Sexual Polymorphism in *Moehringia lateriflora* (Caryophyllaceae)

TAKASHI SUGAWARA

*Department of Biology, Faculty of Science, Hirosaki University, 3 Bunkyo-cho, Hirosaki, Aomori 036*  
(Present address: Biological Institute and Herbarium, Faculty of Liberal Arts,  
Shinshu University, Asahi 3-1-1, Matsumoto, Nagano 390)

**Abstract** Sexual polymorphism in *Moehringia lateriflora* was investigated in terms of the morphology and reproductive potential of flowers different in sex expression in natural populations. Throughout field survey, two different plants, hermaphrodite and female, were found in the three examined populations. Hermaphrodite flowers are protandrous, and have larger petals and longer filaments. Their anthers produce a large number of pollen grains, although their fertilities vary among and within the populations. Female flowers, on the other hand, have smaller petals, shorter filaments, and abortive anthers that completely lack pollen grains. Despite apparently disadvantageous floral attributes for attracting pollinators, the female flowers usually produce seeds equivalent to the hermaphrodite ones in natural populations. Moreover, stigmas of the female flowers mature earlier relative to flower opening than those of the hermaphrodite ones.

(Received December 14, 1992; Accepted April 19, 1993)

Key words: Caryophyllaceae, female flowers, floral morphology, gynodioecy, *Moehringia*, *Moehringia lateriflora*, sexual polymorphism.

*Moehringia lateriflora* (L.) Fenzl (Caryophyllaceae) is a stoloniferous perennial herb widely distributed in temperate regions of the Northern Hemisphere including Japan and Sakhalin (Halliday, 1964; Ohwi, 1965). In Japan, the species is distributed in Hokkaido, Honshu, Shikoku and Kyushu (Ohwi and Kitagawa, 1983). The plants usually occur on sunny slopes of mountains or hills, where they are matted with spreading stolons. The species generally flowers from late May to July, and has been known to be sexually polymorphic (Tohda, 1960, 1965; Kitamura and Murata, 1961). Tohda summarizes that the plants of *Moehringia lateriflora* produce any of hermaphrodite, female, or male flowers. Kitamura and Murata, however, report that the species is monoecious, having both male and female flowers on one and the same plant. Therefore, based on earlier literatures it is unclear how sexual polymorphism occurs in *Moehringia lateriflora*.

In this study a reinvestigation is made to clarify the exact status of sexual polymorphism in *Moehringia lateriflora* on the basis of flower collections from three different populations. The reproductive potential and the actual seed set of the flowers different in sex expression are also reported.

**Materials and Methods**

Field observations of *Moehringia lateriflora* were made at three different localities in Aomori Prefecture, northernmost Honshu (Fig. 1): (1) Zubonmori (40°43’N, 140°0’E; alt. 10m), near the seaside, (2) Dake (40°37’N, 140°17’E; alt. 410m) and (3) Hyakusawa.
Fig. 1. Map showing the localities of three examined populations.

(40°38'N, 140°21'; alt. 290m), in south and southeast of Mt. Iwaki, respectively. In all of the populations, plants occur in a patchy distribution on sunny slopes. The study plot is ca. 6 x 5m in Zubonmori, ca. 5 x 4m in Dake, and ca. 6 x 6m in Hyakusawa. In the Zubonmori population, the plants grow together with Rosa rugosa Thunb., Dianthus superbus L., Buglossoides zollingeri (DC.) Johnston, Galium verum L. var. asiaticum Nakai, etc., while in the Dake and the Hyakusawa populations they occur together with several perennial herbs such as Anthoxanthum odoratum L., Zoysia japonica Steud., and Haloragis micrantha (Thunb.) R. Br.

For examination of sexual differentiation, more than 20 erect stems with open flowers which belonged to different aggregates were randomly collected in the three populations, and fixed with FAA (formalin-acetic acid-alcohol). After fixation, one flower from each erect stem was sampled, and the following three characters were measured using Olympus camera lucida: petal length, petal width and filament length. The fertility of pollen grains was examined under a microscope as follows: two anthers from each flower were crushed on a glass slide, stained with a drop of cotton blue solution, and kept overnight.

Several plants (erect stems) collected from the study sites were transplanted into the experimental garden of Hirosaki University, and those plants were examined in the following year to check the constancy of sexual form of the flowers born on them.

To estimate the fruit and seed set percentages in natural populations, erect stems were collected at random, and all flowers born on those stems were examined.

