

Is there variation in the effects of primate size as seed dispersers?:

Seed and seedling performance after gut simulation treatments in hydrochloric acid

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Abstract

Primates are reliable seed dispersers due to their foraging patterns and ability to transport seeds several hundred kilometers away from the parent tree. It has been observed in the wild that seeds defecated by primates with longer digestive tracts have more successful seed germination. Within the primate stomach, hydrochloric acid (HCl) is a major gastric acid that helps digest and breakdown foods. Hydrochloric acid may also be beneficial to plants as well; the acid provides corrosion of the seed coat to reduce the time a seed spends dormant. Therefore organisms that swallow seeds indirectly treat seeds with HCl acid baths and provide beneficial seed modifications. In this study, seeds were treated with HCl for two hour intervals to determine the effect on germination and growth to stimulate varying time in the gut of various primate species with varying gut lengths. We found that larger primates (i.e., those with longer digestive tracts) may be more effective seed dispersers as seeds germinated earlier and seedlings performed better the longer the time they spent in the acid (i.e., stimulated gut), although they were also more susceptible to herbivory. These findings demonstrate the positive effects of primates on seedling germination and their potential as seed dispersers.

Keywords: acid baths, endozoochory, gut length, plant-animal interaction, primate, seed dispersal, seed dormancy

Introduction

Primates have a unique interaction with their habitat, especially with plants. The plant and primate interaction (i.e., herbivory) can stimulate growth for plants, disperse seeds and feeds the primates. While the plants provide shelter and food (e.g. fruits, leaves, and nectar), the primates reciprocate by facilitating pollen and seed dispersal. For some small, nocturnal primates, nectar provides an important source of nutrients. Nectar may also supplement a larger

primate's diet when fruits are scarce. As primates feed on nectar and flowers, they collect and disperse pollen on their faces and fur. Through this method of obtaining and then transporting pollen, primates become effective pollinators (Nystrom and Ashmore 2008). More importantly, primates are known for their possible role as seed dispersers. Primates can significantly influence forest regeneration and spatial heterogeneity (Wrangham et al. 1994; Julliot 1997). As a seed disperser, they must be able to successfully transport seeds from one

destination to another without harming the seed. Primates primarily disperse seeds through endozoochory – transporting seeds in the body of a primate and then defecating or spitting them out (Nystrom and Ashmore 2009). After they are defecated or deposited, the fate of the seeds are left to the environmental conditions (e.g. allocation of resources, secondary dispersal, and density of seeds; Chapman 1995; Shepherd and Chapman 1998; Chapman and Russo 2007).

Previous observational primate ecology studies have found that primates can transport seeds up to 500-1000 meters away from the parent tree (Julliot 1996; McConkey 2000). In theory, removing seeds from the parent tree improves seed survival and seed germination (i.e. the escape hypothesis; Howe and Smallwood 1982). The removal from close proximity to the parent tree thus reduces the density- or distance-dependent mortality. Other theories include seeds being deposited in uncompetitive locations that favor germination (colonization hypothesis) and seeds with adaptive morphological and behavioral characteristics being deposited in special, favorable locations (directed dispersal; Howe and Smallwood 1982). While these theories address certain foraging behaviors, whether or not primates directly impact seed germination or performance is still debatable.

When seeds are processed through the primate's digestive system, they are exposed to digestive acids and enzymes. All primate species have similar digestive systems, varying primarily in lengths of the small and large intestines. Food travels through the mouth, stomach, and small and large intestines. The major differences between humans and non-human primates are the relative gut proportions. For humans, the stomach is 10-24% of the total gut volume while 17-20% in orangutans and chimps; the small intestine is 56-67% of the total human gut volume while 23-28% in orangutans and chimps (Milton 1987); this variation in morphology influences the amount of time food stays in the digestive system. For

all primates, after food enters through the mouth, it passes into the stomach where a majority of the chemical and mechanical disintegration of food takes place (Singh 2007). The stomach stores food mixes the food with chyme and then passes the rest of the food onto the small and large intestine. The J-shaped organ controls the digestive processes through changes in pH, viscosity, and density of the gastric content. The food passes through four different phases, each varying in time and motor activity. Eventually, food particles are emptied from the stomach depending on their size. Smaller particles are emptied faster compared to the larger particles (Singh 2007).

