

Reproductive biology of *Hibiscus hamabo* Siebold et Zucc. (Malvaceae)

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| journal or publication title | 植物地理・分類研究 = The journal of phytogeography and taxonomy |
| volume | 52 |
| number | 1 |
| page range | 47-56 |
| year | 2004-07-25 |
| URL | http://hdl.handle.net/2297/48647 |

Hiroki Nakanishi¹ and Naomi Kawara-Kiyoura^{1,2}: **Reproductive biology of *Hibiscus hamabo* Siebold et Zucc. (Malvaceae)**

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Abstract

The reproductive biology of *Hibiscus hamabo* Siebold et Zucc. (Malvaceae) was studied in Nagasaki, Kyushu, southwestern Japan. This species is the northernmost distributed *Hibiscus* species in Japan, and the flowers are similar to those of *H. tiliaceus*, which is a pan tropical and subtropical species. The flowering period was observed to be limited to a month and a half, starting at the beginning of July, peaking in mid-July and ending in mid-August. Eight floral characters, petal length, petal width, style length, anther-stigma distance, anther-anther distance, pistil tip length, number of anthers and floral dry weight, and size of mature fruits and seed dry weight, were measured for two populations. The Togitsu population is small and isolated but surrounded by various ecosystems, and the Saikai population is larger and surrounded by natural vegetation. The measurements of reproductive organs, flower, fruit, seed production and seed weight were greater and more varied in the Saikai population. Pollination experiments with the following four treatments were done for these two populations: hand cross-pollination, hand self-pollination, autonomous self-pollination and open-pollination. The results of fruit sets and seed sets indicated that *H. hamabo* is clearly self-compatible but has inbreeding depression. In open-pollinated flowers, fruit sets of the Togitsu population were significantly greater than those of the Saikai population. Fruit predation in the Togitsu population was also greater than that in the Saikai. A comparison of these results with those of *H. tiliaceus*, a phylogenetically closely related species, indicated that the reproductive systems of *H. hamabo* are characterized by adaptation to the warm-temperate climate. A comparison between the populations suggested that the size of the populations and the ecosystem diversity surrounding them were important for their breeding success.

Key words : floral characters, *Hibiscus hamabo*, phenology, pollination, population.

Hibiscus species (Malvaceae) distributed from the tropics to warm-temperate areas often have attractive and large flowers with conspicuous nectar guides. The flowers are also characterized by a “staminal column”, which is a tube formed by coalescent filaments from which a style protrudes. This morphological contrivance functions as a type of herkogamy which effectively prevents self-pollination. Due to these floral characters, the reproductive biology of some *Hibiscus* species has been studied: *H. moscheutos* L. (Spira 1989; Spira et al. 1992; Kudoh and Whigham 1998), *H. laevis* All. (Klips and Snow 1997), *H. glaber* Matsum. and *H. tiliaceus* L. (Hirota et al. 1999).

Hibiscus hamabo Siebold et Zucc. is a deciduous shrub growing around salt marshes and is distributed from the southern Kanto District

through Tokai, the Kii Peninsula, the western part of Honshu, Shikoku and Kyushu to Amami Island in Japan and to Jeju Island of Korea (Nakanishi 1979, 2000, 2001; Ohba 1989). The flowers are similar to those of *H. tiliaceus*, which is a pan tropical and subtropical species. Although the flower size of *H. hamabo* is one of the largest in the warm-temperate zone of Japan, surprisingly little is known about its reproductive biology.

A comparison of reproductive biology among species belonging to the same genus or section, particularly those of phylogenetically close species, may be important for considering the evolution of reproductive systems. Even within a species, it is important to compare reproductive success among populations of not only different sizes but also different environmental conditions

(Jennersten 1988 ; Aizen and Feisinger 1994).

This study was done for two purposes, to provide information on the breeding system and reproductive efficiency of *H. hamabo*, and to compare the reproductive characters of two different populations, with consideration of the causes of the differences found.

Materials and methods

Study plant and study site

Hibiscus hamabo is the northernmost distributed *Hibiscus* species in Japan (Nakanishi 2003), and may be the northernmost species of the section *Azanza* in the world. Plants grow to a height of 3 to 6 m and branches spread near the ground surface, interweaving with each others. The communities usually consist of only *H. hamabo*, but are restricted to small number of individuals. More than half of all localities in western Kyushu have less than 10 individuals (Nakanishi 2000). The species has conspicuous flowers, approximately 7 cm across ; petals are yellow with a dark red center. Individual flowers generally last a single day.

