Effects of Various Photoperiods on Flowering in
Capsicum frutescens and C. annuum

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There have been several reports on the effects of various photoperiods on flowering in
Capsicum annuum, but few on such effects on other species of the genus Capsicum. In this study,
the flowering under various photoperiods of two C. frutescens lines from the Bonin and Ryukyu
Islands in Japan and C. annuum cv. ‘Takanotsume’ (referred as BON, RYU, and TK, respec-
tively) was investigated. The main differences in flowering between C. frutescens and C. annuum
were evident under long-day photoperiods. TK plants grown under photoperiods longer than 15
h bore flowers normally, whereas BON and RYU plants grown under the same conditions did not
bear flowers at first, because their buds failed to grow, and eventually aborted. BON plants bore
flowers under a 24-h photoperiod, although the time to flowering was much longer than that for
TK plants, but RYU plants exposed to photoperiods longer than 14 h bore no flowers during the
entire experimental period. Therefore, long-day photoperiods strongly inhibit C. frutescens
flower bud growth, and there are interspecific differences in flowering between C. frutescens
and C. annuum and intraspecific differences in flowering between the two C. frutescens genotypes.

Keywords: Bonin Islands, domestication, flower buds, flower differentiation, long day, Ryukyu
Islands, short day

INTRODUCTION

Capsicum peppers are widely cultivated worldwide and are economically important as condi-
ments and vegetables. Flowering is one of the essential stages for pepper production. As
photoperiod and temperature are the primary factors determining the flowering time of many plants
(Zeevaart, 1962), the effects of photoperiod on the development and morphology of flowering in
the genus Capsicum have been studied since the early to mid twentieth century. Auchter and
Harley (1924) investigated the effect of day length on flowering in Capsicum, and demonstrated
that the Ruby King pepper (Capsicum annuum) blossomed and produced mature fruits sooner
under short days. Cochran (1942) found that the time to flower primordia differentiation in the
Perfection pimiento (C. annuum) was shortest under a 12-h photoperiod. Artuygina (1967) ob-
tained similar results with eight sweet pepper varieties, finding that the flowering stages began 8–
12 days earlier under a 12-h photoperiod than under a 14-h photoperiod. However, Masuda and
Murage (1998) obtained the opposite results: Kyomidori peppers (C. annuum) exposed to continu-
ous illumination reached flowering seven days earlier than plants grown under a 12-h photoperiod. The authors proposed that plants in the Solanaceae family are day-neutral. Deats (1925) reported that Large Bell and Bull Nose peppers (\textit{C. annuum}) required a moderately short day for the best seed production, although peppers grown in short days blossomed at nearly the same time as those grown in long days.

As mentioned above, there have been reports on the effects of photoperiod on the flowering of fully domesticated \textit{C. annuum}, but few regarding other species in the genus \textit{Capsicum}. It is important to know the differences in flowering under various photoperiods among species in the genus, from wild to domesticated, to understand the basic physiological characteristics, evolution, origin, distribution, and dispersal of this genus.

\textit{Capsicum frutescens} L., probably native to the New World tropics (Eshbaugh, 1993), is a shrubby, perennial, semi-domesticated, tropical and subtropical plant. \textit{C. frutescens} is now grown widely throughout tropical and subtropical regions, such as Central and lowland South America, southeastern Asia, India, Africa, and the Pacific Islands. \textit{C. frutescens} is mainly cultivated in home gardens and used as a seasoning for daily meals. Its large-scale cultivation and trading is rare, except for the commercial pepper cultivar \textit{C. frutescens} ‘tabasco,’ which is used to produce Tabasco sauce.