As primate species differ in body sizes and digestive proportions, they also have different retention time of food in the gut. For example, ceropithecidae (i.e. old world monkeys such as baboons) have a retention time of 16-36 hours; atelinae (i.e. new world monkeys such as spider and woolly monkeys) have a retention time of 5-35 hours; and hominoidea (e.g. gorillas and chimps) have a retention time of 20-30 hours (Chivers and Hladik 1980). Depending on the food passage rate, primate digestive processes can thin and remove the seed coat and consequently instigate quicker germination (Righini et al. 2004). Few studies, however, have experimentally shown how the primate digestive physiology directly affects seed germination and subsequent plant performance. Many primate ecology studies observe primates in the wild with little control over the primates, their diets, or the environment. In particular, no published studies, to our knowledge, have observed how the digestive system may affect seed germination and seedling performance.

In the primate stomach the main gastric acid, hydrochloric acid (HCl), is produced in order to activate digestive enzymes and break down the food. These gastric or stomach acids secreted by parietal cells have a pH of 1-3 and range from 0.01M to 0.18M HCl (pH 0.8-0.9) (Medeiros and Wildman 2013). Throughout the rest of the digestive tract, nutrients are absorbed and the

inorganic materials are eventually defecated in feces. When primates ingest seeds, the digestive processes introduce the seeds to corrosive acids that may alter the seed coat and subsequently alter seed germination. Studies mimicking animal digestive practices (i.e., in birds) have shown hydrochloric acid increased germination with little loss to viability (Goddard et al. 2009). In horticultural practices, however, acid treatments are used to quickly break down gelatinous coating and extract seeds from pulp (Rajan and Markose 2007). Also acid baths consisting of sulfuric acid or hydrochloric acid are used to scarify seeds. The acid causes thinning of the seed coat but may harm the seed should the acid enter the seed and damage the embryo (Bainbridge 2007). By reducing the thickness of the seed coat, seeds reduce their dormancy time and germinate sooner than seeds that were not treated. Therefore, with increased time in acid, seeds should demonstrate a faster germination due to a higher deterioration of the seed coat. The objective of this study is to experimentally determine the temporal affects of hydrochloric acid bath on the germination of seeds and performance of seedlings to stimulate the amount of time seed stays in a primate gut. We hypothesize that seeds treated longer in hydrochloric acid will germinate faster with higher percentage of germination and increased plant performance.

Materials and Methods

In order to mimic the digestive process in the stomach, seeds were soaked for varying lengths of time in 0.15M HCl and a deionized (DI) water control. The seeds used were roma tomatoes (*Solanum lycopersicum* 'Roma'), watermelons (*Citrullus lanatus* 'Crimson Sweet'), and beans (*Phaseolus vulgaris* 'Burpee's Stringless Green Pod'). In a large petri dish, twenty seeds were separately exposed to either DI water, 2 hours in HCl, 4 hours in HCl, and 6 hours in HCl. Once the seeds were soaked, they were rinsed in DI water and

planted in potting mix soil (equal parts peat, perlite and vermiculite). The seedlings were regularly watered and observed once a week to gather height and leaf length data. Plant height was measured from the base of the plant to the first branch; leaf length was measured from the tip to the base of the leaf without the stem. After a month of growing, the plants were harvested and final measurements were taken. Plant length (i.e., base of the plant to the tip), leaf count, stem diameter and aboveground biomass were measured. Aboveground biomass was determined by weighing all individual plants after 24 h of drying at 70°C. Due to the appearance of white flies, the percentage of white fly colonization was also recorded. To analyze the data, a two-way ANOVA was used with plant species, seed treatment, and their interaction as fixed effects. All analyses were performed with JMP Pro 11 after log-transforming the data.

Results

Significant differences were found among the species, treatment, and their interactions, indicating that amount of time spent in an animal digestive system would influence seed germination and plant performance. While it is not surprising to see differences in growth between the species, the treatment demonstrated significant differences in germination, height (cm) recorded on the second week, leaf length (cm) recorded on the first week, total plant length (cm), aboveground biomass (g) and white fly herbivory (%) (Table 1). No significant differences were found in stem diameter (mm), among the species type or the treatment (Table 1). Significant species by treatment interactions were found for germination, height recorded on the second week, and white fly herbivory responses; all other response variables showed similar reactions to the treatments (Table 1).

