Phenology and Fate of Palm Fruits of two canopy palms: *Welfia regia* and *Euterpe precatoria*

Jean Lee

April 25th 2008

Masters project submitted in partial fulfillment of the
requirements for the Master of Environmental Management degree in the Nicholas School of the Environment and Earth Sciences of Duke University 2008

Table of Contents

Abstract

The CICLOS project, located at La Selva Biogical Research Station in Costa Rica, attempts to document the effects of ENSO on tree growth and builds upon past studies at La Selva, integrating studies of stand dynamics, forest carbon and nutrient cycling, and the hydrological cycle. This study adds a finer microscale understanding of the role of canopy palm fruits in the carbon cycle. The principal objective was to determine the fate of palm fruits (removal versus insect predation versus simple fruitfall) throughout the maturation process. Secondary objectives were to characterize the nutrient content of fruitfall associated with fruiting individuals and in two different overall fertility contexts and to describe fruitfall over time as related to methods used to estimate total crop size of immature and mature fruits. Sixteen canopy palms representing eight individuals each from two species—*Welfia regia* and *Euterpe precatoria*—were selected for phenological observations. During this time period, I quantified the fruitfall as well as categorized the condition of the fruits that fell from the trees, creating categories such as exocarp, mature, immature, partially eaten, aborted, or seed. Assuming fruit fell within a 1.5m radius from the bole, the total weight of fruitfall over the span of six weeks was 1682 g and 451g for *Welfia* and *Euterpe,* respectively. We found that on average 9.95 *Euterpe* fruits and 5.7 *Welfia* fruits fell per week per square meter. The mean crop size for *Euterpe* was 3208, with a mean maximum crop size of 6010. The mean crop size for *Welfia* was 1350, with a mean maximum crop size of 1936. We found that *Euterpe* fruitfall had higher proportions of aborted or immature fruit than *Welfia*. 25% of *Euterpe's* fruit and 10% of *Welfia's* fruit were partially open, indicating consumption of fruits as food resources. We estimated that on average 86% and 62% of the fruits were removed from *Euterpe* and *Welfia,* respectively. Our results showed that it was not possible to predict fruitfall from the estimated crop sizes. Analyses

of the effect of fertility levels show that phosphorus levels in soils positively affect *Euterpe* crop sizes. Our study demonstrates the greater need to understand the natural history of fruitfall as well as fruit removal of the system in order to better quantify and qualify the role of canopy palm fruits in the carbon cycle.

Introduction

Tropical ecosystems play a disproportionate role in the global carbon cycle (Wright 2005, Clark 2007, Clark 2001), and we are still unsure how changes in climate and atmospheric composition will affect the tropical forests (Clark 2007). We have not yet developed a concrete method to quantify the net primary production of tropical rainforests, since our understanding of the production at an ecosystem level is still limited (Clark 2001). In order to understand the carbon cycle in tropical forests, we have to understand the components of net primary productivity, including little known parameters such as belowground carbon storage and flux, and the contribution of reproductive materials such as fruits and flowers to the cycle (Clark 2001). Flowers, fruits, and fruiting parts consist mostly of carbon and nitrogen, and understanding the phenology of these parts will help us better visualize how they might affect the carbon cycle across the landscape over time.

This study took place at La Selva Biological Research Station. La Selva is a tropical forest located in northern Costa Rica, which is dominated by tropical and premontane wet forest. It is located at the confluence of Sarapiqui and Puerto Viejo rivers and totals 1,536 ha in area. The annual rainfall is about 4200mm, and the dry season does not last for long periods of time. The soils at La Selva are primarily alluvial, but there is still a large fertility range. The Organization of Tropical Studies purchased La Selva in 1968, and it has functioned as a biological research station since that time (McDade, 1994).

There are hundreds of active research projects at La Selva (http://ots.duke.edu/en/laselva/projects/index.shtml), and this project is part of the multi-investigator, multi-disciplinary CICLOS project currently being conducted at the station. The

CICLOS project builds upon past studies at La Selva, integrating studies of stand dynamics, forest carbon and nutrient cycling, and hydrological cycles.

The CICLOS project, currently in its 3rd year, attempts to document the effects of El Nino Southern Oscillation (ENSO) on tropical tree growth (Clark et al, 2003). Researchers feed individual findings into a CENTURY ecosystem model to provide an estimate of the stand and ecosystem-level carbon budget, and an understanding of how carbon budgets may be affected by climate change (Prentice et al, 2001). By studying the complex variables involved in feedback mechanisms, the project will help paint a better picture of the constraints and feedback of various ecosystem processes in tropical rainforests.

One set of feedbacks mechanisms that is currently being studied is the relationship between palm reproductive phenology and litter invertebrates and their role in the carbon cycle. Phenology is the study of cyclical biological phenomena, and understanding the phenology of fruiting in the tropical rain forest is important not only from the perspective of resource availability for a wide array of fruit-eating vertebrates, but also in terms of understanding the plant's investment in reproductive parts and its relation to nutrient cycling. Work currently underway with palm phenology allows investigators to track the appearance and maturation of successive crops of fruits and flowers over time for the 6 species of palm that reach into the canopy, operationally defined as palms that grow larger than 10-cm DBH: *Astrocaryum alatum, Astrocaryum confertum, Iriartea deltoidea, Socratea exorrhiza,Euterpe precatoria,* and *Welfia regia*. It is estimated that each fruiting body on the palms—peduncle, fruiting branches, and fruits—may contain 3-4 kg of carbon. (Bynum, unpublished). However, at present, we have little understanding of phenology at finer time scales and of what happens to fruits and flowers after falling from the tree. My study seeks to address these gaps.

My principal objective was to determine the fate of palm fruits (removal versus insect predation versus simple fruitfall) throughout the maturation process at La Selva Biological Station. Secondary objectives were to characterize the nutrient content of fruitfall associated with fruiting individuals and in two different overall fertility contexts, as well as describe fruitfall over time as related to methods used to estimate total crop size of immature and mature fruits.

Currently, there is little knowledge on the fate of the fruits for these palms, and we do not know how fruits are removed from the tree and what happens to fruits once they leave the tree. This is important to understand from the perspective of dispersal and reproductive success, but also in terms of understanding the local carbon budget, since fruits removed from the tree are lost to the immediate system. We hypothesize that removal is most likely by frugivores, and fruitfall may have resulted from two different causes: it could be natural fall or fruit could have been knocked down from the feeding activities from arboreal animals (White, 1994). In addition, we hope to supplement the knowledge by documenting the weights and percentages of fruits that are naturally aborted, immature, or affected by vertebrate and invertebrate damage.

We also wanted to know if crop sizes—the total number of fruits on a palm—could be used to predict fruit fall and vice versa. We hypothesize that fruitfall will decrease over time, since there will be fewer and fewer fruits in the trees as they drop their fruits. If we can predict fruitfall from crop size, it will also provide useful estimates of important pools and fluxes of carbon and nitrogen in the system.

Lastly, we wanted to explore possible controls on crop sizes. We hypothesize that palms experiencing greater nutrient availability will have larger crop sizes. Based on the results from my previous literature reviews, trees with larger crop sizes also have increased fruitfall, this final question will identify a mechanism of how soil nutrients influence the local carbon cycle. We chose palms that were in areas of low soil fertility (utisol/residual) as well as in areas of high soil fertility (inceptisol/alluvial). Soil fertility is often an important regulator of populations and community dynamics in tropical forests, and it will be interesting to see if soil fertility also has an effect on the productivity of palms.

Thus, over the course of the paper, I pose and address the following questions:

1. What condition is the fruit in when it falls?
2. Do crop sizes predict fruitfall over time?
3. How much fruit is removed from the system?
4. Do nutrient levels or DBH control crop sizes?

Methods

The study focused on *Euterpe precatoria* and *Welfia regia*, two of the six canopy palms found at La Selva. The two palms are both abundant at La Selva. *Welfia regia* is typically 7-10 meters tall and 10-15cm in diameter; they are distributed in the Central American region and extends south to the Andean border. *Welfia* fruits are almond shaped, dark red in color, and about 5-7 cm in length. *Euterpe precatoria* is one of the 7 species of the genus, they are found in Central America to northern South America. *Euterpe* fruits are small and round; they are purple in color and about 3cm in diameter when ripe.

Study Area

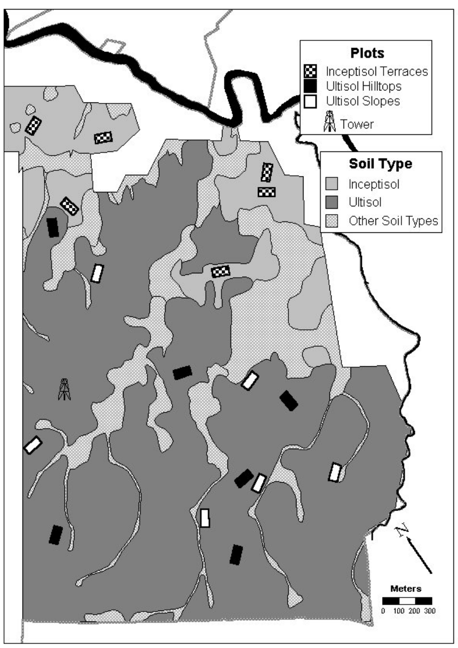


Figure 1. CICLOS plots. The darker shade of represents the residual (utisol) soils, and the lighter shade of gray represents the alluvia (inceptisol) soils.

The study took place in old growth forest at the La Selva Biological Station. The CICLOS plots (Figure 1) are experimental plots set up on different soil and topographic gradients. The focal trees chosen were adjacent to the CICLOS plots, so the soil nutrient data from the plots would be available for analysis. In order to choose specific palms, I went out with other researchers that were working in the plots to look for *Welfia* and *Euterpe.* These two species (out of the possible 6 species) were chosen because they were fruiting during that time. Following CICLOS custom, high fertility plots (on alluvial soils) are labeled as "A" plots, and lower fertility plots (residual soils) were labeled "L". The trees were chosen to be near the CICLOS plots but not in the CICLOS plots, since I did not want to disturb the CICLOS plots. The plots were chosen were A1, A6, L4, and L5. We chose 16 palms total for the study, with 8 boles for each species, and all boles greater than 10 cm dbh. Trees were deliberately chosen for their large crop sizes. Two *Euterpe* were located in the high fertility plots and 4 *Euterpe* in low fertility plots. 7 *Welfia* were located in the high fertility plots, with only 1 *Welfia* in the low fertility plots. For the nutrient analysis portion of this study, the one *Welfia* located in the low fertility plot was removed, since it was only one data point.

Phenology

Fruit crop size was estimated by a method used by Bynum in the CICLOS plots and derived from the system originally developed by Mark Leighton (Cannon et al 2007). The method involves visual determination of phenophase and use of a standardized logarithmic scale to quantify the number of fruits on each canopy palm. Fruits were classified as either mature or immature or in between the mature and immature stages. With this logarithmic scale, the range of each increasing estimation class also increases to accommodate the increasing uncertainty in larger fruit crop estimates. This estimate was used for each infructescence and then the sum of all infructescences amounted to the crop size for a bole at a given point in time. Infructescences were individually located on each bole, and could thus be followed over time. The percent of the infructescence occupied was also recorded; sometimes the infructescences were only 25% full, other times the infructescences were 100% full. Crop size estimates were repeated with every sample once every 5 days.

1,1: 1-3 → 2.5
2,1: 3-7 → 4.5
3,1: 7-10→ 8.5
1,2: 10-30→25
2,2: 30-70→55
3,2: 70-100→85
1,3: 100-400→250
2,3: 400-700→550
3,3: 799-1000→850
1,4: 1000-3000→2500
2,4: 3000-7000→5500
3,4: 7000-10,000→8500

This method was checked for interobserver accuracy; another long term research technician at La Selva also observed the same palms I did and found similar crop sizes. Also, the visual estimations (with binoculars) have been verified by comparing the visual observations with infructescences that have been cut down; when the fruits were manually counted they fell within the same range as the visually estimated fruits. There were 6 total observations in the period of 6 weeks.

Fruitfall Traps

Pimentel and Tabarelli (2004) have established that 83.8% of the fruits of the palm *Attalea oleifera* fall within 2 meters of the parents. Since most of palm fruits fall close to the bole of the tree, I placed 3 traps under each palm, all within 2 meters of the palm. The traps were constructed of 1*1 m of mesh netting mounted on PVC. The PVC was then mounted on rebar that was each 1m high. The traps were then placed at randomly determined starting angles to collect fallen fruits. Fruitfall traps (Smythe, 1970) were placed 1 meter above ground so that none of the ground dwelling frugivores would not have easy access to the fruit. The traps were emptied every 5 days. The total potential fruitfall area underneath the palm is between 7 to 13 square meters, as fruitfall ranges between 1.5 to 2.0 m from the palm. Fallen items were collected every five days, separated by plant part and examined for insect damage or frugivory marks, then counted, weighed fresh, and dried in the oven for 48 hours at 55 degrees C before being weighed again for dry weight.

There were two ways the fruit was quantified. One method quantified the fruit according to actual number of fruit that was in the traps. Since there were not huge numbers of fruit fall, it was possible to individually count and sort the fruit. Another method that was used to quantify fruitfall was to record the dry weight of the fruitfall. We assumed that the fruits that fell in the traps were representative of the fruits that were still in the tree; for example, if insects predated 20% of the fruit in the traps, then we assume that insects also predated 20% of the fruit in the trees.

With both methods, the fruitfall was separated into different categories. Categories included complete fruit, exocarp, seed, and partially eaten, and insect/aborted. Seeds are the mature/ripened ovule. The exocarp is the outer covering of the fruit. Complete fruits had all parts intact (exocarp, mesocarp, and endocarp.) For both *Welfia* and *Euterpe*, the exocarp is a hard husk. Partially eaten seeds are determined by some loss of the exocarp. Since the fruits are not dehiscent, an absence of the exocarp indicates that the fruit has probably been touched by some frugivores. Aborted fruits are fruits that have been aborted—the seed is not properly formed, very small, or there is no seed at all. Immature fruits are fruits that are not yet ripe but have their seeds intact. Immature fruits may have been naturally aborted or have had insect predation. In order to classify fruits that have been eaten by insects, we looked for small holes that were in the exocarp of the fruit, since small holes are often indicators of insect predation. Immature fruit was also cracked open to see if there were larvae or worms in the fruit; if worms or larvae was present, the fruits were then classified as being insect predated. There were also reproductive parts such as peduncles and fruiting branches present in the traps.

Fruits that had the appearance of being partially open were classified as partially eaten, since both palm fruits are not fruits that dehiscent. It can be assumed that the frugivores were either peeling away parts of the endocarp and dropping it or pecking away at the fruit and causing it to drop. The measure of percent partially eaten by count was obtained by dividing the number of partially eaten fruits by the number of total fruits that were in the traps, including partially eaten, insect predated/aborted, and complete fruiting body. The percent immature was also calculated in the same way. In *Welfia*, there was not enough percent aborted for calculations.

Factors influencing crop size

We plotted the DBH of trees against total crop size as well as against the mature crop size. We also looked at the role of nutrients in crop sizes. We were able to obtain nutrient information from the CARBONO project. The soils in the CARBONO plots were sampled in 1998. As detailed by Espleta and Clark (2007), bulk samples were collected for residual and alluvial soils from six cores per depth (0-10cm, 10-30cm, 30-50cm, 50-100 cm) at three regularly spaced intervals. Bulk density was determined by looking at the mean values of each depth from the pits that were adjacent to the three plots. (Espleta and Clark, 2007).

Fruit Removal

Frugivore observations

Tree watches were conducted on 8 of the 16 study trees to estimate the rate of fruit removal by forest arboreal mammals and birds. Initially, each of the 8 trees would be watched for three calendar days between the hours of 6-9am, at dusk around 4-7pm, and at night from 9-11pm.

(Pimentel and Tabarelli, 2004). All visits by vertebrates were recorded and we planned to estimate fruit removal rates using standard methods detailed in Davidar and Morton (1986). Actual observations took place from 6-9am and 1-4pm due to safety reasons, and unfortunately throughout the length of the experiment only one observation period yielded results.

Fruit removed from system

We also calculated the fruit that was removed from the tree. Since we know the total crop size of the palm as well as the total fruitfall for the palm, we were able to estimate the weight of the fruit that has been removed from the system. This estimate was calculated by looking only at mature fruiting branches that had dropped fruit. The equation used was: (1-A/B)*100, A=where A=[(maximum mature crop size) – (mature crop size at the end of the observation period)]*average weight per fruit) + (weight of peduncle + weight of fruiting branches). B= fruitfall scaled up to 1.5 square meters. The weights for all of these numbers are the average dry weights per fruit by maturity phase from the larger dataset of the CICLOS project.

Comparisons of smaller dataset with larger dataset of other investigators

The last part of our study consisted of comparing the smaller dataset with the larger existing dataset from the CICLOS project. Data such as time needed for maturity was available through these datasets, and the larger datasets also include crop sizes that were used for purposes of nutrient analysis. The larger dataset also serves as a comparison to see if the smaller dataset is similar to the larger dataset.

