2011

HEALTHY CHOICES; PREFERENTIAL FORAGING OF INSECTS WITHIN SENESCENT, BUT NUTRIENT-RICH, TROPICAL FLOWERS.

Amie Whigman
CUNY City College

HEALTHY CHOICES:
PREFERENTIAL FORAGING OF INSECTS WITHIN SENESCENT, BUT NUTRIENT-RICH, TROPICAL FLOWERS.

Amie E. Whigham

A thesis submitted in partial fulfillment of the requirements for the degree of Masters of Arts in Biology

DEPARTMENT OF BIOLOGY
THE CITY COLLEGE OF NEW YORK
CITY UNIVERSITY OF NEW YORK COLLEGE

ABSTRACT

Forest floor litter communities include detritivorous, predacious, and parasitic arthropods that feed on, or forage within, the decaying organic material. Although this substrate is heterogenous, little research has investigated the preferential feeding tendencies of these insects. The objective of this study, conducted in the lowland rainforest of French Guiana, was to examine some of the factors that may influence foraging behavior. Plots of forest floor were covered with either leaf or floral litter from three species of Lecythidaceae (Brazil nut family), and insect traps were set within and above each plot. Traps baited with floral litter yielded significantly more insects than those baited with leaf litter. Floral and leaf tissues were subsequently analyzed for moisture, fiber, sugar and nutrient contents. These analyses indicate that floral litter provides a quantitatively richer nutrient source available at a lower energy expenditure, suggesting that insects are operating under optimal foraging strategy.

KEY WORDS

Corythophora amapaensis*,* Couratari stellata**,** *floral nutrients, insect foraging, leaf nutrients,* Lecythis poiteaui*, saproflorivory*

INTRODUCTION

Insects comprise the most diverse group of animals, occupying a remarkable breadth of ecosystems and niches. Within this class is a large group of phytophagous insects that, over numerous independent events, have developed morphological, physiological, behavioral, and ontogenetic adaptations to best fulfill the nutritional requirements necessary for maturation and reproduction (Hochuli 2001, House 1961). Plant-feeding insects may obtain their required nutrients from a variety of plant tissues and, depending on the feeding substrate, are variously classified as root-feeders, sapsuckers, folivores (leaf-feeding), florivores (floral-feeding) or frugivores (fruit-feeding) (Price 2002). Regardless of feeding strategy, the fundamental objective of consuming plant tissue is to obtain the various nutrients, vitamins, and minerals necessary for metabolism, development, and reproduction. Insects largely require similar nutrients in order to sustain these activities (Hochuli 2001), and ideally, a foodstuff would provide all necessary nutrients in appropriate amounts and relative proportions for optimal physiological performance.

In perhaps some of the most widely recognized cases of coevolution, plants have evolved to resist insect attack, developing both chemical and physical defenses (Coley & Barone, 1996). Plants produce an array of secondary metabolites, chemical compounds often unique to particular phylogenetic groups, many of which have anti-feedant roles (Bennett & Wallsgrove 1994, Wink 1987). They range from potent toxins to more subtle disincentives that deter herbivory but prevent rapid evolution of resistance (Hanley *et al.*

2007). Such adaptations are noted in over 200 families of both aquatic and terrestrial plant families (Prychid & Rudall 1999). Physical plant defenses include conspicuous thorns and needles, as well as less obvious structural reinforcements and barriers. Plants with more sclerophyllous leaves, thicker epidermal tissues, and higher proportions of undigestible polysaccharides (fiber) suffer less herbivory than plants without such defenses (Hanley *et al.* 2007, Herms & Mattson 1992). The cellulose in plant cell walls is composed of linear, unbranching glucose chains that fit closely together and form rigid, rod-like structures. Because of this, cellulose is particularly difficult to penetrate enzymatically, requiring a complex of three cellulases that is not present in most insects. In addition, calcium oxalate crystals often aggregate in leaves**,** preventing access to mesophyll cells (Molano-Flores 2001, Ward *et al.* 1997). Silica deposits make plant tissues less penetrable, of a more abrasive texture, and more difficult to digest **(**Baldwin & Preston 1999, Reynolds *et al.* 2009).

A vast majority of herbivorous insects relies on the mechanical breakdown of plant tissue to access nutrients, and many have evolved highly specialized mandibles, digestive enzymes, or other characteristics to counter structural plant defenses (Zudaire *et al.* 1998). However, this "brute-force" tactic requires a large expenditure of energy, and some plants have evolved nutrient imbalances -- offering paltry rewards for costly behavior -- that deter herbivory (Hanley *et al.* 2007, Hochuli 1996). Both the nutritional value and digestibility of tissues must be considered when investigating the feeding patterns of

herbivorous insects (House 1961), including the mandibular work necessary to penetrate plant cell walls and its associated energy cost (Borror *et al.* 1989).

Floral tissues often lack the structural reinforcements of leaf tissue. The walls of floral cells tend to be thinner and easier to penetrate or digest. As a result, floral nutrients are usually more easily accessed than leaf nutrients, though access may require a specialized structure, such as a proboscis, or an evolved toxin resistance (Hochuli 2001).

The reduction in physical defenses may be in part a result of flowers' ephemeral nature within a plant. Approximately 65 percent of tropical flowers could be classified as *single-day flowers*: plants that produce short-lived flowers, opening in bursts and available for pollination for approximately 24 hours. Reid *et al.* (1992) consider short-lived flowers to be a more derived characteristic, as such transitory blossoming in these tropical angiosperms is linked to an advanced biochemical pathway. Primack (1985) hypothesized that reduced longevity is an adaptation in response to the predictability of pollinator arrival: flowers have evolved to attract as many pollinators as quickly as possible.

Modifications in flower morphology, aroma, and coloring have evolved to mirror the broad range of pollinator morphologies and preferences. This variation is especially obvious within the tropics, where biodiversity reaches its maximum and competitive plant-pollinator relationships have driven the evolution of highly specialized characteristics. For instance, bee-pollinated flowers tend to have a sweet aroma and are often white or bright yellow. Bat-pollinated flowers, on the other hand, are usually large and range from white to light purple or green. Most bat-pollinated flowers emit strong

sulfurous odors, especially at night (Faegri & van der Pejl 1971). Regardless of the intended pollinator, pollen offers a rich source of protein. As nitrogen (from protein) tends to be particularly influential in the rate of the physiological development of insects (Scriber & Slansky 1981), floral tissue offers a potentially richer food source than leaf tissue.

Upon pollination, floral organs that are not involved in fruit development often detach from the plant and become available to saproflorivores, a diverse community of insects foraging within abscised flowers **(**Feinstein *et al.* 2007). Though many studies have investigated folivory and communities of leaf litter insects, florivory is still poorly explored. Saproflorivory is even less frequently studied, but has been documented in Colombian scarabs (Noreiga & Calle 2008), Costa Rican drosophilid larvae (Collier & Armstrong 2009), and Neotropical lycenids (Robbins *et al.* 2010). Feinstein *et al.* (2007, 2008) demonstrated that the dense flower falls of Lecythidaceae harbored a community of insects atypical of those found in general leaf litter. These insects were preferentially feeding, seeking shelter and/or ovipositing within the senescent Lecythidaceae flowers.