Plant species and treatment affected how many seedlings emerged (i.e., % germination; Fig.1). Treatment of 2 h in HCl received the

highest germination (20/20 seedlings) while 4 h in HCl received the lowest germination (15/20 seedlings). The watermelon seeds showed an increased response pattern to HCl. With water and 2 h of HCl, watermelon showed the lowest germination (11/20 and 10/20 seedlings respectively), while having the highest germination with 4 and 6 h of HCl (17/20 seedlings for both). The beans demonstrated a stable germination pattern throughout the treatments; the water treatment had the lowest germination (16/20 seedlings) while 2 and 6 h of HCl had the highest germination (19/20 seedlings).

The acid treatments affected not only seed germination but also subsequent seedling performance, as measured by functional plant traits (Table 1; Fig. 2). After two weeks of growth, height demonstrated different responses to the treatment for each species (Fig. 2a). The tomatoes demonstrate a steady positive increase in height across the treatments, the watermelons show an increasing height pattern, and the beans show a slowly decreasing height pattern, especially after 4 h of HCl. In the overall plant length (Fig. 2b), all species show a similar reaction to the treatment; the tomatoes, watermelons, and beans show a 10-20% increase with increasing time in the acid up to a threshold of 4hr whereby they decreased in growth. All three plant species reacted positively (Fig. 2c) to increased exposure of HCl. Beans demonstrated a greater increase in aboveground biomass at 4 and 6 h of HCl while tomatoes and watermelons showed a slight increase.

Surprisingly, biotic interactions (i.e., plant herbivory) also changed across the acid treatments. Throughout the month long growing period, the tomato and bean seedlings attracted white flies to the underside of the leaves (watermelon showed no response). In both species, plants treated with longer exposures of HCl had higher percentage of white fly herbivory (Figure 3). Overall, beans had the

highest biomass as well as the highest herbivory with increasing time in acid.

Discussion

To conclude, tomatoes, watermelons and beans expressed increased germination and performance with HCl treatments. One week after planting, control seeds of tomatoes, watermelons, and beans had the lowest germination (80%, 55%, and 80% respectively) and increased germination with treatments of 6 h of HCl (95%, 85%, and 95% respectively) (Fig. 1). These results clearly demonstrate that longer exposures to HCl will positively affect the germination of seeds. As for seed performance, aboveground biomass increased with treatment while plant height and length expressed a threshold at 4 h in HCl. The results were consistent with our hypothesis that seeds will have quicker time of germination and improved plant performance; the treatments furthermore exhibit a higher percentage of germination. While there was a threshold effect around 4 h in HCl, plant traits clearly increased with HCl treatments. Similarly, a study by Goddard et al. (2009) studying the survival of Benghal dayflower seeds in the gut of mourning doves, found that seeds from dove crops have 92% germination compared to control seeds with 80% germination. When Goddard et al. (2009) stimulated digestion using 0.1M HCl, seeds remained viable. These results clearly demonstrate that exposures to HCl will not harm seeds and will positively affect the germination of seeds; the results also correspond to how ingestion of seeds by primates induces germination. The longer seeds remain exposed to gastric acids in the primate gut, the more likely they are to express faster germination rates. HCl acid deteriorates the seed coat to allow the uptake of nutrients, water and oxygen for quicker germination (Cowlshaw and Dunbar 2000).

Despite the early germination, the height recorded after two weeks demonstrates different

patterns. For the tomatoes, the earlier germination did not seem to affect the heights; the heights of seedlings were the same throughout the different treatments (Fig. 2a). As for the watermelon and beans, an early germination may have resulted in lower heights due to the competition for sunlight. In the bean plots, we noticed the more recent seedlings sprouted branches much higher on the stem than the older seedlings. This effect may be a result of seedlings reacting to the lack of sunlight closer to the ground due to the leaf coverage. Adapting this strategy increases the amount of photosynthesis per unit leaf area with better light conditions (Falster and Westoby 2003). Similar to the height, overall plant length (from stem base to leaf tip) demonstrates how early germination may lead to decreased growth (Fig. 2b). Aboveground biomass, on the other hand, reveals the positive effects of early germination with treatment; while the seedlings may not have grown taller with treatment, they demonstrate increased aboveground biomass with treatment (Fig. 2c). White fly herbivory also correlates with increased exposure to HCl and germination (Fig. 3). While the older leaves attracted more white flies, they were also found on the younger leaves. During the growing period, the white fly herbivory did not seem to affect the growth of the seedlings.