In Japan, \textit{C. frutescens} is cultivated mainly in the Bonin and Ryukyu Islands, where weed forms can be found at forest edges or along roadsides in villages, probably as a result of dispersal by birds. Both areas are famous for \textit{C. frutescens} products marketed to tourists. The eating habits of the Japanese changed after World War II, with a trend toward spicier meals. This trend could lead to large economic benefits from \textit{C. frutescens} cultivation. Moreover, extracts of chilli peppers, especially capsaicinoids, are widely used in food products and in diverse pharmacological and medical applications (Surh and Lee, 1995). Generally, the fruits of \textit{C. frutescens} are so hot that they have potential for industrial production. However, there have been few reports on physiological studies of \textit{C. frutescens} in Japan, including the flowering of these species.

The \textit{C. frutescens} line of the Bonin Islands is very different to that of the Ryukyu Islands, with different morphological characteristics (Yamamoto and Nawata, 2004) and isozyme patterns (Yamamoto and Nawata, 2005). Therefore, the two lines are good models to investigate intraspecific differences in the effects of photoperiod on flowering in \textit{C. frutescens}. In addition, interspecific differences in flowering can be revealed by comparing the characteristics of these lines with \textit{C. annuum} plants cultivated under the same conditions. In this study, the effects of various photoperiods on the flowering of \textit{C. frutescens} lines from the Bonin and Ryukyu Islands and one Japanese hot pepper variety, \textit{C. annuum} cv. ‘Takanotsume’, were investigated to examine interspecific and intraspecific differences in flowering under a controlled environment.

**MATERIALS AND METHODS**

1. **Plant materials**

\textit{C. frutescens} was obtained from markets in the Bonin and Ryukyu Islands. Seeds of these lines, as well as \textit{C. annuum} cv. ‘Takanotsume’ (abbreviated BON, RYU, and TK, respectively), were sown in vermiculite on 21 July 2005 and germinated in an incubator with a fluctuating temperature (16 h at 30°C, 8 h at 20°C) and continuous light, because the seeds of some \textit{C. frutescens} accessions from Southeast and East Asia exhibit dormancy (Yamamoto and Nawata, 2006). The seedlings were transplanted on 8 August 2005 into black vinyl pots (diameter 9 cm, depth 7.5 cm) containing vermiculite and placed in a phytotron (average daily air temperature and humidity 25.4 ±0.1°C and 62.6±0.5%, respectively). Continuous supplemental lighting before the treatments was carried out with six metal halide lamps of 80 μmol m−2 s−1 at plant height for growth before the treatments. Commercial liquid fertilizer solution (0.1% Hyponex; 6 N: 10 P: 5 K: 0.05 Mg: 0.001
Mn: 0.005 B mol/L, Hyponex Japan Corp., Ltd., Osaka, Japan) was applied once a week throughout the experimental period, after the plants were transferred into the phytotron.

2. First experiment

BON, RYU, and TK seedlings were transplanted into plastic pots (diameter 21.5 cm, depth 15 cm) containing vermiculite prior to the treatments. The seedlings were exposed to 6-, 9-, 12-, 15-, 18-, 21-, or 24-h photoperiods from 25 August to 13 November 2005, with three replications. Each day, the seedlings were placed in the phytotron for the light period and then moved back into a dark room (average daily air temperature and humidity 25.3±0.1°C and 64.4±0.8%, respectively) for the dark period. The photoperiod treatment schedule is shown in Table 1.

3. Second experiment

After the first experiment, another experiment was conducted to further observe flower bud formation in BON and RYU. BON and RYU plants grown under a 24-h photoperiod during the first experiment were exposed to 12-h (0700 to 1900), 13-h (0700 to 2000), or 14-h (0600 to 2000) photoperiods, or left in a continuous 24-h photoperiod, and also BON and RYU plants grown under a 12-h photoperiod were exposed to a 24-h photoperiod until 13 December 2005 (with two replications). Finally, plants grown under 15- and 18-h photoperiods in the first experiment were exposed to a 12-h photoperiod (1900 to 0700, light conditions of six metal halide lamps (80 μmol m⁻² s⁻¹ at plant height) and without solar radiation) until 21 December 2005 (with three replications).

