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THE EFFECT OF FLOWERING ON RUBBER PRODUCTION IN GUAYULE (PARTHENIUM ARGENTATUM GRAY)

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THE EFFECT OF FLOWERING ON RUBBER PRODUCTION
IN GUAYULE (PARTHENIUM ARGENTATUM GRAY)

by

Katherine Lucia Willard

A Thesis Submitted to the Faculty of the
DEPARTMENT OF PLANT SCIENCES
In Partial Fulfillment of the Requirements
For the Degree of
MASTER OF SCIENCE

In the Graduate College
THE UNIVERSITY OF ARIZONA

1985
STATEMENT BY AUTHOR

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D. T. Ray

May 1, 1985

D. T. RAY
Professor of Plant Sciences
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# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Chapter</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>LIST OF TABLES</td>
<td>v</td>
</tr>
<tr>
<td>LIST OF ILLUSTRATIONS</td>
<td>vi</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>vii</td>
</tr>
<tr>
<td>1. INTRODUCTION AND LITERATURE REVIEW</td>
<td>1</td>
</tr>
<tr>
<td>2. MATERIALS AND METHODS</td>
<td>12</td>
</tr>
<tr>
<td>3. RESULTS AND DISCUSSION</td>
<td>17</td>
</tr>
<tr>
<td>REFERENCES</td>
<td>50</td>
</tr>
</tbody>
</table>
# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. A Comparison of The Average Fresh Weight, in Grams Per Plant, For Three Flowering Treatments and Four Lines</td>
<td>18</td>
</tr>
<tr>
<td>2. A Comparison of the Average % Dry Weight For Three Flowering Treatments and Four Lines</td>
<td>20</td>
</tr>
<tr>
<td>3. A Comparison of the Average Dry Weight, in Grams Per Plant, For Three Flowering Treatments and Four Lines</td>
<td>21</td>
</tr>
<tr>
<td>4. A Comparison of the Average Plant Height, in cm Per Plant, For Three Flowering Treatments and Four Lines</td>
<td>24</td>
</tr>
<tr>
<td>5. A Comparison of the Average Plant Width, in cm Per Plant, For Three Flowering Treatments and Four Lines</td>
<td>26</td>
</tr>
<tr>
<td>6. A Comparison of the Average % Resin Per Plant For Three Treatments and Four Lines</td>
<td>27</td>
</tr>
<tr>
<td>7. A Comparison of the Average % Rubber Per Plant For Three Treatments and Four Lines</td>
<td>30</td>
</tr>
<tr>
<td>8. A Comparison of the Average Resin Yield, in Grams Per Plant, For Three Treatments and Four Lines</td>
<td>33</td>
</tr>
<tr>
<td>9. A Comparison of the Average Rubber Yield, in Grams Per Plant For Three Treatments and Four Lines</td>
<td>35</td>
</tr>
</tbody>
</table>
### LIST OF ILLUSTRATIONS

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Mean Fresh Weight, in Grams per Plant, of Four Lines for Three Flowering Treatments</td>
<td>19</td>
</tr>
<tr>
<td>2.</td>
<td>Mean Dry Weight, in Grams Per Plant, For Four Lines and Three Flowering Treatments</td>
<td>22</td>
</tr>
<tr>
<td>3.</td>
<td>Mean Height, in cm Per Plant, of Three Flowering Treatments For Four Lines</td>
<td>25</td>
</tr>
<tr>
<td>4.</td>
<td>Mean % Resin Per Plant of Three Flowering Treatments For Four Lines</td>
<td>28</td>
</tr>
<tr>
<td>5.</td>
<td>Mean % Rubber Per Plant of Three Flowering Treatments And Four Lines</td>
<td>31</td>
</tr>
<tr>
<td>6.</td>
<td>Resin Yield, in Grams Per Plant, For Four Lines And Three Treatments</td>
<td>34</td>
</tr>
<tr>
<td>7.</td>
<td>Mean Rubber Yield, In Grams Per Plant, For Three Flowering Treatments and Four Lines</td>
<td>36</td>
</tr>
<tr>
<td>8.</td>
<td>The Relationship Between Plant Height, in cm Per Plant, And Fresh Weight, in Grams Per Plant,</td>
<td>38</td>
</tr>
<tr>
<td></td>
<td>for Three Flowering Treatments and Four Lines</td>
<td></td>
</tr>
<tr>
<td>9.</td>
<td>The Relationship Between Plant Width, in cm Per Plant, and Fresh Weight, in Grams Per Plant,</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td>For Three Flowering Treatments and Four Lines</td>
<td></td>
</tr>
</tbody>
</table>
ABSTRACT

Four guayule lines were tested under three flowering regimes to determine the influence of flowering upon rubber production. Additional data from individual plants included resin production, fresh weight, and % dry weight. The three flowering treatments were: a control where plants flowered and set seed without interference; clipping inflorescences from elongated peduncles just before dehiscence; and removing flower buds as soon as they appeared. At the end of one growing season, no significant differences were found between treatments for either % dry weight or % resin. Plants in the control treatment exhibited significantly lower fresh weight than the plants in the dehiscent treatment but not lower than the non-flowering treatment. In addition, the controls were significantly lower than the other two treatments in total yields of rubber and resin. Significant differences in % rubber were observed between the dehiscent treatment and the treatment in which buds were removed shortly after initiation; however, neither were significantly different from the control. The test will be continued for one more growing season.
CHAPTER 1
INTRODUCTION AND LITERATURE REVIEW

Guayule, *Parthenium argentatum* Gray, provides an excellent source of domestic natural rubber. At the present time nearly all the natural rubber utilized in the world is produced by the rubber tree, *Hevea brasiliensis*. The development of guayule as a commercial rubber producing crop would help satisfy the increasing world demand for natural rubber as well as provide the United States with a dependable domestic source of rubber (Riedl, 1983). Although the quality of rubber produced by guayule is considered to be nearly equal in quality (Berger and Fontanoz, 1983), the cost of growing and extracting guayule rubber is prohibitive enough at this point to prevent it from becoming a successful competitor with *Hevea* rubber (McGinnies and Mills, 1980). This has not always been the case, as the first commercial use of guayule rubber was in 1888 by the New York Belting and Packing Co. The guayule shrubs were imported from Mexico and the rubber extracted by immersion in hot water (McGinnies and Mills, 1980). A mechanical extraction method was developed in 1902 after which the Continental Rubber Company was organized in New York with subsidiary companies in Mexico. These companies represented nearly the entire guayule rubber industry until World War II. Annual yields varied during this period, with a maximum production of 21.5 million pounds in 1910 (McGinnies...
and Mills 1980). Research into cultural practices began in 1912 when it became obvious that natural guayule stands were becoming depleted. The majority of these studies were in California and Arizona due to the threatening nature of the Mexican revolution. This work was carried out under the direction of Dr. W. B. McCallum until the USDA purchased the Continental Rubber Company in 1942 (Hammond and Polhamus, 1965).