The results of this study support the findings of Wrangham et al. (1994), Julliot (1996), and others that germination rates improve after passage through the gut of the primate. The digestive system produces gastric acids to digest foods but also help alter the seed coating. Exposure to gastric acid, stimulated in this experiment with HCl, strips the seed coat for quicker germination. In an experiment by Hafiz et al. (2011), varying time exposures to HCl and mechanical scarification with sandpaper demonstrated higher germination on *Rhynchosia capitata* seeds. After soaking seeds in HCl for 3, 6, and 9 h, germination times improved while soaking seeds in 12, 16, and 18 h, however, had damaging effects on the seeds. Overall, Hafiz et

al. (2011) found that acid treatments and scarification decreased *R. capitata* seed dormancy. For the primates, the gut stimulates an acid bath, leading to increased germination; primates with larger gut volume lead to longer exposures of gastric acid. The acid treatments in this experiment clearly demonstrate an advantageous effect on seed germination with longer exposure to HCl.

Consequently, primates with longer gut retention time, i.e. primates with larger and longer digestive physiology, will be the best dispersers. The longer time the seeds remain in the gut, the more likely the seed coat will be altered to allow quicker germination and shorter seed dormancy. Primates thus provide positive impacts on seedling demographics and performance compared to seeds in the fruit that fall from the tree. In addition to the rapid germination, primates provide some escape from the parent tree where seeds are accumulated under the tree's branches. Compared to those seeds found near the parent tree, digested and defecated seeds may even grow better with primate feces as fertilizer. Other endozoochory studies found that ingestion by tapirs (Capece et al. 2013; Barcelos et al. 2013; O'Farrill et al. 2013), birds (Friguerola et al. 2005; Figuerola et al. 2010; Fricke et al. 2013), cattle (D'hondt and Hoffmann 2010) and beetles (De Vega et al. 2010) positively affect seed germination and plant performance. Ingestion by animals clearly presents valuable seed germination strategies for plants. Throughout generations, plants express traits evolutionary selected by with these frugivorous animals; specifically with animals that have specific eating patterns (e.g., primates and birds), these animals provide ecological and evolutionary consequences such as changes in seed and fruit morphology and structure (Chapman 1995; Encinas-viso et al. 2014). Coevolutionary mechanisms to promote seed dispersal and improve seedling colonization and regeneration may also be evident (Chapman 1995; Lambert and Garber 1998). Primates and

their preference for certain fruit types and morphology may influence evolutionary patterns found among plants.

Conclusion

Primates are major players in their environment and putatively plants benefit from their valuable seed dispersal qualities. While primates feed on fruits, they consume the seeds and disperse seeds through endozoochory. Ingestion by primates with longer gut lengths may provide greater benefits for successful seed germination. Primates provide great advantages to seeds by transferring them away from the parent tree and into open areas. Primates are even known to help expand the forest by defecating on the edges of the forest environments (Cowlshaw and Dunbar 2000). Through this gut simulation study we provide some of the first experimental evidence that primates improve seed germination, and subsequently, plant growth. These data provide evidence that through their seed dispersal activities, primates have larger effects on the sustainability of habitat than appreciated which is a further argument for better primate conservation efforts. Based on this simulation, upcoming future work will further experimentally analyze the effects of gut length on seed and seedling performance by feeding primates of varying sizes and gut lengths common seed, collecting primate feces and growing the seedlings after digestion. We will be using captive primates from the Knoxville Zoo, which include gorillas (*Troglodytes gorilla*), chimpanzees (*Pan troglodytes*), gibbons (*Hylobates lar*), and baboons (*Simia hamadryas*). Our experiment on using HCl for gut simulation indicates that longer exposure to gastric acids improve germination by approximately 15-30%, and thus we expect to see similar results using captive primates at the Knoxville Zoo. Together these results will show that primates are the indirect gardeners of their habitat, directly affecting the forest through