Statistical Analysis

SPSS was used for analysis. We used SPSS for comparison of means, t-tests, and regression models.

Results

We collected a total 1682 grams of fruits and fruiting parts for *Welfia* and a total of 451 g for *Euterpe.* If we assumed fruitfall over an area of 7.07 square meters, the total weight for *Euterpe* fruitfall would have been 1067 g over the span of 6 weeks and the average is 132g per tree and a standard deviation of 143 g. The total weight for *Welfia* 3958 g total and 494 g per tree with a standard deviation of 417 g. Individual fruits of *Welfia* were heavier than those of *Euterpe,* and the total biomass of *Welfia* collected was also more than *Euterpe*, even though there fewer numbers of fruit fell from *Welfia* than from *Euterpe*.

We found that on average 9.95 *Euterpe* fruits and 5.7 *Welfia* fruits fell per week per square meter. We also documented the average weight of each type of fruit (Table 1)

Weight(g)						
Welfia	immature	mature	partially eaten	aborted	seed	exocarp
average	0.58	2.06	1.71	0.94	1.47	0.59
SD	0.10	0.14	0.36	0.10	0.12	0.04
Euterpe						
average	0.30	0.41	0.46	0.09	0.32	0.25
SD	0.03	0.03	0.06	0.01	0.08	0.09

Table 1 Average Weight of Each Type of Fruit

Size of Fruits (cm)

Welfia	average	SD
seed	2.28	0.14
complete fruit	2.88	0.06
partially eaten	2.88	0.10
whole fruit	2.88	0.06
aborted	2.39	0.09
immature	2.88	0.06

Euterpe	average	SD
seed	0.86	0.11
complete fruit	0.86	0.07
partially eaten	0.88	0.08
immature	0.63	0.18
partially eaten	0.88	0.08
aborted/insect	0.63	0.14

Table 2 Average Size of Each Type of Fruit

Fruitfall from both *Euterpe* and *Welfia* palms, regardless of crop size, was less than 50 grams per tree per week; the average was around 31.06 grams. For *Welfia*, the average of the fruitfall per tree was 39.14 grams, and the majority of fruitfall was also less than 50 grams.

In *Euterpe*, 18% of the weight of fruiting bodies that fell in the traps were mature and in *Welfia* 27% of the weight of fruiting bodies is mature. On average, 0.98% of the fruits in *Welfia* were immature, as contrasted with the 7.51% immature in *Euterpe.* In *Euterpe*, there was a large percentage, both by weight and by count, of fruits that had been partially eaten.

By Count	**A plot, N=7**					
Welfia	% partially eaten	% immature	% aborted	% exocarp	% seed	%mature
Average	10.69	0.98	2.21	29.57	19.04	29.13
SD	16.02	1.50	1.33	14.49	11.95	23.42

By Weight	**A plot, N=7**					
Welfia	% partially eaten	% immature	% aborted	% exocarp	% seed	%mature
Average	8.36	0.76	0.93	11.08	17.60	27.93
SD	10.64	0.79	0.59	8.23	14.31	16.95

By Count	**A and L plots, N=8**					
Euterpe	% partially eaten	% immature	% aborted	% exocarp	% seed	%mature
Average	25.14	5.35	16.53	0.36	9.29	12.87
SD	20.43	3.90	11.73	1.01	11.68	8.93

By Weight	**A and L plots, N=8**					
Euterpe	% partially eaten	% immature	% aborted	% exocarp	% seed	%mature
Average	32.36	7.51	5.20	0.05	16.35	18.15
SD	29.19	5.24	3.79	0.15	27.63	16.82

Table 3. Percentage of types of fruits in traps by count and by weight

By Count	**A plots N=2**					
Euterpe	% partially eaten	% immature	% aborted	% exocarp	% seed	%mature
Average	18.24	7.81	20.68	0.00	7.40	12.89
SD	21.16	4.09	7.85	0.00	5.77	7.27

By Count	**L plots N=4**					
Euterpe	% partially eaten	% immature	% aborted	% exocarp	% seed	%mature
Average	27.44	4.53	15.14	0.47	9.93	12.86
SD	21.66	3.84	13.08	1.16	13.50	10.05

By Weight	**A plots N=2**					
Euterpe	% partially eaten	% immature	% aborted	% exocarp	% seed	%mature
Average	32.75	13.50	7.69	0.00	11.15	26.56
SD	36.18	3.87	3.12	0.00	7.79	11.89

By Weight	**L plots N=4**					
Euterpe	% partially eaten	% immature	% aborted	% exocarp	% seed	%mature
Average	29.51	6.43	9.76	0.41	10.59	15.34
SD	6.35	4.72	5.43	0.55	2.38	7.57

Table 4. *Euterpe* Percentage of types of fruits in traps by count and by weight in A plots and L plots (See appendix I—complete fruitfall weights and counts)

The distribution of the fruits in the traps was more representative when we looked at the fruits individually as opposed to by weight. 30% of the fruits that fall in *Welfia* and 12% of the fruits in *Euterpe* were mature fruit. Aborted fruits made up 17% *Euterpe*, as contrasted with the 1.5% insect damaged in *Welfia*. Most of the aborted fruits were because there were insects present in the fruit. The immature fruits for *Euterpe* and *Welfia* were, on average, 5.35%, and 2.64% and respectively.

For *Euterpe,* the A plots and L plots had the same percentage of mature fruit, but the percent weight of the mature fruit was heavier in the A plots than in the L plots.

We also found woody parts of the fruiting structure in the traps; sometimes there were still fruit attached to the fruiting branches. For *Euterpe*, the number of fruits attached to the fallen fruiting branches sometimes numbered over 100. For *Welfia*, the range of fruits attached to the fallen fruiting branches ranged from 10-20 fruits.

The mean crop size for *Euterpe* was 3208 with a standard deviation of 2793; the maximum was 8850 and the minimum was 55. The mean maximum crop size was 6010, the mean mature crop size was 2240 and the mean maximum mature crop size was 4470. The mean immature crop size was 968 and the mean maximum immature crop size was 2760. Crop sizes were larger in the A plots than in the L plots for *Euterpe*.

The mean crop size for *Welfia* was 1350 with a standard deviation of 639. The mean maximum crop size was 1936, the mean mature crop size is 199, and the mean immature crop size was 1150. The mean maximum mature crop size was 536 and the mean immature crop size was 1781. The infructescences were at various stages, ranging from flowering to dead. The percent cover on the fruiting branches also ranged from 0-100%. Based on observations, when a fruiting branch had a high percent cover, it also had a large crop size.

When we ran a regression to determine the relationship between crop size and fruit fall, we found that there was no significant relationship for either *Welfia* or *Euterpe.* The p-value for the regression of crop sizes and fruit fall was 0.65 and 0.3, respectively. The r^2 values were also low. Graphical representations of the data show that the majority of the fruitfall for *Welfia* occurred between crop sizes of 1000-2000 and between 2000-4000 for *Euterpe;* there was no increase in fruitfall as crop sizes increase. When we looked at *Euterpe* fruitfall by weight, we saw that the distribution of *Euterpe* was fairly even across the range of crop sizes.

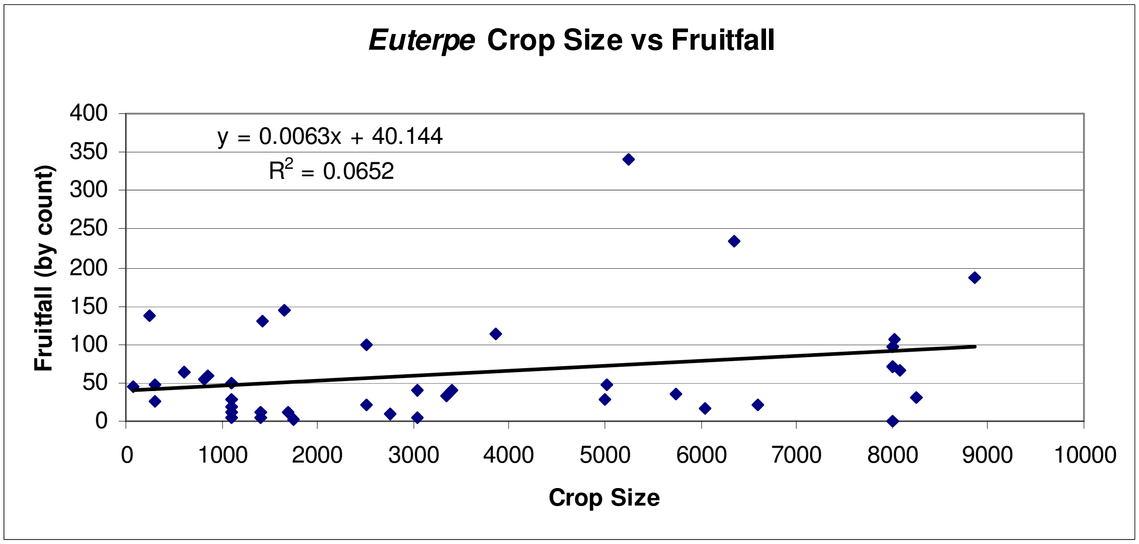


Figure 2 *Euterpe* Crop size vs Fruitfall in Number of Fruits

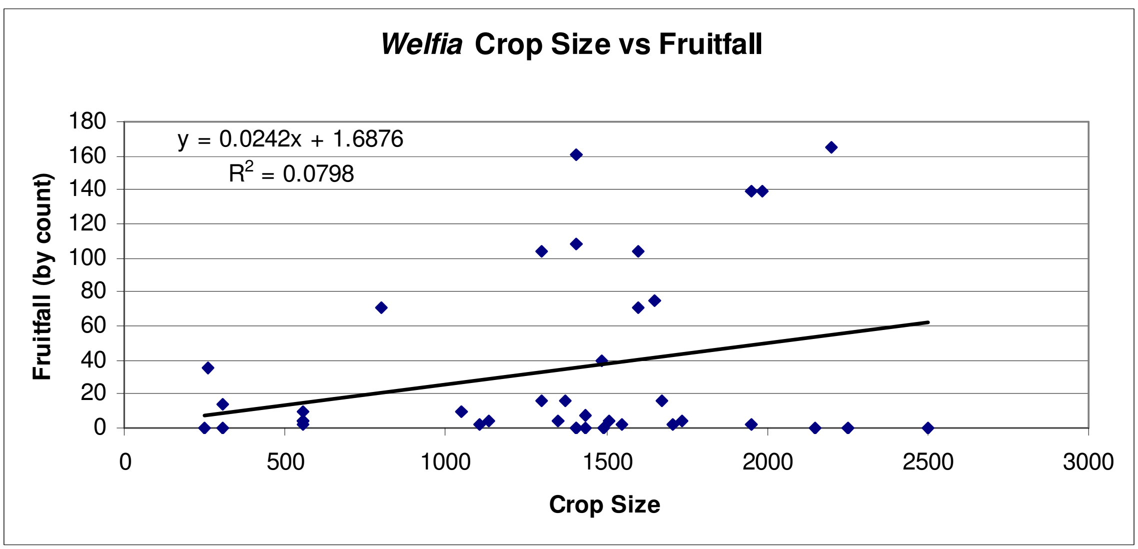


Figure 3 *Welfia* Crop size vs Fruitfall in Number of Fruits

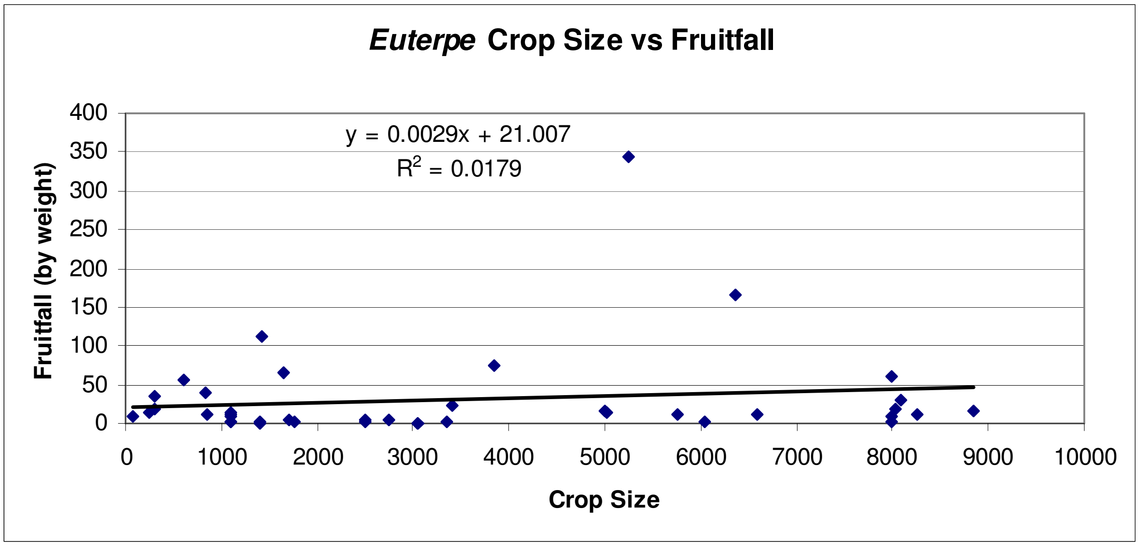


Figure 4 *Euterpe* Crop size vs Fruitfall in Weight (grams)

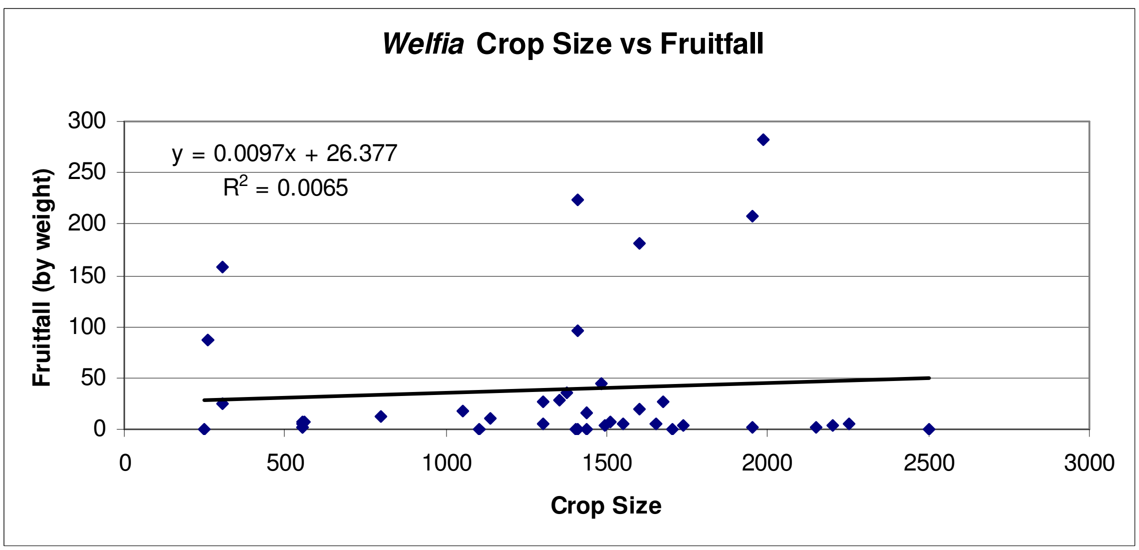


Figure 5 *Welfia* Crop size vs Fruitfall in Weight (grams)

Frugivory Observations

During the entire duration of the study, there was only one frugivory observation. A toucan removed 24 seeds in the span of 60 seconds, and it removed 37 seeds total before it flew away.

Fruit Removed from System

We found that the fruit removed from the system was high for *Euterpe*. The average for the fruitfall for all *Euterpe* trees was 86%, with a standard deviation of 24%. The average fruit removal for *Welfia* is 62%, with a deviation of 23%. However, we do not know how or when these fruits were removed.

We ran a regression of DBH vs crop size to see if there was any effect of DBH on crop sizes, and we found that there was no relationship between the total crop size and the DBH or the mature crop size and DBH.

