Differentiation and Development of Lateral Buds in Castor Plants (*Ricinus communis* L.)*

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Abstract

The complete process of differentiation and development of lateral buds in castor plants was observed. Lateral buds differentiated in ascending order. The nth node lateral bud differentiated synchronously with the differentiation of the (n+3)th leaf on a main stem before the differentiation of the primary raceme. The three uppermost buds differentiated synchronously with the differentiation of the primary raceme. The two or three uppermost buds developed into bearing branches.

Introduction

It is known that the lateral buds at the two or three uppermost nodes start growing when a raceme develops at the apex of a main stem and this process repeated in the primary and higher order branches during the growing period in castor plants. Hanada et al.3, 4) reported that the growth of branches on different nodes on a main stem started simultaneously with a small difference of only about a day, and that the first flowering of the primary raceme, that at the tip of a main stem, took place at the 10 mm-length-stage of the primary branches on the main stem. Hanada5) reported further that the relationship in time between the flowering of the primary raceme and the development of primary branches was not changed by long day treatment which delayed the flowering. However, the differentiation and development in the early stages of the lateral buds, some of which develop into branches, is not clear. The purpose of this study is to clarify the complete process of differentiation and development of lateral buds in castor plants.

Materials and Methods

The experiments were carried out in a field of University of Tsukuba in 1979. Seeds of castor plants cv. Shanghai were sown twice, on June 1st and July 20th, in the planting interval of 0.6 m × 0.5 m. Experiments with the plants sown on June 1st and July 20th are referred to as Exp. 1 and Exp. 2, respectively. Thirty grams of compound fertilizer (N, P2O5, K2O : 14 % each) was applied to each plant as a basal dressing. Plastochron index (P. I.) was used to express the developmental stage of the plant.1, 2) About thirty plants were harvested at every P. I. of the main stem. The differentiation of leaves, lateral buds and the primary raceme on the main stem and the differentiation of leaves and the secondary raceme, defined as those on primary branches, were observed. The entire length of lateral buds were also measured under the dissecting microscope or with the naked eyes. After the flowering of the primary raceme, the entire length of the lateral bud (or the lateral branch) was traced every three days. The leaves and lateral buds on the main stem were numbered in ascending order, the oppositely-arranged leaves (opposite leaves, hereafter) and the buds subtended by the leaves being referred to as number 0. The developmental stage of the plants was expressed by P. I. with a 30 mm reference length. The number of leaves on the main stem was counted, excluding opposite leaves and cotyledons, as mentioned above.

Results

Daily mean temperature during the experiments

The daily mean temperature during the experiments is shown in Fig. 1. It was rather cool from June 1st to June 16th, from June 29th to

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July 23rd and from August 22nd to 31st. The average daily mean temperature for forty days after sowing was 22.7 °C in Exp. 1 and 25.8 °C in Exp. 2.

**Differentiation of leaves on a main stem**

The number of leaves on a main stem at each P. I. stage before the differentiation of the primary raceme is shown in Fig. 2. The differentiation of leaves on a main stem terminated when the primary raceme differentiated. On average 4.6 leaves in Exp. 1 and 4.1 leaves in Exp. 2 had already differentiated on a main stem at P. I. 0, and 6.8 leaves in Exp. 1 and 6.1 leaves in Exp. 2 were found at P. I. 1. These results show that about two new leaves were formed for one P. I. stage from P. I. 0 to P. I. 1. It was observed in Exp. 1 that the primary raceme had already differentiated at P. I. 2 in every plant and in Exp. 2 that primary racemes had differentiated at P. I. 2 or P. I. 3 in some plants. In the plants which had initiated no primary raceme at those stages, the number of differentiated leaves averaged 7.8 and 9.1 at P. I. 2 and P. I. 3, respectively. Thus, about 1.7 or 1.5 new leaves were formed on a main stem during one P. I. stage from P. I. 1 to P. I. 2, or from P. I. 2 to P. I. 3, respectively. It was observed that a primary raceme had differentiated at P. I. 4 in every plant in Exp. 2. It appeared likely that the fifth and sixth leaf differentiated at P. I. 0.20 and P. I. 0.65 respectively in Exp. 1, and that the fifth, sixth, seventh, eighth and ninth leaf differentiated at P. I. 0.45, 0.95, 1.55, 2.15 and 2.85, respectively in Exp. 2 (Fig. 2). That is to say, the difference between the nodal number of the newest leaf initiated and the P. I. increased as the P. I. advanced.