4. Measurement and data analysis

The number of leaves prior to the appearance of the first flower bud and the number of days from the beginning of treatment until the appearance of the first flower bud and the anthesis of the first, second, and third flower nodes were recorded. The plant height, leaf length, and leaf width were measured using a scale. The leaf areas were estimated with the formula $\text{LA} = \text{aL}^\text{W}$ (LA, leaf area; L, leaf length; W, leaf width; TK: a=1.167, b=0.869, and c=0.526; BON: a=0.999, b=0.959, and c=0.670; and RYU: a=1.008, b=0.955, and c=0.644), with the parameters determined by regression using the areas of 100 leaves measured with a leaf area meter (Li-Cor LI-1700, Lincoln, NE, USA). The data from each measurement were analyzed with one-way ANOVA using Microsoft Excel 2000 (Microsoft Corporation, Redmond, WA, USA).

RESULTS

1. First experiment

1.1 Flowering of C. annum cv. ‘Takanotsume’

In TK plants exposed to 6-, 9-, 12-, 15-, 21-, or 24-h photoperiods, the first visible flower bud appeared at about 20 days after the beginning of the treatment. However, under an 18-h photoperiod, the first flower bud appeared significantly later (Table 2). Plants exposed to 6-, 9-, 12-, and 15-h photoperiods had 19.0 to 20.7 leaves prior to the appearance of the first flower bud, with the number of leaves increasing as the photoperiod lengthened (Table 2). The plant height and total leaf area at the appearance of the first flower bud were lower under the 6-h photoperiod than under photoperiods of 12 h or longer (Table 2).

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Table 1 Time schedule of the photoperiod treatment.

<table>
<thead>
<tr>
<th>Time</th>
<th>6h</th>
<th>9h</th>
<th>12h</th>
<th>15h</th>
<th>18h</th>
<th>21h</th>
<th>24h</th>
</tr>
</thead>
<tbody>
<tr>
<td>0700</td>
<td>PHY</td>
<td>PHY</td>
<td>PHY</td>
<td>PHY</td>
<td>DAR</td>
<td>PHY</td>
<td>PHY</td>
</tr>
<tr>
<td>1000</td>
<td>PHY</td>
<td>PHY</td>
<td>DAR</td>
<td>DAR</td>
<td>DAR</td>
<td>PHY</td>
<td>PHY</td>
</tr>
<tr>
<td>1600</td>
<td>DAR</td>
<td>DAR</td>
<td>DAR</td>
<td>DAR</td>
<td>DAR</td>
<td>DAR</td>
<td>DAR</td>
</tr>
<tr>
<td>1900</td>
<td>DAR</td>
<td>DAR</td>
<td>DAR</td>
<td>DAR</td>
<td>DAR</td>
<td>DAR</td>
<td>Always at the phytotron</td>
</tr>
</tbody>
</table>

* PHY plants were moved to the phytotron.
* DAR plants were moved to the darkroom.
Plants exposed to 6-, 9-, 12-, and 15-h photoperiods bore flowers normally on the first and higher flower nodes, whereas some plants exposed to photoperiods longer than 18 h did not bear flowers on the first or second nodes because their buds aborted (Table 2). Plants exposed to photoperiods longer than 18 h bore flowers normally on the third and higher flower nodes, as did plants exposed to photoperiods of 15 h or shorter.

The time to flowering from the beginning of treatment was shortest under the 9- and 12-h photoperiods, and the number of days to anthesis at each node was also lower than under other photoperiods. The time to anthesis at each node was significantly longer under long days, such as 18-, 21-, and 24-h photoperiods, than under a 12-h photoperiod (Table 2).