The field study was carried out at two sites, Shishigawa in Togitsu-cho and Minamikushijima in Saikai-cho, which are ca. 12 km and 30 km, respectively, northwest of Nagasaki City, Kyushu, southwestern Japan (Fig. 1). The climate is warm-temperate with a mean annual temperature of 16.9°C and a total annual precipitation of 1,993 mm in Nagasaki (1971–2000, National As-

tronomical Observatory 2002). At Shishigawa in Togitsu-cho, which faces the Oomura Bay, the *H. hamabo* community is composed of ten individuals of *H. hamabo* and a few individuals of *Pittosporum tobira*, *Euonymus japonicus* and other ever-green shrubs. The neighborhood of this community contained various ecosystems, such as paddy fields, abandoned paddy fields, streams, residential areas and evergreen broad-leaved forests, but no other population of *H. hamabo* was found. This population is hereafter referred to as the Togitsu population. At Minamikushijima in Saikai-cho, the *H. hamabo* community is developed along a narrow strait surrounded by evergreen broad-leaved forests dominated by *Castanopsis cuspidata* var. *sieboldii* and composed of about forty individuals of *H. hamabo*. This is hereafter referred to as the Saikai population. Other *H. hamabo* populations are found near this population.

Phenology

The flowering phenology and dispersal period were studied in the Togitsu population. For flowering phenology, we visited the study site every other day from early July to the end of August for two years (2001–2002) and counted the number of flowers in a section of a larger individual of *H. hamabo* because it was impractical to check all the flowers of a plant in the community. The part comprised approximately one-third of the whole plant. For the dispersal phenology, ten seed traps consisting of plastic baskets, 70 cm in diameter and 40 cm in depth, were set on the ground of the population. We counted the number of seeds in all traps every two weeks from October 2001 to June 2002.

Floral and fruit morphology

Flowers were randomly selected and eight floral characters were measured (Fig. 2) of two populations: petal length (PeL), petal width (PW), style length (SL), anther-stigma distance (ASD), which is the nearest distance between the uppermost anther and the lowermost stigma, anther-anther distance (AAD), which is the distance between the lowermost anther and the uppermost anther, pistil tip length (PiL), which is the dark red portion of the upper part of the pis-

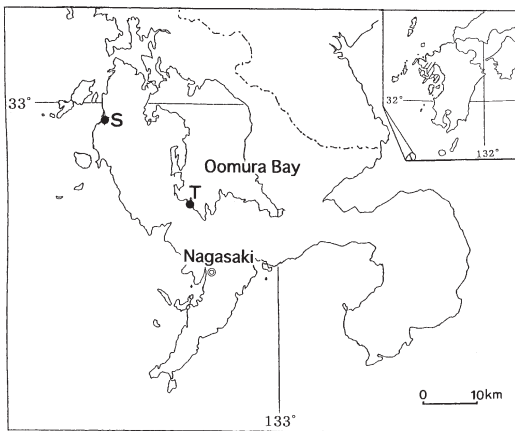


Fig. 1. Map showing the localities investigated. T, Togitsu population ; S, Saikai population.