The Emergency Rubber Project was initiated in 1942 due to the unavailability of rubber from the Far East. Natural rubber was in high demand for strategic purposes, therefore a need to develop a stable domestic source was realized. Under the direction of the USDA, research progressed at a rapid rate with almost 3 million pounds of rubber being produced in only 3-1/2 years. The project was abandoned after World War II once the importation of Hevea rubber was resumed and the imminent strategic need had subsided. Nearly all research in guayule was abandoned by 1959 (Hammond and Polhamus, 1965).

Guayule is a native species of the Chihuahuan Desert of Northern Mexico and Southern Texas. The geographical range of guayule is scattered throughout the central plateau of Mexico. Plants are generally found in spotty stands, presumably only where environmental conditions are ideally suited for proper growth and reproduction (Müller, 1946).

Although the native range of guayule is limited, it can be grown successfully in other areas of the Southwest with proper agronomic practices. Guayule has been grown on an economic scale in Texas, Arizona, and California (Hammond and Polhamus, 1965). All these areas are
characterized by low rainfall and consequently are faced with a limited, and rapidly shrinking, amount of available water for irrigation. Many of the farms in these areas are presently growing crops which require large quantities of water to complete a growing season. Thus, if guayule could be developed into a viable agronomic crop it would possibly require much less water than the conventional crops in these areas of low rainfall. Guayule in its natural range grows between elevations of 600M and 2,150M above sea level with the majority of prominent stands found between 1550M and 2000M (Polhamus, 1962).

Within its elevational habitat, guayule has affinities for specific soil types. It is typically found on calcareous, well drained, gravelly soils, usually on slopes near higher hills. It is almost never found on alluvial soils unless there is a gravelly area associated with it (Muller, 1946). The average yearly rainfall for this region is 21 to 50cm (Muller, 1946). Cooperrider and Culley, as described in Polhamus (1962) believe that guayule actually requires more rainfall than this, and substantiate their idea by the fact that shrubs are often found growing in outwash areas characterized by soils with high infiltration rates. They estimate that irrigation due to natural runoff may increase the yearly amount of available water to 30 to 60cm annually. This explains why plants grown in Tucson, which has an average annual rainfall of about 28cm, do not prosper without supplemental irrigations.

Guayule grows as a dense shrub and can reach heights of 1M in natural stands; however, most of the shrubs are found to be approximately
50cm high (Hammond and Polhamus, 1965). Initial branching occurs just above the soil surface. Each branch terminates in an inflorescence, after which two or three of the uppermost lateral buds grow into new branches. This pattern continues whenever conditions are suitable for growth, forming a compact, symmetrical shrub. Growth occurs primarily when daytime temperatures are warm and adequate moisture is present. This growth pattern indicates that while flowering is related to temperature and availability of moisture, it is an indirect relationship. Vegetative growth is the direct result of favorable environmental conditions while flowering is a subsequent consequence (Hammond and Polhamus, 1965).

The shape and color of guayule leaves varies between lines and in response to the climatic conditions under which shrubs are grown. Generally, leaves appear lanceolate with any degree of lobing from deeply lobed to almost entire. They range from 6 to 7 mm long and 2 to 2-1/2 mm wide during the summer, to a much stouter winter leaf of 1 to 3 mm long and 3 to 7 mm wide. The color ranges from a grey-green when adequate water is available, to a silvery grey when the plant is experiencing water stress. Leaves persist on the plant until early December after which they shrivel, die and are eventually shed. This continues until only a terminal leaf cluster remains in early February (Muller, 1946). During this period assimilates, including rubber or rubber precursors, are thought to be translocated from the leaves to the stem (Garrot, 1984).
Guayule roots are similar to those produced by many arid plants. As long as there is no impeding hardpan layer, a strong tap root will develop and grow to excessive depths. Usually such hardpans are impossible to avoid and the tap root does not penetrate more than 1M. Fiberous roots are concentrated in the top 18 cm of the soil with a possible lateral spread of up to 3M (Polhamus, 1962). This extensive development of fibrous roots close to the soil surface is needed for efficient harvesting of water from sporadic rainfalls in its native habitat.

As previously stated, flowering is a response to active vegetative growth induced by proper moisture and temperature conditions. First year seedlings planted in Tucson during the fall can be expected to flower in early to mid-March. The initial flowering is usually characterized by a single inflorescence, since the plant is still growing as a single stem. Shortly after this first flowering, branching will begin and the number of flowers observed on a single plant will increase exponentially throughout the growing season. Profuse flowering will continue as long as the proper moisture and temperature regimes persist (Hammond and Polhamus, 1965). The guayule inflorescence is a one-sided compound cyme, borne on a single peduncle which raises it above the level of the foliage. Each flower consists of five unisex pistillate ray florets, each in association with two sterile disc florets. The remaining disc florets produce viable pollen but have an abortive pistil (Hammond and Polhamus, 1965). Since only the ray florets have functional ovaries the maximum number of achenes produced
per flower head is five. Even under optimum conditions, only 35% of the achenes will become fully developed (Artschwager, 1943). Despite this low viability rate, large numbers of achenes may develop in one growing season due to the large number of inflorescences produced per plant as observed in this study. Lack of flowering and subsequent achene development would presumably lead to the use of assimilates in other plant functions. When flowering heads were removed from wheat, new patterns of translocation were established within two to three days (Austin and Edrich, 1975). Assimilates were found to be translocated to other developing tillers and sink areas. Assuming this same transition will occur in guayule, the question is whether assimilates will be used to produce more rubber, other storage compounds such as carbohydrates, or metabolized for use in increasing plant growth.