1.2 Flowering of *C. frutescens* from the Bonin Islands

The first visible BON flower bud appeared earliest on plants grown under a 12-h photoperiod, followed by plants grown under a 9-h photoperiod (Table 3). The time to appearance of the first flower bud was significantly delayed, by about 5 to 14 days, in long days, and was also nearly 10 days longer under a 6-h photoperiod, the shortest photoperiod tested, than under a 12-h photoperiod (Table 3). Plants exposed to 9- and 12-h photoperiods had significantly fewer leaves prior to the appearance of the first flower bud (Table 3). Long days resulted in a greater number of leaves prior to the first flower bud than with a 12-h photoperiod (Table 3). The plant height at the appearance of the first flower bud was greatest under the 15-h photoperiod, followed by plants under photoperiods longer than 18 h, and was lower under photoperiods shorter than 12 h (Table 3). The total leaf area was greatest under the 15-h photoperiod, and decreased as the photoperiod lengthened, with smaller leaves being produced. The leaf area under 9- and 12-h photoperiods was smaller than that under long days except for the 24-h photoperiod, due to the lower number of leaves.

<table>
<thead>
<tr>
<th>Table 2</th>
<th>The effect of various photoperiod on flowering of <em>C. annuum</em> cv. Takanotsume (TK).</th>
</tr>
</thead>
<tbody>
<tr>
<td>First visible bud appeared</td>
<td>No. of days from beginning of treatment until</td>
</tr>
<tr>
<td></td>
<td>1st node</td>
</tr>
<tr>
<td>6h</td>
<td>20.0⁺</td>
</tr>
<tr>
<td>9h</td>
<td>19.0⁺</td>
</tr>
<tr>
<td>12h</td>
<td>19.0⁺</td>
</tr>
<tr>
<td>15h</td>
<td>18.3⁺</td>
</tr>
<tr>
<td>18h</td>
<td>25.7⁺</td>
</tr>
<tr>
<td>21h</td>
<td>21.0⁺</td>
</tr>
<tr>
<td>24h</td>
<td>20.3⁺</td>
</tr>
</tbody>
</table>

Values followed by different letters are significantly different at the 5% level.

⁺ some plant did not bear flowers on the first or second nodes because their buds did not grow well and were aborted (A, n=B; A = the average of data of B plant(s) which bore flowers).

<table>
<thead>
<tr>
<th>Table 3</th>
<th>The effect of various photoperiod on flowering of <em>C. frutescens</em> from the Bonin Islands (BON).</th>
</tr>
</thead>
<tbody>
<tr>
<td>First visible bud appeared</td>
<td>No. of days from beginning of treatment until</td>
</tr>
<tr>
<td></td>
<td>1st node</td>
</tr>
<tr>
<td>6h</td>
<td>38.3⁺</td>
</tr>
<tr>
<td>9h</td>
<td>31.3⁺</td>
</tr>
<tr>
<td>12h</td>
<td>28.7⁺</td>
</tr>
<tr>
<td>15h</td>
<td>41.0⁺</td>
</tr>
<tr>
<td>18h</td>
<td>42.7⁺</td>
</tr>
<tr>
<td>21h</td>
<td>37.0⁺</td>
</tr>
<tr>
<td>24h</td>
<td>35.3⁺</td>
</tr>
</tbody>
</table>

FBA⁺: flower-bud abscission.

† only one plant bore flowers on the first to third nodes. (A, n=1; A = the data of one plant which bore flowers).

NG no growth of buds.

Values followed by different letters are significantly different at the 5% level.
leaves that had emerged prior to the first flower bud in these conditions.

Under photoperiods of 12 h or shorter, only plants exposed to a 12-h photoperiod and one plant exposed to a 9-h photoperiod bore flowers on the first and higher flower nodes; the buds of the others dropped before flowers finally opened on the fourth to sixth nodes. Unlike TK plants, which under all photoperiods bore flowers on at least the third and higher flower nodes, plants exposed to photoperiods of longer than 15 h did not bear flowers during the first experiment because the buds aborted, although flower differentiation was observed (Fig. 1).