Voucher specimens are temporarily deposited in Hirosaki University, and shall be transferred to the Makino Herbarium (MAK), Tokyo Metropolitan University.
Results and Discussion

1) Sex expression in natural populations

Each erect stem of *Moehringia lateriflora* has one to three inflorescences (cymes), and usually bears one to four flowers per cyme. Flowers are small, whitish, and actinomorphic; each flower has five sepals, five petals, ten stamens and a compound ovary with three to four free styles. Five nectar-producing glands (nectaries) are present at the base of five stamens alternating with the petals (Fig. 2), as in other species of the family (Dulberger and Horovitz, 1984; Tsukui and Sugawara, 1992), and they exude nectar during a flowering period. Although no exact observations on pollinators were made, some small insects (ex., beetles and hover-flies) have obviously visited the flowers.

In all of the three populations examined, hermaphrodite and female flowers (Fig. 2A, B) are common. In addition, some intermediate flowers (Fig. 2C) which have a lower pollen fertility (mean: 24.2%, see also Tab. 1) are found in the Hyakusawa population. In earlier studies (Tohda, 1960, 1965; Kitamura and Murata, 1961), male flowers have also been reported for the species. In my field survey, however, I have never encountered male flowers in the three populations.

In natural populations, most of the erect stems examined bore either female or hermaphrodite flowers on inflorescences, though inflorescences possessing both female and hermaphrodite flowers were rarely found in a few stems. Plants transplanted into the experimental garden consistently bore one of the two different flowers during two years of the
Fig. 3. Stigmas prior to flower-opening in female (A) and hermaphrodite (B) flowers of *Moehringia lateriflora*. Scale bar represents 200μm.

Table 1. Pollen fertility (%) of hermaphrodite flowers examined in three populations of *Moehringia lateriflora*

<table>
<thead>
<tr>
<th>Population (year of sampling)</th>
<th>N*</th>
<th>Mean ± S.D.</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zubonmori (1991)</td>
<td>5</td>
<td>81.0 ± 6.8</td>
<td>70.2 – 88.1</td>
</tr>
<tr>
<td>Zubonmori (1992)</td>
<td>20</td>
<td>84.4 ± 8.5</td>
<td>66.4 – 97.1</td>
</tr>
<tr>
<td>Dake (1991)</td>
<td>10</td>
<td>60.0 ± 2.9</td>
<td>55.9 – 65.4</td>
</tr>
<tr>
<td>Dake (1992)</td>
<td>18</td>
<td>59.4 ± 3.2</td>
<td>51.1 – 64.3</td>
</tr>
<tr>
<td>Hyakusawa (1992)</td>
<td>24</td>
<td>95.5 ± 3.3</td>
<td>86.9 – 99.1</td>
</tr>
<tr>
<td>Hyakusawa (1992)</td>
<td>24</td>
<td>24.2 ± 11.0</td>
<td>1.0 – 43.5</td>
</tr>
</tbody>
</table>

* N: Number of flowers examined
* : Pollen fertility in intermediate flowers with more or less abortive stamens as shown in Fig. 1C.

Table 2. Averages of petal length, petal width, and filament length in hermaphrodite and female flowers examined in three populations of *Moehringia lateriflora*

<table>
<thead>
<tr>
<th>Population</th>
<th>Petal length (mm)</th>
<th>Petal width (mm)</th>
<th>Filament length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± S.D.</td>
<td>Mean ± S.D.</td>
<td>Mean ± S.D.</td>
</tr>
<tr>
<td>Zubonmori</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hermaphrodite (N=46)*</td>
<td>6.5 ± 0.6</td>
<td>3.3 ± 0.2</td>
<td>3.3 ± 0.2</td>
</tr>
<tr>
<td>Female (N=47)</td>
<td>4.7 ± 0.4</td>
<td>2.6 ± 0.2</td>
<td>1.1 ± 0.2</td>
</tr>
<tr>
<td>Dake</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hermaphrodite (N=21)</td>
<td>6.0 ± 0.2</td>
<td>3.3 ± 0.1</td>
<td>3.1 ± 0.1</td>
</tr>
<tr>
<td>Female (N=23)</td>
<td>5.0 ± 0.3</td>
<td>2.4 ± 0.2</td>
<td>1.1 ± 0.2</td>
</tr>
<tr>
<td>Hyakusawa</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hermaphrodite (N=21)</td>
<td>6.4 ± 0.2</td>
<td>2.9 ± 0.2</td>
<td>3.2 ± 0.1</td>
</tr>
<tr>
<td>Female (N=21)</td>
<td>4.8 ± 0.3</td>
<td>2.1 ± 0.2</td>
<td>1.0 ± 0.1</td>
</tr>
<tr>
<td>Intermediate (N=13)</td>
<td>4.8 ± 0.2</td>
<td>2.0 ± 0.1</td>
<td>2.4 ± 0.3</td>
</tr>
</tbody>
</table>

* N: Number of flowers examined
investigations. Therefore, as far as based on the three examined populations, *Moehringia lateriflora* is either unisexual (female) or bisexual (hermaphrodite) depending on plants.

In the present study, however, frequency of plants with different sexual forms of the flowers was not examined in each population.