The purpose of this study is to quantify the nutritional value of food resources available within this unique trophic niche. I hypothesized that, relative to fallen leaves, fallen flowers would have increased moisture and nutrient contents, and that these nutrients would be more easily accessible. Fallen flowers would therefore supply insects with a richer energy source available at a lower energy expense than fallen leaves. I further hypothesized that, because of the anticipated nutritional benefits of fallen flowers,

traps placed amidst fallen flowers would yield more individual insects than traps placed amidst leaf litter.

METHODS

Study Site:

All field studies and sample collections were conducted in the lowland forest of Les Eaux Claires. This homestead is located approximately 7 km north of the small village of Saül in central French Guiana (3˚37-39'N, 53˚12-13'W). This area has two dry seasons: the first between July and November, and the second a minor two-week period in March or April (Berkov & Tavaklian 1999). This study site was selected because it is particularly species rich in Lecythidaceae (Mori & Prance 2006 onward), which are the subject of this study.

Study System (Lecythidaceae):

Lecythidaceae comprise a diverse family of trees with Pan-tropical distribution but are particularly species rich and abundant in the Amazonian forests. Lecythidaceae are ecologically dominant in this part of the world (Steege *et al.* 2006), where they have been estimated to account for a third of the trees present (Mori & Prance 2006 onward).

The flowers of most Lecythidaceae are large and showy, produced at high densities per tree but only available for pollination for approximately one day. The androecia are conspicuous, some with exposed staminal rings and, in the more derived species, fleshy

hoods and coils (Tsou & Mori 2007). Staminal rings are comprised of densely packed stamens that produce large volumes of pollen (Mori & Prance 2006 onward). The flowering brevity of Lecythidaceae, coupled with the evolution of complex androecial morphologies, are related to the specialization of Lecythidaceae pollinators noted within the family (Table 1).

After the initial flowering burst, successfully pollinated ovules will begin to develop, whereas the androecia and petals immediately detach and drop to the forest floor. The broad petals separate and are often displaced by wind. The denser androecia, however, typically remain intact and accumulate under the tree from which they are released (Mori & Prance 2006 onward). This large volume of floral matter carpets the forest floor and provides a potential feeding ground for numerous insects **(**Feinstein *et al.* 2007).

Field Collections:

For this study, I focused on three species of Lecythidaceae: *Corythophora amapaensis* Pires ex S. A. Mori & Prance, *Couratari stellata* A. C. Smith and *Lecythis poiteaui* O. Berg (Fig. 1; subsequently abbreviated CA, CS, and LP, respectively). Collections were made by Alec Baxt during peak flowering times (September 2007, dry season, to January 2008, rainy season), from previously identified and vouchered trees (Berkov & Tavakilian 1999) (Table 1). Freshly fallen androecia and dead, intact, unsorted leaves were collected from underneath the study trees. Intact buds were collected directly

from tree canopies to determine whether nutrients were retranslocated prior to flower abscission. All samples were carefully inspected for signs of perturbation or decay and then briefly dipped in 70 percent EtOH prior to drying (using solar, silica, or oven dehydration).

In addition, floral longevity observations were recorded for CA androecia over a 10-day period. Ten CA androecia were collected as the species came into flower, half of which were placed under the tree (protected), half in the open (exposed). Flower longevity observations were considered indirect and informal assessments of tissue durability.

Tissue Analyses

Percent moistures were calculated as [(W-D/W) x 100], for which W represents the total wet weight recorded when samples were collected and D represents the total dry weight recorded when samples were fully dehydrated (Trautman & Richard 1996). Due to equipment failure, W for samples collected from CA-Q and CA-O (suffixes indicate individual tree, Table 1) were not measured on site. These samples were rehydrated in the lab. To determine a standard rehydration time, samples with known W were boiled for 15, 20, or 25 minutes, then cooled between two moist paper towels. These materials were then weighed to determine the difference between field W and rehydration W. Twenty-five minutes was determined to be an adequate rehydration time. The CA-Q and CA-O samples were subsequently boiled for 25 minutes and weighed.

Analyses of fiber, sugar and nutrient contents were performed at Ward Agricultural Testing Laboratories in Kearney, Nebraska. Acid detergent tests were performed to determine the proportion of undigestible cell components (fiber). An acidic detergent solution dissolves the soluble components of the cell wall and indicates the proportion of remaining undigestible material – cellulose, lignin and heat-damaged proteins. Larger values indicate reduced digestibility (Schroeder 1994).

To determine the amount of free sugars present in the samples, total invert sugar was measured. Invert sugars (glucose and fructose) result from the the hydrolysis of sucrose. Often, the more free sugars present in the material, the sweeter the taste.

Macronutrients ($\geq$ 100 mg kg^{-1}) evaluated in this study included carbon, nitrogen, potassium, phosphorus, calcium, magnesium, and sulfur. Micronutrients ($\leq$ 100 mg kg^{-1}) included zinc, iron, manganese, and copper (Raven *et al.* 2005). Macro and micronutrients are, by definition, present in quantities that differ by orders of magnitude. To adjust for this, all macronutrient percentage data and all micronutrient parts per million (ppm) data were converted to mg g^{-1} before proceeding with statistical analyses.

Insect Trapping

When the study trees were in flower, four 1-m^2 plots were established beneath each tree; two plots were covered with leaf litter and two with floral litter. Floral litter plots contained species-specific androecia. Leaf litter plots contained leaves that were not necessarily derived from the specific study trees.

A clear plastic pan trap was placed within the center of each plot, and a hanging trap (baited appropriately with floral or leaf litter) was secured 1 m above each plot. Pan traps contained one inch of water with a few drops of liquid detergent, added to break the surface tension. Traps were visited and emptied daily for a period of three days. Insects were identified per Imes (1992) and Marshall (2006) to the level of order under a stereoscopic microscopic (Nikon model SMZ645). I do not make assumptions about the feeding guilds of insects collected in the traps, but consider them *floral-foraging* (collected from floral traps) or *leaf-foraging* (collected from leaf traps).

Data Analyses

I used JMP Version 5.0.1.2 to perform ANOVAs and Student's *t*-tests, and Minitab Release 15 for Principal Components Analysis (PCA).

Tissue Analyses

Because I had two types of floral tissue (bud and androecia), I first used a Student's *t*-test to identify any significant difference between bud and androecial moisture, fiber, sugar and nutrient contents. When there were no significant differences, bud and androecial data were pooled as "floral tissue," and a second *t*-test analyzed floral tissue vs. leaves. When there were significant differences between bud and androecial samples, an ANOVA was used to analyze differences among androecia, buds and leaves.