1.3 Flowering of C. frutescens from the Ryukyu Islands

The first visible RYU flower bud appeared earliest under the 12-h photoperiod, similar to BON plants, and buds appeared at around 40 days under 9-, 15-, 18-, 21-, and 24-h photoperiods (Table 4). The time to the appearance of the first flower bud was significantly delayed under the 6-h photoperiod. Plants grown under a 12-h photoperiod had the lowest number of leaves prior to the appearance of the first flower bud (Table 4). This number was around 30 under 9-, 15-, 18-, 21-, and 24-h photoperiods, and was significantly larger under the 6-h photoperiod (Table 4). The plant height at the time of the first flower bud appearance was greatest under the 6-h photoperiod, measured 30.3 to 34.5 cm under 9-, 15-, 18-, 21-, and 24-h photoperiods, and was lowest under the 12-h photoperiod (Table 4). The total leaf area decreased as the photoperiod lengthened under photoperiods longer than 15 h, as for BON plants. Plants grown under a 12-h photoperiod had the smallest total leaf area, owing to the low number of leaves that had emerged prior to the appearance of the first flower bud, and those grown under the 6-h photoperiod had the largest leaf area, due to the large number of leaves produced because of the great delay in flower bud differentiation.

The flowering properties of RYU differed from those of TK and BON. Buds of RYU plants exposed to a 12-h photoperiod grew normally and flowered, but the buds on plants grown under any of the other photoperiods aborted throughout the experimental period. RYU plants did not pro-

![Fig. 1](image)

**Fig. 1** Flower bud abortion under long day photoperiods. (A) Flower bud differentiation was observed at first, then (B) buds aborted under long day photoperiods.

<table>
<thead>
<tr>
<th>No. of days from beginning of treatment until First visible bud appeared</th>
<th>Anthesis</th>
<th>No. of leaves prior to the first flower bud</th>
<th>At the first flower bud appearance</th>
<th>Plant height (cm)</th>
<th>Total leaf area (cm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>6h</td>
<td>65.3</td>
<td>NG</td>
<td>NG</td>
<td>45.3</td>
<td>39.7</td>
</tr>
<tr>
<td>9h</td>
<td>37.7</td>
<td>NG</td>
<td>NG</td>
<td>29.3</td>
<td>24.0</td>
</tr>
<tr>
<td>12h</td>
<td>29.0</td>
<td>46.3</td>
<td>50.2</td>
<td>53.9</td>
<td></td>
</tr>
<tr>
<td>15h</td>
<td>37.0</td>
<td>NG</td>
<td>NG</td>
<td>28.0</td>
<td>34.5</td>
</tr>
<tr>
<td>18h</td>
<td>41.3</td>
<td>NG</td>
<td>NG</td>
<td>29.0</td>
<td>33.3</td>
</tr>
<tr>
<td>21h</td>
<td>40.0</td>
<td>NG</td>
<td>NG</td>
<td>31.3</td>
<td>33.7</td>
</tr>
<tr>
<td>24h</td>
<td>38.7</td>
<td>NG</td>
<td>NG</td>
<td>31.0</td>
<td>32.7</td>
</tr>
</tbody>
</table>

NG: no growth of buds

Values followed by different letters are significantly different at the 5% level.
duce buds at all under the 6- and 9-h photoperiods, even though BON plants grown under the same conditions produced buds and bore flowers on the fourth to sixth flower nodes.

2. Second experiment

All BON plants began to produce buds and reached flowering in two to three weeks after transfer from a continuous 24-h photoperiod to 12-, 13-, or 14-h photoperiods, and plants grown under a continuous 24-h photoperiod also reached flowering in about two weeks (Table 5). No growth of new buds was observed at first on BON plants that were transferred from a 12-h photoperiod to a 24-h photoperiod, but new buds began to appear about one month later. RYU plants flowered in 27 to 30 days under 12- and 13-h photoperiods, but no new bud growth was observed under 14-h or continuous 24-h photoperiods, even after one month (Table 5). In addition, no new bud growth was observed during the entire experimental period on RYU plants that were transferred from a 12-h photoperiod to a 24-h photoperiod.