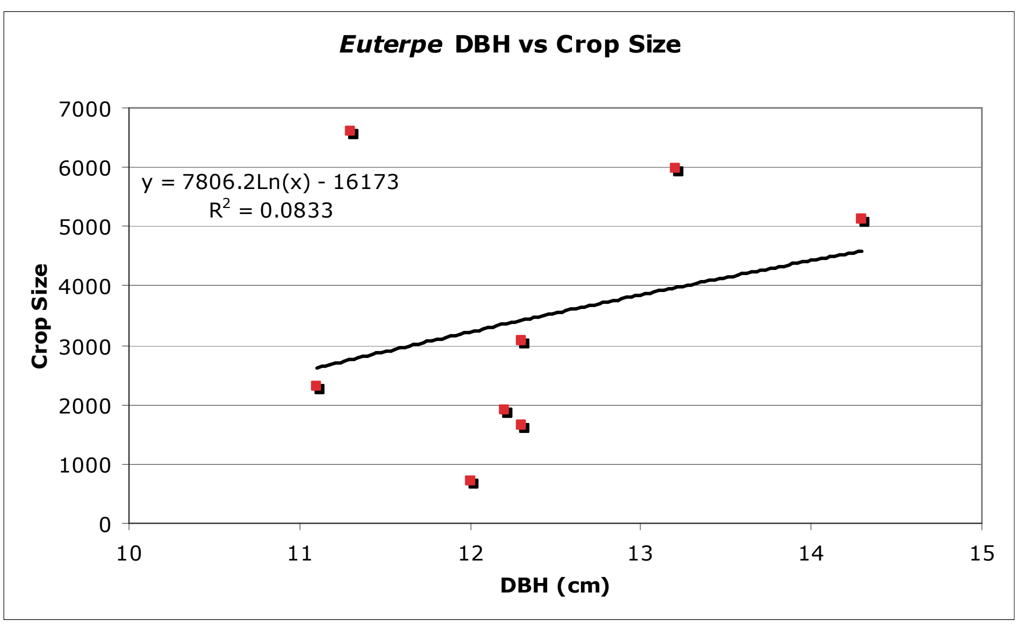


Figure 6 *Euterpe* DBH vs Crop size

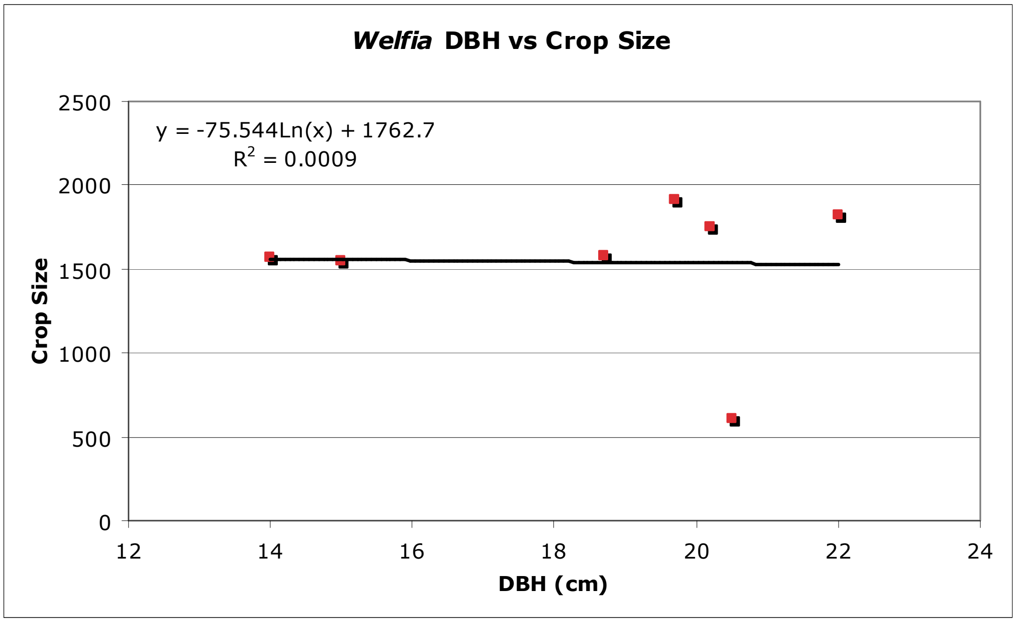


Figure 7 *Welfia* DBH vs Crop size

(See Appendix I for graphs of *Welfia* DBH vs Mature Crop Size)

Nutrient Analysis

Since it was likely that soil samples would be highly correlated (high phosphorus may lead to lower levels of nitrogen), we ran a correlation matrix and found that nitrogen and phosphorous were highly correlated. See Appendix II: Nutrient Analysis

For the nutrient analyses aspect of the data, we found that there was no correlation between crop sizes for *Welfia* and the nitrogen, phosphorous, or carbon content of the soil within the A plots. There was only one data point in the L plot, so we did not use it for analysis. However, there is a positive relationship between the crop sizes for *Euterpe* and the phosphorus levels of the A plots and L plots.

As there were not enough points to run a regression to analyze the effect of phosphorous on crop sizes, I ran a comparison of means on SPSS. The results showed that the means are significantly different from each other and higher phosphorous levels have higher crop sizes for *Euterpe*. In the comparison of means chart below, we see that there was a significant difference between the phosphorous levels of 4.64 (L4 plot) and 4.09 (L5 plot) when compared with the 9.11 (A6 plot) for *Euterpe*. While the crop sizes of 4.09 were larger than the crop sizes at phosphorous level of 4.64, they are not significantly larger; however, the crop sizes are significantly larger when the phosphorus level was at 9.11. We also found that nitrogen had a significant negative effect on crop size for *Euterpe*.

Multiple Comparisons
Dependent Variable: CS
Tukey HSD

		Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
(I) N	(J) N				Lower Bound	Upper Bound
18.28 A6	18.48 L4	5095.2917	854.55992	0	3024.1686	7166.4147
	19.09 L5	3619.4583	740.0706	0	1825.8132	5413.1035
18.48 L4	18.28 A6	-5095.2917	854.55992	0	-7166.4147	-3024.1686
	19.09 L5	-1475.8333	740.0706	0.125	-3269.4785	317.8118
19.09 L5	18.28 A6	-3619.4583	740.0706	0	-5413.1035	-1825.8132
	18.48 L4	1475.8333	740.0706	0.125	-317.8118	3269.4785

Based on observed means.

Table 5. Comparison of Means for *Euterpe* crop sizes with nitrogen levels

Multiple Comparisons
Dependent Variable: M
Tukey HSD

		Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
(I) N	(J) N				Lower Bound	Upper Bound
18.28 A6	18.48 L4	4411.9583	613.08193	0	2926.0846	5897.832
	19.09 L5	3363.2083	530.94453	0	2076.404	4650.0127
18.48 L4	18.28 A6	-4411.9583	613.08193	0	-5897.832	-2926.0846
	19.09 L5	-1048.75	530.94453	0.13	-2335.5544	238.0544
19.09 L5	18.28 A6	-3363.2083	530.94453	0	-4650.0127	-2076.404
	18.48	1048.75	530.94453	0.13	-238.0544	2335.5544

Based on observed means.

Table 6. Comparison of Means for *Euterpe* mature crop sizes with nitrogen levels

Multiple Comparisons
Dependent Variable: CS
Tukey HSD

(I) P	(J) P	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval Lower Bound	Upper Bound
4.09 L4	4.64 L5	1475.83	740.07	0.13	-317.81	3269.48
	9.11 A6	-3619.46	740.07	0.00	-5413.10	-1825.81
4.64 L5	4.09 L4	-1475.83	740.07	0.13	-3269.48	317.81
	9.11 A6	-5095.29	854.56	0.00	-7166.41	-3024.17
9.11 A6	4.09 L4	3619.46	740.07	0.00	1825.81	5413.10
	4.64 L5	5095.29	854.56	0.00	3024.17	7166.41

Table 7. Comparison of Means for *Euterpe* crop sizes with phosphorus levels

Multiple Comparisons
Dependent Variable: M
Tukey HSD

(I) P	(J) P	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval Lower Bound	Upper Bound
4.09 L4	4.64 L5	1048.75	530.94	0.13	-238.05	2335.55
	9.11 A6	-3363.21	530.94	0.00	-4650.01	-2076.40
4.64 L5	4.09 L4	-1048.75	530.94	0.13	-2335.55	238.05
	9.11 A6	-4411.96	613.08	0.00	-5897.83	-2926.08
9.11 A6	4.09 L4	3363.21	530.94	0.00	2076.40	4650.01
	4.64 L5	4411.96	613.08	0.00	2926.08	5897.83

Table 8. Comparison of Means for *Euterpe* mature crop sizes with phosphorus levels

There were not enough *Welfia* observations to run the same test for *Welfia*. However, within the alluvial plots there were different measures of phosphorus, so I ran an independent samples t-test to see if there were differences in crop size due to the two phosphorous levels. The two phosphorus levels are within similar soil fertility plots (both are alluvial), and there was no difference between the crop sizes due to the phosphorous levels. The p-value for the t-test was 0.49 for both nitrogen and phosphorus.

The positive relationship for *Euterpe* was significant at with a p-value of 0.008 and negative for *Welfia* with a p-value of 0.014. See Appendix II: Nutrient Analysis.

Discussion

Fruitfall

Actual distribution of fruits in traps was deduced from looking at the percent of fruit by weight as well as by count. Aborted fruits in *Euterpe* were not fairly represented if we only look at the number of fruits by weight, since aborted fruits are lighter. (See Table 1, Table 4). 17% of the number of fruits caught in *Euterpe* was aborted fruits, whereas the aborted fruits only represented 5% of the total weight in the traps. However, from a nutrient information standpoint, using the weight of the fruits will compensate for the different lesser nutrient content of immature or aborted fruits as compared to whole or complete fruit.

As our primary objective was to determine the fruits that were removed by insect predation versus frugivores activity versus simple fruitfall, we can look the fruits that fell in the traps at the traps as a method of qualifying what the fate of the fruits.

White (1994) had hypothesized that the percent weight of unripe (immature or aborted) fruits may be overrepresented in the fruit traps compared to in the trees. White (1994) pointed out that immature fruits fall when they are knocked down by frugivore activity, whereas mature fruit fall naturally. However, this may not be the case in our study. Given the large number of partially eaten fruits, I would hypothesize that partially open fruit were the ones handled by the "sloppy" eaters that knock down many fruits as they eat. Given the high number of fruits knocked down, I do not think that the number and weight of immature fruits are misrepresented in the fruit traps.

Euterpe and *Welfia* may both overproduce seeds in order increase the chance of dispersal. The Janzen Connell model (Janzen 1970, Connell 1971) predicts the seeds that drop directly under the tree will mostly not germinate and become seedlings, because they are too close to the parent tree and most likely not be able to survive. Thus, the number of seeds that are aborted due to insects or any other unknown reason may not actually be a significant loss for *Euterpe*, as they produce large numbers of seeds in order to attract more frugivores and increase the probability of seed dispersal.

Euterpe had more partially eaten fruit than *Welfia*. The smaller fruit size of *Euterpe* makes it a more likely food resource for frugivores. Consequently, there is a higher probability that *Euterpe* fruits were handled by frugivores. *Euterpe* also had a higher percentage of fruits that were immature and aborted; some of which were due to insect predation. A possible reason for this is because *Euterpe* produces smaller but more fruit, and with less investment per fruit, the tree can afford to have more fruit aborted. The percentage of insect and aborted fruits range from 2% to 33%, with an average of 17% and a standard deviation of 11%, a low proportion compared to many other trees in the tropics.

The higher percentage of partially eaten fruits could have implications for the fates of the fruits after they fall. A study by Silvius and Fragoso (2002) showed that an increase handling of fruits and seeds could also reduce the predictability of seed fate. The study showed that when large rodents and primates handle the fruit they actually increase the probability that there will be predation by insects such as beetles, since they expose parts of the fruit. They also found that different forms of handling would affect the rate of insect infestation differently.

Predation by insects is a major cause of seed mortality (Janzen, 1982, Terborgh, 1993), and close associations have been found between the palms in genus *Attalea* and bruchid beetles; up to 50% of fallen fruits have been predated by insects (Wright, 2001) There may be similar associations in *Euterpe* that have yet to be explored. It is also possible that the insect predation happened after the fruits fell from the traps, since fallen fruits stayed in traps for up to 5 days before collection.

There were a large number of *Welfia* exocarps and seed in the traps compared to *Euterpe*, and for *Welfia* there were numerous discarded exocarps around the palms as well. One possible explanation is the eating habits of the frugivores that utilize *Welfia* as a food resource. Capuchins monkeys generally remove the fleshy part of the fruit and dispose of the exocarp, so the exocarp found around the palms may have been dropped by the frugivores eating them. It would be relatively easy to remove the fruit flesh from the exocarp or spit out the seed after the fleshy part of the fruit is consumed. Another possibility is that because *Euterpe* fruits are smaller, frugivores that consume it are more likely to swallow the entire fruit and not leave the exocarp, or eat the exocarp but drop the seeds. While the exocarp found in the fruitfall traps for *Welfia* may suggest the fruits were eaten —specifically the fleshy parts of the fruit, the absence of exocarp does not necessarily mean that fruit was not removed from the tree; it is possible the fruit was eaten whole.

Actual distribution of fruits in traps was deduced from looking at the percent of fruit by weight as well as by count. Aborted fruits in *Euterpe* were not fairly represented if we only look at the number of fruits by weight, since aborted fruits are lighter. (See Table 1, Table 4). 17% of the number of fruits caught in *Euterpe* was aborted fruits, whereas the aborted fruits only represented 5% of the total weight in the traps. However, from a nutrient information standpoint, using the weight of the fruits will compensate for the different lesser nutrient content of immature or aborted fruits as compared to whole or complete fruit.

Phenology

Our mean crop sizes of 3208 (n=8) for *Euterpe* are about the same as the mean crop sizes of the larger palm dataset (mean =3085, n=69). However, our mean maximum crop size is 6010, compared to the mean maximum crop size of 4999 of the larger palm dataset. *Welfia* deviated more, with a mean crop size of 1350 (n=7) as compared with the mean crop size of 258 (n=127). The mean max crop sizes were also high, with the data collected displaying a mean of 1936 and whereas the long term larger dataset had a mean maximum crop size of 849. There are large standard deviations associated with the crop sizes, which is a possible reason for the discrepancy between the two datasets. The reason for this is because we chose palms with more fruits to improve our probably of frugivory observations, so the selection of palms was nonrandom—two of the *Euterpe* palms in the A plots had maximum crop sizes 8850.

Crop size as a predictor of fruitfall

We initially hypothesized that fruitfall would decrease over time as the fruiting branches dropped more and more of their fruits. Our results contradicted these predictions. Fruitfall did not decrease over time, primarily because increasing numbers of branches were becoming mature enough to drop fruits continuously throughout the study period. Also, we were surprised to find that mature crop sizes were not good predictors of weekly fruitfall; larger mature crop sizes in the tree did not lead to an increase in fruitfall in traps. If the study period was increased, it is possible we would observe a decrease in crop sizes as the fruiting season ends.

We also predicted a correlation between crop size and fruit fall, but found that in actuality, crop sizes were not good predictors of fruitfall; larger crop sizes did not lead to an increase fruitfall in traps. One of the reasons for this might be the week-to-week data correlation;

each week's crop size is closely tied to the crop size of the previous week and often builds upon it.

As crop sizes do not reflect the phenophases of the numerous fruiting branches of the palms, it is difficult to use crop size as a predictor. Though the numerical crop sizes may not have changed for the specific palm, one mature fruiting branch may have dropped its fruits while another newer fruiting branch has matured. Looking only at the mature fruits would not lend more insight, since there have been observations where one fruiting branch dropped the majority of its fruits as another immature branch became mature. As there is no method of ensuring dropped fruits are always from the fruiting branches with the most ripened fruit, tracing the history of a specific infructescence will not be a viable option, either. This may be because new fruits are often produced as mature fruits drop. These problems are illustrated in the graph below. If one only looks at the mature crop size from week 1 as a starting point to week 6 as an ending point, it appears that the crop sizes for mature fruit changes only slightly from week 1 to week 6, but what is actually occurring is that the immature fruits are becoming mature, and mature fruits are dropping, as is evident from the sharp decrease in immature fruit between week 3 and 4.

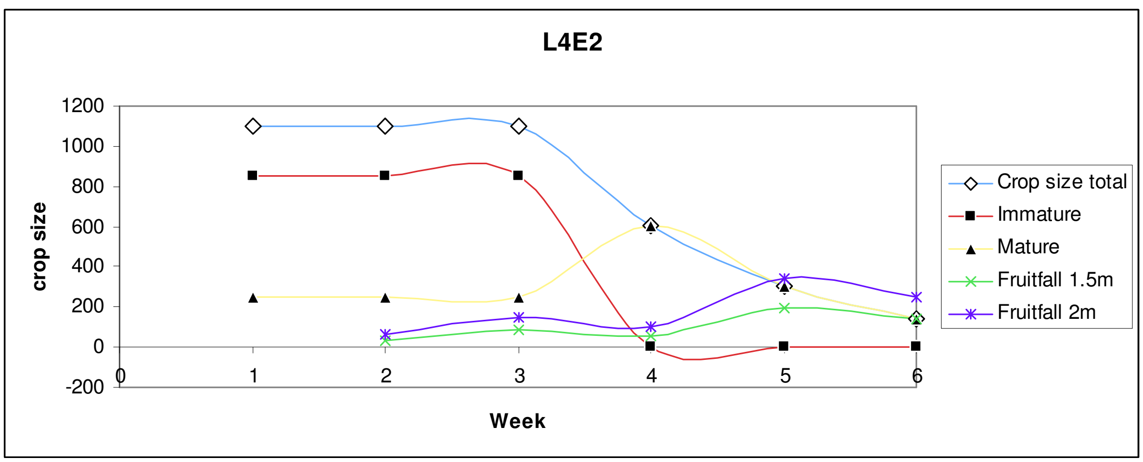


Figure 7. Crop size, Phenophase, and Fruitfall of an *Euterpe* palm. (For all 16 palms see Appendix III: Crop Size, Phenophase, and Fruitfall over six weeks)

While *Euterpe* and *Welfia* may not have the sharply peaking characteristics of other trees, longer periods of observation would still be beneficial. From the larger CICLOS dataset, we found that the mean of the length of the reproductive cycle for *Euterpe* was 7.5months, with a minimum of 3 months and a maximum of 12 months; *Welfia* had an average reproductive cycle of 12 months with minimum of 5 months and a maximum of 19 months. (Bynum and Stitch, pers. comm.) If the trees were observed for longer, then we would be able to paint a more accurate picture of when the fruits reach their maximal maturity.