I also made interspecific comparisons between two species of flowers (CA and LP, CS was represented by a single sample) to determine if the different species had

different nutrient contents. Interspecific leaf comparisons were not made because leaf samples did not necessarily represent material from the individual study trees.

To identify and visualize general trends within leaf and floral data, I included all significantly different nutrient data in a PCA, a multivariate technique that reduces the dimensionality of the data and highlights patterns. However, PCA requires a normal and unbounded data set (Sokal & Rohlf 1995). My data were proportional, with a minimum value of zero and maximum value of one. As the proportion of one variable increased, the proportion of one or more other variables necessarily decreased. According to Sokal and Rohlf (1995), proportional data can be normalized by using the angular transformation $\arcsin(p^{1/2})$. Therefore, all data were angularly transformed prior to the PCA.

The analysis included both macro and micronutrient variables, and values were distributed over a broad scale. To standardize values and reduce the spread of the data, a correlation matrix was used for the PCA. Absolute values of elements of the unit eigenvector within the correlation matrix represent the weighted contribution of each variable to each principal component. Positive and negative values indicate the directionality along the axes. I report eigenvectors and a score plot for the first two principal components.

Insect Trapping

The data for pan and hanging traps were pooled for analysis. Student's *t*-tests were used to identify differences in leaf and floral trap yields. An ANOVA was used to identify any differences in trap yield among flowers from the three study species of Lecythidaceae.

RESULTS

Floral Durability

Protected and unprotected treatments of CA androecia led to stark differences in appearance (Fig. 2). Due to an unusually rainy dry-season, CA flowers placed in the sun, removed from the protection of the overhead branches, were observed to be swollen from rain and discolored**.** Flowers in the shade, protected from the elements by canopy branches, were notably less swollen and still retained their original coloration. After ten days, exposed flowers had completely lost their original shapes. Flowers under the canopy, on the other hand, retained their shape and became dry and brittle**.** Very little mold was noted on these flowers, and insect activity was minimal.

Tissue Analyses

Percent moisture differed across the three tissue types ($F=54.03_{2, 10}$, $P < 0.0001$), but not interspecifically ($P = 0.68$). Leaves differed most notably, with a percent moisture approximately half that of androecia (means ± SE: leaves 44.2 ± 6.2, androecia 85.4 ± 0.7, buds 72.7 ± 3.6) (Fig. 3). For all other tissue analyses, bud and androecia samples

did not differ significantly (all $P > 0.05$) and differences are reported as leaf vs. "floral tissue" (androecia and bud, collectively).

Leaf tissue contained significantly more fiber, calcium, magnesium, iron and manganese than floral tissue (fiber: $t = -11.01$, df =18, $P < 0.0001$; Ca: $t = -11.1$, df = 18, $P < 0.0001$; Mg: $t = -3.5$, df = 18, $P = 0.003$; Fe: $t = -3.336$, df = 18, $P = 0.004$; Mn: $t = -11.165$, df = 18, $P < 0.0001$) (Table 2, Fig. 4).

Sugar, nitrogen, phosphorus, potassium, sulfur and zinc were all found at significantly higher levels in floral tissue samples (Sugar: $t = 3.3$, df = 14, $P = 0.005$; N: $t = 4.01$, df = 18, $P = 0.0008$; P: $t = 11.6$, df = 18, $P < 0.0001$; K: $t = 16.9$, df = 18, $P < 0.0001$; S: $t = 2.4$, df = 18, $P = 0.03$; Zn: $t = 3.3$, df = 13.8, $P = 0.005$) (Table 2, Fig.4). There were no significant differences between floral and leaf carbon or copper levels.

Corythophora amapaensis samples contained significantly more fiber, calcium, magnesium and manganese (fiber: $t = 7.07$, df = 8, $P < 0.0001$; Ca: $t = 4.19$, df = 5, $P = 0.01$; Mg: $t = 3.9$, df = 9, $P = 0.004$; Mn: $t = 3.7$, df = 4, $P = 0.02$) than LP. *Lecythis poiteaui* samples contained significantly more sugar, nitrogen, phosphorus, potassium and sulfur (Sugar: N: $t = -8.2$, df = 11, $P < 0.0001$; P: $t = -9.4$, df = 10, $P < 0.0001$; K: $t = -3.3$, df = 7, $P = 0.01$; and S: $t = -6.8$, df = 11, $P < 0.0001$) (Table 2, Fig. 4). There were no significant interspecific differences in carbon, copper, iron, or zinc (all $P > 0.05$)

PCA

Principal Component 1 accounted for 64.5 percent of the variability in the data. Floral and leaf tissue were separated along this axis (Table 3). Principal Component 2 accounted for 10.8 percent of the variability in the data. Both axes contributed to separating the three species of flowers into distinct clusters (Table 3, Fig. 4).

Insect Trapping

Flower traps yielded a mean (± SE) of 11.6 (± 2.2) insects, significantly more than the leaf traps (4.8 ± 1.3) (t = 2.7, df = 24.5, P = 0.01). The dominant orders collected were Coleoptera and Hymenoptera (mostly ants). Ratios among orders were similar for leaf and flower traps, except that Diptera were almost never recovered from leaf traps. Among the floral traps, CA (12.6 ± 2.4) and CS (12.8 ± 3.7) were sometimes more productive than LP (6.8 ± 3.7), though these yields were not significantly different ($F = 2.8_{2, 21,}$ P = 0.08).

DISCUSSION

Not All Plant Parts Are Created Equal

The Principal Component Analysis shows a clear separation along Principal Component 1 into two distinct and disparate groups: leaves and flowers. The variables contributing most to this separation were the higher levels of fiber, calcium and manganese in leaves (all with negative eigenvectors) versus the higher levels of sugar, phosphate, potassium, nitrogen and sulfur in flowers (all with positive eigenvectors)

(Table 3, Fig. 4). Within the flower cluster, data points were separated along both components, further teasing apart C*ouratari stellata*, *Corythophora amapaensis* and *Lecythis poiteaui* samples. The variables contributing most to the separation along PC2 were sulfur and fiber (both with negative eigenvectors) versus zinc (positive eigenvector). This indicates that there is a quantitative difference in the nutritional content between leaves and flowers as well as among the three species of flowers.

Floral Tissue as a Richer Foodstuff

Floral litter seems to offer a quantitatively richer food source than leaf litter, containing more free sugars and macronutrients (N, P, K and S). Nitrogen and sugar may be enriched within floral tissue due to the nitrogen in protein-rich pollen and the sugars in nectar. However, these nutrients also represent an essential metabolic cohort, and efficient cycling of this cohort is crucial to a plant's longevity. However, nutrients may be disproportionately withdrawn and recycled from various plant tissues during the process of retranslocation (Kadir & Van Cleemput 1995).