their foraging and eating patterns. Historically, primates also affect the evolutionary patterns of plant structures and morphology (Chapman 1995; Lambert and Garber 1998; Encinas-Viso et al. 2014). In observational studies around the world, the loss of primates leads to unstable forest environments (Julliot 1997; Gowlshaw and Dunbar 2000; McConkey 2000; Nystorm and Ashmore 2008). With further in-depth studies of primate impact on the environment, especially regarding their seed dispersal capabilities (e.g. endozoochory and removing seeds from the parent tree), we can predict regeneration patterns of the forest. Primates distinctly modify their environment simply through eating habits, making primates crucial inhabitants of the forest. Without studies to further promote their significance, they may lose the consideration of conservationists and, ultimately, the world.

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Table 1: The effects of acid treatments on seed germination and seedling performance. All data were log-transformed before analysis with two-factor ANOVA on JMP.

Response Variable	Species		Treatment		Species*Treatment	
	F	P	F	P	F	P
Germination ¹ (%)	5.9650	0.0030	4.0836	0.0076	2.9476	0.0088
Height ¹ (cm)	308.7394	0.0001	0.8959	0.4442	0.3099	0.9313
Height ² (cm)	339.2916	0.0001	3.5351	0.0157	4.3159	0.0004
Leaf Length ¹ (cm)	152.2117	0.0001	3.4536	0.0174	0.9654	0.4496
Leaf Length ² (cm)	343.7517	0.0001	1.2225	0.3025	0.5442	0.7742
Leaf Count*	23.563	0.0001	0.7678	0.5138	0.1152	0.9945
Stem Diameter* (mm)	0.4758	0.6223	1.3157	0.2717	0.4739	0.8269
Total Plant Length* (cm)	75.6087	0.0001	3.9728	0.0094	1.2034	0.3079
Aboveground Biomass* (g)	54.1154	0.0001	3.4299	0.0188	1.4485	0.2002
White Fly Herbivory* (%)	146.4558	0.0001	6.2188	0.0005	2.2466	0.0421

¹ Data collected one week after planting

² Data collected two weeks after planting

* Data collected three weeks after planting, while harvesting plant

Figure Legends

Figure 1: The percent of germination of the tomato, watermelon, and bean seedlings by treatment of DI water, two hours in HCl, four hours in HCl, and six hours in HCl one week after planting. The highest germination for tomatoes was at two hours (100%) and the lowest at four hours (75%). The highest germination for watermelons was at four and six hours (95%) and lowest at two hours (50%). The highest germination for beans was at two and six hours (95%) and the lowest with DI water (80%). From water to six hours of HCl, overall plant germination increased about 15-30%.

Figure 2: The average height (a), overall length (b), and total aboveground biomass (c) of the tomato, watermelon, and bean seedlings by treatment of DI water, two hours in HCl, four hours in HCl, and six hours in HCl. Plant height (a) demonstrate different reactions to the treatment per species while plant length (b) and aboveground biomass (c) have similar patterns with the treatments.

Figure 3: The average percentage of white fly herbivory on seedlings for each species per treatment. Tomatoes and beans demonstrate an increase in herbivory with treatment; watermelons did not have any herbivory.

Figure 1.

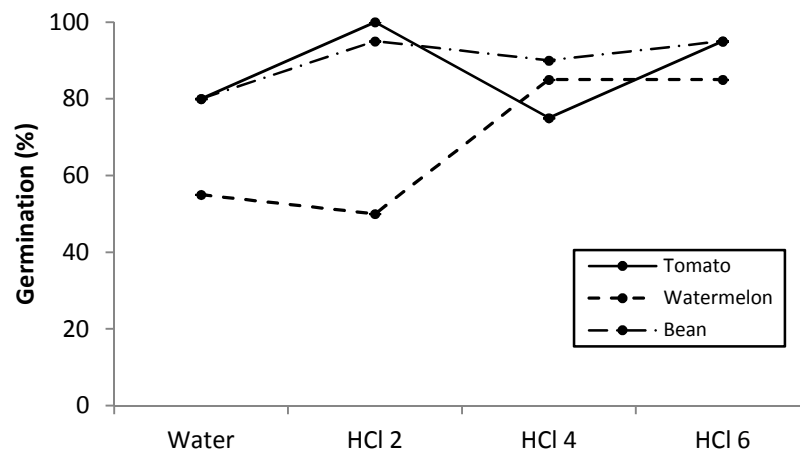


Figure 2.

