THE ROLE OF LEAVES IN THE PERCEPTION AND INHIBITION OF THE
FLOWERING STIMULUS IN SUGARCANE

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SUMMARY
Studies were conducted to determine the effects on flowering response of the removal of selected leaves from sugarcane plants during the induction period. It has been shown that the removal of mature leaves 3 and 4 from plants of the variety US 48-34 resulted in earlier flowering compared to undefoliated controls. Furthermore, the removal of the spindle or leaf 1 or leaf 2 resulted in delay and reduced intensity of emergence of the inflorescences. The inhibitory effect of lower leaves on flowering can best be interpreted by assuming that the lower leaves produce a transmissible inhibitor which prevents growth of the inflorescence primordium.

INTRODUCTION
Day length is a critical factor for the induction of flowering in plants. It is generally accepted that leaves respond to a proper combination of light and darkness, produce a flowering stimulus which is translocated to the apex, where it initiates an inflorescence or flower primordium. Hence the removal of all leaves on a plant during the period when day length is inductive to flowering will result in inhibition of flowering. Evidence has been put forward to support the view that this is the case in sugarcane. The question which arises therefore is what would be the effect of flowering of sugarcane if only selected leaves were removed during the induction period. The object of this preliminary experiment is to throw some light on this problem.

MATERIAL AND METHODS

Planting
Single-eyed cuttings of the variety US 48-34 were planted in 6" × 5" polythene pots in June 1966, the young plants were raised in the glass house and on the 1st of October 1966, they were transplanted to 2' × 1'6" polythene bags and placed in the field. There were two young plants per bag and fertilizers were applied at transplanting.
Experimental design

A randomised block design was adopted; there were two blocks each consisting of ten plots and two polythene bags constituted one plot.

Treatments

The treatment consisted in removing selected leaves from plants of different plots; before carrying out the defoliation it was necessary to define leaf position and number, this being illustrated in Fig. 1. The last leaf showing a visible leaf mark was considered as the first leaf, all the leaves within the first leaf being defined as the spindle. The treatments are given in Table 1 and are represented diagrammatically in Fig. 2.

On the 16th January the first defoliation was carried out according to schedule

Fig. 1. Leaf position and number.

in Table 1. From the 16th January to the 24th February the shoots were allowed to grow and by the end of that period the shoots had again a spindle and four leaves, hence a second defoliation was carried out (Fig. 2).

The day lengths in Mauritius varied from 13 h 14 min light on the 16th January to 11 h 54 min on the 1st of April, and are given in Table 2.

George has shown that in Mauritius, the maximum flowering response for the
Fig. 2. Diagrammatic representation of the leaf cutting treatments.

TABLE 1

<table>
<thead>
<tr>
<th>Code</th>
<th>Leaves cut</th>
<th>Leaves left on plant</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>S + 1st + 2nd + 3rd + 4th</td>
<td>Nil</td>
</tr>
<tr>
<td>B</td>
<td>1st + 2nd + 3rd + 4th</td>
<td>Spindle (S)</td>
</tr>
<tr>
<td>C</td>
<td>S + 2nd + 3rd + 4th</td>
<td>1st</td>
</tr>
<tr>
<td>D</td>
<td>S + 1st + 3rd + 4th</td>
<td>2nd</td>
</tr>
<tr>
<td>E</td>
<td>S + 1st + 2nd + 4th</td>
<td>3rd</td>
</tr>
<tr>
<td>F</td>
<td>S + 1st + 2nd + 3rd</td>
<td>4th</td>
</tr>
<tr>
<td>G</td>
<td>S + 1st + 2nd</td>
<td>3rd + 4th</td>
</tr>
<tr>
<td>H</td>
<td>S + 1st</td>
<td>2nd + 3rd + 4th</td>
</tr>
<tr>
<td>I</td>
<td>S</td>
<td>1st + 2nd + 3rd + 4th</td>
</tr>
<tr>
<td>J</td>
<td>Nil</td>
<td>S + 1st + 2nd + 3rd + 4th</td>
</tr>
</tbody>
</table>

TABLE 2

<table>
<thead>
<tr>
<th>Date</th>
<th>Day length</th>
</tr>
</thead>
<tbody>
<tr>
<td>15 Jan.</td>
<td>13 h 14 min</td>
</tr>
</tbody>
</table>

The variety C.P. 36–13 occurred when the plants were subjected to natural day lengths from the 23rd of February to the 16th March. The fact that the second defoliation was carried out on the 24th of February is therefore of significance.
RESULTS

Date of emergence

The dates of emergence of the inflorescences were recorded for each plot, a mean date of emergence was calculated for each treatment and is shown in Table 3, column 2, as the number of days to emergence recorded from the 1st of April. Furthermore, the distribution in time of the dates of emergence was considered and, for each plot, the upper and lower quartiles were not considered, the data recorded in the inter-quartile range was averaged, this derived variate is shown in Table 3 column 3.