As senescence initiates in mature leaves, nutrients are retracted for breakdown, redistribution and reuse (Wooley *et al.* 1958). Leaves successfully retranslocate approximately 50 percent of N and P, and 25-40 percent of K (Villela & Proctor 1999), though the efficiency of retranslocation fluctuates with annual rainfall and soil quality (Nadkarni & Matelson 1992, Ochieng & Erftemeijer 2001).

Nutrients are retranslocated from the flowers of certain species (Bieleski 1995), but the process is usually less efficient. In Magg's (1985) study of litter fall and retranslocation, abscised flowers represented less than 15 percent of the total litter biomass collected, but accounted for up to 57 percent of the total nutrients available. Bloom et al. (1985) relate flower production and nutrient retranslocation to economic theory and speculate that, in many species, floral tissue is so ephemeral that retranslocation would be too costly (Bloom *et al.* 1985). Producing pollinator-attractive reproductive organs is a high-risk investment: it often drains nutrient reserves. However, the potential benefit of producing nutrient-rich flowers, fruits and seeds outweighs the cost, so long as the tissues are sustained for only short durations. It is more cost-efficient, then, to abscise flowers quickly after pollination (Bloom 1985, Hocking 1981).

Though the nutrient content of leaves is lower than that of floral tissue, leaf tissue is not completely barren of nutrients, and does offer significantly higher levels of calcium magnesium, iron and manganese. All of these have direct photosynthetic associations, which may well account for their elevated levels in leaves.

Moisture, though not formally recognized as a nutrient, may play a significant role in insect foraging strategy. Moisture can be a limiting resource, even in a rainforest, particularly during the dry season (when most Lecythidaceae are in flower). My results indicate that androecia offer nearly twice the percent moisture of leaves (84.4% androecia, 72.6% bud, 44.2% leaf). The difference between bud and androecia probably reflects vacuole expansion in the androecia. These values fell within other published moisture

content ranges: leaf litter 39-62 percent (Taylor 1998), floral tissue 84-89 percent (Dahiya 2002, Westgate & Grant 1998) and buds 53-81 percent (Kindu *et al.* 2008).

Floral Tissue as an "Easy Meal"

Not only does senescent floral tissue offer an abundance of nutrients, but these nutrients appear to be more readily accessible than those in leaf tissue. Leaves contained more than twice as much undigestible fiber as flowers. This is most likely due to the lignin-reinforcement of supportive sclerenchyma tissue (Buxton & Redfearn 1997, Facelli & Pickett 1991). Calcium, too, was found at levels more than double those of floral tissue. The accumulation of calcium in mature leaves is thought to play a role in the initiation of leaf senescence (Chou & Kao 1992), and retranslocation of calcium from leaves is minimal (Fife *et al.* 2008, Saur *et al.* 2000). The increased levels of calcium, coupled with the higher proportion of undigestible fibers, restrict access to leaf nutrients and would require foraging insects to invest more mechanical energy for a lower nutrient return.

Assuming that a more fibrous feeding substrate requires more mandibular work, insects may be operating under optimal foraging strategy, preferentially foraging amongst litter that will provide the largest output of nutrients at the lowest energy expenditure. Many insects are known to be able to discriminate between food sources and alter behavior accordingly (Charnov 1976, Goulson 1999, Waldbauer & Friedman 1991). Smallegange *et al.* (2007) observed *Pieris brassicae,* a folivorous caterpillar, migrating up

branches to preferentially feed on available flower buds. Caterpillars that fed on flowers experienced significantly faster growth rates than those that fed on leaves. Floral litter traps also yielded predatory arthropods, perhaps due to the increased likelihood of finding prey in floral piles. Floral litter is both conspicuous and aromatic, qualities that may influence an insect's foraging decision (Bernays 2001).

Interspecific Floral Comparisons

Although the nutrient differences between flowers and leaves were consistent with my expectations, the intraspecific differences in flowers were not. Though *Couratari stellata* was only represented by a single sample, and was not included in the ANOVA, it did separate from the other flower samples along both axes in the PCA (Table 3, Fig. 4).

The *C. stellata* flower had the highest level of nitrogen, but was moderately low in free sugars (Table 2). This was surprising because, of the three species analyzed, it is the only one that rewards its bee pollinators with nectar, and has a corresponding reduction in stamens (and presumably in pollen) (Knudsen & Mori 1996). Equally surprising was the particularly high sulfur level in *C. stellata,* even though *Lecythis poiteaui* flowers emit a strong sulfurous odor. This is an uncommon property noted almost exclusively in bat-pollinated flowers (Feinstein *et al.* 2008). Knudsen & Mori (1996) did not detect any sulfur compounds in *C. stellata* floral volatiles; *C. stellata* wood, however, is rich in sulfur compounds (Berkov et al. 2000), and the flowers develop a fetid aroma as they senesce (A. Berkov pers. obs). Feinstein *et al*. (2008) even reared a couple stratiomyid flies,

which are primarily associated with flowers from *L. poiteaui,* from *C. stellata* flowers. As insects often locate food through aromas in upwind drafts (Bernays 2001), these flies may have been attracted to *C. stellata* by its sulfurous notes associated with floral senescence.

Bat-pollinated *L. poiteaui* flowers were also high in nutrients, offering a rich source of sugar, nitrogen, phosphorus and potassium (Table 2). While *L. poiteaui* flowers were relatively nutrient-rich, they were lowest in fiber (Table 2), which contributed to their intermediate position along the second PCA axis (Table 3, Fig. 4). This reduction in fiber probably contributes to the alacrity with which *L. poiteaui* androecia decay. While *Corythophora amapaensis* androecia retained their shapes for 10 days (Fig. 2), *Lecythis poiteaui* androecia rapidly deteriorate into a viscous deposit within just one or two days (Feinstein *et al*. 2008).

Relative to the other species in this study, *C. amapaensis* flowers might be considered "leaf-like." They produce a weak aroma dominated by green leaf volatiles, and, rather than nectar, offer fodder pollen as a reward to pollinators (Knudsen & Mori 1996). The androecia are comparatively small, and due to their color they do not stand out as distinctly from the leaf litter (at least to a human, A. Berkov, pers. obs.). They group with other flowers along the first axis of the PCA (Fig. 4), but are closer to leaves because they are moderately high in fiber, calcium and magnesium (Table 2). They are also relatively low in nitrogen and sulfur, but high in zinc, which distinguishes *C. amapensis* from other flowers along PC2. Floral fiber content may be related to androecial morphology, with higher content in *C. amapaensis*, in which the androecial

hood is closely appressed, and *C. stellata*, in which the androecium forms a complex coil (Fig. 1).