**Differentiation of primary raceme**

In Exp. 1, four or five leaves were found at the tip of a main stem at P. I. 0 in the plants whose primary raceme had not differentiated yet. At P. I. 1, all the plants which had four or five leaves had initiated primary racemes on the apices, and six or seven leaves had differentiated in the plant which had no primary raceme yet.

In Exp. 2, seven or eight leaves were found at P. I. 2. At P. I. 3, all the plants which had seven or eight leaves had primary racemes on the apices, and nine or ten leaves existed in the plants which had no primary raceme (Table 1). It may be suggested, therefore, that in the plants which had n leaves ultimately, the primary raceme differentiated in the period between differentiation of the nth leaf and differentiation of the \((n + 1)\)th leaf in the plants which formed more than n leaves. Thus, in the plants which had five leaves in Exp. 1, the primary raceme seemed to differentiate after P. I. 0.2 and before
Table 1  Number of differentiated leaves and node number of uppermost differentiated lateral bud at each P. I, stage in plants with primary raceme not differentiated and in plants with primary raceme differentiated

<table>
<thead>
<tr>
<th>State of the plants</th>
<th>P. I. of the plants (main stem)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td><strong>Exp. 1</strong></td>
<td></td>
</tr>
<tr>
<td>primary raceme not differentiated</td>
<td>4 (26)</td>
</tr>
<tr>
<td>node of uppermost bud</td>
<td>1 (26)</td>
</tr>
<tr>
<td>primary raceme differentiated</td>
<td>5 (1)</td>
</tr>
<tr>
<td>node of uppermost bud</td>
<td>5 (1)</td>
</tr>
</tbody>
</table>

**Exp. 2**

| primary raceme not differentiated | 4 (21) | 5 (2) | 6 (20) | 7 (2) | 8 (6) | 9 (21) | 10 |
| node of uppermost bud | 0 (1) | 1 (20) | 1 (20) | 2 (4) | 4 (6) | 6 (12) | 7 |

| primary raceme differentiated | 5 (0) | 4 (2) | 6 (2) | — | 7 (1) | 8 (5) | 9 (10) | 10 |
| node of uppermost bud | — | — | — | — | — | — | — |

Note *: The value in the parenthesis is number of plants

Table 2  Number of differentiated leaves on the lateral bud on each node at each P. I, stage in plants with secondary raceme not differentiated

<table>
<thead>
<tr>
<th>node number of lateral bud</th>
<th>P. I. of the plants (main stem)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
</tr>
<tr>
<td><strong>Exp. 1</strong></td>
<td></td>
</tr>
<tr>
<td>cotyledonary</td>
<td>1.7</td>
</tr>
<tr>
<td>0</td>
<td>0.3</td>
</tr>
<tr>
<td>1</td>
<td>-0.9</td>
</tr>
<tr>
<td>2</td>
<td>-2.0</td>
</tr>
<tr>
<td>3</td>
<td>-2.0</td>
</tr>
<tr>
<td>4</td>
<td>-2.0</td>
</tr>
<tr>
<td>5</td>
<td>-2.0</td>
</tr>
</tbody>
</table>