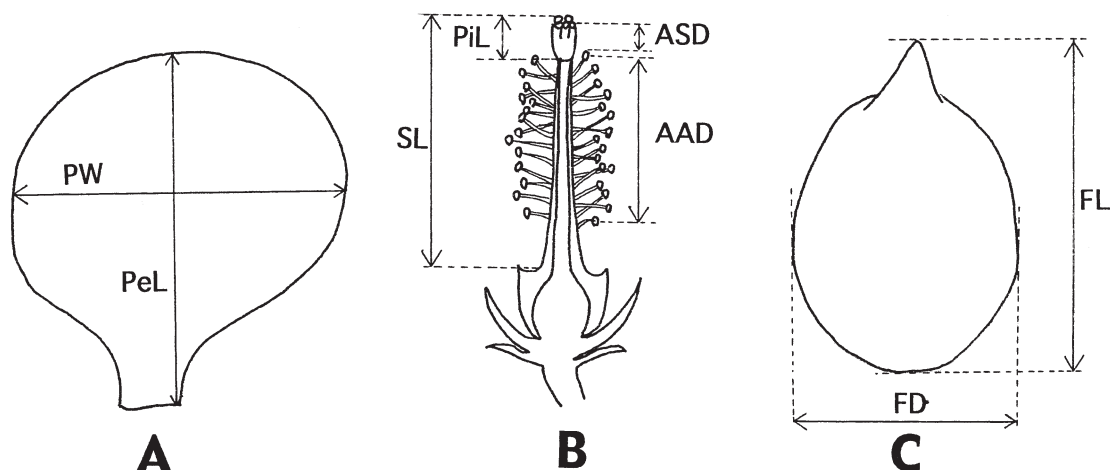


Fig. 2. Measured part of flower and fruit of *Hibiscus hamabo*. A: petal. PeL, petal length; PW, petal width. B: longitudinal section of the central portion of flower. SL, style length; ASD, anther-stigma distance; AAD, anther-anther distance; PiL, pistil tip length. C: fruit. FL, fruit length; FD, fruit diameter.

til, number of anthers and dry floral weight. Individual flowers of *H. hamabo* last a single day and fall the next day. Fallen flowers, which included corolla, stamens and pistil excluding the ovary were collected and dried for about three weeks in the laboratory, after which each flower was weighed using a Sartorius analytical balance (Chyo Balance Corporation, Tokyo, Japan). Thirty-nine flowers from three individuals in the Togitsu population and 58 flowers from five individuals in the Saikai were measured except for dry floral weight ($n=28, 26$). The variation in floral and fruit characters is small among individuals in the same population (Nakanishi unpublished).

To compare the size of mature fruits between the two populations, fruit length (FL) and fruit diameter (FD) (Fig. 2) were measured for 52 and 54 fruits in the Togitsu and Saikai populations, respectively. Number of seeds per fruit (30 fruits in Togitsu and 32 fruits in Saikai) was counted, and mature seeds were weighed in 100-seed lots.

Pollination experiments

Pollination experiments were done with the following four treatments at the two populations: hand cross-pollination, hand self-pollination, autonomous self-pollination and open-pollination. For the former two treatments, newly opened flowers on randomly selected individuals were hand-pollinated in the morning

prior to pollinator visitation. Dehiscing anthers from a randomly selected plant far away from maternal plants in each population were used as the pollen source for hand cross-pollination treatments. Cross pollination treatments were conducted on 26 flowers in the Togitsu population and 59 in the Saikai population. For hand self-pollination, dehiscing anthers were brushed against stigma lobes of the same flower on 23 in Togitsu and 57 in Saikai. After each treatment, flowers were tagged and bagged. To test the autonomous self-pollination, 25 flowers in Togitsu and 53 in Saikai were bagged in the morning and 26 open pollinated flowers in Togitsu and 51 in Saikai were also tagged and bagged the next morning. The bags were used to prevent additional pollinations of the hand- and autonomous pollination experiments. The paper bags were water-proof and were left in place until the end of experiments to protect fruit for all treatments.

Approximately three weeks later, bags were removed and fruit and seed sets were checked for each treatment. Fruits were classified into four types: normal mature fruit, which had enlarged ovaries and was bigger than 2.5 cm in length; damaged mature fruit, which was mature fruit damaged by moth larva; immature fruit, including no fruits, with only a naked pedicel remaining, which lacked developing seeds and was usually smaller than 1 cm in

length; and damaged immature fruit including no fruits, with only the insect's feces remaining. Fruit sets were determined by the rate of mature fruits, including damaged mature fruits, to the total number of fruits, except for the last type which could not be determined to be fertilized or unfertilized due to insect attack. Seed sets were determined by the rate of mature seeds in normal mature fruits which were not attacked by seed predators. Mature seeds were determined by distinguishing enlarged seeds from aborted ones, which were flat and shrivelled.

Pollinator and fruit predation

To identify floral visitors of *H. hamabo*, we carried out observations during pollination experiments in the flower season of 2002. Observations were made by visual scanning in the two populations and pollinators were recorded. Pollinators that were not identified in the field were captured for later identification.

Many fruits that have been bored by moth larva are found during the fruiting season. To estimate the level of fruit predation, we checked 52 fruits in the Togitsu population and 54 fruits in the Saikai population in mid-October. Preyed on fruits included not only bored fruits but also those which had larvae inside, even though they had not been bored. The larvae were captured and raised to the adult stage for identification.