Due to their comparatively nutritious flowers, I expected *L. poiteaui* and *C. stellata* to have higher trap yields than *C. amapaensis*, but in this study *L. poiteaui* flower-trap yields were consistently low, while some traps from the other two species occasionally had high yields. This was not consistent with rearing data (Feinstein *et al.* 2008) or anecdotal observations (A. Berkov pers. obs.) suggesting that, relative to *C. amapaensis*, *C. stellata* androecia should be a preferred substrate. Trap yields may have been influenced by flowering phenology and seasonal changes in insect activity (Coley & Barone 1996). *Corythophora amapaensis* blooms during the early part of the dry season and *C. stellata* during the late dry season (Coley & Barone 1996). In this experiment, *C. stellata* traps were set when trees had passed their flowering peak, and this may have affected trap yield.

Lecythis poiteaui trap yields may have been depressed because the foul-smelling floral volatiles that attract bats and flies might actually deter other insects. Additionally, the rapid disintegration of senescing flowers could present adverse conditions for both oviposition and foraging. Feinstein *et al.* (2008) found that drosophilids were able to complete their rapid life cycles and emerge in abundance, while immature stratiomyids were conspicuous due to their large size, but seldom survived to the adulthood.

Implications and Future Analyses

Senescent flowers were, as predicted, more nutritious and more easily digestible than dead leaves, but the flowers analyzed were heterogeneous, and nutrient levels did not conform with the expectations that one might have based on floral volatiles, pollination syndromes, or trap yield. It appears insects are preferentially foraging in the more energy-rich substrate available at lower energy costs, though I can not with certainty conclude that the increased insect prevalence is due strictly to nutrient content and resource availability. Aromatic attraction, for instance, may have influenced insect foraging. To determine if intrinsic characteristics of flowers do in fact regulate communities of foraging insects, I would need to include more plant species, greater replication within plant species and, if traps are employed, more trap replication. Gut analyses of trapped insects could be conducted in order to definitively conclude that insects are preferentially feeding as opposed to seeking out shelter or laying eggs (Feinstein *et al.* 2007).

While Feinstein *et al.* (2007) reared a range of phytophagous insects from Lecythidaceae flowers, including Coleoptera, Diptera, Hymenoptera, Lepidoptera and Thysanoptera, the insects collected in this study were not representative of these earlier rearing studies, indicating that oviposition is certainly not the only motivation behind the floral foraging. I conclude that the increased insect activity observed among forest-floor flower falls is due to the nutrients that fallen flowers readily make available (perhaps advertised by aroma and color) and that foraging is the driving force behind my observations.

Though the overall nutrient content of Lecythidaceae floral litter was significantly higher than the nutrient content of leaf litter, in the broad scheme of things, this difference is relatively small. Mattson (1980) compares the nitrogen content of various plant tissues, including angiosperm leaf litter, for which nitrogen content ranged from 0.5 to 3 percent. Both the leaf and floral litter investigated in this study fall within this range, suggesting that, though differences in foodstuff may be subtle, they can have significant impacts on a delicately balanced ecosystem.

ACKNOWLEDGEMENTS

I would like to acknowledge the National Science Foundation (NSF Rig:0542276) and PSC-CUNY (PSC-REG-37-1065) for the funding that made this project possible. I would also like to acknowledge the people who graciously contributed, either directly or indirectly, by offering guidance and support. First, Dr. Amy Berkov, for her continued support and direction as my mentor. Also, Alec Baxt for his intensive field work and sample collections that were used for the analyses in this study; Dr. Scott Mori for vouchering collected samples; my committee members, Dr. Robert P. Anderson and Dr. Jane Gallagher, for their valuable feedback and guidance, and all the CCNY students and faculty who have helped me along the way with my endeavors in biology.

LITERATURE CITED

Baldwin, I. T. & Preston, C. A. 1998. The eco-physiological complexity of plant responses to insect herbivores. *Planta* 208:137-145.

Bennett, R. N. & Wallsgrove, R. M. 1994. Secondary metabolites in plant defence mechanisms. *New Phytologist* 127:617-633.

Berkov A. & Tavakilian G. 1999. Host utilization of the Brazil nut family (Lecythidaceae) by sympatric wood-boring species of *Palame* (Coleoptera, Cerambycidae, Lamiinae, Acanthocinini). *Biological Journal of the Linnean Society* 67:181-198.

Berkov A., Meurer-Grimes B. & Purzycki K. 2000. Do Lecythidaceae specialists (Coleoptera: Cerambycidae) shun fetid tree species? *Biotropica* 32:440-551.

Bernays, E. A. 2001. Neural limitations in phytophagous insects: implications for diet breadth and evolution of host affiliation. *Annual Review of Entomology* 46:703-727.

Bieleski, R. 1995. Onset of phloem export from senescent petals of daylily. *Plant Physiology* 109:557-565.

Bloom, A. J., Chapman, S., III & Mooney, H. A. 1985. Resource limitations in plants--an economic analogy. *Annual Review of Ecology and Systematics* 16:363-392.

Borror, D., Joyce, C. A. Triplehorn and Norman F. Johnson. 1989. *Introduction to the Study of Insects* (6th edition). Saunders College Publishing, Philadelphia. 800 pp.

Buxton, D.R. & Redfearn, D. D. 1997. Plant limitations to fiber digestion and utilization. *The Journal of Nutrition* 127:814S-818S.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9:129-136.

Chou, C. M. & Huei, K.C. 1992. Methyl jasmonate, calcium, and leaf senescence in rice. *Plant Physiology 99:1693-1694*

Coley, P. D. & Barone, J. A. 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27:305-335.

Dadd, R. H. 1970. Relationship between filtering activity and ingestion of solids by larvae of the mosquito *Culex pipiens*: a method for assessing phagostimulant factors. *Journal of Medical Entomology* 7:708-712

Dahiya, D. S., Unnikrishnan, D., Gupta, A. K., Sehrawat, S.K. & Siddiqui, S. 2003. Dehydration of annual chrysanthemum (*C. coronarium*). *Acta Horticulturae* (ISHS) 620:359-362

Facelli, J. M. & Pickett, S. T. A. 1991. Plant litter: its dynamics and effects on plant community structure. *The Botanical Review* 57:1-32.

Faegri, K. & Van der Pijl, L. 1979. *The principles of pollination ecology* (3rd edition). Pergamon Press, New York. 242 pp.

Feinstein, J., Mori, S. A. & Berkov, A. 2007. Saproflorivory: a diverse insect community in fallen flowers of Lecythidaceae in French Guiana. *Biotropica* 39:549-554.

Feinstein J., Purzycki, K. L., Mori, S. A., Hequet, V. & Berkov, A. 2008. Neotropical soldier flies (*Stratiomyidae*) reared from *Lecythis poiteaui* in French Guiana: Do bat-pollinated flowers attract saprophiles? *Journal of the Torrey Botanical Society* 135:200-207.

Fife, D. N., Nambiar, E. K., & Saur, E. 2008. Retranslocation of foliar nutrients in evergreen tree species planted in a Mediterranean environment. *Tree Physiology* 28:187-196.

Goulson, D. 1999. Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution. *Perspectives in Plant Ecology, Evolution, and Systematics* 2:185-209.