**Exp. 2**

| cotyledonary             | 1.1 | 1.7 | 2.1 | 2.4 | 3.1 | 2.9 | 3.0 | 2.5 |
| 0                        | 0.1 | 1.6 | 2.1 | 2.4 | 2.9 | 3.1 | 3.1 | 3.1 |
| 1                        | -1.0 | 1.0 | 2.0 | 2.7 | 3.9 | 3.6 | 4.1 | 4.2 |
| 2                        | -2.0 | -0.2 | 1.0 | 2.5 | 3.3 | 3.5 | 3.9 | 3.8 |
| 3                        | -2.0 | -1.2 | 1.0 | 2.5 | 3.3 | 3.5 | 3.9 | 3.8 |
| 4                        | -2.0 | -1.9 | -0.8 | 0.5 | 2.5 | 3.5 | 4.4 | 4.8 |
| 5                        | -2.0 | -2.0 | -1.7 | 0.3 | 1.6 | 3.0 | 4.0 | 4.8 |
| 6                        | -2.0 | -2.0 | -2.0 | 0.1 | 1.8 | 3.1 | 3.8 | 5.0 |
| 7                        | -2.0 | -2.0 | -2.0 | 0.3 | 2.4 | 3.6 | 4.0 | above 5 |
| 8                        | -2.0 | -2.0 | -2.0 | 0.2 | 2.4 | 3.7 | 4.0 | above 5 |

Notes *: The number in this Table indicates the state of bud in average as follows;
-2 : No bud differentiated.
-1 : A bud differentiated, but no prophyll differentiated.
0 : Prophyll differentiated.
Positive number : Number of leaves on lateral bud excluding prophyll.
** : Data shown about plants with five leaves in Exp. 1 and eight leaves in Exp. 2.
Fig. 2. Differentiation of leaves or lateral buds on the main stem in the plants which had no primary raceme at each P. I. stage.

Note

- leaves on the main stem in Exp. 1.
- leaves on the main stem in Exp. 2.
- Lateral buds in Exp. 1.
- Lateral buds in Exp. 2.

Differentiation of leaves or lateral buds on the main stem in the plants which had no primary raceme at each P. I. stage.

Differentiation of lateral buds

The differentiation process of lateral buds on a main stem differed depending on the differentiation of the primary raceme. The differentiation of lateral buds at each P. I. stage of a main stem before the differentiation of primary raceme is given in Fig. 2. It was clearly shown that the differentiation of lateral buds took place in ascending order from the lower node toward the upper node before the differentiation of the primary raceme. The lateral bud on the first node had already differentiated at P. I. 0 both in Exp. 1 and Exp. 2. At P. I. 1, the lateral bud had differentiated on the third node in most plants in Exp. 1 and Exp. 2, with a few exceptions, in which the fourth node lateral bud had already differentiated. The average nodal number of the uppermost bud which had differentiated at P. I. 2 and at P. I. 3 was 4.33 and 6.22, respectively. The second, third, fourth, fifth and sixth node lateral buds seemed to have differentiated at P. I. 0.5, 1.0, 1.8, 2.4 and 2.9, respectively (Fig. 2). Also the differentiation of the second, third, fourth, fifth and sixth node buds seemed to take place at almost the same time as the differentiation of fifth, sixth, seventh, eighth and ninth leaf (Fig. 2).

The results indicate that the nth node bud differentiated simultaneously with the differentiation of the \((n+3)\)th leaf before the differentiation of the primary raceme. No lateral bud was found at three, sometimes four, uppermost leaf axils at any growing stage before differentiation of the primary raceme. On the other hand, in every plant on which primary raceme was found at the tip, a lateral bud was observed at any node up to the tip (Table 1). These results indicate that the three or four uppermost buds, which remain undifferentiated before the differentiation of the primary raceme, differentiated at the same time immediately after the differentiation of the primary raceme.