Rubber is found in all parts of the guayule plant, but is present in greater amounts in the stems and roots (Artschwager, 1943). Unlike Hevea, where rubber is found in the form of a latex in lactifera, the majority of guayule rubber is stored within the cells of the vascular rays of the phloem and xylem in plants over 1 year of age (Artschwager, 1943). The secondary xylem and phloem is not as developed in younger plants, thus the greatest proportion of rubber is found in the primary cortex, pith, xylem parenchyma, and the epithial cells of the resin canals. In mature plants the phloem tissues contain a greater percentage of the rubber than the xylem. In the stems and branches the inactive phloem may contain three times more rubber than the xylem with the difference in the roots being even greater (Curtis, 1947). Thus,
plants which favor phloem production over xylem production should exhibit greater potentials for higher rubber yields. This anatomical trait can be either genetically selected for or induced by altering environmental factors to create a situation more suitable for phloem production.

Although the accumulation of rubber in the leaves is relatively insignificant, the leaves may have a profound effect upon rubber accumulation in other tissues. Spence and McCallum, described in Polhamus 1962), removed leaves from growing plants during the fall and observed a pronounced decrease in rubber accumulation in the stems. This study suggests the possibility of a precursor produced in the leaves which is subsequently translocated to the site of rubber accumulation. The period of most rapid rubber accumulation is from late fall to early spring (Higgins and Backhaus, 1983). This change in rate of rubber accumulation demonstrates that some change in the flow of assimilates has occurred. This coincides with a period of reduced growth and flowering and with the systematic shedding of leaves. Thus, the change may be the result of a change in the sink-source balance caused by the absence of growth, or it may be a means of conserving carbohydrates from the leaves. It is still unanswered as to whether the leaves contain a stored precursor which has been produced throughout the months of rapid growth or if the change from an actively growing plant to one of relative quiescence causes a change in the distribution of assimilates from the still photosynthesizing leaves. In either case, the increased production of leaves may lead to greater rubber accumulation. Plants
deprived of flowers during the growing season may create either a source of assimilates for the production of greater plant biomass, an increase of rubber storage capacity by increasing the amount of stem tissue, or an increase in the amount of leaf area available for producing and possibly storing rubber precursors. These plants may also redirect the energy normally utilized in flowering and achene development into the direct production of rubber.

Renewed interest in guayule has developed since 1975 due to the increased cost of rubber from foreign sources. Future needs for natural rubber are predicted to far exceed present amounts provided by Hevea plantations (Bragg and Lacewell, 1983). It is hoped that through improvement in cultural methods, rubber extractions, and genetic lines, coupled with increased prices for natural rubber, guayule can present itself as an economical agronomic crop. In order to do this the cost of growing guayule must be reduced while rubber yields are increased. Since rubber content is contingent upon the size of the plant and the % rubber in the plant tissues, both of these factors must be maximized to obtain optimum yields (Ray, Garrot, and Rose 1983).

Manipulation of irrigation is one method which can be controlled to effect rubber yields. Tingy and Foote (1947) designed an experiment to measure the influence of spacing and irrigation on rubber % and total yield. The low level irrigation resulted in plants with the highest % rubber but plants were smaller than in the other treatments, thus resulting in the lowest yields. The heaviest irrigation produced the largest plants but with very low % rubber. This treatment also resulted
in low rubber yields. The intermediate treatment proved to be the overall highest yielder. This result was also found by Garrot (1984). Thus, irrigation scheduling is one key to producing the highest yielding shrubs and conserving water as well. Once proper moisture levels are determined for a certain line under specific growing conditions, irrigations can be timed by using the crop water stress index (Garrot, 1984). This method provides an accurate way to monitor the plants and determine when irrigations should be applied by measuring the amount of stress being experienced by the plants.

Studies to measure the effects of light intensity concluded that higher weights and rubber percentages were generally produced under higher light intensities (Benedict, 1950). Diurnal temperatures also have an effect on rubber yields. Various temperature treatments were compared under conditions of abundant moisture and high fertility (Bonner and Galston, 1947). It was found that constant temperatures of either 27°C or 4 - 7°C resulted in little or no rubber accumulation. However, when day and night temperatures fluctuated with a daytime temperature of 27°C and night temperatures of 2 - 10°C, rapid increases in rubber concentration resulted.

Several studies have been done to determine the effect of flowering on vegetative growth in other plants. Work with tomato showed increased vegetative growth with partial flower removal (Hurd, Gay, and Mountfield, 1979). Similar results were found in a study conducted to determine the fate of assimilates following ear removal in wheat (Austin and Edrich, 1975). Labeling of intact tillers with carbon 14, they
found 80 to 92% of the labeled carbon was eventually transferred to the developing ear in closest proximity. In plants where ears were removed, carbon 14 was quickly transported to other developing tillers and roots. They determined that new patterns of translocation were established within 2 to 3 days after ear removal to facilitate transport of assimilates from the photosynthesizing flag leaf of the removed tiller to other sink areas.

A study was conducted on another rubber-producing plant, Kok-saghyz (*Taraxacum sahghz*, Rod.), to correlate flowering to rubber and resin production (Mashtakov, Belchikova, and Leonova, 1940). In this study it was found that rubber yield was higher in the plants that flowered. In order to better understand why this occurred, it is best to examine the method used to induce flowering. Kok-saghyz populations typically exhibit low levels of flowering during the first year of cultivation. The relative amount of flowering can be increased by changing the method of cultivation to one which provides more favorable growing conditions. The plants which were induced to flower were the ones which had the genetic potential to take advantage of improved conditions and flower in their first year. The authors noted that flowering plants demonstrated increased growth determined by root size and weight, height, number and weight of leaves, and diameter of the basal rosette. These plants had slightly higher levels of % rubber at the onset of flowering than the non-flowering plants, but by the end of the flowering cycle the % rubber in the non-flowering plants exceeded that of the
flowering plants. When considering total rubber yield, the flowering plants far outproduced the non-flowering due to their larger size.

To date, very little work has been done to determine the effect of flowering upon rubber production and accumulation in guayule. In an unpublished study by Benedict (1948), as described by Higgins and Backhaus (1983), a faster rate of rubber accumulation was found in plants which were not allowed to flower. Measurements for rubber yield were made by Higgins and Backhaus (1983) on plants induced to flower using photoperiods. They found no affect when analyzing the plants only a few days after the appearance of the first flower primordia. These studies do not give information about comparative yields between flowering and non-flowering plants over one growing season; however, they do suggest that the influence of flowering is one which deserves further study. Thus, it was the purpose of the present study to quantify the effects of flowering upon rubber yields.
CHAPTER 2

MATERIALS AND METHODS

Seeds from lines 593, N396, 11619 and 11591 were collected from individual plants in increase plots located in Mesa, Arizona, during June of 1982. Care was taken to select plants exhibiting a minimum amount of morphological variation which is a common occurrence within guayule lines. Line 593 plants were short, symmetrical, compact plants with more branching than the other lines. Both 11619 and 11591 were relatively tall, not as compact with few branches. Neither appeared to be as dense or have the consistent symmetrical shape of the 593 shrubs. These two lines were very similar in shape and size and were often difficult to distinguish from each other. The N396 line was intermediate in size and branching pattern to 593 and the other two lines.