Hanley, M. E., Lamont, B. B., Fairbanks, M. M. & Rafferty, C. M. 2007. Plant structural traits and their role in anti-herbivore defence. *Perspectives in Plant Ecology, Evolution and Systematics* 8:157-178.

Herms, D. A. & Mattson, W. J. 1992. The dilemma of plants: to grow or defend. *The Quarterly Review of Biology* 67:283-335.

Hew, C. S. & Yip, K. C. 1987. Respiratory metabolism in isolated orchid petal cells. *New Phytologist* 105:605-612.

Hew, C. S. & Yip, K. C. 1991. Respiration of orchid flower mitochondria. *Botanical Gazette* 152:289-295.

Hochuli, D. F. 1996. The ecology of plant/insect interactions: Implications of digestive strategy for feeding by phytophagous insects. *Oikos* 75:133-141.

Hochuli, D. F. 2001. Insect herbivory and ontogeny: How do growth and development influence feeding behaviour, morphology and host use? *Austral Ecology* 26:563-570.

Hocking, P. J. 1982. Accumulation and distribution of nutrients in fruits of castor bean (*Ricinus communis L.*). *Annals of Botany* 49:51-62.

House, H. L. Effects of different proportions of nutrients on insects. *Entomology Experiments and Applications* 12:651-669.

Imes, R. 1992. *The Practical Entomologist.* Fireside Publishing, New York. 160 pp.

Kadir, W. R. & Van Cleemput, O. 1995. Nutrient retranslocation during the early growth of two exotic plantation species. *Proceedings of the International Congress on Soils of Tropical Forest Ecosystems* 6:96-101.

Kindu, M., Glatzel, G., Sieghardt, M., Birhane, K., & Taye, B. 2008. Chemical composition of the green biomass of indigenous trees and shrubs in the highlands of central Ethiopia: Implications for soil fertility management. *Journal of Tropical Forest Science* 20:167-174.

Maggs, J. 1985. Litter fall and retranslocation of nutrients in a refertilized and prescribed burned *Pinus ellottii* plantation. *Forest Ecology and Management* 12:253-268.

Mattson, W. J. Jr. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* 11:119-161.

Molano-Flores, B. 2001. Herbivory and calcium concentrations affect calcium oxalate crystal formation in leaves of *Sida* (Malvaceae). *Annals of Botany* 88:387-391.

Mori, S. A. & Prance, G. T. 2006 onward, accessed 2010. *The Lecythidaceae Pages* (http://sweetgum.nybg.org/lp/index.html). The New York Botanical Garden, Bronx, New York.

Nadkarni, N. M. & Ferrell-Ingram, K. 1992. Biomass and nutrient dynamics of fine litter of terrestrially rooted material in a neotropical montane forest, Costa Rica. *Biotropica* 24:113-120.

Noriega, J. A. A. & Calle, C. J. 2008. Consumption of *Gustavia hexapetala* (Aublet) Smith (Lecythidales: Lecythidaceae) by the dung beetle *Eurysternus plebejus* Harold (Coleoptera: Scarabaeidae). *The Coleopteris Bulletin* 62:455-460.

Ochieng, C. A. & Erftemeijer, P. L. 2002. Phenology, litterfall and nutrient resporption in *Avicennia marina* (Forssk.) Vierh in Gazi Bay, Kenya. *Trees - Structure and Function* 16:167-171.

Primack, R. B. Longevity of individual flowers. 1985. *Annual Review of Ecology and Systematics* 16:15-37.

Prychid, C. & Rudall, P. 1999. Calcium oxalate crystals in monocotlydons: a review of their structure and systematics. *Annals of Botany* 84:725-739.

Raven, P. R., Evert, R. & Eichhorn, S. E. 2005. *The Biology of Plants* (7th ed.). New York, W. H. Freeman. 686 pp.

Reid, M. S. & Wu, M. J. 1992. Ethylene and flower senescence. *Plant Growth Regulation* 11:37-43.

Robbins, R. K., Aiello, A., Feinstein, J., Berkov, A., Caldas, A., Busby, R. C. & Duarte, M. 2010. A tale of two species: detritivory, parapatry, and sexual dimorphism in *Lamprospilus collucia* and *L. orcidia* (Lycaenidae: Theclinae: Eumaeini). *Journal of Research on the Lepidoptera* 42:64-73.

Saur, E., Nambiar, E. K. & Fife, D. N. 2000. Foliar nutrient retranslocation in *Eucalyptus globulus. Tree Physiology* 20:1105-1112.

Schroeder, J. W. 1994, accessed 2010. Interpreting Forage Analysis (http://www.ag.ndsu.edu/pubs/plantsci/hay/r1080w.htm) AS-1080 North Dakota State University, Fargo, North Dakota.

Scriber, J. M. & Slanksy, F. Jr. 1981. The nutritional ecology of immature insects. *Annual Review of Entomology* 26:183-211.

Sokal, R. R. & Rohlf, F. J. *Biometry* (3rd edition). W. H. Freeman and Company, New York. 887 pp.

Sotelo, A., Lopez-Garcia, S. & Basurto-Pena, F. 2007. Content of nutrient and antinutrient in edible flowers of wild plants in Mexico. *Plant Foods and Human Nutrition* 62:133-138.

Steege, H. ter, Pitman, N. C. A., Phillips, O. L., Chave, J., Sabatier, D., Duque, A., Molino, J. F., Prevost, M. F., Spichiger, R., Castellanos, H., von Hildebrand, P. & Vasquez, R. 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* 443:444-447.

Trautmann, N. & Richard, T. 1996, accessed 2009. Moisture Content. (http://cwmi.css.cornell.edu/resources.htm) Cornell Waste Management Institute, Cornell University, Ithaca, New York.

Tsou, C. H. & Mori, S. A. 2007. Floral organogenesis and floral evolution of the Lecythidoideae. *American Journal of Botany* 94:716-736.

Villela, D. M. & Proctor, J. 1999. Litterfall mass, chemistry, and nutrient retranslocation in a monodominant forest on Maraca Island, Roraima, Brazil. *Biotropica* 31:198-211.

Waldbauer, G. P. & Friedman, S. 1991. Self-selection of optimal diets by insects. *Annual Review of Entomology* 36:43-63.

Ward, D., Spiegel, M. & Saltz, D. 1997. Gazelle herbivory and interpopulation differences in calcium oxalate content of leaves of a desert lily. *Journal of Chemical Ecology* 23:333-346.

Westgate, M. E. & Thomson-Grant, D. L. Water deficits and reproduction in maize. *Plant Physiology* 91:862-867.

Wink, M. 1987. Plant breeding: importance of plant secondary metabolites for protection against pathogens and herbivores. *TAG Theoretical and Applied Genetics* 75:225-233.

Woolley, J. T., Broyer, T. C. & Johnson, G. V. 1958. Movement of chlorine within plants. *Plant Physiology* 33:1-7.