Results

Phenology

The flowering period of the Togitsu population lasted ca. a month and a half (Fig. 3). In 2001, flowering began at 2 July, reached a peak at 18 July, decreased from the beginning of August and ended on 20 August (Fig. 3). In 2002, the flowering period started earlier: flowering was already well underway on 2 July, reached a peak on 10 July and ended on 5 August (Fig. 3). This pattern was also found in all other individuals in the Togitsu population. Only a few flowers were produced in the population from mid-August to late September.

The seed dispersal period of the Togitsu population was long, and continued from October, 2001, to July of the next year (Fig. 4). There

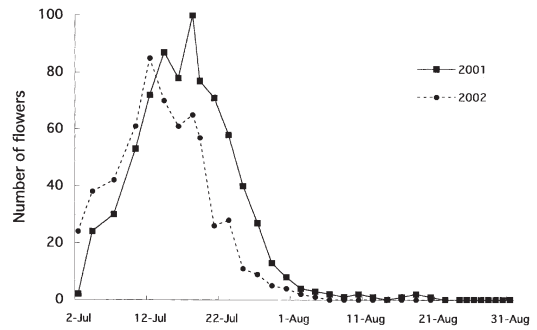


Fig. 3. Flowering phenology of *Hibiscus hamabo* for the Togitsu population in 2001 and 2002. Number of flowers in a part of a large individual were counted every other day. The flowering period in 2002 occurred earlier than in 2001.

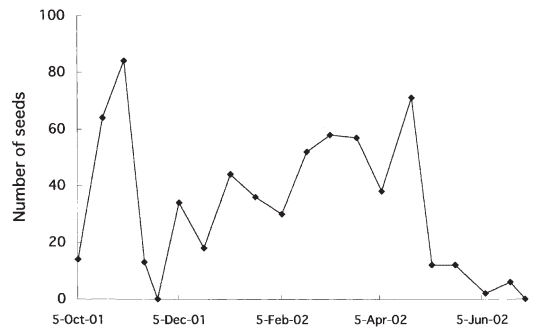


Fig. 4. Seed dispersal phenology of *Hibiscus hamabo* for the Togitsu population from October 2001 to June 2002. Number of seeds shows the total number of seeds fallen in seed traps.

were two peaks of seed fall. One was clear at the beginning of November and the other was a weak peak during the spring of the next year (Fig. 4).

Floral and fruit morphology

Petal length (PeL), petal width (PW), style length (SL) and anther-anther distance (AAD) of flowers in the Saikai population were significantly larger and more varied than those in the Togitsu population (Table 1). Pistil tip length (PiL), number of anthers and dry floral weight of flowers in the Saikai were also larger than those in the Togitsu, but the difference was not significant (Table 1). Anther-stigma distance (ASD) of flowers in Saikai was significantly smaller than that in Togitsu ($P < 0.001$, U-test).

Both fruit length and width in Saikai were significantly larger than those in Togitsu ($P <$

Table 1. Measurements of eight floral characters (mean±S.D) of each population

| | Togitsu population | Saikai population | Sign. level* |
|------------------------------|-------------------------|-------------------------|--------------|
| Petal length (PeL) | 48.0±3.4 mm (n=39) | 51.1±3.7 mm (n=58) | P<0.001 |
| Petal width (PW) | 45.4±3.7 mm (n=39) | 48.8±4.7 mm (n=58) | P<0.001 |
| Style length (SL) | 23.6±2.3 mm (n=39) | 24.7±2.3 mm (n=58) | P<0.05 |
| Anther-stigma distance (ASD) | 4.1±0.8 mm (n=39) | 3.2±0.9 mm (n=58) | P<0.001 |
| Anther-anther distance (AAD) | 13.0±1.5 mm (n=39) | 15.9±2.3 mm (n=58) | P<0.001 |
| Pistil tiplength (PiL) | 6.3±0.5 mm (n=39) | 6.4±0.8 mm (n=58) | n.s. |
| Number of anthers | 51.0±3.2 (n=18) | 51.8±6.7 (n=58) | n.s. |
| Dry floral weight | 170.1±21.9 mg (n=28) | 179.0±20.7 mg (n=26) | n.s. |

n=Number of flowers investigated.