For studies of phenology, longer studies over substantial periods of time would be more informative (Toriola, 1998). This study also concluded that if fruit fall was to reflect fruit abundance, then there would be displays of “sharply peaked” fruiting season over the span of a 4-6 week period; this did not occur for this data since fruiting branches were continuously fruiting during the observation period.

In addition to the phenology of palms as a possible reason for the unpredictability of fruit fall, another possibility is that the majority of the fruits were removed before they fell. A tree with a crop size of 4000 may have 3000 of its fruits removed by frugivores and thus only 1000 fruits fallen to the forest floor; a tree with only 2000 fruits would also have roughly 1000 fruits removed so only 1000 would fall. While we were unable to observe frugivores eating the fruits of the focal palms, we were still able to estimate the weight of fruit that was removed from the local system, as discussed below. While it is an estimate, it serves the purpose of answering our question on how much of the nutrients from the fruit are potentially lost from the system.

Fruit Removal

There are several possible reasons for lack of frugivory observations. While palms are a common and important food resource, the likelihood that frugivores would be removing fruit from the 8 focal palms during the time of observation would be small since tropical forests contain such a diverse array of food resources in addition to palms. Another possibility is that even though we chose palms with larger crop sizes for frugivory observations, they may not have been substantially larger than neighboring palms or other food resources. In the future, I would recommend the use of camera traps. The observation periods that I conducted were only 4 hours at a time at one of the eight chosen trees, but cameras would be able to monitor the activity surrounding the tree more closely and capture the number of fruits frugivores are removing, the duration they stay in an area, and the rate of fruit removal per minute.

Once we know the rate of fruit removal by frugivores such as toucans or monkeys, we may be able to combine the data obtained with other observation methods. For example, some studies have used transect methods and listened for birds in the area to get an idea of what species of birds are eating the fruit. Moegenburg and Levey in 2003 used vocalizations of the parrots to figure out the location of the birds and the estimated time of visit to the plots. We may be able to estimate the numbers of fruit that are being removed based on the data on how many fruits are removed per minute and how many minutes the birds are in the plot.

Despite a lack of frugivory observations, we were able to use estimated crop sizes and our data on the weight of fruitfall to estimate the weight of fruit that was removed by them from the system. While it is an estimate, it serves the purpose of answering our question on how much of the nutrients from the fruit are lost from the system.

Euterpe had a larger percentage of fruit removed (86% compared to 62% in *Welfia*). One reason is because *Euterpe* is smaller and thus more accessible to a wider variety of frugivores. We note that these are rough calculations and there may be less removed than calculated, since heavier fruiting parts that may not have fallen—such as peduncles or fruiting branches—were included in the calculations of total weight that should have fallen from the tree. The large removal of the crop sizes may also support the idea that palms are important resources, and in this study we have not accounted for fruits that have fallen and what happens to them after they fall.

We would also like to note that fruits are likely to be removed from the system after they fall, and this is also an important factor to considering in terms of nutrient losses. Observationally, there were rarely whole fruits left on the ground around the bole, possibly indicating that they are carried away quickly once they fell. Agoutis, capuchins, peccaries (Peres, 1997, Henry 1999, Brewer and Rejmanek, 1999), and other ground dwelling animals remove and consume the fruits after they have already fallen, helping the seed dispersal process. A study by Brewer (1999) documented mammals taking fruit and burying it elsewhere for consumption later. Terrestrial mammals often serve as secondary seed dispersers, and it would be interesting to see how much fruit is removed from the system after it falls.

Thus, in order to account for the loss of nutrients to the system after the fruits fall, we can also place mammal traps or make seed piles and tag seeds to trace how many fruits are removed after fruitfall as well as how far the seeds travel. However, it is also important to remember that fruits from adjacent palms may also be moving into the local system. Since palms are often close to each other, it is highly likely that fruits are moving out of one local system into another, and vice versa.

Factors influencing Crop Sizes

Chapman et al (1992) found that DBH was a good measure of fruit productivity for tropical trees, but we found that DBH was not a good predictor of for crop sizes of the palms. This was not unexpected, since canopy palms invest more energy in increasing height. Thus, we saw no correlation between crop sizes and DBH, and DBH was not a good predictor of crop sizes. There was actually a slight negative correlation (y = -727.87Ln(x) + 2344.3, R-squared value of 0.3, see Graph 4) for mature crop sizes vs *Welfia* DBH. One explanation for this may be as the palms grow larger they are more limited in nutrients for fruitbearing and thus less fruits become mature. However, we would need more data before we can investigate this possibility in further detail.

Our results with nutrient analysis showed that phosphorus had a significant positive effect on *Euterpe*. This was unexpected, since previous studies showed that there were more *Euterpe* for in lower fertility plots (Clark and Clark, 1995). Clark and Clark (1995) found that *Euterpe* were more abundant in steeper slopes and poorer soils; *Welfia regia* was found in the area across all nutrient gradients. *Euterpe's* abundance varied significantly with the different types of soils, and the presence and absence of the *Euterpe* was strongly dependent on topographic position (Clark and Clark 1995).

Since it is difficult to separate out the factors of topography and soil at La Selva, it is highly possible the distribution of *Euterpe* is affected more by the elevation than by the soil and that soil nutrients limit distribution but not crop size. Further exploration with larger sample sizes and possibly phosphorus treatments are needed to better understand the controls on crop sizes of *Euterpe*.

Conclusions

The importance of palms in tropical regions in undeniable, yet there is still little known about the natural history of the fruitfall as well as the contribution of the fruits to the local nutrient cycle. The project, as part of the larger CICLOS project, is important for understanding the fate of fruits both from the standpoint of fruit availability to frugivores as well as how fruits may contribute to the carbon cycle. Litter invertebrates, arboreal frugivores, and tree reproduction are all factors that may contribute as well as be affected by the carbon cycle.

Our study contributed to the natural history knowledge of *Euterpe precatoria* and *Welfia regia*. We were able to quantify fruitfall over a period of six weeks and determine the fates of the fruits throughout the maturation process. We found that fallen fruiting bodies can be categorized into the following categories: partially eaten, aborted, immature, and mature, and seeds. We were also able to establish that crop sizes are not good predictors of fruitfall, and this is largely due to the constant fruit production over time.

While our frugivory observations did not yield the rate of fruit removal for the two palm species, we were able to estimate that on a weight basis 86% of the *Euterpe* fruit and 62% of *Welfia* fruit was lost from the system before falling from the palm. Our study showed that large numbers of fruits were being removed from the area directly below the palm boles studied. Future studies will be able to create a more accurate picture by also looking at the fruits that are removed by ground dwelling frugivores.

We found that DBH had no effect on crop sizes, mostly likely because palms do not have secondary growth and therefore DBH does not necessarily reflect age or reproductive status. We found that higher phosphorus levels do not significantly affect crop sizes in *Welfia* but they do significantly positively affect crop sizes of *Euterpe*, despite the limited distribution of *Euterpe* in richer soils.

A greater understanding of how palms will respond to climate change and consequently affect fruit production and the carbon cycle is important on both the population level and on the landscape scale. Palms are abundant and widely distributed at La Selva: their role in the ecosystem as sources of food for frugivores and their potential to play an important role in the carbon cycle cannot be overlooked. There is indeed a greater need for natural history observations and investigating the factors that could help us quantify fruitfall more accurately, since this will be instrumental to quantifying and qualifying the role of palms in the carbon budget.

Acknowledgements

I would like to thank the KLN internship fund for making this project possible, Danilo Villegas for his help in the field, Dr. Dan Richter for program advising, the CICLOS project for providing information and infrastructural support, and most of all Dr. Nora Bynum for her continued patience, advice, support, and encouragement throughout the project.

Bibliography

1. Clark, D. (2007) Detecting Tropical Forests' Responses to Global Climatic and Atmospheric Change: Current Challenges and a Way Forward. *Biotropica* 39, 4-19
2. Clark, D.A., *et al.* (2001) Measuring Net Primary Production in Forests: Concepts and Field Methods. *Ecological Applications* 11, 356-370
3. Clark, D.A., *et al.* (1995) Edaphic and Human Effects on Landscape-Scale Distributions of Tropical Rain Forest Palms. *Ecology* 76, 2581-2594
4. Clark, D.B., *et al.* (1998) Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. *Journal of Ecology* 86, 101-112
5. Clark, D.B., *et al.* (1999) Edaphic Factors and the Landscape-Scale Distributions of Tropical Rain Forest Trees. *Ecology* 80, 2662-2675
6. Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rainforest trees. *Dynamics of populations*, 298-231
7. Davidar, P., and Morton, E.S. (1986) The Relationship Between Fruit Crop Sizes and Fruit Removal Rates by Birds. *Ecology* 67, 262-265
8. Denslow, J.S., and Moermond, T.C. (1982) The effect of accessibility on rates of fruit removal from tropical shrubs: An experimental study. *Oecologia* 54, 170-176
9. Dixon, R.K., *et al.* (1994) Carbon Pools and Flux of Global Forest Ecosystems. *Science* 263, 185-190
10. Espeleta, J.F., and Clark, D.A. (2007) Multi-Scale Variation In Fine-Root Biomass In A Tropical Rain Forest: A Seven-Year Study. *Ecological Monographs* 77, 377-404
11. Fischer, K.E., and Chapman, C.A. (1993) Frugivores and Fruit Syndromes: Differences in Patterns at the Genus and Species Level. *Oikos* 66, 472-482
12. Galetti, M., and Aleixo, A. (1998) Effects of palm heart harvesting on avian frugivores in the Atlantic rain forest of Brazil. *Journal of Applied Ecology* 35, 286-293
13. Howe, H.F., and Kerckhove, G.A.V. (1979) Fecundity and Seed Dispersal of a Tropical Tree. *Ecology* 60, 180-189
14. Izawa, K., and Mizuno, A. (1977) Palm-fruit cracking behavior of wild black-capped capuchin (Cebus apella). *Primates* 18, 773-792
15. Justiniano, M.J., and Fredericksen, T.S. (2000) Phenology of Tree Species in Bolivian Dry Forests1. *BIOTROPICA* 32, 276-281
16. Korine, C., *et al.* (2000) Fruit characteristics and factors affecting fruit removal in a Panamanian community of strangler figs. *Oecologia* 123, 560-568
17. Moegenburg, S.M., and Levey, D.J. (2003) Do Frugivores Respond to Fruit Harvest? An Experimental Study of Short-Term Responses. *Ecology* 84, 2600-2612
18. Nathan, R., and Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* 15, 278-285
19. Newstrom, L.E., *et al.* (1994) A New Classification for Plant Phenology Based on Flowering Patterns in Lowland Tropical Rain Forest Trees at La Selva, Costa Rica. *Biotropica* 26, 141-159
20. O'Brien, J.J., *et al.* (2008) Phenology and Stem Diameter Increment Seasonality in a Costa Rican Wet Tropical Forest. *Biotropica* 40, 151-159

21. Rich, P.M., *et al.* (1986) Height and Stem Diameter Relationships for Dicotyledonous Trees and Arborescent Palms of Costa Rican Tropical Wet Forest. *Bulletin of the Torrey Botanical Club* 113, 241-246
22. Russo, S.E. (2003) Responses of dispersal agents to tree and fruit traits in Virola calophylla (Myristicaceae): implications for selection. *Oecologia* 136, 80-87
23. Scariot, A., *et al.* (1995) Flowering and Fruiting Phenologies of the Palm Acrocomia aculeata: Patterns and Consequences. *Biotropica* 27, 168-173
24. Smythe, N. (1989) Seed Survival in the Palm Astrocaryum standleyanum: Evidence for Dependence upon its Seed Dispersers. *Biotropica* 21, 50-56
25. Steven, D.D. (1983) Reproductive Consequences of Insect Seed Predation in Hamamelis Virginiana. *Ecology* 64, 89-98
26. Terborgh, J., *et al.* (1993) Predation by vertebrates and invertebrates on the seeds of five canopy tree species of an Amazonian forest. *Plant Ecology* 107-108, 375-386
27. Toriola, D. (1998) Fruiting of a 19-Year Old Secondary Forest in French Guiana. *Journal of Tropical Ecology* 14, 373-379
28. van Schaik, C.P., *et al.* (1993) The Phenology of Tropical Forests: Adaptive Significance and Consequences for Primary Consumers. *Annual Review of Ecology and Systematics* 24, 353-377
29. Vitousek, P.M., and Denslow, J.S. (1986) Nitrogen and Phosphorus Availability in Treefall Gaps of a Lowland Tropical Rainforest. *The Journal of Ecology* 74, 1167-1178
30. Vitousek, P.M., and Denslow, J.S. (1987) Differences in Extractable Phosphorus Among Soils of the La Selva Biological Station, Costa Rica. *Biotropica* 19, 167-170
31. Wang, Y.-H., and Augspurger, C. (2006) Comparison of seedling recruitment under arborescent palms in two Neotropical forests. *Oecologia* 147, 533-545
32. White, L.J.T. (1994) Patterns of Fruit-Fall Phenology in the Lope Reserve, Gabon. *Journal of Tropical Ecology* 10, 289-312
33. Wright, S. (2005) Tropical Forests in a changing environment. *TRENDS in Ecology and Evolution* 20, 553-560
34. Wright, S.J., and Duber, H.C. (2001) Poachers and Forest Fragmentation Alter Seed Dispersal, Seed Survival, and Seedling Recruitment in the Palm Attalea butyraceae, with Implications for Tropical Tree Diversity1. *BIOTROPICA* 33, 583-595

Appendix I: Weight, Count, and Percent of Fruits per Palm

Trees were tagged and number according to Soil Type and Plot Number (as was designated by the CICLOS plots) and tree species ID.

COUNT

Welfia	% partially eaten	% immature	% aborted	% exocarp	% seed	%mature
A1WI	3.61	1.20	0.00	33.04	26.79	8.93
A1W2	7.41	0.00	3.70	7.41	1.85	77.78
A1W3	46.38	0.00	2.63	18.29	9.76	31.71
A1W4	8.57	0.00	3.70	45.24	35.71	16.67
A6W1	0.00	0.00	2.33	38.98	27.12	32.20
A6W2	2.30	4.02	1.20	20.11	10.87	10.87
A6W3	6.56	1.64	1.92	43.94	21.21	25.76
L4W1*	0.00	14.29	0.00	85.71	0.00	0.00
sum	74.83	21.15	15.49	292.72	133.31	203.91
average	9.35	2.64	1.94	36.59	16.66	25.49
SD	15.31	4.91	1.46	23.96	12.95	24.00

WEIGHT (g)

Welfia	% partially eaten	% immature	% aborted	% exocarp	% seed	%mature
A1WI	1.16	0.08	0.00	4.34	8.40	4.14
A1W2	1.59	0.00	0.54	0.44	0.25	15.47
A1W3	30.35	0.00	1.26	4.31	5.73	27.19
A1W4	11.79	1.89	1.89	22.86	39.95	30.14
A6W1	0.00	0.89	0.89	16.51	28.86	52.50
A6W2	4.41	1.67	1.11	12.37	14.35	19.97
A6W3	9.22	0.83	0.83	16.73	25.67	46.12
L4W1*	0.00	0.00	0.00	2.09	0.00	0.00
sum	58.53	5.35	6.52	79.65	123.22	195.51
average	7.32	0.67	0.82	9.96	15.40	24.44
SD	10.28	0.78	0.64	8.25	14.64	18.54

*L4W1 data was not used due to lack of fruits on palm during time of observation

COUNT

Euterpe	% partially eaten	% immature	% aborted	% exocarp	% seed	%mature
A6E1	3.28	4.92	26.23	0.00	11.48	18.03
A6E2	33.21	10.70	15.13	0.00	3.32	**7.75**
L4E1	56.92	1.54	24.62	0.00	1.54	13.85
L4E2	37.50	9.72	20.83	0.00	2.78	26.39
L5E1	36.30	8.90	5.69	2.85	26.33	3.20
L5E2	29.87	3.90	33.77	0.00	0.65	12.99
L5E3	2.17	2.17	2.17	0.00	28.26	0.00
L5E4	1.89	0.94	3.77	0.00	0.00	20.75
sum	201.14	42.79	132.22	2.85	74.36	102.96
average	25.14	5.35	16.53	0.36	9.29	12.87
SD	20.43	3.90	11.73	1.01	11.68	8.93

WEIGHT (g)