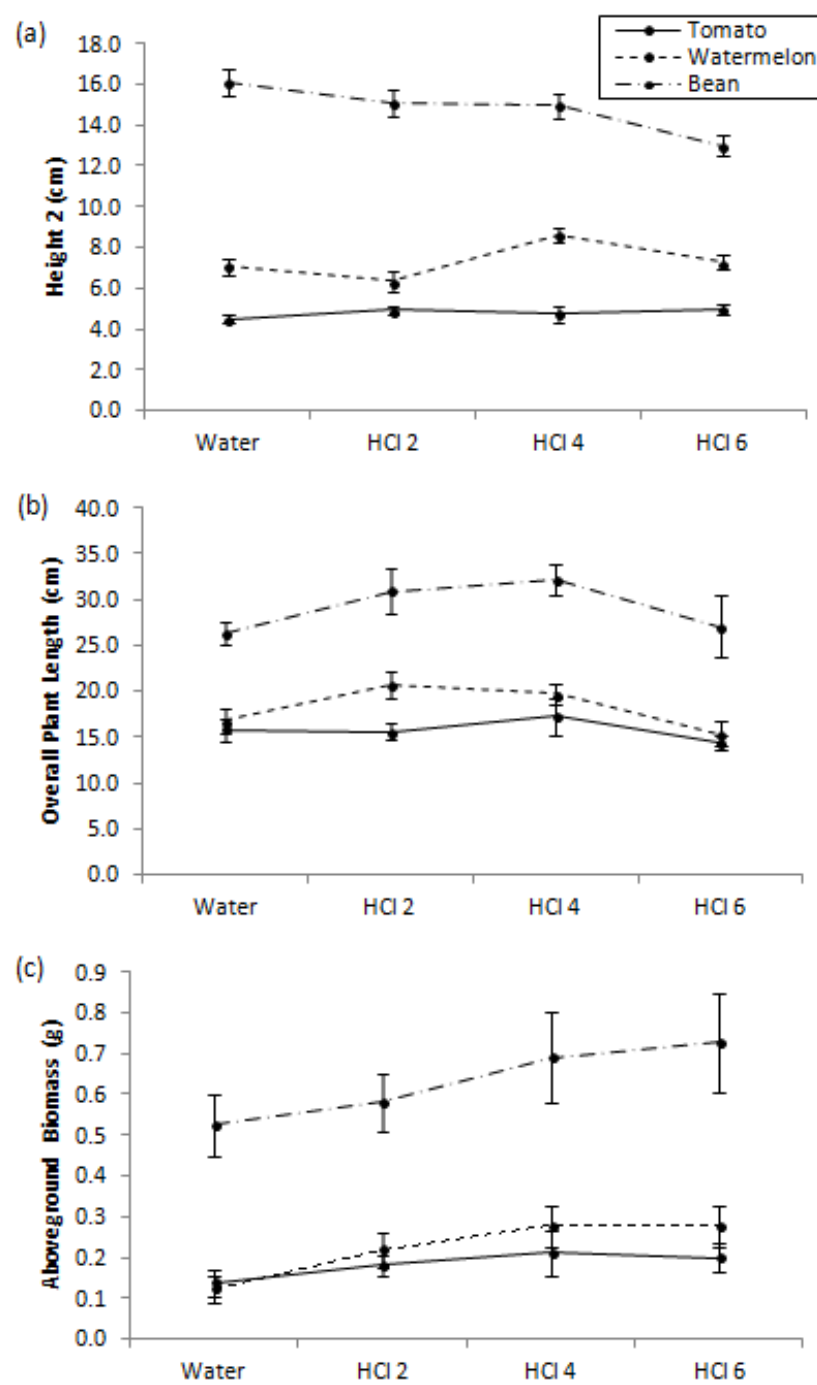


Figure 3.