*Significant differences between two populations by U-test.

Table 2. Fruit size, seed number and seed weight (mean±S.D) of each population

| | Togitsu population | Saikai population | Sign. level* |
|---------------------------|-----------------------|-----------------------|--------------|
| Fruit length | 25.7±2.8 mm (n=52) | 26.9±1.9 mm (n=54) | P<0.001 |
| Fruit diameter | 15.0±0.9 mm (n=52) | 16.3±1.6 mm (n=54) | P<0.001 |
| Number of seeds per fruit | 45.4±3.9 (n=30) | 52.5±6.0 (n=32) | P<0.001 |
| Seed weight per 100 seeds | 1.56±0.06 g (n=15) | 1.78±0.04 g (n=16) | P<0.001 |

n=Number of fruits investigated.

*Significant differences between two populations by U-test.

0.001, U-test, Table 2). Number of seeds per fruit and seed weight per 100 grains were also significantly greater for Saikai than for Togitsu (P<0.001, U-test, Table 2).

Pollination experiment

In fruit set, there were some differences among treatments and between the two populations (Table 3). The rates for hand cross-pollinated flowers were the highest in both populations (89.5% in Togitsu and 76.1% in Saikai). The rates for open pollinated flowers and that for hand self-pollinated were the second highest percentages in the Togitsu and the Saikai populations, respectively. The rates for auto-self pollinated flowers were low (66.7% in Togitsu and

56.5% in Saikai). These fruit set rates differed significantly among treatments between auto self-pollination and open pollination in Togitsu, and between hand cross-pollination and auto self-pollination, hand cross-pollination and open pollination in Saikai (Table 4). There were no significant differences between the two populations except for the open-pollination where the fruit set of the Togitsu population was significantly higher than that of the Saikai (P<0.005, G-test, Table 3). The rates of damaged immature fruits which could not be determined to be fertilized or unfertilized due to insect attack were 18.0% in the Togitsu population and 24.5% in Saikai. The total damaged fruits comprised 35.0% of the Togitsu population and 39.1% of the Saikai.

Number of seed set in fruits varied more among treatments and between the two populations than did fruit set (Table 5). The rates for hand cross-pollinated flowers were the highest in both populations (64.1% in Togitsu and 72.2% in Saikai). The rates for autonomus self-pollinated flowers were the lowest (23.8% in Togitsu and 26.0% in Saikai). There were significant differ-

ences among some treatments but no differences among other treatments (Table 6). For all treatments, seed sets of the Togitsu population were lower than those of the Saikai population except in open pollination, but there were no significant differences between the two populations (Table 5).

Table 3. Number of fruits and fruit set under four pollination treatments of the two populations

| | Togitsu population | | | | | Saikai population | | | | | Sign. level** |
|------------------------|--------------------|-------------------|----------|---------------------|-------------------|-------------------|-------------------|----------|---------------------|-------------------|---------------|
| | mature | damaged mature | immature | damaged immature | fruit set* (%) | mature | damaged mature | immature | damaged immature | fruit set* (%) | |
| Hand cross-pollination | 14 | 3 | 2 | 7 | 89.5 | 24 | 11 | 11 | 13 | 76.1 | n.s. |
| Hand self-pollination | 13 | 2 | 3 | 5 | 83.3 | 22 | 4 | 15 | 16 | 63.4 | n.s. |
| Auto.self-pollination | 12 | 2 | 7 | 4 | 66.7 | 20 | 6 | 20 | 7 | 56.5 | n.s. |
| Open pollination | 10 | 11 | 3 | 2 | 87.5 | 7 | 11 | 15 | 18 | 54.5 | P<0.005 |

* Number of mature and damaged mature fruits/Total number of fruits except damaged immature fruits×100

**Significant differences between two populations by G-test.

Table 4. Correlation by G-test for fruit set of each pollination treatment in the two populations

| | Togitsu population | | | Saikai population | | |
|-------------------|--------------------|------------------|-------------------|-------------------|------------------|-------------------|
| | Hand cross-polli. | Hand self-polli. | Auto. self-polli. | Hand cross-polli. | Hand self-polli. | Auto. self-polli. |
| Hand self-polli. | n.s. | — | — | n.s. | — | — |
| Auto. self-polli. | n.s. | n.s | — | P<0.05 | n.s | — |
| Open polli. | n.s. | n.s | P<0.005 | P<0.005 | n.s | n.s |