Differentiation of lateral buds

Differentiation of leaves on a lateral bud

Table 2 shows the differentiation of leaves on a lateral bud at each P. I. stage in the plants with five final leaves on the main stem in Exp. 1 and in the plants with eight final leaves in Exp. 2. The differentiation of the primary raceme seemed to take place in the stage between P. I. 0.2 and 0.7 in the plants with five final leaves in Exp. 1 and between P. I. 2.2 and 2.9 in the
plants with eight leaves in Exp. 2, as mentioned above. Before the differentiation of the primary raceme, more leaves were found in the lower buds than in the upper buds. After the differentiation of the primary raceme on the main stem, the differentiation of leaves proceeded more rapidly in the upper node lateral buds than in the lower node lateral buds. That is, the differentiation of leaves proceeded at the rate of one or more leaves for one P. I. stage in the two or three uppermost buds and at a lower rate of less than a leaf for one P. I. stage in the buds at the two or three lowest nodes. It was observed that the two uppermost buds had the largest number of differentiated leaves and that lower node lateral buds had less leaves than upper node buds in the later stage, in the plants whose secondary racemes had not differentiated yet.

Differentiation of secondary racemes

Differentiation of secondary racemes took place on the two or three uppermost buds, and rarely on the lower buds (Fig. 3). The final number of leaves on the uppermost primary branch was $4.5 \pm 1.39$ in Exp. 1 and $3.8 \pm 1.17$ in Exp. 2. The differentiation of the secondary raceme took place at P. I. $(n-4)$ to $n$ in Exp. 1 and P. I. $(n-3)$ to $(n-1)$ in Exp. 2, depending on the final number of leaves on the branch. (Fig. 3)

The differentiation of the secondary raceme on the lower node branch took place later than that of upper node branch.

Growing process of lateral buds

Fig. 4 and Fig. 5 show the growth in length of lateral buds in the plants with five leaves in Exp. 1 and in the plants with eight leaves in Exp. 2. The length of lateral buds increased rapidly after differentiation. The growth was inhibited to some extent after the bud attained about one to ten mm in length in lower node buds. The final length of lateral buds on lower nodes did not reach 100 mm. The two or three uppermost buds continued vigorous growth without inhibition and bore secondary raceme
on the apices. The growth of the third node lateral bud was less vigorous than that of the two uppermost buds.

**Discussion**

The number of differentiated leaves at a certain P. L. stage was slightly greater in Exp. 1 than Exp. 2 (Fig. 2). The daily mean temperature was higher during Exp. 2 than Exp. 1 (Fig. 1). The difference in number of leaves between the two experiments seems to be caused by the faster expanding of leaves in Exp. 2, since expanding of a leaf is more sensitive to temperature than differentiation of a leaf.8)

About 1.5 new leaves differentiated on the average during the period of one P. L. This suggests that the differentiation of leaves was faster than the expanding of leaves. As the result, unexpanded young leaves accumulated in the apex, similar to tobacco and maize.8) But, it is not known whether the increasing rate of accumulation of unexpanded young leaves in the apex is constant throughout the growing period or not. The number of leaves on a main stem was as little as four to ten in these experiments. However, the number of leaves on a main stem in castor plants cultivated in the tropical area is generally much more than ten, some times as many as forty.7) It is not known if the relationship observed in this experiment between the differentiation rate of leaves and rate of P. I. is applicable to castor plants which have more leaves on their main stems in the tropics.

Differentiation of lateral buds before the differentiation of primary raceme is different from
that after the differentiation of primary raceme. It was found that the \( n \)th bud differentiated simultaneously with the differentiation of \( (n+3) \)th leaf on a main stem, and that the three or four uppermost buds did not differentiate before the differentiation of primary raceme, without exception (Fig. 2 and Table 1). The differentiation of lateral buds was related more closely to the differentiation of leaves than to the plastochron index. This relationship between the differentiation of lateral buds and leaves on main stem seems not to be changed throughout the growing period before the differentiation of the primary raceme.

The three uppermost buds differentiated at the same time, immediately after the differentiation of the primary raceme. This differentiation behavior is much different from that in sunflower (unpublished).