Euterpe	% partially eaten	% immature	% aborted	% exocarp	% seed	%mature
A6E1	7.17	16.23	9.90	0.00	16.66	9.90
A6E2	58.33	10.76	5.49	0.00	5.64	5.49
L4E1	72.36	11.62	10.13	0.00	1.57	10.13
L4E2	6.39	0.92	0.88	0.00	0.30	0.88
L5E1	49.38	4.51	2.69	0.42	24.80	2.69
L5E2	55.77	9.14	8.30	0.00	0.89	8.30
L5E3	7.93	3.99	1.67	0.00	80.97	1.67
L5E4	1.59	2.90	2.52	0.00	0.00	2.52
sum	258.92	60.08	41.57	0.42	130.83	41.57
average	32.36	7.51	5.20	0.05	16.35	5.20
SD	29.19	5.24	3.79	0.15	27.63	3.79

Total Weight (grams) Collected Over Six Weeks

WELFIA	Immature	Mature	Partially Eaten	Aborted	Seed	Exocarp
A1WI	0.37	20.16	5.67	0.00	40.94	21.15
A1W2	0.00	74.41	7.65	2.61	1.23	2.10
A1W3	0.00	55.18	61.60	2.55	11.63	8.75
A1W4	1.19	18.96	7.42	1.19	25.13	14.38
A6W1	0.68	39.86	0.00	0.68	21.91	12.54
A6W2	3.26	38.98	8.60	2.17	28.01	24.14
A6W3	0.77	42.62	8.52	0.77	23.72	15.46
L4W1*	0.00	0.00	0.00	0.00	0.00	1.77
sum	6.26	290.16	99.47	9.97	152.57	100.28

EUTERPE	Immature	Mature	Partially Eaten	Aborted	Seed	Exocarp
A6E1	2.46	5.30	1.09	1.50	2.52	0.00
A6E2	6.35	10.71	34.41	3.24	3.33	0.00
L4E1	2.26	2.48	14.05	1.97	0.30	0.00
L4E2	1.66	7.95	11.57	1.59	0.54	0.00
L5E1	5.05	4.65	55.31	3.02	27.78	0.47
L5E2	3.78	9.11	23.06	3.43	0.37	0.00
L5E3	0.16	0.00	0.32	0.07	3.29	0.00
L5E4	0.57	9.62	0.31	0.50	0.00	0.00
sum	22.29	49.81	140.12	15.30	38.13	0.47

Total Number of Fruits Collected Over Six Weeks

WELFIA	Immature	Mature	Partially Eaten	Aborted	Seed	Exocarp
A1WI	1.35	10.00	4.05	0.00	30.00	37.00
A1W2	0.00	42.00	4.00	2.00	1.00	4.00
A1W3	0.00	26.00	38.03	2.16	8.00	15.00
A1W4	0.00	7.00	3.60	1.56	15.00	19.00
A6W1	0.00	19.00	0.00	1.37	16.00	23.00
A6W2	7.40	20.00	4.23	2.22	20.00	37.00
A6W3	1.08	17.00	4.33	1.27	14.00	29.00
L4W1	1.00	0.00	0.00	0.00	0.00	6.00
sum	10.83	141.00	58.23	10.57	104.00	170.00

EUTERPE	Immature	Mature	Partially Eaten	Aborted	Seed	Exocarp
A6E1	3.00	11.00	2.00	16.00	7.00	0.00
A6E2	29.00	21.00	90.00	41.00	9.00	0.00
L4E1	1.00	9.00	37.00	16.00	17.12	1.85
L4E2	7.00	19.00	27.00	15.00	0.47	0.00
L5E1	25.00	9.00	102.00	16.00	79.41	0.00
L5E2	6.00	20.00	46.00	52.00	0.00	0.00
L5E3	1.00	0.00	1.00	1.00	0.71	0.00
L5E4	1.47	32.38	2.94	5.89	4.33	0.00
sum	73.47	121.38	307.94	162.89	118.04	1.85

Total Weight (grams) of Fruitfall Collected Over Six Weeks
Assuming fruit fell within 1.5 meters to 2 meters from bole of palm

WELFIA	1m^2	7.07 m^2	12.57m^2
A1WI	162.46	1146.95	2040.46
A1W2	160.37	1132.24	2014.30
A1W3	67.65	477.62	849.70
A1W4	20.97	148.04	263.37
A6W1	25.31	178.69	317.90
A6W2	65.07	459.38	817.26
A6W3	30.80	217.47	386.89
L4W1	28.10	198.36	352.88
sum	560.73	3958.75	7042.76
average	70.09	494.84	880.34
SD	59.09	417.16	742.14

EUTERPE	Total	7.07 m^2	12.57m^2
A6E1	5.05	35.64	63.40
A6E2	19.67	138.84	247.01
L4E1	6.47	45.69	81.28
L4E2	60.30	425.75	757.42
L5E1	37.33	263.58	468.91
L5E2	13.78	97.31	173.12
L5E3	1.35	9.56	17.00
L5E4	6.57	46.40	82.55
sum	150.53	1062.76	1890.69
average	18.82	132.85	236.34
SD	20.31	143.38	255.07

Fruit Removed

	weight that would have fallen	1.5m	% weight of fruitfall on ground	%weight of fruit lost
A6E1	2407.30	35.68	1.48	98.52
A6E2	2517.79	139.01	5.52	94.48
L4E1	2041.80	45.75	2.24	97.76
L4E2	586.32	426.27	72.70	27.30
L5E1	2634.41	263.90	10.02	89.98
L5E2	968.93	97.43	10.06	89.94
L5E3	441.70	9.57	2.17	97.83
L5E4	612.75	46.46	7.58	92.42
A1WI	1937.36	1148.34	59.27	40.73
A1W2	1444.56	1133.62	78.47	21.53
A1W3	1937.36	478.20	24.68	75.32
A1W4	1637.88	148.22	9.05	90.95
A6W1	978.20	178.91	18.29	81.71
A6W2	978.20	459.94	47.02	52.98
A6W3	978.20	217.73	22.26	77.74
L4W1	522.36	198.60	38.02	61.98

Average Percent Removed and Standard Deviation for *Euterpe*: 86.03%, SD 23.98%
Average Percent Removed and Standard Deviation for *Welfia*: 62.87%, SD 23.35%

Appendix II: Nutrient Analysis

Correlation Matrix of Crop Sizes with Nutrients
CS=Crop size

EUTERPE
Correlations

		CS	C	N	CN	NP	P	K	CA	MG	FE
CS	Pearson Corr.	1	-0.68	-0.317	-0.42	-0.567	0.617	0.661	0.369	-0.52	0.011
	Sig. (2-tailed)	.	0	0.028	0.003	0	0	0	0.01	0	0.943
	N	48	48	48	48	48	48	48	48	48	48
C	Pearson Corr.	-0.68	1	0.444	0.638	0.819	-0.896	-0.978	-0.521	0.747	0.01
	Sig. (2-tailed)	0	.	0.002	0	0	0	0	0	0	0.945
	N	48	48	48	48	48	48	48	48	48	48
N	Pearson Corr.	-0.317	0.444	1	-0.407	0.878	-0.795	-0.249	-0.996	0.927	-0.892
	Sig. (2-tailed)	0.028	0.002	.	0.004	0	0	0.088	0	0	0
	N	48	48	48	48	48	48	48	48	48	48
CN	Pearson Corr.	-0.42	0.638	-0.407	1	0.08	-0.231	-0.784	0.325	-0.034	0.776
	Sig. (2-tailed)	0.003	0	0.004	.	0.587	0.114	0	0.024	0.817	0
	N	48	48	48	48	48	48	48	48	48	48
NP	Pearson Corr.	-0.567	0.819	0.878	0.08	1	-0.988	-0.682	-0.917	0.993	-0.566
	Sig. (2-tailed)	0	0	0	0.587	.	0	0	0	0	0
	N	48	48	48	48	48	48	48	48	48	48
P	Pearson Corr.	0.617	-0.896	-0.795	-0.231	-0.988	1	0.785	0.845	-0.964	0.434
	Sig. (2-tailed)	0	0	0	0.114	0	.	0	0	0	0.002
	N	48	48	48	48	48	48	48	48	48	48
K	Pearson Corr.	0.661	-0.978	-0.249	-0.784	-0.682	0.785	1	0.333	-0.594	-0.217
	Sig. (2-tailed)	0	0	0.088	0	0	0	.	0.021	0	0.139
	N	48	48	48	48	48	48	48	48	48	48
CA	Pearson Corr.	0.369	-0.521	-0.996	0.325	-0.917	0.845	0.333	1	-0.956	0.848
	Sig. (2-tailed)	0.01	0	0	0.024	0	0	0.021	.	0	0
	N	48	48	48	48	48	48	48	48	48	48
MG	Pearson Corr.	-0.52	0.747	0.927	-0.034	0.993	-0.964	-0.594	-0.956	1	-0.657
	Sig. (2-tailed)	0	0	0	0.817	0	0	0	0	.	0
	N	48	48	48	48	48	48	48	48	48	48
FE	Pearson Corr.	0.011	0.01	-0.892	0.776	-0.566	0.434	-0.217	0.848	-0.657	1
	Sig. (2-tailed)	0.943	0.945	0	0	0	0.002	0.139	0	0	.
	N	48	48	48	48	48	48	48	48	48	48
MN	Pearson Corr.	-0.206	0.278	0.984	-0.562	0.779	-0.675	-0.073	-0.965	0.846	-0.958
	Sig. (2-tailed)	0.16	0.056	0	0	0	0	0.621	0	0	0
	N	48	48	48	48	48	48	48	48	48	48
AL	Pearson Corr.	0.512	-0.735	-0.934	0.052	-0.991	0.96	0.579	0.961	-1	0.67
	Sig. (2-tailed)	0	0	0	0.724	0	0	0	0	0	0
	N	48	48	48	48	48	48	48	48	48	48

WELFIA
Correlations

		CS	C	N	CN	NP	P	K	CA	MG	FE
CS	Pearson Corr.	1	0.109	0.109	0.109	0.109	-0.109	-0.109	-0.109	-0.109	0.109
	Sig. (2-tailed)	.	0.491	0.491	0.491	0.491	0.491	0.491	0.491	0.491	0.491
	N	42	42	42	42	42	42	42	42	42	42
C	Pearson Corr.	0.109	1	1	1	1	-1	-1	-1	-1	1
	Sig. (2-tailed)	0.491	.	0	.	.	.	.	0	0	0
	N	42	42	42	42	42	42	42	42	42	42
N	Pearson Corr.	0.109	1	1	1	1	-1	-1	-1	-1	1
	Sig. (2-tailed)	0.491	0	.	.	.	.	.	0	.	0
	N	42	42	42	42	42	42	42	42	42	42
CN	Pearson Corr.	0.109	1	1	1	1	-1	-1	-1	-1	1
	Sig. (2-tailed)	0.491	.	.	.	.	0	.	.	.	.
	N	42	42	42	42	42	42	42	42	42	42
NP	Pearson Corr.	0.109	1	1	1	1	-1	-1	-1	-1	1
	Sig. (2-tailed)	0.491	.	.	.	.	0	.	.	.	0
	N	42	42	42	42	42	42	42	42	42	42
P	Pearson Corr.	-0.109	-1	-1	-1	-1	1	1	1	1	-1
	Sig. (2-tailed)	0.491	.	.	0	0	.	.	.	0	.
	N	42	42	42	42	42	42	42	42	42	42
K	Pearson Corr.	-0.109	-1	-1	-1	-1	1	1	1	1	-1
	Sig. (2-tailed)	0.491	.	.	.	.	.	.	.	0	.
	N	42	42	42	42	42	42	42	42	42	42
CA	Pearson Corr.	-0.109	-1	-1	-1	-1	1	1	1	1	-1
	Sig. (2-tailed)	0.491	0	0	.	.	.	.	.	.	.
	N	42	42	42	42	42	42	42	42	42	42
MG	Pearson Corr.	-0.109	-1	-1	-1	-1	1	1	1	1	-1
	Sig. (2-tailed)	0.491	0	.	.	.	0	0	.	.	0
	N	42	42	42	42	42	42	42	42	42	42
FE	Pearson Corr.	0.109	1	1	1	1	-1	-1	-1	-1	1
	Sig. (2-tailed)	0.491	0	0	.	0	.	.	.	0	.
	N	42	42	42	42	42	42	42	42	42	42
MN	Pearson Corr.	-0.109	-1	-1	-1	-1	1	1	1	1	-1
	Sig. (2-tailed)	0.491	.	.	0	.	0	.	.	.	.
	N	42	42	42	42	42	42	42	42	42	42
AL	Pearson Corr.	0.109	1	1	1	1	-1	-1	-1	-1	1
	Sig. (2-tailed)	0.491	.	.	.	.	.	.	.	0	.
	N	42	42	42	42	42	42	42	42	42	42

EUTERPE
Multiple Comparisons
Dependent Variable: CS
Tukey HSD

(I) P	(J) P	Mean Difference I-J	Std. Error	Sig.	95% Confidence Interval Lower Bound	Upper Bound
4.09	4.64	2146.25	647.97	0.01	338.30	3954.20
	6.92	2455.38	1181.75	0.24	-841.91	5752.67
	7.55	2649.38	1492.82	0.40	-1515.84	6814.60
	9.11	-2769.50	792.81	0.01	-4981.59	-557.42
4.64	4.09	-2146.25	647.97	0.01	-3954.20	-338.30
	6.92	309.13	1232.58	1.00	-3129.99	3748.25
	7.55	503.13	1533.37	1.00	-3775.25	4781.51
	9.11	-4915.75	866.76	0.00	-7334.18	-2497.33
6.92	4.09	-2455.38	1181.75	0.24	-5752.67	841.91
	4.64	-309.13	1232.58	1.00	-3748.25	3129.99
	7.55	194.00	1824.25	1.00	-4895.99	5283.99
	9.11	-5224.88	1314.51	0.00	-8892.61	-1557.16
7.55	4.09	-2649.38	1492.82	0.40	-6814.60	1515.84
	4.64	-503.13	1533.37	1.00	-4781.51	3775.25
	6.92	-194.00	1824.25	1.00	-5283.99	4895.99
	9.11	-5418.88	1599.98	0.01	-9883.10	-954.67
9.11	4.09	2769.50	792.81	0.01	557.42	4981.59
	4.64	4915.75	866.76	0.00	2497.33	7334.18
	6.92	5224.88	1314.51	0.00	1557.16	8892.61
	7.55	5418.88	1599.98	0.01	954.67	9883.10

Based on observed means.

WELFIA
Multiple Comparisons
Dependent Variable: CS
Tukey HSD

(I) P	(J) P	Mean Difference I-J	Std. Error	Sig.	95% Confidence Interval Lower Bound	Upper Bound
4.09	4.64	-187.56	477.76	1.00	-1562.83	1187.71
	6.92	924.14	498.11	0.43	-509.71	2357.99
	7.55	1187.88	472.00	0.12	-170.81	2546.58
	9.11	168.87	434.69	1.00	-1082.40	1420.14
	10.96	864.92	372.68	0.19	-207.86	1937.71
4.64	4.09	187.56	477.76	1.00	-1187.71	1562.83
	6.92	1111.70	520.97	0.27	-387.94	2611.34
	7.55	1375.44	496.06	0.07	-52.51	2803.40
	9.11	356.43	460.70	0.97	-969.72	1682.58
	10.96	1052.48	402.72	0.10	-106.77	2211.74
6.92	4.09	-924.14	498.11	0.43	-2357.99	509.71
	4.64	-1111.70	520.97	0.27	-2611.34	387.94
	7.55	263.74	515.69	1.00	-1220.71	1748.20
	9.11	-755.27	481.77	0.62	-2142.08	631.54
	10.96	-59.22	426.66	1.00	-1287.39	1168.96
7.55	4.09	-1187.88	472.00	0.12	-2546.58	170.81
	4.64	-1375.44	496.06	0.07	-2803.40	52.51
	6.92	-263.74	515.69	1.00	-1748.20	1220.71
	9.11	-1019.01	454.72	0.22	-2327.97	289.94
	10.96	-322.96	395.87	0.96	-1462.50	816.58
9.11	4.09	-168.87	434.69	1.00	-1420.14	1082.40
	4.64	-356.43	460.70	0.97	-1682.58	969.72
	6.92	755.27	481.77	0.62	-631.54	2142.08
	7.55	1019.01	454.72	0.22	-289.94	2327.97
	10.96	696.05	350.54	0.35	-313.00	1705.10
10.96	4.09	-864.92	372.68	0.19	-1937.71	207.86
	4.64	-1052.48	402.72	0.10	-2211.74	106.77
	6.92	59.22	426.66	1.00	-1168.96	1287.39
	7.55	322.96	395.87	0.96	-816.58	1462.50
	9.11	-696.05	350.54	0.35	-1705.10	313.00

Based on observed means.