Line 593 was developed by the Continental Rubber Company. During the time of extensive research with the Emergency Rubber Project, several lines of guayule were developed which were considered superior to wild plants in accumulating rubber. Line 593 was considered the standard to which all new guayule lines were compared. Lines N396 and 11619 were compared to 593 with varying results depending upon the location where they were tested (Hammond and Polhamus, 1965). Line N396 was superior in yield to 593 in Texas, but was lower in Salinas, California. In Salinas, line 11619 was the highest yielder. Thus,
environmental influences cannot be generalized in terms of their effect on yields but need to be considered on a local basis depending upon the line being grown.

All achenes were treated with a 0.525% solution of hyperchlorite for 20 minutes and air-dried. Treated seeds were mixed with fine vermiculite at the rate of 2g of seed per 300g vermiculite in a germinating tray 700cm squared. Trays were placed in a germinator at 33°C and watered two times daily for five days. Germinated seeds were then transplanted bare-rooted to a 3 x 3 x 10cm open-bottomed paper sleeve and grown in a shade house at 80% light until late October, 1983.

Two plots were prepared at the University of Arizona Campus Agricultural Research Center in Tucson, Arizona. Each plot consisted of eight raised beds running north-south 76cm apart. Seedlings were transferred from the shadehouse and hand transplanted 30cm apart onto one-row beds. The two plots had a final width of 6M and a length of 15M or 0.09 ha. Each plot contained four completely randomized blocks consisting of four lines and three flowering treatments planted in treatment units of five plants each. This design resulted in eight treatment units on all beds, bordered at each end with five border plants. The six inside beds were planted with treatment units, while the two outside beds contained border plants. None of the border plants were included in the analysis. Each block contained twelve treatment units or two ranges of six units each running east-west across the six inside beds.
Plants were furrow irrigated immediately following transplanting to facilitate stand establishment. All non-surviving seedlings were replaced by November 30th after which plants became quiescent until growth resumed in late winter. There was 100% survival after the initial spring irrigation was applied on March 16, 1984. This irrigation coincided with the first observance of plant flowering. Irrigations were timed so that the crop water stress index (Garrot, 1984) was at or below 0.3. This insured that the plants did not experience stress due to inadequate moisture, and caused profuse flowering. Weed control was accomplished by manual removal.

The three flowering treatments were begun when flowering commenced in March, 1984. The three treatments consisted of: a control (C) consisting of plants that were allowed to flower normally without interference; (D), clipping flowers from already elongated peduncles at first dehiscence; and (NF), removing flower buds from the plants as soon after initiation as possible. Treatments were performed two or three times per week, depending upon the amount of flowering, from March 16 until October 15.

In the NF treatment, the buds were removed while still deep in the leaf axils, close to the growing point of the stem. Although great care was taken when removing these buds, it was difficult to avoid pinching off part of the meristematic regions at the same time. Pollen dehiscence was determined by the first appearance of pollen on the fertile disc florets. Some inflorescences were clipped earlier if it was
thought that the next field visit would find them at a stage past dehiscence. In this way, few of the inflorescences in the D treatment progressed to the stage of ovule development.

The inflorescence terminates the growth of the stem upon which it is bourne. Subsequently lateral branches appear which will also eventually terminate in an inflorescence (Hammond and Polhamus, 1965). When flowering began in March, plants generally had one to four inflorescences since most were either monopodial or had few branches. The number of inflorescences produced per plant gradually increased as the plants became larger and as temperature and day length became more conducive to growth. Flowers were particularly prolific right after irrigations or heavy rains. An abundance of buds was evident within 6-7 days after water was applied. By mid-summer flowering reached a peak of about 20 to 60 inflorescences per plant when examined two times per week. By early September this began to taper off until flowering ceased in late October.

Two plants from each treatment unit were measured for plant height and width, then harvested on January 4, 1985. Width measurements were taken in both directions and averaged. Each plant was analyzed individually for fresh weight, % dry weight, total dry weight, % and total resin, and % and total rubber using the solvent extraction procedure (Garrot, Rubis, Johnson, and Dill, 1980). All weight measurements were done in grams. Plant height and width was recorded in centimeters. The remaining plot was left for a continuation of the study for a second year.
The data were analyzed as a randomized complete block design. Mustat was used to determine a two factor ANOVA, with the factors being the three flowering treatments and the four lines, at the 0.05 significance level. Mean separations were performed at the 0.05 significance level using LSD.
CHAPTER 3

RESULTS AND DISCUSSION

Measurements in plant fresh weight (Table 1 and Figure 1) found the D treatment with a mean of 557g per plant, the NF treatment with a mean of 508g per plant, and the C treatment with a mean of 448g per plant. Significant differences in fresh weight were found between the D and C flowering treatments with D plants having the highest value and C plants the lowest. The NF treatment was intermediate in value and was not significantly different from the other two. Line 11619 had a mean fresh weight of 526g per plant, line 11591 had a mean of 517g per plant, line N396 had a mean of 520g per plant, and line 593 had a mean of 472g per plant. There were no significant differences between lines for fresh weight. Line 11619 had the highest value followed by lines 11591, N396, and 593 respectively.

There were no significant differences between treatments or lines for % dry weight (Table 2). The same order of values observed for fresh weight was found for % dry weight. The D treatment was highest, 58.1%, followed by NF treatment, 57.5%, and finally the C treatment, 57.2%. Line 11619 was highest, 58.2%, followed by line 11591, 57.7%, line N396, 57.6%, and line 593, 57.0%.

Values for total dry weight (Table 3 and Figure 2) found the D treatment with a mean of 323g per plant, the NF treatment with a mean
Table 1. A Comparison of The Average Fresh Weight, in Grams Per Plant, For Three Flowering Treatments and Four Lines.