To investigate the effect of photoperiod on the flowering of BON and RYU, plants grown under 15- and 18-h photoperiods in the first experiment were transferred to a 12-h photoperiod (1900 to 0700, light from six metal halide lamps without solar radiation). Both BON and RYU plants produced flower buds and flowered in 25 to 33 days (BON) or 32 to 38 days (RYU), slightly longer than the time to flowering of plants transferred from a continuous 24-h photoperiod to a 12-h photoperiod (0700 to 1900, light from solar radiation) (Table 5).

DISCUSSION

1. Interspecific differences in flowering in Capsicum

Plants in each of the three pepper lines, TK, BON, and RYU, developed flower buds earliest when grown under a 12-h photoperiod, suggesting that they are all short-day plants. This result agrees with the conclusions of Auchter and Harley (1924), Cochran (1932, 1942), and Artyugina (1967), but conflicts with that of Masuda and Murage (1998), who claimed that species in the Solanaceae family, which includes the genus Capsicum, are day-neutral. In TK, the first flower buds appeared in 19.0 to 25.7 days, and their appearance was not remarkably delayed under any of the photoperiods tested, whereas in BON and RYU, the time to the appearance of the first flower

<table>
<thead>
<tr>
<th>Table 5 Changing photoperiods of BON and RYU.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>First experiment</strong></td>
</tr>
<tr>
<td><strong>Photoperiod</strong></td>
</tr>
<tr>
<td>BON <strong>24h</strong></td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>RYU <strong>12h</strong> Normal</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td><strong>15h</strong></td>
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<td></td>
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<tr>
<td></td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td><strong>18h</strong></td>
</tr>
<tr>
<td></td>
</tr>
</tbody>
</table>

* NG no growth of buds.

** MHL lightening of 6 metal halide lamps almost without solar radiation.
bud was longer (28.7 to 42.7 days and 29.0 to 65.3 days, respectively) and was delayed markedly under conditions that were unsuitable for these lines. *C. frutescens* (BON and RYU) appears to be more late-maturing than *C. annuum* (TK), a trait that was very evident under the unsuitable conditions. The number of leaves prior to the appearance of the first flower bud and the plant height at this time were greater in BON and RYU than in TK under the same photoperiods, another indication that *C. frutescens* is late-maturing.

Deats (1925) reported that pepper plants do not form flowers in a photoperiod with a day length of 6.5 h, but Auchter and Harley (1924) reported the formation of both buds and flowers in this crop under a 7-h photoperiod. Thus, Cochran (1942) concluded that a day length of 7 h is about the lower limit for flower primordia differentiation in *Capsicum*. However, both *C. annuum* and *C. frutescens* exhibited flower differentiation under a 6-h photoperiod in our study, although the time to the appearance of the first flower bud in BON and RYU was strongly delayed and the buds aborted under these conditions, probably due to a reduced accumulation or abnormal distribution of photosynthates. Therefore, it appears that a day length of around 6 h is the lower limit for flower differentiation in *C. annuum* and *C. frutescens*.

TK plants grown under long days developed more leaves prior to the appearance of the first flower bud than those grown under short days, a result that conflicts with the results of Rylski (1972), who claimed that fewer leaves formed prior to the appearance of the first flower in California Wonder under long days than under short days. The height of TK plants at the first visible flower bud appearance was also higher under long days than under short days, which agrees with the results of Cochran (1942) and Dorland and Went (1947). These results suggest that plants grown under long days use more photosynthates during their growth. This trend was also observed in BON and RYU, but in addition, the severe delay in the time to the first flower bud appearance in BON and RYU caused by a 6-h photoperiod resulted in increases in the number of leaves produced prior to the appearance of the first flower bud, the plant height, and the total leaf area at the appearance of the first flower bud.