Euterpe crop size

Coefficients

Model		Unstandardized Coefficients		Standardized	t	Sig.
		B	Std. Error	Beta		
1	(Constant)	253.427	942.771		0.269	0.789
	P	455.284	168.661	0.283	2.699	0.008
a	Dependent Variable: CS					

Euterpe mature crop size

Coefficients

Model		Unstandardized Coefficients		Standardized	t	Sig.
		B	Std. Error	Beta		
1	(Constant)	-1135.8	603.279		-1.883	0.063
	P	520.021	107.926	0.465	4.818	0
a	Dependent Variable: M					

Welfia crop size

Coefficients

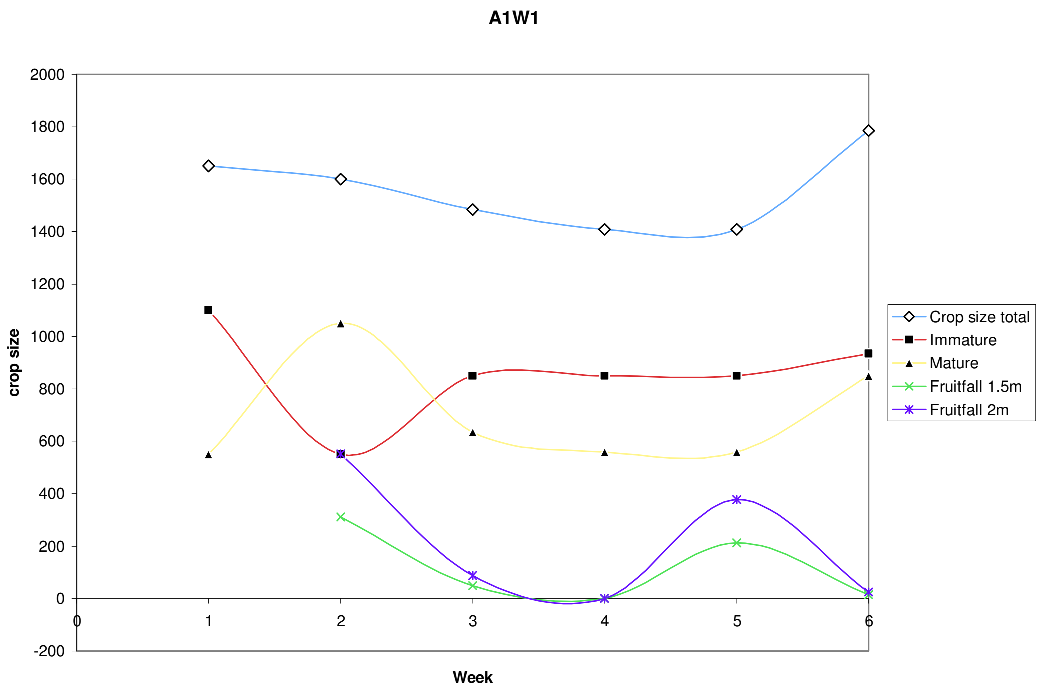
Model		Unstandardized Coefficients		Standardized	t	Sig.
		B	Std. Error	Beta		
1	(Constant)	2015.779	393.373		5.124	0
	P	-112.263	45.413	-0.173	-2.472	0.014
a	Dependent Variable: CS					

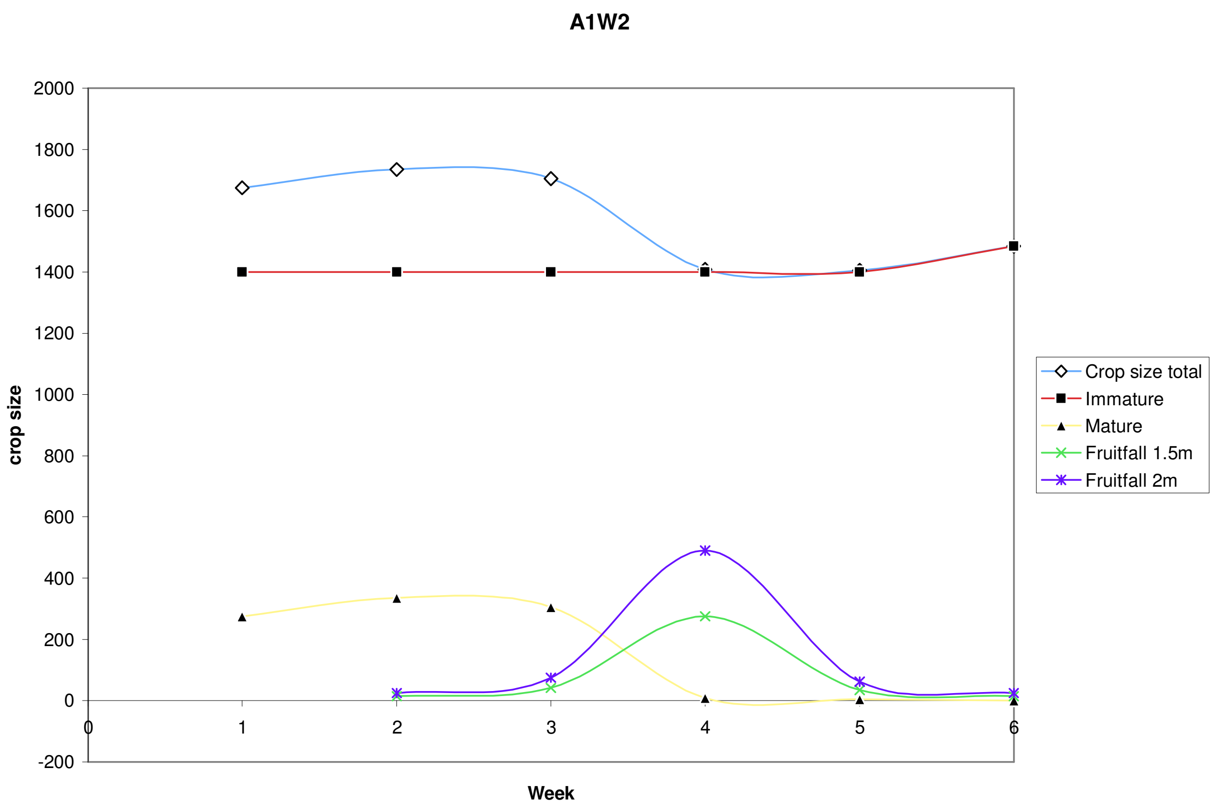
Welfia mature crop size

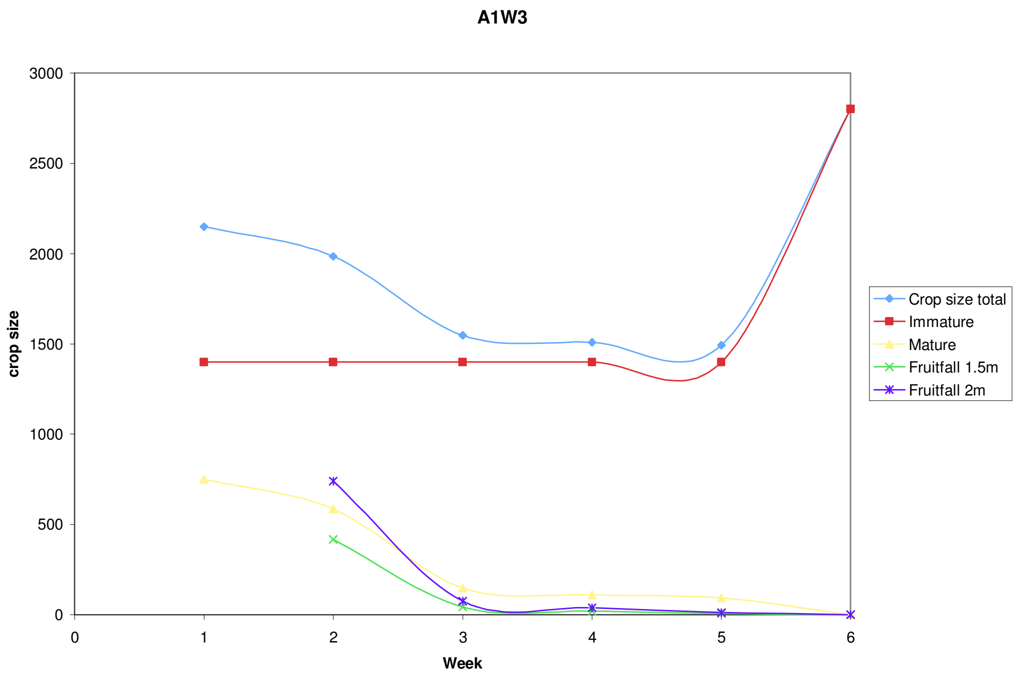
Coefficients

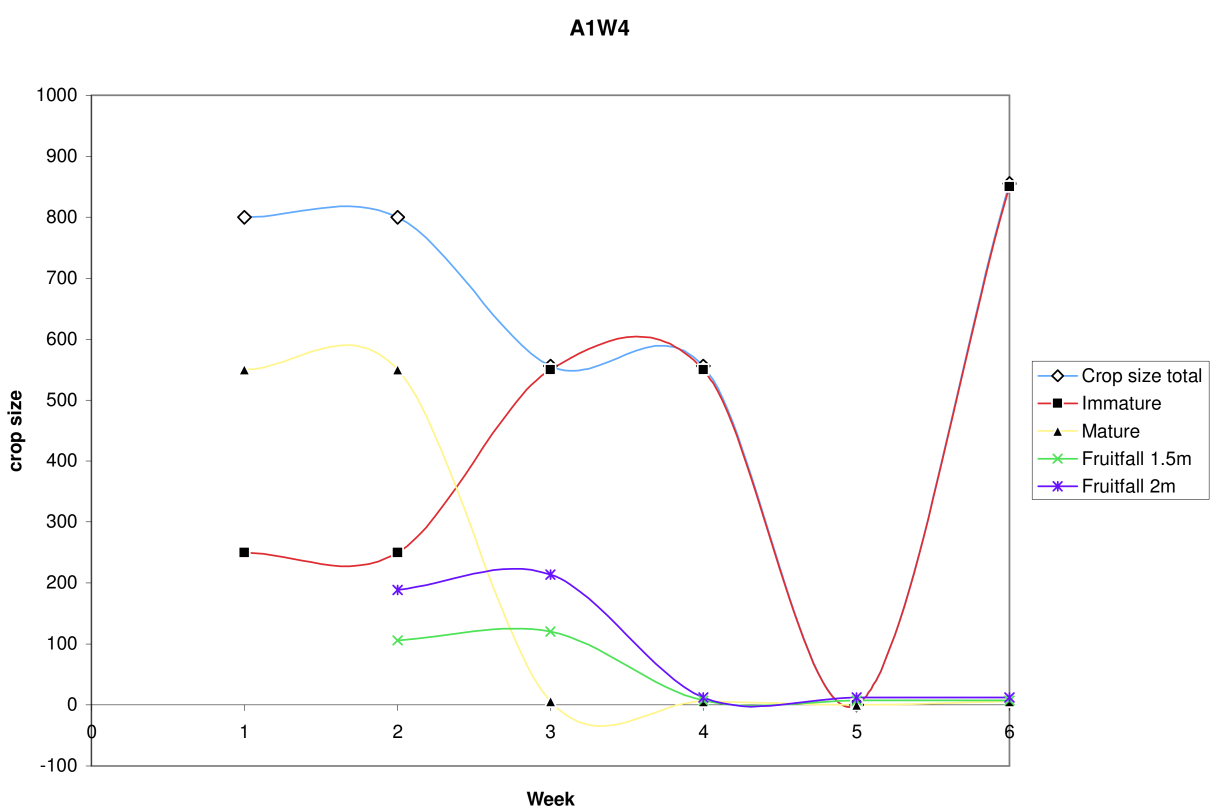
Model		Unstandardized Coefficients		Standardized	t	Sig.
		B	Std. Error	Beta		
1	(Constant)	861.672	183.959		4.684	0
	P	-60.055	21.237	-0.198	-2.828	0.005
a	Dependent Variable: M					

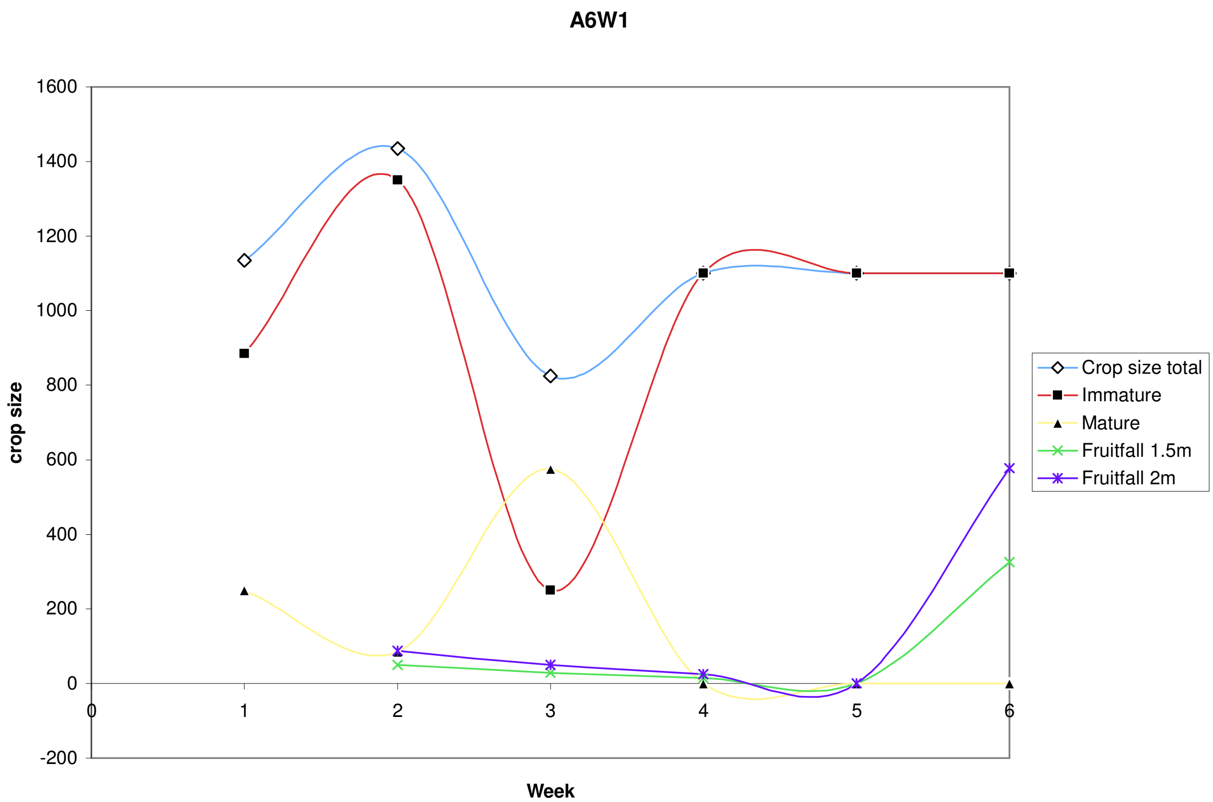
Appendix III. Crop Size, Phenophase, and Fruitfall over Six Weeks