<table>
<thead>
<tr>
<th>(A) Treatment</th>
<th>Average Fresh Weight, in Grams, of All Lines in Each Treatment</th>
<th>(B) Line</th>
<th>Average Fresh Weight, in Grams, of All Treatments in Each Line</th>
</tr>
</thead>
<tbody>
<tr>
<td>D</td>
<td>557a*</td>
<td>11619</td>
<td>526a</td>
</tr>
<tr>
<td>NF</td>
<td>508ab</td>
<td>11591</td>
<td>517a</td>
</tr>
<tr>
<td>C</td>
<td>448b</td>
<td>N396</td>
<td>502a</td>
</tr>
</tbody>
</table>

D: Inflorescences clipped at dehiscence.
NF: Inflorescences clipped at initiation.
C: Control

* Values followed by like letters are not significantly different at the 0.05 level.
Fig. 1. Mean Fresh Weight, in Grams per Plant, of Four Lines for Three Flowering Treatments.
Table 2. A Comparison of the Average % Dry Weight For Three Flowering Treatments and Four Lines

<table>
<thead>
<tr>
<th>(A) Treatment</th>
<th>Avg. % Dry Weight of All Lines in Each Treatment</th>
<th>(B) Line</th>
<th>Avg. % Dry Weight of All Treatments In Each Line</th>
</tr>
</thead>
<tbody>
<tr>
<td>D</td>
<td>58.1a*</td>
<td>11619</td>
<td>58.2a</td>
</tr>
<tr>
<td>NF</td>
<td>57.5a</td>
<td>11591</td>
<td>57.7a</td>
</tr>
<tr>
<td>C</td>
<td>57.2a</td>
<td>N396</td>
<td>57.6a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>593</td>
<td>57.0a</td>
</tr>
</tbody>
</table>

D: Inflorescences clipped at dehiscence.
NF: Inflorescences clipped at initiation.
C: Control

* Values followed by like letters are not significantly different at the 0.05 level.
Table 3. A Comparison of the Average Dry Weight, in Grams Per Plant, For Three Flowering Treatments and Four Lines.

<table>
<thead>
<tr>
<th>(A) Treatment</th>
<th>Avg. Dry Weight, In Grams, of All Lines In Each Treatment</th>
<th>(B) Line</th>
<th>Avg. Dry Weight, In Grams, of All Treatments In Each Line</th>
</tr>
</thead>
<tbody>
<tr>
<td>D</td>
<td>323a*</td>
<td>11619</td>
<td>306a</td>
</tr>
<tr>
<td>NF</td>
<td>293ab</td>
<td>11591</td>
<td>299ab</td>
</tr>
<tr>
<td>C</td>
<td>256b</td>
<td>N396</td>
<td>289ab</td>
</tr>
<tr>
<td></td>
<td></td>
<td>593</td>
<td>269b</td>
</tr>
</tbody>
</table>

D: Inflorescences clipped at dehiscence.

NF: Inflorescences clipped at initiation.

C: Control

* Values followed by like letters are not significantly different at the 0.05 level.
Figure 2. Mean Dry Weight, in Grams Per Plant, For Four Lines and Three Flowering Treatments.
of 293g per plant, and the C treatment with a mean of 256g per plant. Line 11619 had a mean value of 306g per plant, line 11591 had a mean of 299g per plant, line N396 had a mean of 289g per plant, and line 593 had a mean of 269g per plant. Significant differences were only found between the D and C treatments. Once again the same trend was observed between lines. Significant differences were found only between the highest line, 11619, and the lowest, 593.

Measurements in plant height (Table 4 and Figure 3) found no significant differences between treatments. Both the NF and D treatments had a mean height of 20cm. The C treatment had a mean height of 19cm. Significant differences were found between lines. Lines 11619 and 11591 had mean heights of 21cm, line N396 had a mean height of 19cm, and line 593 had a mean height of 17cm. Lines 11619 and 11591 were tallest and were significantly taller than N396 and 593. Line N396 was significantly taller than 593.

There were no significant differences found in plant width (Table 5) between treatments or between lines. Mean width for the D treatment was 18cm followed by the C and NF treatments, each with a mean width of 17cm. Line 593 had a width of 18cm, followed by lines 11619, N396, and 11591, each with a mean width of 17cm.

Measurements for % resin (Table 6 and Figure 4) found no significant differences between treatments. The NF treatment had a mean of 6.4%, followed by the C treatment and the D treatment, each with a mean of 6.0%. Differences between lines were significant. Line 11619 had a
Table 4. A Comparison of the Average Plant Height, in cm Per Plant, For Three Flowering Treatments and Four Lines.

<table>
<thead>
<tr>
<th>(A) Treatment</th>
<th>Avg. Plant Height, In cm, Of All Lines In Each Treatment</th>
<th>(B) Line</th>
</tr>
</thead>
<tbody>
<tr>
<td>NF</td>
<td>20a*</td>
<td>11619</td>
</tr>
<tr>
<td>D</td>
<td>20a</td>
<td>11591</td>
</tr>
<tr>
<td>C</td>
<td>19a</td>
<td>N396</td>
</tr>
</tbody>
</table>

NF: Inflorescences clipped at initiation.
D: Inflorescences clipped at dehiscence.
C: Control

* Values followed by like letters are not significantly different at the 0.05 level.
Figure 3. Mean Height, in cm Per Plant, of Three Flowering Treatments For Four Lines.
Table 5. A comparison of the Average Plant Width, in cm Per Plant, For Three Flowering Treatments and Four Lines.

<table>
<thead>
<tr>
<th>(A) Treatment</th>
<th>Avg. Plant Width, in cm, Of All Lines In Each Treatment</th>
<th>(B) Line</th>
<th>Avg. Plant Width, in cm, Of All Treatments In Each Line</th>
</tr>
</thead>
<tbody>
<tr>
<td>D</td>
<td>18a*</td>
<td>593</td>
<td>18a</td>
</tr>
<tr>
<td>C</td>
<td>17a</td>
<td>11619</td>
<td>17a</td>
</tr>
<tr>
<td>NF</td>
<td>17a</td>
<td>N396</td>
<td>17a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>11591</td>
<td>17a</td>
</tr>
</tbody>
</table>

D: Inflorescences clipped at dehiscence.
C: Control
NF: Inflorescences clipped at initiation.

* Values followed by like letters are not significantly different at the 0.05 level.
Table 6. A Comparison of the Average % Resin Per Plant For Three Treatments and Four Lines.