Table 5. Seed set (mean±S.D) under four pollination treatments of the two populations

| | Togitsu population | Saikai population | Sign. level* |
|------------------------|----------------------|----------------------|--------------|
| Hand cross-pollination | 64.1±17.5% (n=14) | 72.2±15.3% (n=24) | n.s. |
| Hand self-pollination | 41.1±19.6% (n=13) | 47.3±18.5% (n=22) | n.s. |
| Auto. self-pollination | 23.8±22.1% (n=12) | 26.0±22.3% (n=20) | n.s. |
| Open pollination | 54.4±20.6% (n=10) | 46.1±26.4% (n=7) | n.s. |

n=Number of normal matured fruits examined which were not attacked by seed predators.

*Significant differences between two populations by U-test.

Table 6. Correlation by U-test for seed set of each pollination treatment in the two populations

| | Togitsu population | | | Saikai population | | |
|-------------------|--------------------|------------------|-------------------|-------------------|------------------|-------------------|
| | Hand cross-polli. | Hand self-polli. | Auto. self-polli. | Hand cross-polli. | Hand self-polli. | Auto. self-polli. |
| Hand self-polli. | P<0.05 | — | — | P<0.001 | — | — |
| Auto. self-polli. | P<0.001 | n.s | — | P<0.001 | P<0.01 | — |
| Open polli. | n.s | n.s | P<0.001 | P<0.05 | n.s | n.s |

Pollinator and fruit predation

The compositions of pollinators differed somewhat between the two populations (Table 7). In the Togitsu population, the most frequent pollinator was *Apis mellifera* Linnaeus, which is a naturalized bee that comprised 58.8% of all pollinators observed (N=34), and was followed by *Papilio helenus nicconicolens* Butler and *Parnara guttata* Bremer et Grey. *Papilio xuthus* Linnaeus and *Byasa alcinous* Klug, both of which are Papilionidae, were also observed. In the Saikai population, *P. helenus nicconicolens* was the most frequent, followed by *P. memnon thunbergii* Siebold. *Papilio xuthus*, *B. alcinous* and *Parnara guttata* were also found. Some ant species often visited the flowers but did not contribute to pollination.

The moth larva which bored fruits of *H. hamabo* was *Rehimena surusalis* (Walker). This moth is known as a specialist predator of *Hibiscus* species (Inoue 1982; Miyata 1983; Murase 2000). The fruit predation rate was 94.2% in the Togitsu population and 74.1% in the Saikai. There was a significant difference between the two populations ($P < 0.05$, G-test).

Discussion

The flowering season of *H. hamabo* has been generally described as occurring from July to August (Ohwi and Kitagawa 1983; Ohba 1989). The flowering peak clearly occurred in mid-July, and only a few flowers were found in August in the Togitsu population. This tendency was also

found in the Saikai population. The flowering period in 2002 occurred earlier than in 2001. This may have been because the winter to spring months were unusually warm in 2002. The beginning of the cherry blossom season of *Prunus yedoensis*, which is one of the best known plants for phenology in Japan was six days earlier than average for Nagasaki in the spring of 2002 (Nagasaki Marine Observatory 2003). Monthly average temperatures in 2002 were warmer by 1.7°C in January, 0.3°C in February, 1.5°C in March, 0.7°C in April and 0.4°C in May than those in 2001 (Nagasaki Marine Observatory 2002). The flowering season of *H. tiliaceus* is from June to August in the Bonin Islands (Hirota et al. 2000) and the Ryukyu Islands (Ohba 1989), both of which are subtropical, and is also known to last almost throughout the year in the tropics (e.g. Smith 1981). These flowering durations are longer than that of *H. hamabo*, mainly due to the warmer climate. In spite of the different temperature conditions between 2001 and 2002, the flowering durations of *H. hamabo* were almost the same. This indicates that the flowering duration of *H. hamabo* may be fairly fixed, unlike that of *H. tiliaceus*.