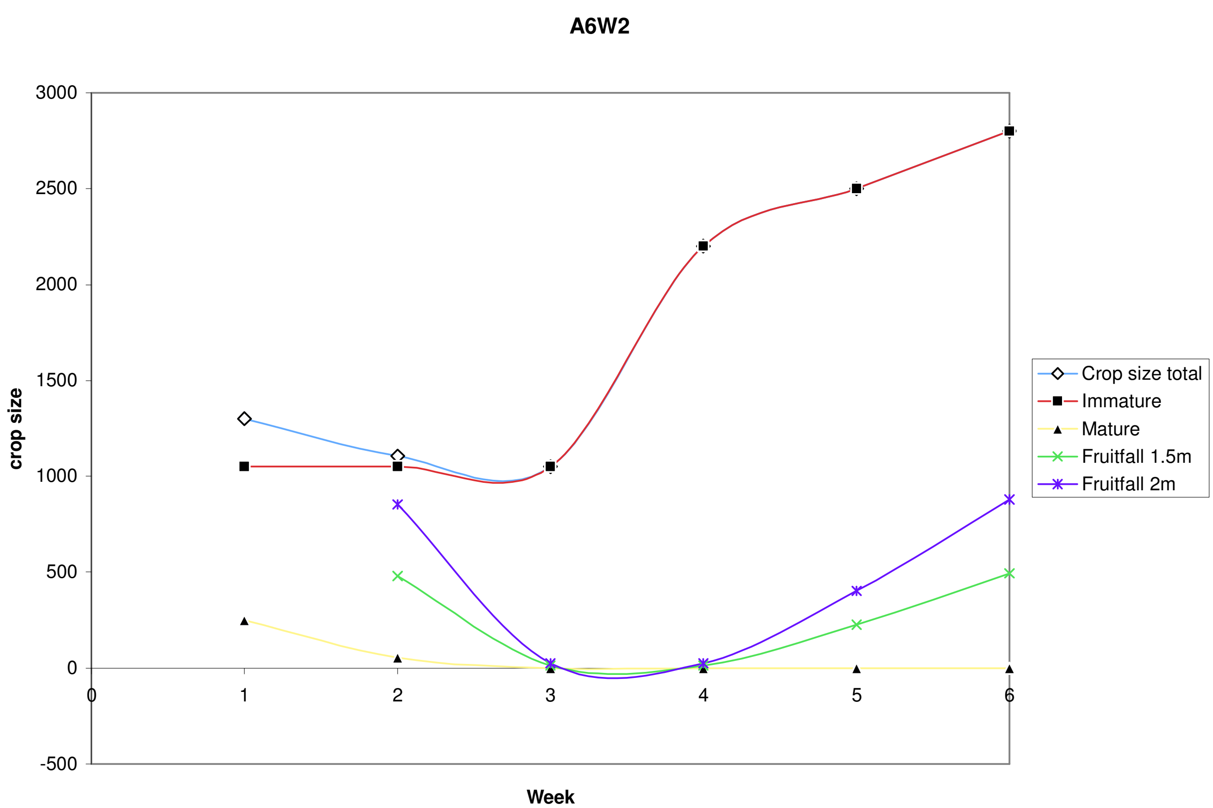


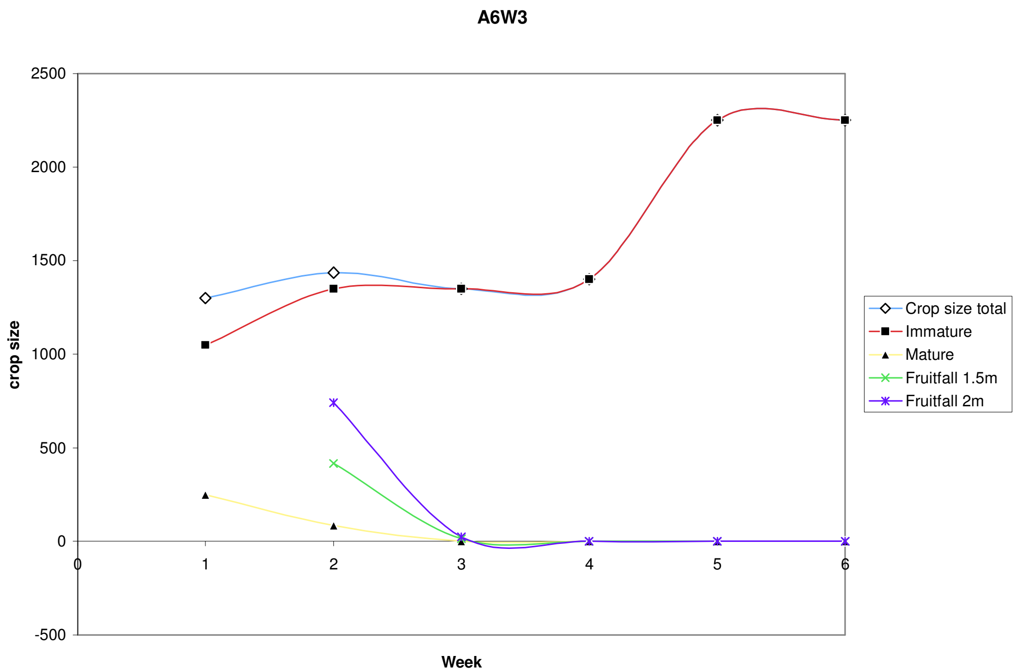


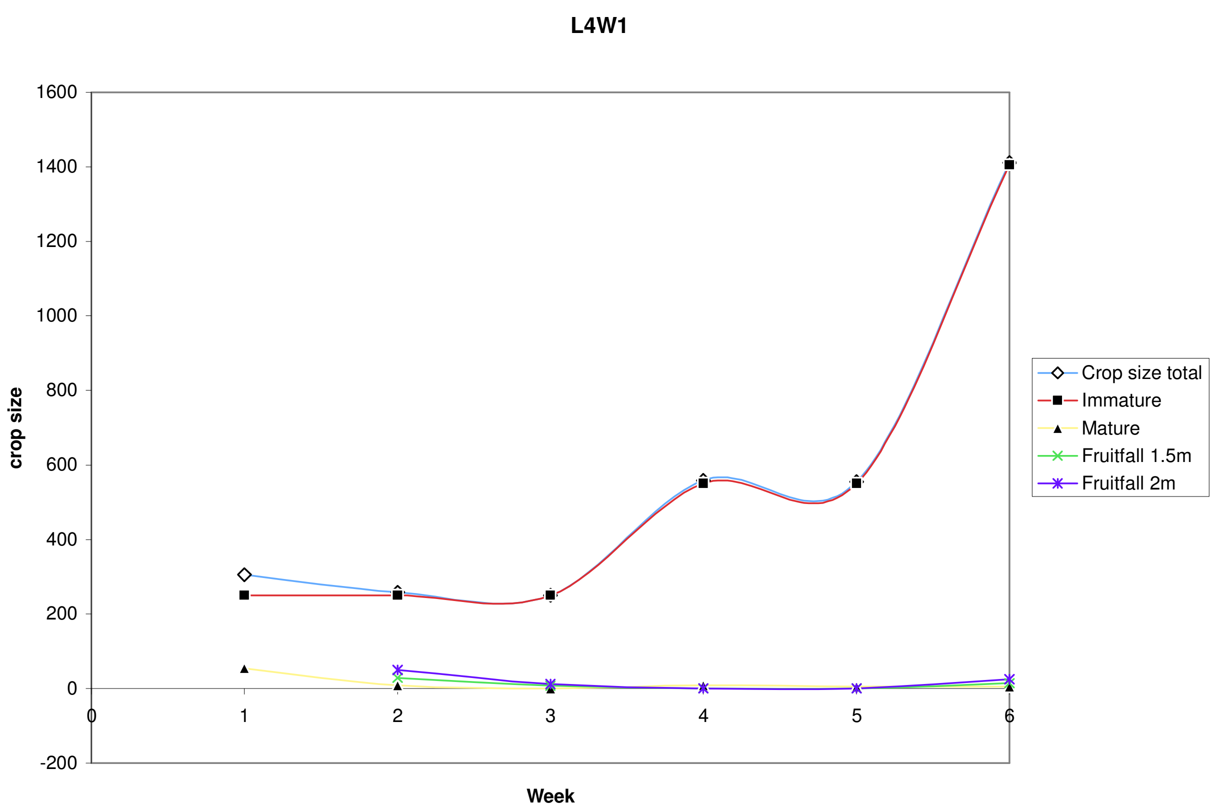

A1W3
3000
2500
2000
1500
1000
500
0
0
1
2
3
4
5
6
crop size
Week
Crop size total
Immature
Mature
Fruitfall 1.5m
Fruitfall 2m

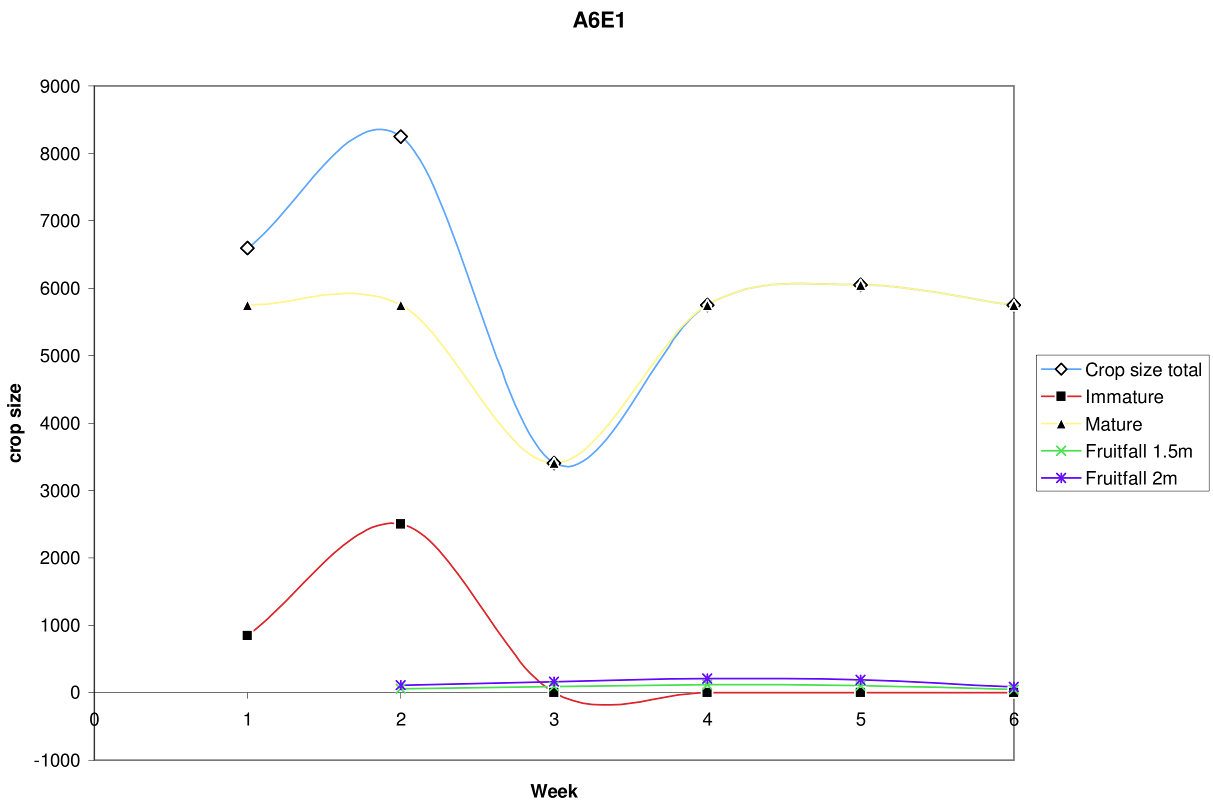

A1W4
1000
900
800
700
600
500
400
300
200
100
0
-100
0
1
2
3
4
5
6
crop size
Week
Crop size total
Immature
Mature
Fruitfall 1.5m
Fruitfall 2m

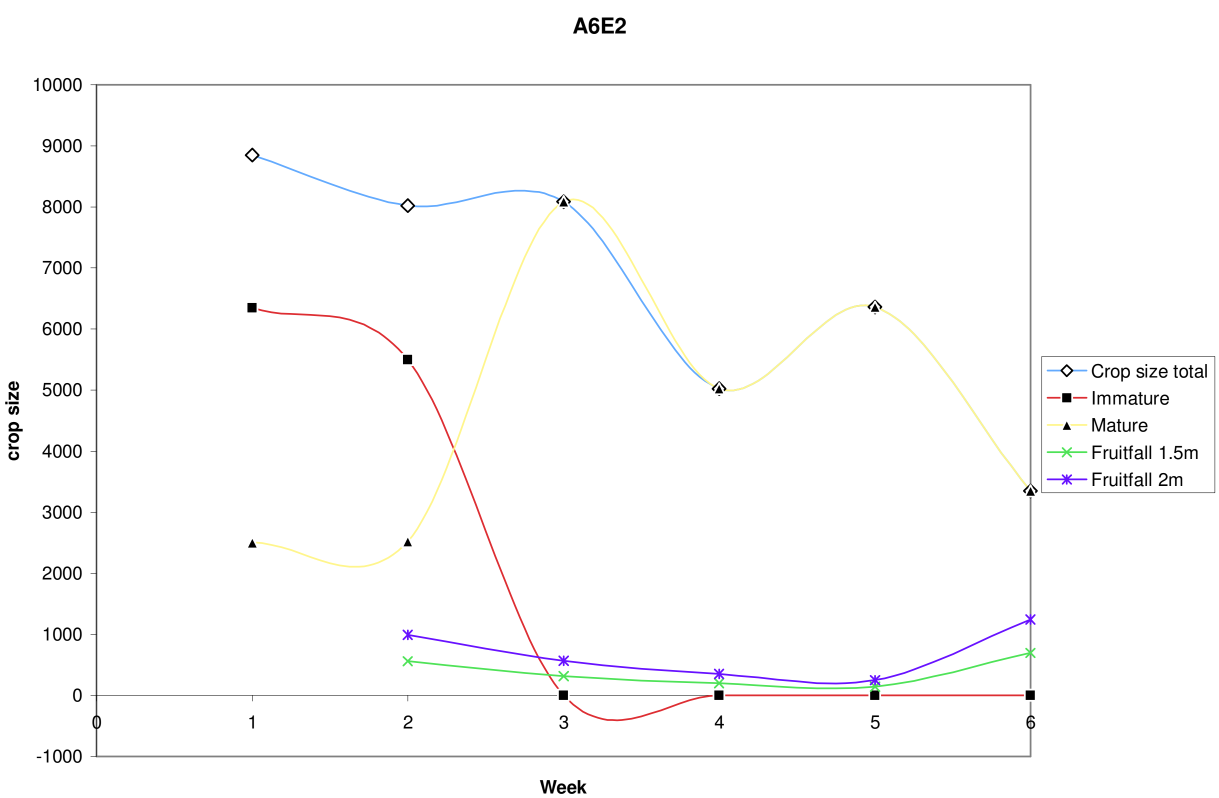

A6W1
1600
1400
1200
1000
800
600
400
200
0
-200
crop size
0
1
2
3
4
5
6
Week
Crop size total
Immature
Mature
Fruitfall 1.5m
Fruitfall 2m

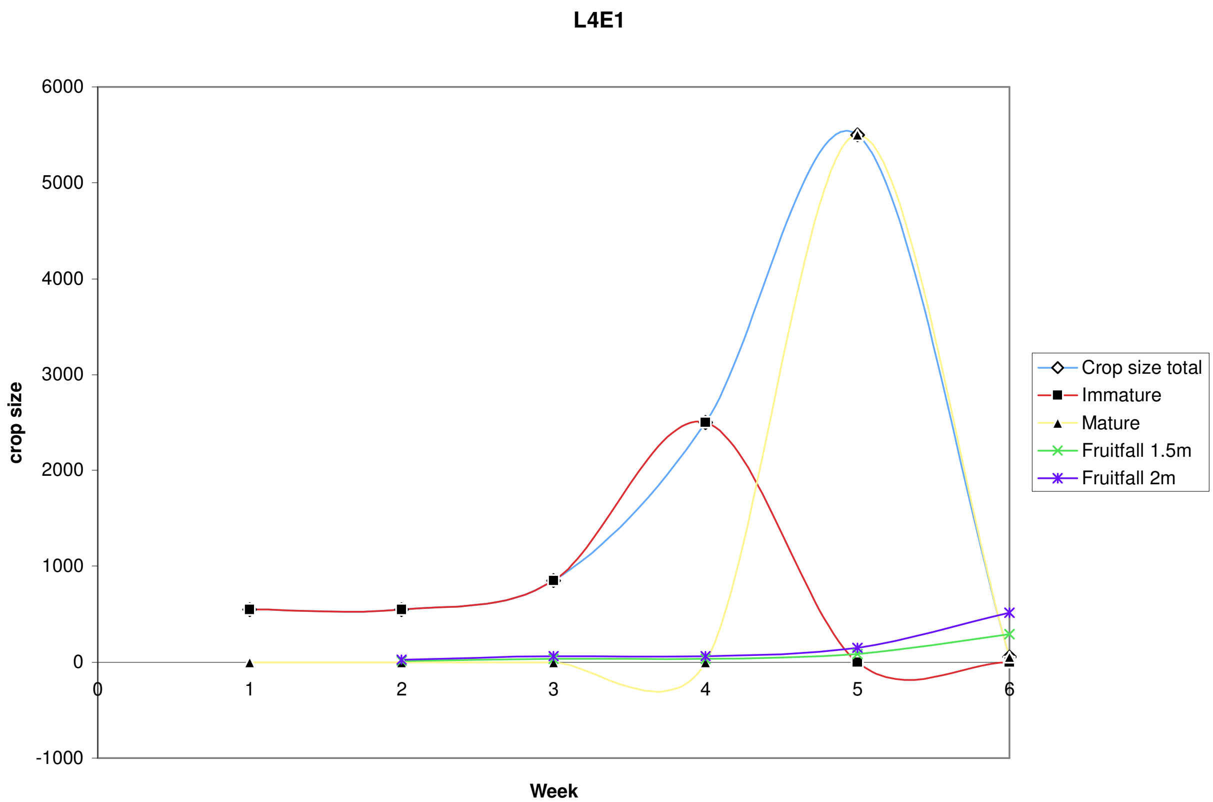

A6W2
3000
2500
2000
1500
1000
500
0
-500
crop size
0
1
2
3
4
5
6
Week
Crop size total
Immature
Mature
Fruitfall 1.5m
Fruitfall 2m