2) *Floral attributes in hermaphrodite and female flowers*

Floral structures of hermaphrodite and female flowers are shown in Figure 2. Hermaphrodite flowers are protandrous. As the flowers open, anthers of five outer stamens alternating with petals dehisce first, and then (one or two days later in general) anthers of the inner stamens dehisce. When the flowers open and all anthers dehisce, the styles are still positioned below the anthers (Fig. 2A), and their stigmatic tissues (papillae) are not developed well enough yet (Fig. 3B). Two to three days later, the styles gradually extend upward and spread out obliquely (Fig. 2A4), and they now have well-developed, receptive stigmatic tissues.

In the female flowers, on the other hand, stamens become abortive early in flower development; their filaments fail to extend upward and their anthers completely lack pollen grains (Fig. 2B2). While the flowers are still closed, styles are already elongated upward (Fig. 2B4), and their stigmas mature earlier and become receptive sooner relative to flower opening (Fig. 3A), rather than in case of hermaphrodite ones. This earlier stigma maturation would be significant for extending the chance of pollination to the female flowers.

Anthers of the hermaphrodite flowers produce a large number of pollen grains. Fertilities of pollen grains of the hermaphrodite flowers examined in the three populations are presented in Table 1. The fertilities considerably differ among the populations, but are fairly constant within a population during the two examined years (i.e., 81% and 84% in Zubonmori, 59% and 60% in Dake, and 96% in Hyakusawa).

Averages of petal length and width, and filament length in the hermaphrodite and the female flowers in the three populations are summarized in Table 2. Petal length and width of the female flowers are significantly shorter (t-test, p < 0.001), as in other gynodioecious species such as *Iris douglasiana* (Uno, 1982), *Saxifraga granulata* (Stevens and Richards, 1985), and *Thymus vulgaris* (Assouad et al., 1978). In addition, filaments of the female flowers were significantly shorter than those of the hermaphrodite ones (t-test, p < 0.001).

Comparisons in ovule numbers per ovary are also presented in Table 3. There was no significant difference in mean ovule number between hermaphrodite and female flowers in any population during two years of the study (t-test, P > 0.05).

As already mentioned above, some intermediate flowers which show a lower pollen fertility (mean: 24%, range: 1.0-43.5%) are found in the Hyakusawa population. Anthers of those flowers are smaller in size than those of the hermaphrodite flowers (Fig. 2C), and degenerative particularly in the inner stamens. Moreover, their petals are also smaller (Tab. 2), as in those of the fully female flowers. In the present study, however, ovule numbers per ovary in the intermediate flowers were not examined. In addition, it is uncertain as to whether the sexual condition in such flowers is genetically stable or not.

3) *Pollination experiments and fruit sets in natural populations*

As 11 female flowers were bagged, they produced no fruits, thus indicating that no apomixis occurred. When 15 hermaphrodite flowers were bagged prior to anthesis, they set no fruits. Of 43 artificially self-pollinated hermaphrodite flowers, only eight flowers set fruits each of which contains several seeds ranging one to seven (mean: 4.0). These results suggest that the hermaphrodite flowers are partially self-compatible despite their protandrous
nature, and also depend on insect pollinators to set fruits and seeds.

Table 4 shows the fruit and seed set percentages in hermaphrodite and female flowers examined in Dake and Zubonmori populations. In general, both hermaphrodite and female flowers produce well fruits and seeds in each population. The seed set percentage in the Zubonmori population tends to be higher in female flowers than in hermaphrodite flowers (t-test, \( p < 0.001 \)). On the other hand, the fruit set percentage is considerably different among the populations. This difference may be caused by a varying distribution pattern of the hermaphrodite and female plants in each population. Indeed, in the Zubonmori population the hermaphrodite plants are scattered and intermingled with the female ones, while in the Dake population both the hermaphrodite and the female plants occur in separate aggregates.

As presented above, the present investigations revealed that both the hermaphrodite and the female flowers are commonly found in the three investigated populations of *Moehringia lateriflora*. The hermaphrodite flowers have larger petals and are protandrous, while the female flowers have smaller petals and their stigmas mature earlier relative to flower opening than those of the hermaphrodite flowers. In natural populations, the female flowers well produce seeds equivalent to the hermaphrodite ones, although they appear disadvantageous for attracting pollinators because of smaller flower size as well as of the lack of pollen grains.
I am grateful to Dr. H. Tohda of Tohoku University for helpful advice during the course of this work, and to Dr. H. Tobe of Kyoto University for critical reading of the manuscript.

References


に、柱頭組織の成熟が開花から2〜3日以上後になるが、雌花は開花時にはすでに柱頭組織を発達させ、受粉可能な状態にあることも明らかになった。（〒036 弘前市文京町 3 弘前大学理学部生物学教室；現在の住所 〒390 松本市旭3-1-1 信州大学教養部生物学教室）