Zudaire, E., Simpon, S. & Montuenga, L. 1998. Effects of food nutrient content, insect age and stage in the feeding cycle on the FMRFamide immunoreactivity of diffuse endocrine cells in the locust gut. *The Journal of Experimental Biology* 201:2971-2979.

TABLES

Table 1. Study species of Lecythidaceae.

Spp.[1]	Tree, Voucher[2]	Collection Dates	Floral Characteristics[3]: color, aroma, diameter, # stamen (mean)	Pollinator
CA	Q, M24147 O, M24145	Sept - Oct 2007	Pink - dark red/purple, sweet, 4cm, 200	bee
CS		Nov 2007	White - pale yellow, sweet, 4cm, 45	bee
LP	T, M24175 U, M24176	Jan 2008	White - pale green, sulfurous, 11cm, 1000	bat

[1] CA=*Corythophora amapaensis,* CS=*Couratari stellata*, LP=*Lecythis poiteaui*.
[2] Unique letter codes are followed by voucher numbers collected by S. A. Mori and deposited at New York Botanical Garden and CAY. CS samples were collected from several unvouchered trees; flower identity was confirmed by S. A. Mori.
[3] Floral characteristics and pollinators are from Mori & Prance (2006 onwards).

Table 2. Fiber, sugar and nutrient content of floral and leaf tissue (mean ± SE).

	Floral				Leaf	
	CA	CS[1]	LP	Collective[2]		P value[3]
Fiber mg g^{-1}	335.8 ± 19.3[a]	325	158.0 ± 15.2[b]	233.4 ± 26.4	693.0 ± 35.9	<0.0001
Sugar mg g^{-1}	43.2 ± 9.5[a]	17.2	57.5 ± 7.5[b]	49.5 ± 6.1	2.6 ± 0.2	<0.0001
Macronutrients mg g^{-1}						
C	458.3 ± 3.5[a]	ND	465.5 ± 2.5[a]	463.1 ± 4.3	449.3 ± 14.6	NS
N	15.5 ± 0.7[a]	22.2	21.8 ± 0.5[b]	19.6 ± 0.8	15.2 ± 0.6	0.0008
P	1.2 ± 0.06[a]	1.5	1.9 ± 0.05[b]	1.6 ± 0.08	0.41 ± 0.05	<0.0001
K	12.0 ± 0.8[a]	14.8	15.4 ± 0.6[b]	14.1 ± 0.5	2.4 ± 0.3	<0.0001
Ca	1.9 ± 0.1[a]	0.84	1.0 ± 0.1[b]	1.3 ± 0.1	7.8 ± 0.5	<0.0001
Mg	2.06 ± 0.08[a]	1.82	1.7 ± 0.07[b]	1.8 ± 0.1	2.6 ± 0.3	0.003
S	1.9 ± 0.07[a]	4.7	2.5 ± 0.06[b]	2.4 ± 0.2	1.9 ± 0.1	0.03
Micronutrients mg g^{-1}						
Fe	0.1 ± 0.04[a]	0.06	0.1 ± 0.03[a]	0.1 ± 0.06	0.5 ± 0.09	0.004
Zn	0.045 ± 0.008[a]	0.02	0.027 ± 0.006[a]	0.03 ± 0.004	0.015 ± 0.006	0.005
Mn	0.05 ± 0.006[a]	0.009	0.01 ± 0.005[b]	0.03 ± 0.02	0.4 ± 0.03	<0.0001
Cu	0.01 ± 0.0008[a]	0.01	0.01 ± 0.0006[a]	0.02 ± 0.004	0.03 ± 0.006	NS

[1] CS represented by a single sample; therefore only CA and LP were included in the interspecific analyses. ND indicates that no carbon data was obtained from the CS sample. When CA and LP floral materials are significantly different ($P < 0.05$), the data are labeled with different superscript letters.

[2] Includes pooled data from all species of bud and androecia samples

[3] Comparison between collective floral data and leaf data. NS indicates that there was no significant difference.

Table 3. Principal Component Analysis of nutrient content in leaves and flowers. Elements of the unit eigenvector are given for the first two principal components. Larger absolute values of the elements of the eigenvectors contribute greatest to the separation along each axis. Elements of the unit eigenvector and the percentage of variation among the specimens explained by each axis are also presented.

Variable	PC1	PC2
Fiber	- 0.302	- 0.351
Sugar	0.329	- 0.218
N	0.329	- 0.218
P	0.340	0.045
K	0.352	0.043
Ca	- 0.336	- 0.066
Mg	- 0.242	- 0.121
S	0.211	- 0.632
Zn	0.172	0.578
Fe	- 0.268	0.139
Mn	- 0.350	- 0.059
Cu	- 0.118	- 0.051
Eigenvalue	7.736	1.302
Variation Explained	64.50%	10.80%

FIGURES

Figure 1. Photographs of *Corythophora amapaensis* (CA), *Couratari stellata* (CS) (taken by C. A. Gracie), and *Lecythis poiteaui* (LP) (taken by S. A. Mori) flowers, respectively (Mori & Prance 2006 onward).

