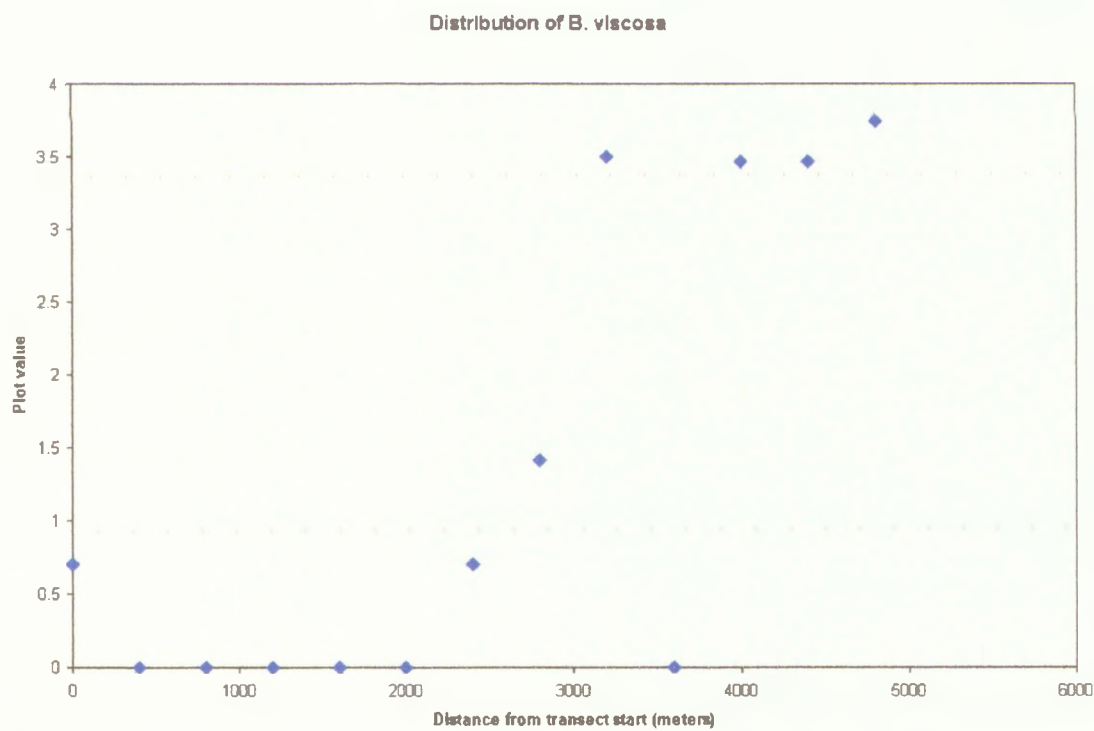


Figure 7. Distribution of *B. viscosa* along the altitudinal gradient of Santa Cruz Island.

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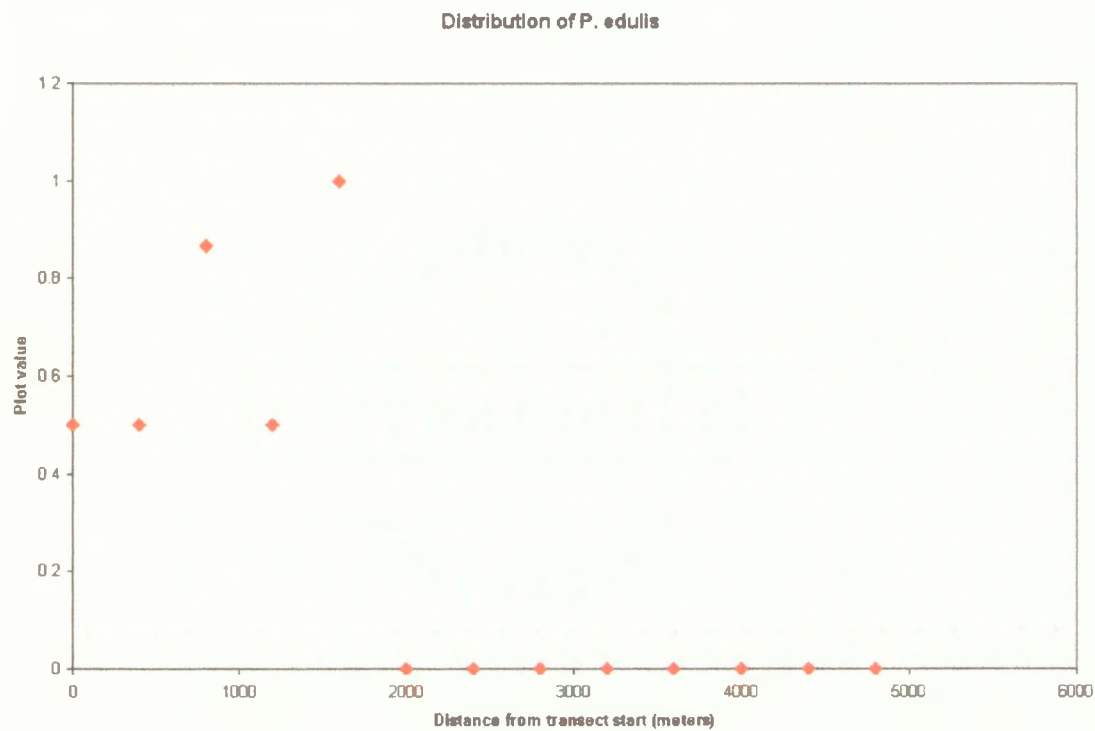