In contrast, the leaf area of BON and RYU plants was reduced and that of TK was slightly reduced by longer days, such as those of 21 and 24 h, likely because plants exposed to long days produced smaller leaves and dropped leaves earlier. Adams and Langton (2005) reviewed the effect of photoperiod on the leaf area and leaf production rate, and showed that six of the 50 species tested (12%) produced larger or longer leaves in short days. Ezekiel and Bhargava (1991) reported that long days resulted in a smaller individual leaf size in potato (*Solanum tuberosum*). Prolonging the light period to continuous light without a dark break causes leaf injury, characterized by leaf chlorosis and necrosis, in potato (Cao and Tibbits, 1991), eggplant (Murage et al., 1996), and tomato (Hillman, 1956). It appears that leaves age more rapidly under long days than under short days, possibly because under long days the organs do not receive the break in work provided by night. Thus, abscission of individual leaves occurred quickly under long days. These results show that the leaves of some *Capsicum* species remain smaller and/or are injured by long days, especially under nearly continuous light.

Under photoperiods of 12 h or shorter, flowering in *C. annuum* and *C. frutescens* differed. TK plants bore flowers regularly on the first and higher flower nodes under photoperiods shorter than 12 h, but only BON and RYU plants grown under a 12-h photoperiod flowered similarly. The buds of BON plants grown under shorter photoperiods dropped until flowers bloomed on the fourth to sixth nodes, and RYU plants grown under 6- and 9-h photoperiods did not produce buds at all during the first experimental period. This is probably because *C. frutescens* requires more photosynthates to bear flowers than *C. annuum*, and/or *C. frutescens* uses low amounts of photosynthates because of its high respiration rate, due to its much larger leaf area than that of *C. annuum* (Tables 2, 3, and 4).

The crucial difference in flowering between *C. annuum* and *C. frutescens* was the reaction to
long days. TK plants grown under photoperiods longer than 15 h did not flower well on the first or second nodes, but bore flowers normally on the third and higher flower nodes. However, BON and RYU plants exposed to photoperiods longer than 15 h bore no flowers during the first experimental period because their buds aborted, although flower differentiation was observed and enough photosynthates appeared to accumulate to allow flowering. Long days strongly inhibited *C. frutescens* flower bud growth. Photoperiod affects not only the time to flowering but also node and branch formation and the overall balance between reproductive and vegetative growth (Laing et al., 1984; Wallace, 1985). It appears that unknown substances regulate *Capsicum* flower bud growth, and they are produced or accumulated during the dark period. TK did not flower well initially under long days, but recovered rapidly through some unknown mechanism, which may enable this line to accumulate the substances important for flower bud growth, even under long days. In contrast, BON and RYU could not recover to bear flowers under these conditions.

Plant hormones, including abscisic acid (ABA), auxin, cytokinin, gibberellic acid (GA₃ and GA₄), and indoleacetic acid (IAA), are thought to influence flower bud formation (Chen, 1990; Gao et al., 2002; Ito et al., 2004; Koshita and Takahara, 2004; Pal and Ram, 1978; Ulger et al., 2004). These hormones may be related to *Capsicum* flower bud growth, with those that have a positive effect on flower formation being produced during the dark period, and/or those that exhibit an inhibitory effect on flower bud growth being accumulated under long days.