<table>
<thead>
<tr>
<th>(A) Treatment</th>
<th>Avg. % Resin of All Lines In Each Treatment</th>
<th>(B) Line</th>
<th>Avg. % Resin of All Treatments In Each Line</th>
</tr>
</thead>
<tbody>
<tr>
<td>NF</td>
<td>6.4a*</td>
<td>11619</td>
<td>6.8a</td>
</tr>
<tr>
<td>C</td>
<td>6.0a</td>
<td>11591</td>
<td>6.3b</td>
</tr>
<tr>
<td>D</td>
<td>6.0a</td>
<td>N396</td>
<td>6.2b</td>
</tr>
<tr>
<td></td>
<td></td>
<td>593</td>
<td>5.3c</td>
</tr>
</tbody>
</table>

NF: Inflorescences clipped at initiation.
C: Control.
D: Inflorescences clipped at dehiscence.

* Values followed by like letters are not significantly different at the 0.05 level.
Figure 4. Mean % Resin Per Plant of Three Flowering Treatments For Four Lines.
mean of 6.8%, line 11591 had a mean of 6.3%, line N396 had a mean of 6.2%, and line 593 had a mean of 5.3%. Line 11619 was significantly higher than all the other lines. Lines 11591 and N396 followed in that order and were not significantly different from each other. The lowest value was that for line 593 which was significantly lower than the other 3 lines.

Significant differences in % rubber (Table 7 and Figure 5) were found for treatments and for lines. The NF treatment had a mean of 3.9% the C treatment had a mean of 3.6%, and the D treatment had a mean of 3.5%. The NF plants were highest and significantly different from the lowest value, recorded for the D treatment. The C plants were intermediate and were not significantly different from either NF or D plants. Line 11619 had a mean of 4.2%, line N396 had a mean of 3.8%, line 11591 had a mean of 3.6%, and line 593 had a mean of 3.0%. Line 11619 was significantly higher than the other 3 lines. Lines N396 and 11591 followed in that order and were not significantly different from each other. Line 593 was significantly lower than the other 3 lines.

Significant differences were found for resin yield (Table 8 and Figure 6) between treatments and lines. The NF and D treatments both had a mean yield of 19g per plant and the C treatment had a mean yield of 16g per plant. The D and NF treatments were highest and significantly different from the lowest value for the C treatment. Line 11619 had a mean yield of 21g per plant, line 11591 had a mean yield of 19g per plant, line N396 had a mean yield of 18g per plant, and line 593 had a mean yield of 14g per plant. Line 11619 expressed the highest value
Table 7. A Comparison of the Average % Rubber Per Plant For Three Treatments and Four Lines.

<table>
<thead>
<tr>
<th>(A) Treatment</th>
<th>Avg. % Rubber of All Lines In Each Treatment</th>
<th>(B) Line</th>
<th>Avg. % Rubber of All Treatments In Each Line</th>
</tr>
</thead>
<tbody>
<tr>
<td>NF</td>
<td>3.9a*</td>
<td>11619</td>
<td>4.2a</td>
</tr>
<tr>
<td>C</td>
<td>3.6ab</td>
<td>N396</td>
<td>3.8b</td>
</tr>
<tr>
<td>D</td>
<td>3.5b</td>
<td>11591</td>
<td>3.6b</td>
</tr>
<tr>
<td></td>
<td></td>
<td>593</td>
<td>3.0c</td>
</tr>
</tbody>
</table>

NF: Inflorescences clipped at initiation.

C: Control.

D: Inflorescences clipped at dehiscence.

* Values followed by like letters are not significantly different at the 0.05 level.
Figure 5. Mean % Rubber Per Plant of Three Flowering Treatments
And Four Lines.
followed by 11591, N396, and 593 respectively. Line 11619 was significantly higher than lines N396 and 593. Line 11591 was only significantly different from line 593. Line 593 was significantly lower than the other 3 lines.

Differences in rubber yield (Table 9 and Figure 7) were significant for treatments and lines. The NF and D treatments both had a mean yield of 11g per plant and the C treatment had a mean yield of 9g per plant. The NF and D treatments were highest followed by the C treatment. Both NF and D treatments were significantly different from the C treatment, but not from each other. Line 11619 had a mean yield of 13g per plant, lines 11591 and N396 both had mean yields of 11g per plant, and line 593 had a mean yield of 8g per plant. Yield for line 11619 was significantly higher than the other 3 lines. Lines N396 and 11591 were not significantly different from each other, but were significantly higher than 593. Line 593 was significantly lower than the other 3 lines.

Measurements made on plant height (Table 4) and width (Table 5) reveal an interesting relationship to the plants fresh weight (Table 1). There were no differences in plant height or width between the three treatments; however, there was a difference between treatments for plant fresh weight (Figures 8 and 9). Since there were no differences in plant dimensions but there were differences in plant weight, it leads to the conclusion that the heavier plants were denser. These plants were characterized by more branching or by increases in stem size caused by
Table 8. A Comparison of the Average Resin Yield, in Grams Per Plant, For Three Treatments and Four Lines.

<table>
<thead>
<tr>
<th>(A) Treatment</th>
<th>Avg. Resin Yield, In Grams, Of All Lines In Each Treatment</th>
<th>(B) Line</th>
<th>Avg. Resin Yield, In Grams, Of All Treatments In Each Line</th>
</tr>
</thead>
<tbody>
<tr>
<td>D</td>
<td>19a*</td>
<td>11619</td>
<td>21a</td>
</tr>
<tr>
<td>NF</td>
<td>19a</td>
<td>11591</td>
<td>19ab</td>
</tr>
<tr>
<td>C</td>
<td>16b</td>
<td>N396</td>
<td>18b</td>
</tr>
<tr>
<td></td>
<td></td>
<td>593</td>
<td>14c</td>
</tr>
</tbody>
</table>

D: Inflorescences clipped at dehiscence

NF: Inflorescences clipped at initiation

C: Control

* Values followed by like letters are not significantly different at the 0.05 level.
Figure 6: Resin Yield, in Grams Per Plant, For Four Lines And Three Treatments.
Table 9. A Comparison of the Average Rubber Yield, in Grams Per Plant
For Three Treatments and Four Lines

<table>
<thead>
<tr>
<th>(A) Treatment</th>
<th>Avg. Rubber Yield, In Grams, Of All Lines In Each Treatment</th>
<th>(B) Line</th>
<th>Avg. Rubber Yield, In Grams, Of All Treatments In Each Line</th>
</tr>
</thead>
<tbody>
<tr>
<td>NF</td>
<td>11a*</td>
<td>11619</td>
<td>13a</td>
</tr>
<tr>
<td>D</td>
<td>11a</td>
<td>N396</td>
<td>11b</td>
</tr>
<tr>
<td>C</td>
<td>9b</td>
<td>11591</td>
<td>11b</td>
</tr>
<tr>
<td></td>
<td></td>
<td>593</td>
<td>8c</td>
</tr>
</tbody>
</table>

NF: Inflorescences clipped at initiation.
D: Inflorescences clipped at dehiscence.
C: Control.