Figure 8. Distribution of *P. edulis* at the Caseta and El Chato. This species does not have a discernable linear relationship with the altitudinal gradient, but its abundance decreases at a distance of about two kilometers into the reserve.

Chapter Four – Discussion

Do tortoises eat the fruits of Psidium guajava and Passiflora edulis?

Analysis of tortoise scats collected at both the Caseta and El Chato sites indicates that tortoises regularly consume the fruits of the invasive species *P. guajava* and *P. edulis*. Their selection of this fruit is consistent with other observations on tortoise feeding behavior. Tortoises have been observed spending up to an hour at a time grazing on the fallen fruits of the tree *Hippomane mancinella* (Rodhouse et al. 1975). Tortoises also make the fruit of the endemic Galápagos guava tree (*Psidium galapageium* Hook. f.) a large part of their diet when it is available (Cayot 1987, Fowler de Neira and Johnson 1985).

Do tortoises pass viable seed through their digestive tracts?

The results of the seed germination trials for *P. edulis* show a significant difference between the germination percentages for ingested and noningested seed. The higher germination percentage for ingested seeds indicates that passage through an animal's gut promotes seed germination. Seeds removed from ripe fruit have a thick seed coat, and are also covered with a thick pulp. Mechanical or chemical abrasion is often necessary for germination of this type of seed (Stiles 1989, Traveset 1998).

It is not known at this time which, if any, native bird species play a role in the dispersal of *P. edulis*, or whether introduced vertebrates such as pigs and goats disperse the seed. Rick and Bowman mention an anecdotal account from mainland Ecuador describing cultivation methods for passionfruit, including instructions to field hands on where to defecate after consumption of ripe fruits (Rick and Bowman 1961). This

information suggests that humans in Galápagos should be considered a potential dispersal agent for *P. edulis*, and human behavior should be modified accordingly in park areas.

Guava does not require passage through an animal gut for germination.

Somarriba tested germination percentages between ripe, fallen fruit and seed ingested by cattle, and found no significant differences (Somarriba 1986). In my seed germination experiments, a higher percentage of the control seeds than the tortoise ingested seeds germinated. While the difference is significant, tortoises do pass viable seed through their digestive tracts, which suggests that they may still play an important role in dispersal. Guava has been naturalized in the Galápagos for more than eighty years, and most of its dispersal agents are not yet clearly identified, nor are they known for wild guava in mainland South America (Somarriba 1986). A closely related species, *Psidium cattleianum*, has become an aggressive invader in Hawaii and is spread by introduced birds and feral pigs (Huenneke and Vitousek 1990). Schofield mentions that feral cattle eat the fruits of *P. guajava* and suggests that their trampling of native vegetation may aid in establishment of seedlings (Schofield 1989). Recent work in Galápagos indicates that cattle can disperse guava seed (Henderson 2001). Other observations suggest that at one point in time, feral cattle may have played a role in the suppression of guava trees.

Eckhardt and Kastadalen both note that cattle ate the shoots of young trees, and that it was not until the population of feral cattle on Santa Cruz was brought under control by hunting that the thickets of guava trees began to establish themselves (Eckhardt 1972, Kastadalen 1982).

Evidence from other studies suggests that the Galápagos tortoise can be an effective seed dispersal agent. The tortoise is probably the primary dispersal agent of the



endemic Galápagos tomato (*Lycopersicon cheesmanii* Riley). Young captive specimens of *Geochelone elephantopus porteri* were fed seeds of the Galápagos tomato by Rick and Bowman. The ingested seeds passed through the tortoises in 11 to 21 days, and germinated at percentages between 60 and 81% (Rick and Bowman 1961). Untreated control seeds from the same ripe fruits did not germinate in this experiment, although other observations have indicated that seed from ripe fruit will eventually germinate (Rick and Bowman 1961, Tye 2003).