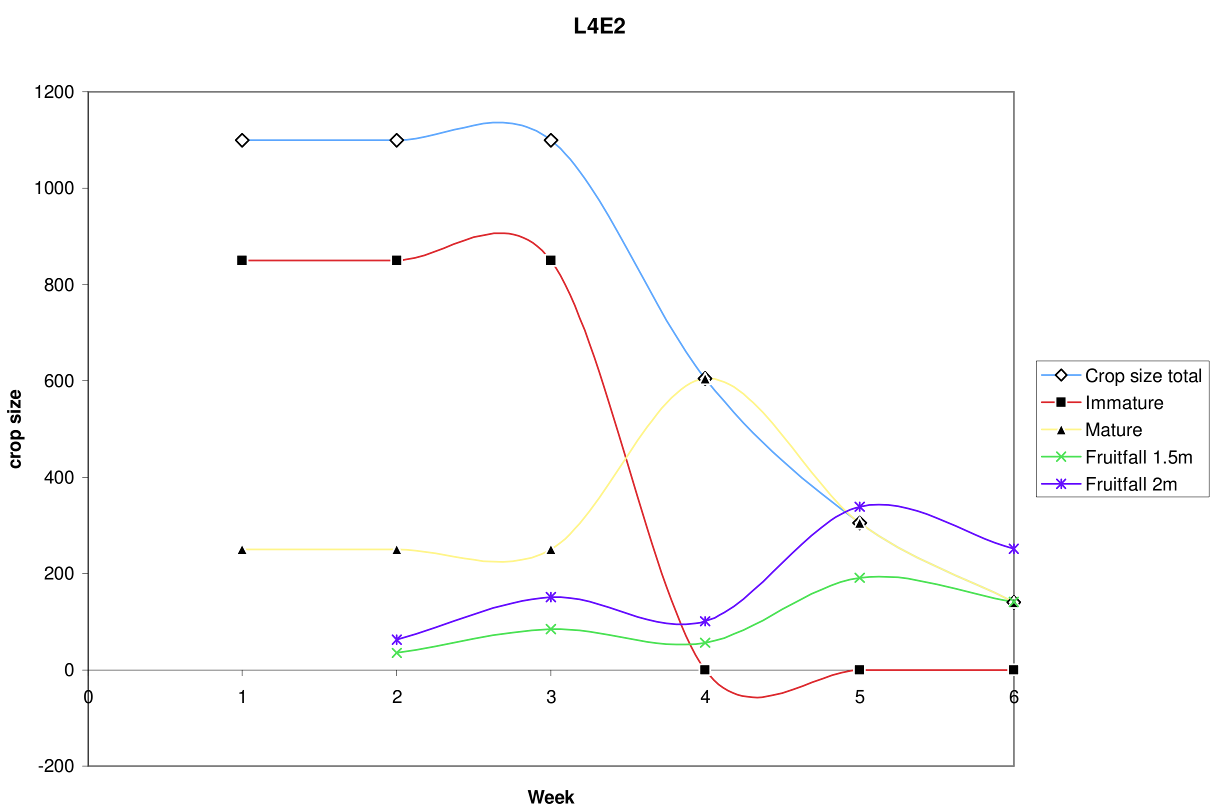

A6W3
2500
2000
1500
1000
500
0
-500
crop size
0
1
2
3
4
5
6
Week
Crop size total
Immature
Mature
Fruitfall 1.5m
Fruitfall 2m

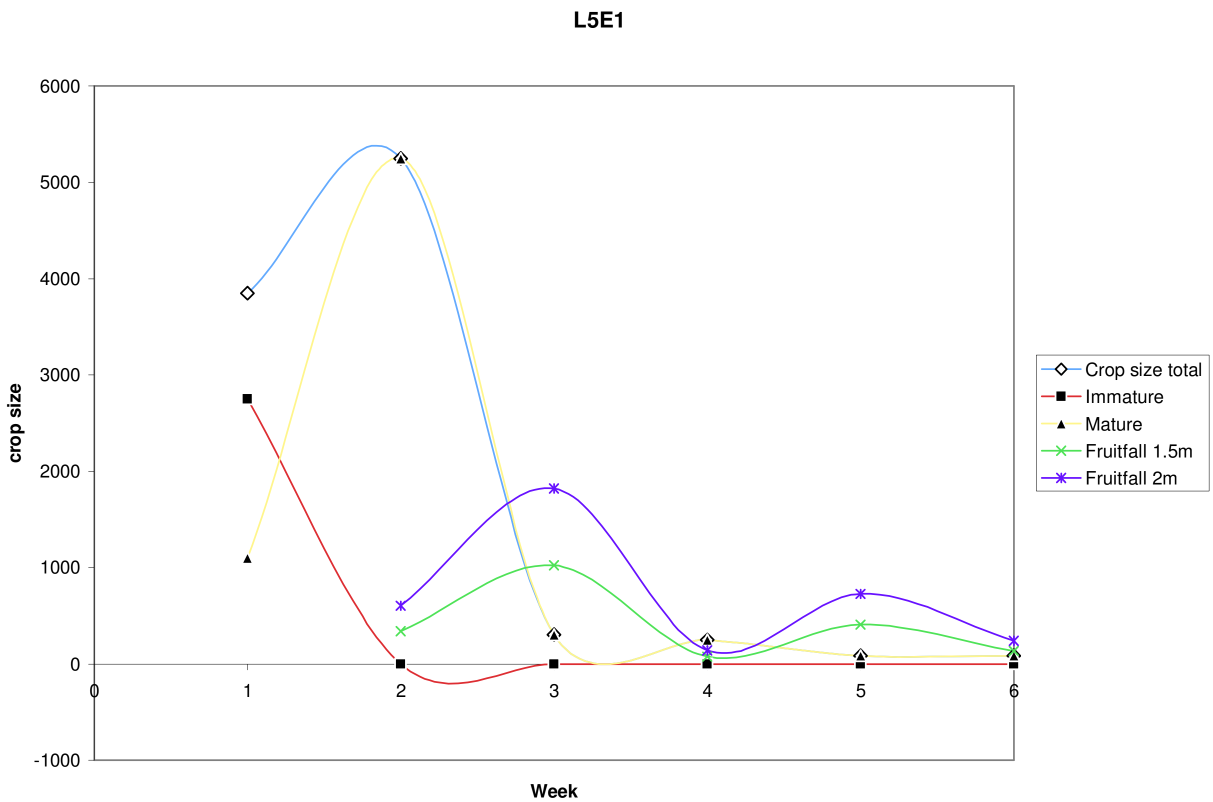

L4W1
1600
1400
1200
1000
800
600
400
200
0
-200
crop size
0
1
2
3
4
5
6
Week
Crop size total
Immature
Mature
Fruitfall 1.5m
Fruitfall 2m

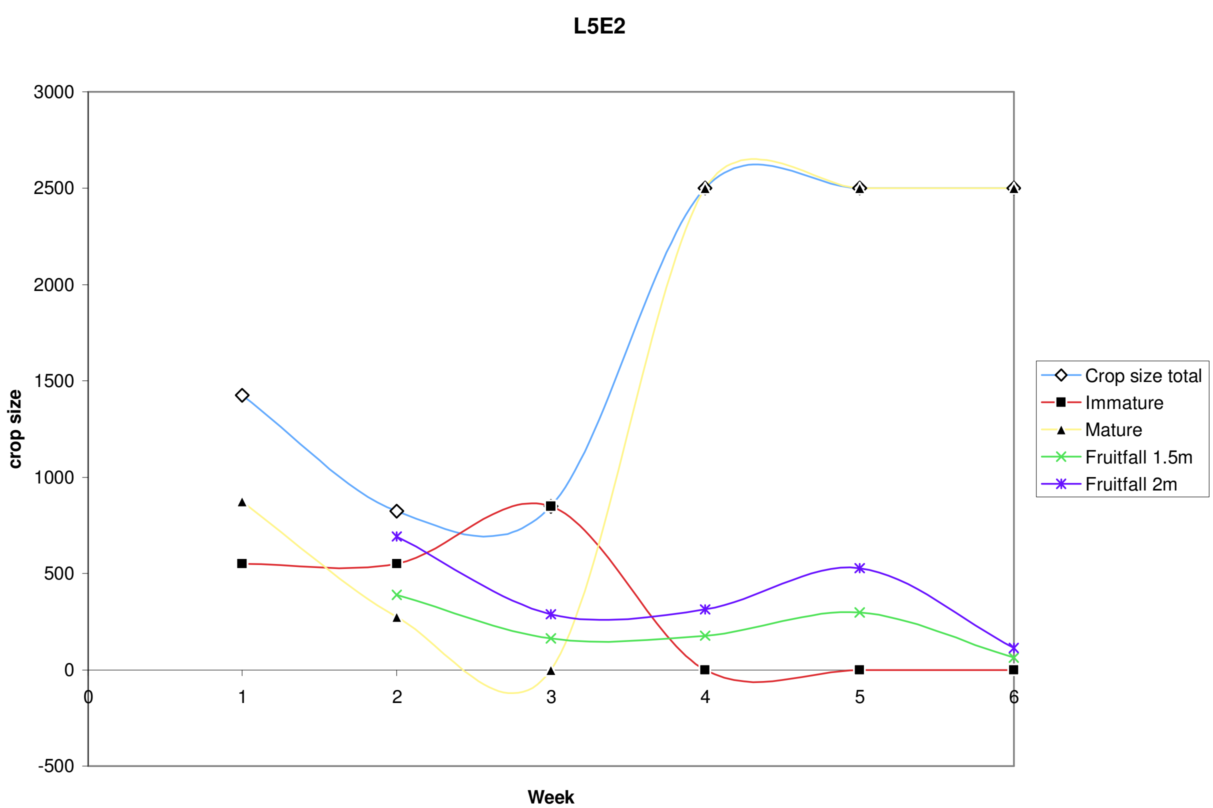

A6E1
9000
8000
7000
6000
5000
4000
3000
2000
1000
0
-1000
crop size
0
1
2
3
4
5
6
Week
Crop size total
Immature
Mature
Fruitfall 1.5m
Fruitfall 2m

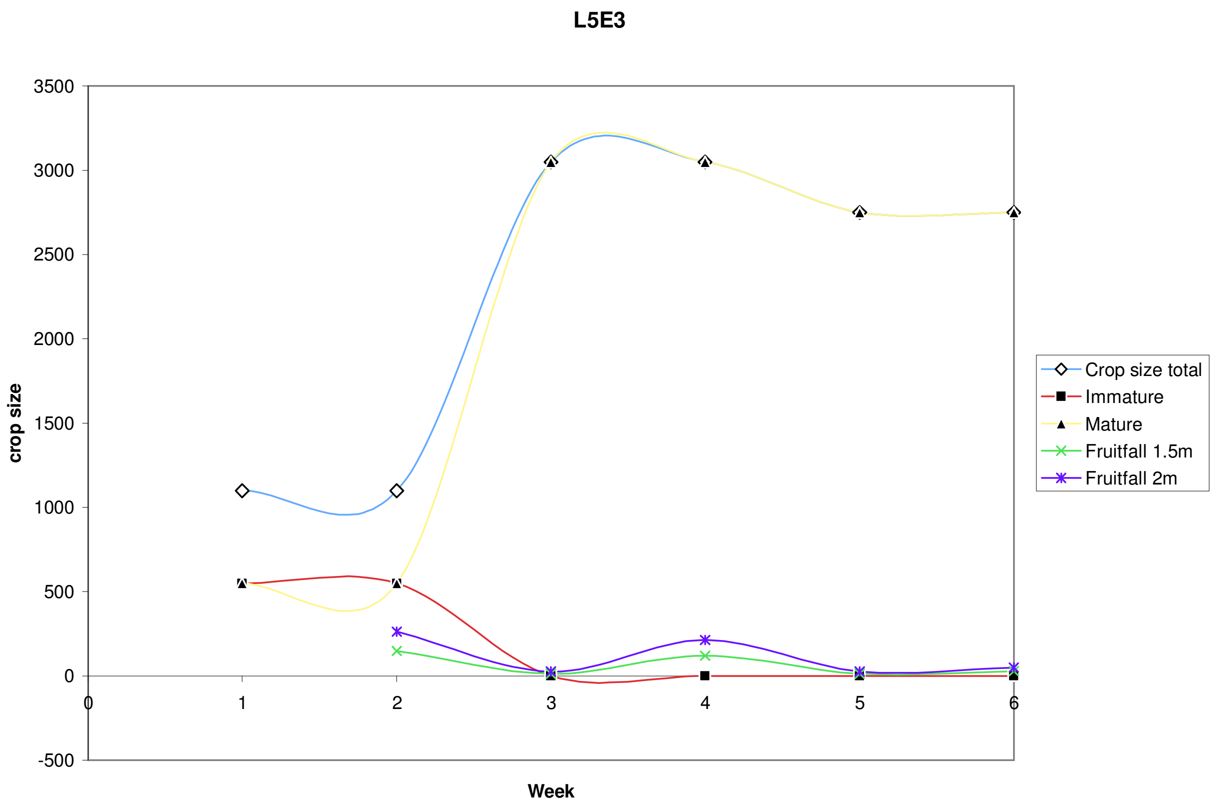

A6E2
10000
9000
8000
7000
6000
5000
4000
3000
2000
1000
0
-1000
crop size
0
1
2
3
4
5
6
Week
Crop size total
Immature
Mature
Fruitfall 1.5m
Fruitfall 2m

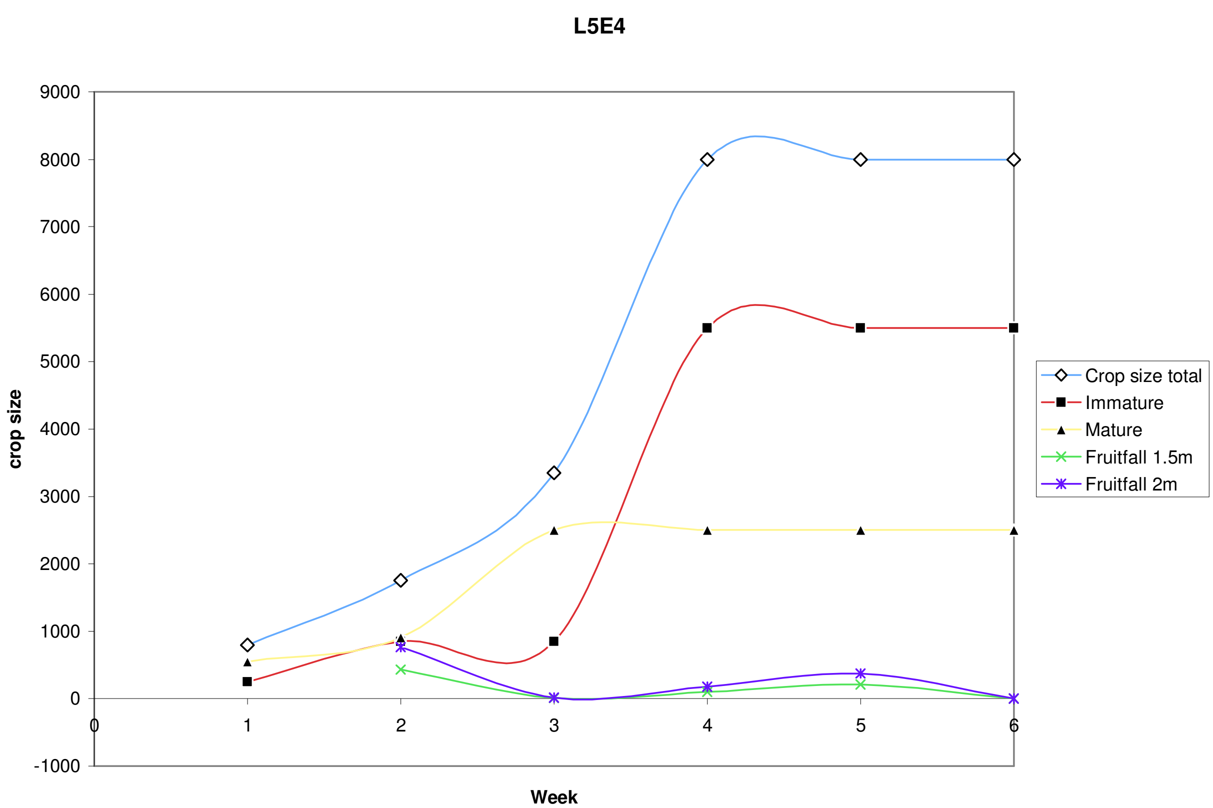

L4E1
6000
5000
4000
3000
2000
1000
0
-1000
crop size
0
1
2
3
4
5
6
Week
Crop size total
Immature
Mature
Fruitfall 1.5m
Fruitfall 2m


L4E2
1200
1000
800
600
400
200
0
-200
crop size
0
1
2
3
4
5
6
Week
Crop size total
Immature
Mature
Fruitfall 1.5m
Fruitfall 2m


L5E1
crop size
6000
5000
4000
3000
2000
1000
0
-1000
0
1
2
3
4
5
6
Week
Crop size total
Immature
Mature
Fruitfall 1.5m
Fruitfall 2m


L5E2
crop size
3000
2500
2000
1500
1000
500
0
-500
0
1
2
3
4
5
6
Week
Crop size total
Immature
Mature
Fruitfall 1.5m
Fruitfall 2m


L5E3
3500
3000
2500
2000
1500
1000
500
0
-500
crop size
0
1
2
3
4
5
6
Week
Crop size total
Immature
Mature
Fruitfall 1.5m
Fruitfall 2m


L5E4
9000
8000
7000
6000
5000
4000
3000
2000
1000
0
-1000
crop size
0
1
2
3
4
5
6
Week
Crop size total
Immature
Mature
Fruitfall 1.5m
Fruitfall 2m