2. **Intraspecific differences in flowering in *Capsicum frutescens***

Among photoperiods equal to or shorter than 12 h, BON plants flowered normally on the first and higher nodes under the 12-h photoperiod, but those grown under 6- and 9-h photoperiods did not show normal flowering, suggesting that the assimilation and dissipation of hormones in BON plants under 6- and 9-h photoperiods may not have been well balanced, resulting in flower bud abscission before flowering and delayed flowering until the fourth to sixth nodes (Table 3). In contrast, RYU plants grown under 6- and 9-h photoperiods did not produce flower buds or reach flowering during the first experimental period; only RYU plants exposed to a 12-h photoperiod reached flowering (Table 4). BON appears to be able to adapt to very short days and flower, although this process took much longer than in TK, whereas under 6- and 9-h photoperiods, all RYU buds aborted during the first experimental period. This observation also agrees with the large delay in the time to the appearance of the first flower buds in RYU grown under a 6-h photoperiod.

Under photoperiods longer than 15 h, BON and RYU plants formed no buds during the first experimental period, as mentioned above. Therefore, the second experiment was conducted after the first experiment to further examine this lack of flowering in these lines (Table 5). All BON plants transferred from a continuous 24-h photoperiod to 12-, 13-, and 14-h photoperiods began forming buds and reached flowering in two to three weeks, and plants under a continuous 24-h photoperiod also reached flowering in about two weeks. In contrast, RYU plants reached flowering under the 12- and 13-h photoperiods, but no new bud growth was observed in RYU plants under 14-h or continuous 24-h photoperiods. It appears that BON has a mechanism to develop flower buds even under long days, like TK, but needs a much longer period to bear flowers than TK. However, RYU did not reach flowering under 14-h and continuous 24-h photoperiods, but this inhibition was overcome by 12- and 13-h photoperiods, suggesting that the day length is a very important factor for RYU. The critical day length for RYU appears to be between 13 and 14 h. This result agrees with the findings that no growth of new BON buds was observed at first after transfer from a 12-h photoperiod to a 24-h photoperiod, but that new flower buds appeared about one month later, whereas no buds were observed during the entire experimental period on RYU plants transferred from a 12-h photoperiod to a 24-h photoperiod (Table 5).

Both BON and RYU plants transferred from 15- and 18-h photoperiods to a 12-h photoperiod (1900 to 0700, with artificial light and without solar radiation) produced flower buds and reached flowering in 25 to 33 days (BON) and 32 to 38 days (RYU), although the time to flowering was
slightly longer than in plants transferred to a 12-h photoperiod (0700 to 1900, with solar radiation) (Table 5). This result supports the idea that the inhibition of flowering in BON and RYU by long days was not caused by a reduced accumulation of photosynthates due to the high rate of respiration under the low light intensity but, instead, was caused by the length of the night, which appears to be very important for flower bud growth in both BON and RYU.

Yamamoto and Nawata (2006) reported that accessions of C. frutescens from Southeast and East Asia appear to be at various stages of domestication, from weedier to fully domesticated. Because the BON and RYU lines are at an intermediate stage between wild and domesticated, they may still contain some genes that inhibit flower differentiation or flower bud growth under long days. The differences in the reactions to long days in BON and RYU reveal the gene diversity of C. frutescens in Southeast and East Asia. In contrast, TK appears to have lost these genes during the domestication process, like other fully domesticated varieties of C. annuum such as “Ruby King” (Auchter and Harley, 1924), “Hatvani Hajtató,” “Soroksári Hajtató,” and “California Wonder” (Máthé and El-Bahadili, 1989), and “Kyomidorì” (Masuda and Murage, 1998), which showed normal flowering and flower bud growth under a continuous 24-h photoperiod. However, it is not known how wild C. annuum reacts to long days, that is, whether C. annuum was originally able to bear flowers normally under very long days.

In conclusion, the photoperiod affects not only the time to flowering in Capsicum, but also the growth of C. frutescens flower buds. Semi-domesticated C. frutescens and fully domesticated C. annuum exhibit interspecific differences in flowering and fruiting habits, especially in the reaction to long days, under controlled conditions, and there is also an intraspecific difference between the two C. frutescens genotypes. It will be necessary to determine whether these differences are caused by the stage of domestication. Further studies are required on the flowering of wild C. annuum and other species of the genus Capsicum.

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