Differentiation of lateral buds took place in ascending order, and the bud started development in the same order before the differentiation of primary raceme. The lateral buds on the lower nodes developed rapidly until the bud attains 1 mm to 10 mm long, and the growth was inhibited thereafter. This is the same behavior as seen in rice plants which are exposed to an unfavorable environment. The growth-inhibition of lateral buds in the lower nodes in castor plants, however, is likely caused by internal factors before the differentiation of the primary raceme, since this phenomenon is commonly observed even under favorable conditions.

The two or three uppermost buds, on the contrary, continued growing without inhibition to bear secondary racemes at the apices. It was clearly shown that a upper node lateral bud develops more vigorously than a lower node lateral bud in differentiation of leaves as well as in length.

Summary

Castor plants were grown twice (Exp. 1 and Exp. 2) in order to clarify the complete process of differentiation and development of lateral buds in castor plants.

The results were as follows:

1. The fifth and sixth leaves seemed to differentiate at P. I. 0.20 and 0.65 respectively in Exp. 1. In Exp. 2, on the other hand, the fifth, sixth, seventh, eighth and ninth leaf seemed to differentiate at P. I. 0.45, 0.95, 1.55, 2.15 and 2.85, respectively. About 1.5 leaves were produced during the period in which one P. I. advanced.

2. When the growing stage was expressed by \((P. I. - \text{total number of leaves on the main stem})\), the differentiation of the primary raceme took place at the stage -4 to -5.

3. The differentiation of the \( n \)th bud took place simultaneously with the differentiation of \((n+3)\)th leaf, and no bud differentiated at the three or four uppermost nodes before the differentiation of the primary raceme. The three uppermost buds differentiated immediately after the differentiation of the primary raceme.

4. The lower buds on the main stem tended to have more leaves than the upper buds, before the differentiation of the primary raceme. The upper buds formed leaves more rapidly than the lower buds, after the differentiation of the primary raceme.

5. Differentiation of secondary raceme took place earlier in the upper bud than in the lower bud. As the result, the total number of leaves on a primary branch was larger in a lower bud than in a upper bud.

6. The length of lateral buds increased rapidly after their differentiation. The growth of the buds, except for the three uppermost buds, was inhibited after the buds attained 1 to 10 mm in length. The two or three uppermost buds grew up rapidly to bear secondary racemes at the apices.

Literature cited


摘 要

ひまにおける側芽数の分化及び発育

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ひまにおける側芽数の分化及び発育の全過程を明らかにする事を目的とし、実験1、実験2）圃場に生育させ、実体顕微鏡下及び肉眼にて観察を行なった。尚、主茎葉数及び側芽数の節位は対生葉及びその節を0とし、上方に向って番号を付した。結果は以下に示す通りである。
1. 実験1では第5葉及び第6葉はそれぞれP. I. 0.20及び0.65に分化すると考えられた。実験2では第5・6・7・8・9葉はそれぞれP. I. 0.45・0.95・1.55・2.15・2.85に分化すると考えられた。P. I. 1以降はP. I. が1進む毎に約1.5葉増加した。
2. （P. I. 一主茎総葉数）によって第1花房の分化期を表わすと、ほぼ4かから5の時に第1花房が分化すると考えられた。
3. 第1花房分化直後において、第n節側芽数と第(n + 3)節がほぼ同時に分化すると考えられ、最上位の3または4節の側芽数が未分化していた。最上位3～4節の側芽数は第1花房の分化直後にほぼ同時に分化した。
4. 第1花房分化直後に下位節側芽数ほど多くの葉を持つ傾向であった。第1花房の分化後は上位節側芽数のほうが葉の分化を急速に行なった。
5. 第2花房は上位節側节数の花房ほど早く分化し、その結果、上位節側节数ほど1次側枝総葉数が少なかった。
6. 側节数は側芽数分化後急速に長くなるが、最上位の3節の側芽数を除き1〜10mmの長さに達した頃から伸長の抑制が始まった。最上位の2または3節の側芽数は抑制されることなく急速に生長を続け、その先端に第2花房を着生した。