* Values followed by like letters are not significantly different at the 0.05 level.
Fig 7. Mean Rubber Yield, in Grams Per Plant, for Three Flowering Treatments and Four Lines.
increased secondary phloem and xylem production. Since neither stem size or branching were measured, these conclusions can only be inferred by the height, width, and fresh weight measurements taken; however, I consider them to be valid assumptions.

One of the concerns during this study was that removal of newly initiated buds in the NF treatment would also remove part of the meristematic regions of the plant and cause the initiation of more branching. If this were the case, the NF treated plants would be expected to have the heaviest fresh weight; however, this was not observed (Table 1). The fresh weight of these plants is intermediate to that of the other two treatments and is not significantly different from either of them. The D treatment, which could not have been induced to branch more due to pruning, was found to be heaviest.

It is interesting to note that the D treatment exhibits the greatest fresh weight and is substantially different from the C plants. It was expected that the NF plants would have the greatest fresh weight since they had the largest amount of assimilates available for vegetative growth due to complete flower removal. I believe the timing of flower removal is responsible for making the D treatment, rather than the NF treatment, result in the heaviest plants.

When buds were removed in the NF treatment, the plant responded immediately initiating new buds within 3 to 4 days. The plants in the D treatment did not react in this manner. Three to four days after treating the D plants, newly initiated buds were relatively fewer than
Fig. 8. The Relationship Between Plant Height, in cm Per Plant, And Fresh Weight, in Grams Per Plant, for Three Flowering Treatments and Four Lines.
Fig. 9. The Relationship Between Plant Width, in cm Per Plant, and Fresh Weight, in Grams Per Plant, For Three Flowering Treatments and Four Lines.
in the NF treated plants. Although no actual counts were taken, it was evident that the NF plants had a substantially greater number of buds present than the D plants after a subsequent removal. Thus, it appears that the NF plants were redirecting much of their energy into bud initiation.

By allowing the peduncles to elongate and flowers to develop to the stage of dehiscence before removing the inflorescence, two processes were affected. First, although there is some lignification of the peduncle (Artschwager, 1943) and further development of the inflorescence, the majority of this growth is brought about by cell elongation rather than cell divisions. This process of peduncle lignification is relatively insignificant when considering the overall scheme of energy consumption of the plant. A greater amount of energy would be needed later for ovule and achene development. The processes of achene, and ovule development are halted by the removal of the almost mature inflorescence, thus this potential sink for energy supplying assimilates is removed. At the same time a physiological process seems to be slowed down or temporarily stopped by allowing the inflorescence to progress to the stage of dehiscence. A threshold appears to have been crossed which satisfies the plant's need to produce achenes. Both flower initiation and achene production require substantial amounts of energy. It appears that plants in the D treatment redirected their energy gained by inflorescence removal into vegetative growth rather than achene development or flower initiation. These increases in fresh and dry
weight, (Table 1 and 3) are possibly due to increased stem thickening caused by increased production of secondary phloem and xylem. The D plants appeared to have about the same flower initiation rate as the controls, therefore, plants in these two treatments would be expected to have similar branching patterns. The difference in fresh weight between the C and D treatments is thus due to increased stem size, rather than increased branching.

The plants in the NF treatment, however, presented a different situation. In this case, buds were removed when they were very small, therefore the threshold for physiological change that is necessary for achene production in the plant was never reached. The plants responded by persistently attempting to flower and produce achenes, however futile the effort proved. In this manner some of the energy gained by not producing achenes was exploited for additional attempts at producing flowers rather than for greater vegetative growth.

The control plants were the smallest of the three treatments. If the C and D treatments are assumed to have a similar rate of flower initiation, which should be true if the above explanation of physiological change is correct, then differences between the two treatments would be due to achene development in the C treatment. This indicates that the energy used for achene development significantly reduced the weight of the plants. It also indicates that achene development is a higher energy consumptive process than flower initiation. If continuous flower initiation was as energy demanding, then the NF treatment
would be closer in fresh weight to the C treatment than to the D treatment. Although the NF weights were not significantly different from the C weights, there was an actual mean difference of 61 grams between the two treatments, which in itself may prove to be significant on a per hectare basis when considering total rubber yields. This difference indicates that the energy gained by not having achenes present on the plant is partially utilized to increase the amount of flowers initiated. On a commercial scale, flower suppression would be accomplished by altering the plant's hormonal balance with chemicals. This would prevent any initiation of flower buds and consequently all the plant's energy would be directed to vegetative growth. Greater increases in fresh weight and rubber yield may result with chemical flower suppression than by manual removal of buds as was done in this study. Subsequent flower suppression was accomplished by chemical means, changing the plant's hormonal balance so as to stimulate vegetative growth instead of flower initiation, greater increases in fresh weight by non-flowering plants may be obtained than was found in this study.

When comparing the four lines for morphological differences, each one appears to have its own particular growth habit. Although differences between lines were not significant, measurements in plant height and width (Tables 4 and 5) showed substantial differences between three of the four lines for height, and no differences between lines for width. Since there are no differences in fresh weight or plant width between lines but there are differences in plant height, plants from
lines 593 and N396 would have either greater numbers of branches or increased stem size to compensate for the extra height of 11619 and 11591 plants and still maintain the same weight (Table 1).

These measurements are completely consistent with the plant's appearance in the field. Although differences in fresh weight between treatments reveals an interesting relationship, differences in total dry weight are more important to consider since this is the variable upon which estimates for resin and rubber yield are based. Since there were no significant differences in % dry weight for either treatments or lines (Table 2), the differences in total dry weight (Table 3) are a direct reflection of the differences in fresh weight (Table 1). In the comparison of treatment means for dry weight, the same relationship is found as was present for fresh weight; the C plants expressed the smallest value and were significantly different from the D treatment plants which had the highest value. The NF plants were intermediate in total dry weight and were not significantly different from either of the other two treatments.

When comparing means for the four lines, the same order is also found as for fresh weight (Table 1), with line 593 being the lowest mean followed by N396, 11591 and 11619, respectively. There was a significant difference between lines 593 and 11619, however, where before there was none. This change is due in part to the fact that smaller numbers are expressed in total dry weight than fresh weight, therefore a smaller difference will result in significance. Also, even though % dry weights
were not significantly different, line 11619 did have the greatest %
dry weight, 58.22, while 593 had the least, 56.96 (Table 2).