TABLE 3

<table>
<thead>
<tr>
<th>Treatment Code</th>
<th>Leaves left on plant</th>
<th>Mean no. of days to emergence(^a) Preliminary data</th>
<th>Mean no. of days to emergence(^a) Derived data</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>nil</td>
<td>22</td>
<td>19</td>
</tr>
<tr>
<td>B</td>
<td>Spindle</td>
<td>14*</td>
<td>13*</td>
</tr>
<tr>
<td>C</td>
<td>1st</td>
<td>17</td>
<td>10*</td>
</tr>
<tr>
<td>D</td>
<td>2nd</td>
<td>25</td>
<td>19</td>
</tr>
<tr>
<td>E</td>
<td>3rd</td>
<td>23</td>
<td>23</td>
</tr>
<tr>
<td>F</td>
<td>4th</td>
<td>25</td>
<td>23</td>
</tr>
<tr>
<td>G</td>
<td>3rd + 4th</td>
<td>35**</td>
<td>35**</td>
</tr>
<tr>
<td>H</td>
<td>2nd + 3rd + 4th</td>
<td>24</td>
<td>20</td>
</tr>
<tr>
<td>I</td>
<td>1st + 2nd + 3rd + 4th</td>
<td>22</td>
<td>21</td>
</tr>
<tr>
<td>J</td>
<td>S + 1st + 2nd + 3rd + 4th</td>
<td>21 + LSD P 0.05 = 7 LSD P 0.05 = 3</td>
<td>21 + LSD P 0.01 = 9 LSD P 0.01 = 5</td>
</tr>
</tbody>
</table>

\(^a\) Referenced as from 1st April.
\(^\star\) Significant at \(P = 0.05\).
\(^\star\star\) Significant at \(P = 0.01\).
\(^\star\star\star\) Significant at \(P = 0.001\).

Preliminary and derived data for mean emergence dates for the treatments follow a similar pattern. When only spindle or leaf 1 or 2 is left on the plant, flowering was found to occur earlier than in the control, whereas when leaf 3 or 4 is present, flowering occurred slightly later and finally when leaves 3 and 4 are left together on the plant, flowering took place markedly later than in the control.

Intensity of emergence and initiation of inflorescence

The percentage of emergence for each treatment was calculated; this is shown in Table 4. In order to carry out a statistical analysis it was necessary to transform the percentage into angles where the angle = \(\arc\sin\sqrt{\text{percentage}}\) (Snedecor18). At the end of the experiment, on 22nd of June, the stalks which had not emerged were dissected and the presence or absence of a primordium was noted. It was apparent that in some cases the inflorescence primordia were reverting to the vegetative stage. The percentage of stalks which had initiated an inflorescence was
calculated for each plot. These percentages were also transformed into angles and are shown in Table 4.

It follows from Table 4 that the presence of leaf 3 or 4 singly or in combination reduces emergence compared to the control, it is also apparent that the older the leaf left on the plant the lower the percentage of emergence, and furthermore, when both leaves 3 and 4 are left on the plant emergence is lowest. These results were significant.

On the other hand there was a very great variability in the percentage initiation, the standard error was very great and none of the treatments were significantly different from the control. However, in the treatments where leaves 3, 4 or 3 and 4 were left on the plant, percentage initiation was markedly lower than the control but failed to reach significance at $P = 0.05$ level.

**DISCUSSION**

*Relative sensitivity of leaves in perceiving the flowering stimulus*

Khudairi et al.\textsuperscript{13,14} showed that the young expanding leaves were the most effective for perceiving the flowering stimulus in *Xanthium*. In the present experiment it has been shown that presence of leaf 1 only resulted in earlier flowering, compared to the presence of either leaf 2 or 3 or 4 respectively and that the delay in flowering increased gradually with the presence of older leaves on the plant. Also, plants with the spindle only did not flower earlier than plants with leaf 1, in fact they flowered somewhat later, although the difference was not statistically significant (Table 3). It seems therefore that presence of leaf 1 is vital for optimum flowering and that
the leaves within the spindle may be considered as too young and leaves 2, 3, 4, as too old. However, this does not account for the facts that plants with all the leaves 1, 2, 3, 4, flowered significantly later than plants with either the spindle or leaf 1 or leaf 2 only; and plants with leaves 3 and 4 flowered less and later than plants with either leaves 3 or 4 only (Tables 3 and 4).