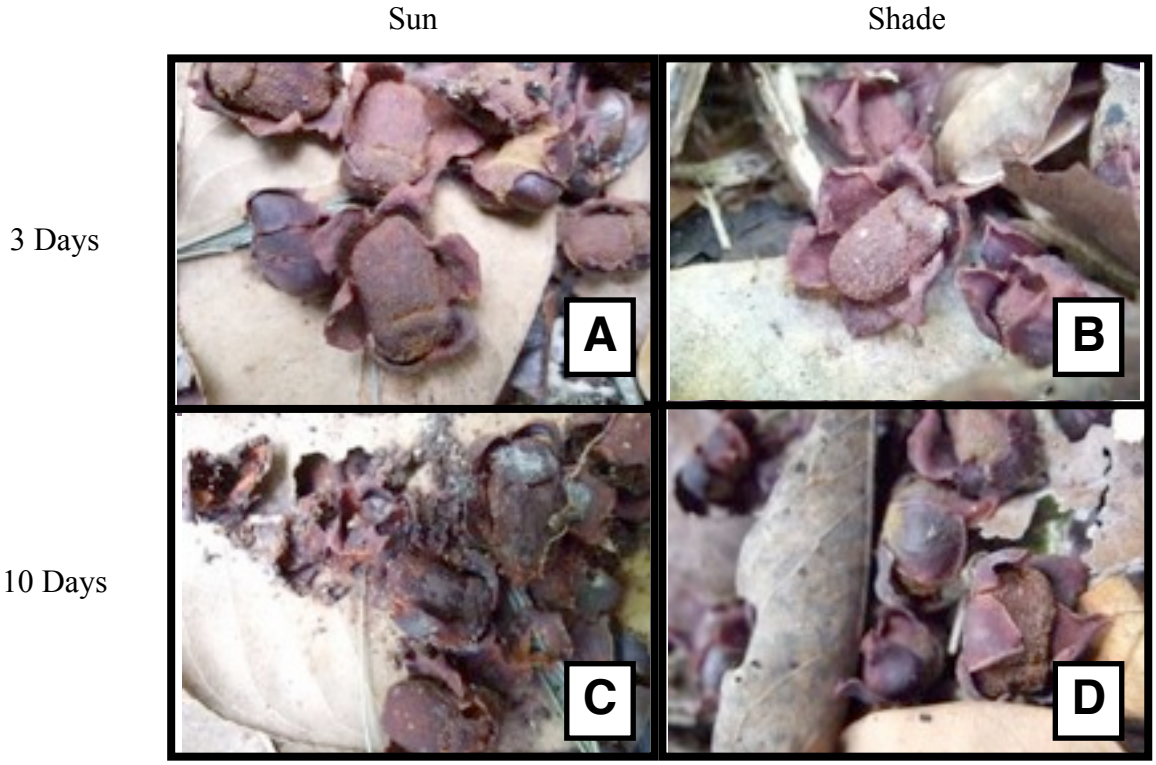

Figure 2. Floral decay of *Corythophora amapaensis* left in the sun (exposed) and shade (sheltered). Images were taken by Alec Baxt and show the effects of sun (A, B) and shade (C, D) treatments of androecia after three (A, C) and ten (B, D) days. Flowers left in the sun, unprotected from the rain, deteriorated quickly by comparison.

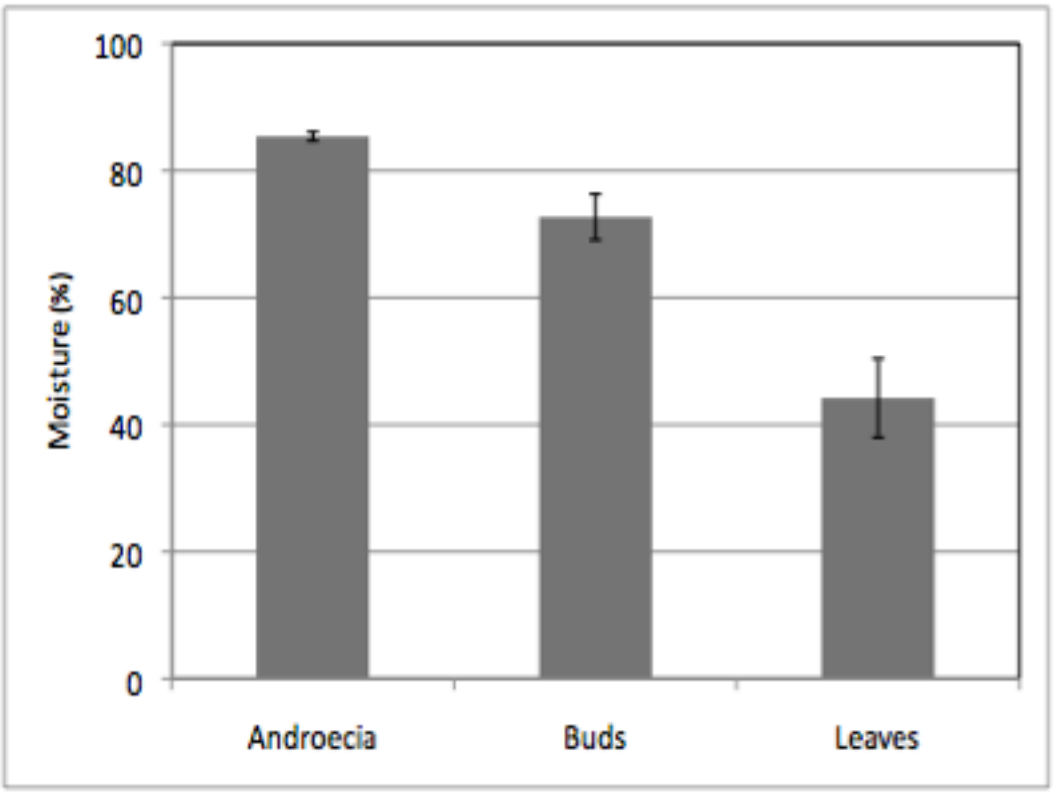

Figure 3. Mean moisture content of the plant tissues (% ± SE).

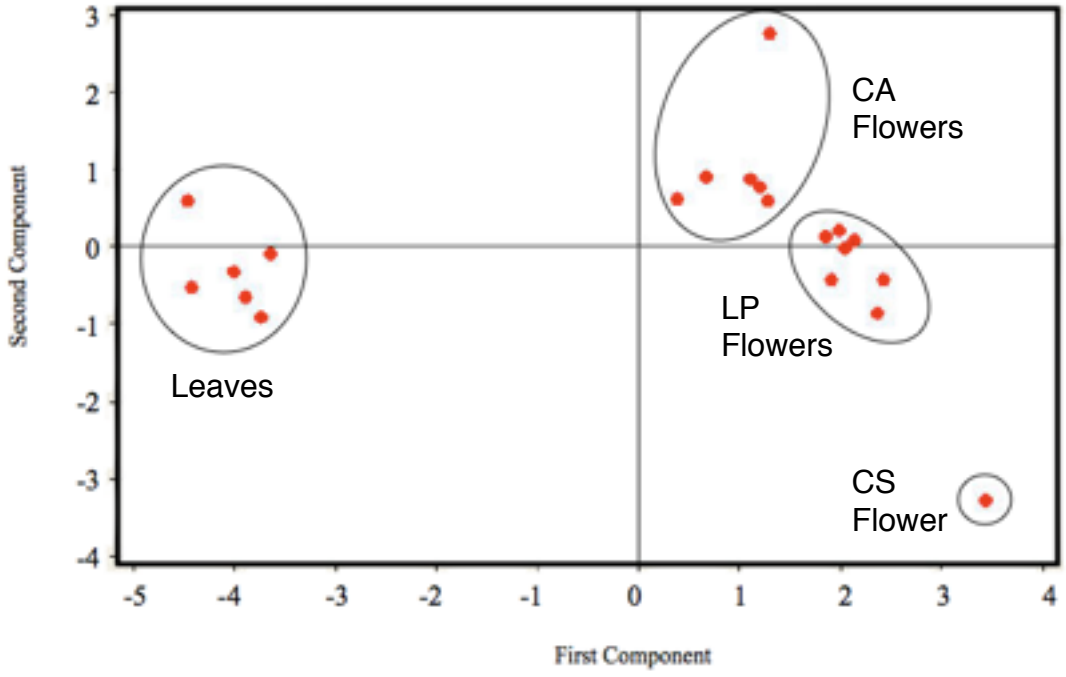

Figure 4. PCA of nutrient content of leaves and flowers from three species of Lecythidaceae. Ellipses indicate distinct clusters of like tissues, as labeled. The first and second components account for 75 percent of the variation within the data.