However, while the flowering period was limited to a month and a half, the dispersal period continued for over half a year. The capsule is apically opened so that the seeds don't fall immediately, and seed fall may be influenced by wind. Nevertheless, there were two falling peaks. The first peak, occurring at the beginning of No-

Table 7. Pollinator visitors to two *Hibiscus hamabo* populations

| Togitsu population | | Saikai population | |
|--------------------------------------|---------------|--------------------------------------|---------------|
| Pollinator | Frequency (%) | Pollinator | Frequency (%) |
| Lepidoptera | | Lepidoptera | |
| <i>Papilio helenus nicconicolens</i> | 14.7 (5)* | <i>Papilio helenus nicconicolens</i> | 41.7 (5)* |
| <i>Parnara guttata</i> | 14.7 (5) | <i>Papilio memnon thunbergii</i> | 25.0 (3) |
| <i>Papilio xuthus</i> | 3.0 (1) | <i>Papilio xuthus</i> | 8.3 (1) |
| <i>Cephonodes hyles</i> | 3.0 (1) | <i>Byasa alcinous</i> | 8.3 (1) |
| <i>Byasa alcinous</i> | 3.0 (1) | <i>Parnara guttata</i> | 8.3 (1) |
| Hymenoptera | | Hymenoptera | |
| <i>Apis mellifera</i> | 58.5 (20) | <i>Andrena</i> sp. | 8.3 (1) |
| <i>Andrena</i> sp. | 3.0 (1) | | |

*Numbers of individuals are shown in parentheses.

vember, was clear and may be due to fall by capsule opening. The second peak, in spring, was weak and may be due to fall by the capsule breaking. Such a long dispersal period might be useful to avoid predation after seed fall and to enhance the chances of dispersal by sea-currents. The seeds of *H. hamabo* are known to be dispersed by sea-currents (Nakanishi 1985).

The results of floral character measurements indicated that the flowers of *H. hamabo* were clearly smaller than those of *H. tiliaceus* and *H. glaber* reported by Hirota et al. (2000). It appears to be a common phenomenon that among phylogenetically close species, northern distributed species often have smaller flowers. Hirota et al. (2000) studied reproductive success in *H. glaber* and *H. tiliaceus* in the Bonin (Ogasawara) Islands, which are in the subtropics and reported that their anther-stigma distances (ASD) were 5.3–5.8 mm and 7.8 mm, respectively. Compared with these values, the distance of *H. hamabo* (4.1 mm in the Togitsu population and 3.2 mm in the Saikai population) is considerably close. The fact that the anther-stigma distance of *H. hamabo* distributed in warm-temperate areas is shorter than those of phylogenetically close-related *Hibiscus* species distributed in subtropical and/or tropical areas is remarkable, and may be related to pollinator availability. Studies on *H. laevis* showed that flowers in the more northern parts of North America have a shorter anther-stigma distance than those in southern areas (Klips and Snow 1997). In hand self-pollination experiments both fruit set and seed set of *H. hamabo* have greater rates compared with those of *H. tiliaceus* and *H. glaber* reported by Hirota et al. (2000). These reproductive characters of *H. hamabo* may be caused by the adaptation to warm-temperate climate.

Both hand self-pollinated flowers and autonomous self-pollinated flowers bore fruits and seeds, indicating that *H. hamabo* is clearly self-compatible. The fact that seed sets for hand cross-pollinated flowers in both populations were significantly greater than that for hand self-pollinated flowers suggests that *H. hamabo* has inbreeding depression. This result is similar to the finding for *H. tiliaceus*, but not for *H. glaber*,

whose inbreeding depression is comparatively weak (Hirota et al. 2000). *H. hamabo* and *H. tiliaceus* grow in similar salt-marsh stands, unlike *H. glaber*, which is found in inland dry scrub in the Bonin Islands.

The reproductive organs including flower, fruit size and seed weight are obviously larger in the Saikai population. The causes for these differences are not clear. The findings that both the number of seeds per fruit and seed weight in the Saikai population were greater than those in the Togitsu population, suggest that the difference may not be due to nutritional differences between the two populations. The Togitsu population must have been influenced by the effects of inbreeding depression, because the population is an isolated small one, and is growing on a closed bay area. Only anther-stigma distance (ASD) of flowers in the Saikai population was significantly smaller than that in the Togitsu population. This indicates the potential for stigmas to contact anthers and, therefore, for self-pollination. However, in autonomous self-pollinated flowers, fruits and seed sets were not significantly different between the two populations. The difference of anther-stigma distance (ASD) between the two populations may not be enough to cause a difference in the autonomous self-pollination.