It thus appears that the lower leaves, 3 and 4 are inhibitory not only because they may be less sensitive in perceiving the flowering stimulus, but also because they may either produce a solute stream which may dilute or prevent the flowering stimulus from reaching the apex, or they may act as sinks for the flowering stimulus or they may produce a transmissible flowering inhibitor.

Lincoln et al.\textsuperscript{15} working with \textit{Xanthium} presented evidence to support the view that the flowering stimulus is translocated with the stream of assimilates in the phloem. Further evidence is obtained by the work of Chailakhjan and Butenko\textsuperscript{6} on \textit{Perilla crispa} discussed by Zeevaart\textsuperscript{16} in his review of the physiology of flowering. Hence, in the course of further discussion it will be assumed that the flowering stimulus is translocated with the assimilate stream.

\textit{Older leaves produce a solute stream which may dilute or prevent the flowering stimulus from reaching the apex.}

Hartt \textit{et al.}\textsuperscript{14} have shown that lower leaves of the sugarcane plant translocate less assimilates and at a slower rate than upper leaves. They further showed that the removal of the upper leaves resulted in increased translocation of assimilates from the lower leaves upwards and that removal of lower leaves resulted in a slight increase in translocation downwards, and as the effect on translocation is much greater when the upper leaves are removed compared with the lower leaves, competition from the lower leaves is much weaker than from the upper leaves. Hence it is unlikely that the inhibitory effect of lower leaves in this experiment can be attributed to the production of a competitive stream of assimilates by these leaves. Evans\textsuperscript{7} showed that short-day leaves either above or below a long-day leaf inhibited flowering in the long-day plant \textit{Lolium tumulentum}. He further showed\textsuperscript{7} that the inhibitory effect could not be attributed to a competition between assimilate streams coming from the short-day leaves.

\textit{Lower leaves may act as sinks for the flowering stimulus}

Hartt \textit{et al.}\textsuperscript{14} working with the sugarcane variety H. 37-1933, showed that lower leaves received only 1\% \textsuperscript{14}C in six weeks when \textsuperscript{14}CO\textsubscript{2} was fed to the upper leaves, and therefore cannot act as a sink for the assimilates. It thus seems that the possibility of lower leaves acting as a sink for the flowering stimulus and thus causing inhibition or delay of flowering in sugarcane is unlikely. Evans\textsuperscript{7} also showed that this possibility must be ruled out as an explanation for the inhibitory effect of short-day leaves in \textit{L. tumulentum}.

\textit{Lower leaves produce a transmissible flowering inhibitor}

Guttridge\textsuperscript{9,10} and Thompson and Guttridge\textsuperscript{11}, working with the short-day plant
strawberry presented evidence that leaves under long-day conditions produced a transmissible flowering inhibitor. Evans\(^7\) also arrived at the conclusion that the production of a flowering inhibitor by short-day leaves could best explain the results he obtained with the long-day plant *L. tumulentum*. The results of the present experiment can be best interpreted by assuming that the mature leaves 3 and 4 produce a flowering inhibitor. Thus the removal of leaves 3 and 4 from plants results in an elimination of the source which produces these inhibitors and hence leads to heavier and earlier flowering. On the other hand the presence of leaves 3 and 4 together on the plant results in the production of a greater amount of inhibitors compared to the presence of only leaf 3 or 4 alone and this is probably why plants with leaves 3 and 4 flower later than plants with leaf 3 or 4 only.

**The role of the inhibitor**

There is no significant difference in percentage initiation between the different treatments whereas the percentage emergence is significantly lower than the control in treatments A, E, F, G and H. The percentage emergence was lowest in treatment G where both leaves 3 and 4 were left on the plant. It thus appears that the flowering inhibitor prevents the growth of the primordium after initiation and does not affect the initiation process itself. However, this last point has to be confirmed as the results of percentage initiation were highly variable and the S.E. was very large.

**ACKNOWLEDGEMENTS**

The author wishes to express his thanks to Mr. R. Antoine for his interest and helpful criticism during the preparation of this paper.

Credit is given to Mr. M. Pérombelon, formerly Geneticist at this Institute, who had contributed to the planning of the experimental work before his resignation.

**REFERENCES**


Discussion

P. G. C. Brett: Applauded the paper and expressed opinion that a technique for inducing heavier flowering was indicated.

C. S. Loh: We have experimented with stripping the matured leaves below +3 leaf which promotes flowering but no flowering occurs if the mature leaves below +3 remain. It seems that flowering and non-flowering is physiologically reversible.

P. Noel: Has anyone experience of the low sucrose content of noble cane?

D. I. T. Walker: Yes, we have.

P. G. C. Brett: Mentioned the result of removing leaves in Australia.