The Galápagos native tree *Hippomane mancinella* is a member of the family Euphorbiaceae, and contains a white, toxic latex substance in its leaves and fruit. Tortoises regularly consume the fruit and pass it whole through their guts (Cayot 1987, Rodhouse et al. 1975, Thornton 1971). It appears to have no serious effect on the animal. Rodhouse et al. speculate that tortoises may in fact be the dispersal mechanism for the tree, as trees are often found in clusters relatively far away from other trees (Rodhouse et al. 1975).

Although reptiles are not as well known as seed dispersal agents as birds and many mammals, the literature contains several examples of tortoises around the world as potentially significant agents of plant dispersal (Stiles 1989, Traveset 1998). Box turtles have been noted to increase the germination percentages of native plants in Virginia (Braun and Brooks, Jr. 1987). Moll and Jansen demonstrated that although semi-aquatic turtles in Costa Rica did not significantly increase the germination percentage of riparian flora, they still pass viable seed through their guts and may be important in local plant dispersal (Moll and Jansen 1995). The spur-thighed tortoise, *Testudo graeco* enhanced germination of four of five species examined, with an average time of retention in the

digestive tract of 5.3 days (Cobo and Andreu 1988). Leopard tortoises (*Geochelone pardalis*) were found to eat grasses, succulents, and forbs from 26 plant families and to pass viable seed from seven families (Milton 1992). The Aldabran giant tortoise (*Geochelone gigantea* Schweigger) may be a particularly significant dispersal agent for the Aldabra atoll. Seed from 28 different species of vascular plants germinated after passing through tortoises' guts (Hnatiuk 1978). The tortoise, in fact, may be the primary dispersal agent for *Stachytarpheta jamaicensis*, which was introduced by humans to another section of the atoll (Hnatiuk 1978).

Can tortoises disperse seed to sites suitable for establishment of seedlings?

Seeds that remain viable in a tortoise's digestive tract may be spread to locations either far from or near to the parent plant, depending upon the tortoise's behavior. Daily tortoise behavior is consistent, with two main activities: resting and eating (Cayot 1987, Rodhouse et al. 1975). Tortoises also may travel during the day, with recorded distances varying between 21 m and 413 m with a mean distance of about 155 m (Rodhouse et al.). They are more likely to travel long distances during dry conditions, when food is not as readily available (Cayot 1987, Rodhouse et al. 1975).

Tortoises frequently follow established paths, although they are also capable of clearing their way through thick vegetation (Cayot 1987, Fowler de Neira and Johnson 1985, Rodhouse et al. 1975). The main paths at both study sites are heavily traveled by tortoises, and many animals were observed resting or feeding on or near these pathways. A wide distribution of passionfruit was also noted along these paths in the upper

elevations, although it is not clear whether this is the result of tortoise dispersal or some other agent.

Rick and Bowman observed that seed passage through the digestive tract of their captive tortoises took between 11 and 21 days (Rick and Bowman 1961). Information on the other extant giant tortoise *Geochelone gigantea* gives a similar range of time, related to climatic conditions. The mean time for food passage is 27 days, but during the wet season digestion may take only six days, and during the dry season it may take up to fifty (Hnatiuk 1978). Assuming average daily travel of 155 m, a relatively active tortoise could travel more than two kilometers in a two week period. Viable seed could then be dispersed to safe sites at a large radius from the parent plant.

What constitutes a safe site for establishment of *Passiflora edulis* or *Psidium guajava* in the Galápagos? Unlike the other described vegetation zones on Santa Cruz Island, the patchy nature of the transition zone makes it difficult to discern individual species distribution patterns. Reeder and Riechert found that species dominance varied throughout the transition zone and could only correlate that variation with shifts in altitude (Reeder and Riechert 1975).

My vegetation analysis revealed some distribution patterns, again relating primarily to the altitudinal gradient. Four species demonstrated an observable relationship to the gradient. The abundance of both *H. mancinella* (Figure 5) and *Sida* spp. (Figure 6) decreases as the altitudinal gradient decreases. *B. viscosa* (Figure 7) becomes quite prevalent at distances between 2400 and 5000 meters from the study sites. *P. edulis* (Figure 8) does not show a strictly linear relationship to the altitudinal gradient but its distribution appears, at this point in time, to be primarily limited to between 2 and

3 kilometers towards the coast from both El Chato and the Caseta, although two plants were observed at a distance of nearly 5 kilometers away from the park boundary. There may be a subtle shift in the vegetation community at about 3 kilometers from the boundary as canopy cover decreases and the terrain becomes more open. The presence of *Sida* spp. tapers off here, and *B. viscosa* becomes more prevalent. *H. mancinella* is still present, although it occurred with less frequency in the study plots. The distribution of *S. occidentalis*, present at middle elevations, begins to thin out here as well.