Differences in % resin and % rubber exhibit the same trends, with NF the greatest, followed by the C plants and finally the D
treatment which was smallest for both lines (Tables 6 and 7). There
were no significant differences for % resin. The surprising point in
these data is that the control plants exhibit higher values than the
plants in the D treatment. If increased rubber production is thought
to be a result of increased availability of nutrients due to lack of
flowering and consequently achene production, then % rubber should be
lowest in the C treatment. The key to explaining this result is under­
standing the relationship of % rubber and % resin to dry weight. As
was previously explained, relative availability of assimilates for
vegetative growth resulted in the D treatment having the highest fresh
weight and dry weight, followed by NF plants and finally C plants
(Tables 1 and 3). The values for total dry weight express the weight
of the entire plant discounting water. Rubber and resin % represent
the proportion of the dry weight comprised of these compounds. Thus,
it is possible that the total weight of either rubber or resin is least
in the C plants and greatest in the other two treatments due to greater
plant size but other components contributing to plant dry weight are
present in relatively greater amounts than rubber or resin at this time
in the D plants. This is evident when examining the results for rubber
and resin yield (Tables 8 and 9). In both cases, there is no signifi­
cant difference between yields of the NF and D treatments; however, both
are significantly greater than the controls.
The fact that % resin and % rubber are lowest for the D treatment (Tables 6 and 7) is not in spite of the fact that these plants had the greatest amount of assimilates available for growth but rather as a result of it. Since evidence from this study indicates that the increase in plant dry weight is not due to increases in plant dimensions in the D treatment, and presumably is not due to excessive branching since branching is a direct result of flowering., then it may be assumed that the increased weight is due to greater amounts of secondary xylem and phloem. Since the plants used in this study were still relatively young, a large portion of the rubber and resin is still contained in the primary tissues. The excessive growth exhibited by the D plants caused this amount of rubber and resin to be less on a percent basis when related to total dry weight. It should also be noted that these plants were harvested in December at the beginning of the optimum time for rubber accumulation, November to March. If the harvest had been done in March the D plants may have expressed a much higher % rubber value.

This idea does not adequately explain the relationship between the C and NF treatments. Although the differences between the two are not significant, they do occupy the same relative position for both variables. For some reason, the preference for increasing other dry weight constituents instead of rubber is not as pronounced in the NF treatments. This may be because the increase in total dry weight is not as great as it was for the D plants, therefore, assimilates were partitioned differently. There also is the possibility that a slight
increase in resin production was realized as a reaction to injury inflicted by bud removal. If rubber production is positively related to resin production in guayule, this reaction could cause greater rubber production. If the D plants are indeed characterized by a relative increase in secondary phloem and xylem, then these plants may have much greater potential for accumulating rubber due to increased available storage tissue during the important rubber accumulating months.

The final analysis of total yields for rubber and resin indicates that plant size is a more significant factor than percentages of these compounds present. During the second year of the study the differences in partitioning of assimilates for growth may realize a more substantial increase in % rubber and resin. This would consequently have a more profound affect upon yields.

Differences in % resin and resin yield and % rubber and rubber yield between lines are significant. In all cases, line 593 expressed the lowest values followed by line N396 and line 11591, respectively, with line 11619 having the highest value. Line 11619 was always significantly higher than the other three lines in % resin, % rubber, and rubber yield, but not significantly different from line 11591 in resin yield, although it did average more than two grams greater. Line 593 was significantly lowest in all cases, thus representing the poorest in rubber and resin yields and % rubber and resin of all the lines tested. Lines N396 and 11591 were always intermediate to 11619 and 593 in rubber and resin yields and rubber and resin %. The relationship between lines
593 and 11619 was similar to the results recorded by Hammond and Polhamous (1965) where the two lines were compared in Texas and California.

These results can be explained in part by the differences in morphological structure between the four lines. As was previously mentioned, lines 593 and N396 were more compact, characterized by more branching than the other two lines. Lines 11591 and 11619 were less compact and did not have a dense appearance. Since no differences in fresh weight were found, lines 11591 and 11619 appeared to produce more secondary growth than the other lines. Plants characterized by profuse branching would have a greater proportion of primary tissues which have been shown to contain lower quantities of rubber, and presumably resin as well, since the resin canals are not developed in these tissues (Artschwager, 1943). Differences in relative flowering between lines may also have had an affect. Since branching is considered to be a reaction to flowering in guayule, then it should be assumed that lines 593 and N396 had produced more flowers than 11591 or 11619. Unfortunately no data were collected on numbers of flowers produced by each line. When making casual observances while removing buds and inflorescences in the NF and D treatments, however, the 593 and N396 lines did indeed seem to flower in a much more prolific manner.

This may explain why yield comparisons of lines 593 and 11619 at various locations produced opposite results (Hammond and Polhamous, 1965). Line 593 may find conditions more conducive to flowering in
Tucson and Texas than in the Salinas Valley, thus producing low rubber yields in these locations. Line 11619 on the other hand, experiences the opposite effect. Factors contributing to this change may be day length, light intensity, diurnal fluctuations in temperature, relative humidity or a combination of any of these conditions.

Changes in the nine variables observed in this study can be attributed to the three flowering treatments or differences between lines. Differences between flowering treatments were most dramatically expressed as changes in fresh weight. I feel this contributed the greatest toward changes in rubber yield and resin yield. In order to further qualify where this change in fresh weight occurred, measurements should be taken of branching amount and stem thickness and compared between treatments on a similar study. There also should be counts taken on the number of flowers produced by plants in each of the treatments to determine quantitatively how much less the D treatment plants flowered than the NF treatment plants.

The other consideration in this study is that the flower buds were removed manually. If this process is to be used on a commercial scale, flower suppression will be accomplished by chemical means. Artschwager (1943) contends that flowering triggers the formation of secondary phloem and xylem. Since these tissues are most important for rubber storage (Artschwager, 1943) complete elimination of flowering may be detrimental to rubber accumulation. Studies should be done to determine if flowering is necessary for development of secondary xylem and
phloem and proper applications of flowering suppressants determined accordingly.

Increases in rubber yield of 22% were found in the D treatment over the C treatment. This increase may prove substantial enough to consider reducing or eliminating flowering in a commercial operation. This increase must first be realized with a chemical suppressant, however, and the cost of applying the suppressant must be low enough to still consider the rubber increase an economic gain.
REFERENCES