A lack of data on soil types and precipitation throughout the southwestern section of Santa Cruz Island limits the scope of vegetation analysis. The altitudinal gradient clearly corresponds with a moisture gradient. The Scalesia zone and upper elevations of the transitional zone are cooler and more densely forested, with persistent misty conditions even during the dry season (Cayot 1987, Itow 1965, Jackson 1997). The lower sections of the transition zone and the arid zone are warmer, drier, and more open, with fewer stands of trees and shrubs (Cayot 1987, Itow 1965, Jackson 1997, Reeder and Riechert 1975). Itow has correlated plant species dominance with the altitudinal gradient and percentage of lava cover, finding again that lava cover decreases as altitude increases and moisture increases (Itow 1965, 1966).

At this point, *P. guajava* appears to be limited in its potential range in this section of the island to the Scalesia zone and top of the transition zone, in and around the agricultural zone boundary. It does not persist past the first kilometer into the reserve. *P. edulis*, however, is able to establish itself throughout the transition zone. Moil reported in 1990 that the distribution of *P. edulis* was limited to areas close to the park boundary;

the spread of passionfruit deeper into the tortoise reserve is therefore a matter of great concern and should be monitored closely.

Conclusions

The spread of alien plants and animals is cause for concern throughout the world's ecosystems. Many exotics have both ecological and economic impacts on native ecosystems, and it has been argued that biological invasion should be considered a component of anthropogenic global change (Vitousek 1994, Vitousek et al. 1997). The Galápagos archipelago has been affected by human behavior since 16th century, but the impacts have become more severe in the last half of the 20th century. The rapid growth of the islands' resident human population and the increase in tourism corresponds to an exponential increase in the numbers of non-native plant species present in the islands as agricultural activity has increased to support a growing population (Mauchamp 1997, Tye 2001b).

Invasive species, plant and animal, are the greatest threat to the biodiversity of this unique archipelago (Tye 2001b). Through cooperation between the Galápagos National Park Service and the Charles Darwin Research Station, active eradication and control efforts are underway for a range of invasive taxa in Galápagos. An understanding of the ecological relationships, such as seed dispersal behavior, between native and non-native species improves the effectiveness of these control programs. Ultimately, however, changes in the behavior of the islands' short and long term residents and visitors will determine whether the biodiversity of the Galápagos will be lost or protected.

Appendix 1, Index Species

Species	Family	Zone	Form	Status
<i>Cassia occidentalis</i>	Caesalpiniaceae	arid/transition	herb	native
<i>Bastardia viscosa</i>	Malvaceae	arid	herb	native
<i>Sida</i> spp.	Malvaceae	Scalesia	herb	native
<i>Pennisetum purpureum</i>	Poaceae	arid/Scalesia	herb	introduced
<i>Lantana peduncularis</i>	Verbenaceae	arid	shrub	endemic
<i>Lantana camara</i>	Verbenaceae	arid/Scalesia	shrub	introduced
<i>Hippomane mancinella</i>	Euphorbiaceae	coast/arid/trans	tree	native
<i>Zanthoxylum fagara</i>	Rutaceae	arid/Scalesia	tree	native
<i>Acacia rorudiana</i>	Mimosaceae	arid/transition	tree	endemic
<i>Psidium galapageium</i>	Myrtaceae	arid/Scalesia	tree	endemic
<i>Psidium guajava</i>	Myrtaceae	Scalesia	tree	introduced
<i>Scalesia pedunculata</i>	Asteraceae	Scalesia	tree	endemic
<i>Opuntia echios</i>	Cactaceae	arid/transition	tree	endemic
<i>Cordia lutea</i>	Boraginaceae	arid	tree	native
<i>Momordica charantia</i>	Cucurbitaceae	arid/transition	vine	introduced
<i>Passiflora colinvauxii</i>	Passifloraceae	Scalesia	vine	endemic
<i>Passiflora edulis</i>	Passifloraceae	Scalesia	vine	introduced
<i>Passiflora foetida</i>	Passifloraceae	arid/Scalesia	vine	native

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