Composition and frequency of pollinators may vary due to the time of day, temperature, and weather, etc. (e.g. Herrera 1988), so that it is difficult to compare populations far away from each other. Nevertheless, it is conspicuous that naturalized *Apis mellifera* appear only in the Togitsu population. The absence of *A. mellifera* in the Saikai population may be due to the environment of a dominant evergreen broad-leaved forest. In the Togitsu population, fruit and seed sets in open-pollinated flowers were similar to hand-pollinated flowers, suggesting that sexual reproduction was not pollen-limited. In open-pollinated flowers, both fruit and seed sets in the Togitsu population were greater than in the Saikai population. These may be due to the frequent visitation of *A. mellifera* in the Togitsu population, which is surrounded by various ecosystems such as paddy fields, abandoned paddy fields, streams, residential sections, and evergreen broad-leaved forests. It is conspicuous that

both the fruit set and seed set of open pollination in *H. hamabo* were far greater than those in *H. tiliaceus* and *H. glaber* studied in Bonin Island, where the important pollinator for them was only *A. mellifera* (Hirota et al. 1999). Aside from *A. mellifera* in the Saikai population, the most important pollinator of *H. hamabo* flowers was Papilionidae butterflies. These large butterflies are known to be attracted to red (Tanaka 1991, 1993). *Hibiscus hamabo* has flowers with not only a red center but also a dark red stigma surrounded by yellow anthers, which must be attractive to these butterflies.

The fruit predation rate in the free condition was very high, 94.2% in the Togitsu population and 74.1% in the Saikai. The result was far larger than in pollination treatments. This may be due to the fact that the pollination treatments were bagged. The fruits in the Togitsu population were significantly more preyed on than those in the Saikai population. This may be due to differences in the conditions of the populations. The Saikai population is larger in size and is surrounded by natural conditions. It may be considered that the Saikai population is affected by a limited predator. In any case, fruit predation by moth larvae greatly influences the reproductive success of *H. hamabo*.

Some characters related to the reproductive systems of *H. hamabo* such as shorter flowering duration, smaller flower size, shorter anther-stigma distance and higher seed set rate in self-pollination may have been adapted to the warm-temperate climate. The differences in pollination and predation observed between the two populations suggest that the inbreeding success is influenced by the ecosystem diversity surrounding the populations of the species.

Acknowledgements

We are grateful to Dr. Hiroshi Kudoh of Kobe University for providing some of the references. Insects were kindly identified by Prof. Shuichi Ikudome of Kagoshima Women's Junior College (bees) and Mr. Katsumi Sibahara of Isahaya Commercial High School (moths). We are also thankful to Miss Keiko Fukuda, Miss Natsuki Tajiri, Mr. Takashi Minami and Mr. Tarou Iwaki for their support in the field study.

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- (Received January 8, 2004; accepted June 25, 2004)
- 中西弘樹¹・清浦(川良)奈緒美^{1,2}:ハマボウの繁殖生物学的研究
- ハマボウ (*Hibiscus hamabo* Siebold et Zucc.) は日本中南部と韓国済州島の海岸部に生育し、フヨウ属オオハマボウ節 (*Azanza*) の中で最も北に分布する種である。本種の繁殖生態について、2つの個体群で開花と散布フェノロジー、花と果実の形態、果実の被食などの調査と受粉実験を行ない、近縁種のオオハマボウ (*H. tiliaceus* L.) やモンテンボク (*H. glaber* Matum.) と比較した。開花期間は7月初旬から8月中旬までの約1ヵ月半であり、春に暖かい年では開花が早くなったが、開花期間は変わらなかった。散布期間は10月から翌年の6月までと長く、11月初旬と4月の2つの種子落下のピークがあった。花の形態や受粉システムを近縁種と比較すると、花が小さいこと、開花期間が短いこと、葯と柱頭の距離が短いこと、人工自家受粉による結果率および結実率が高いことなどから、ハマボウは暖温帯に適応した繁殖生態をしていると考えられる。結果率、結実率とも人工他家受粉、人工自家受粉、自動自家受粉の順に低下したが、結果率に有意差はなく、結実率には有意差があった。ハマボウは自家和合性があるが、近交弱勢を示す植物であることがわかった。
- 花の形態、果実の大きさ、種子重などから、西海個体群の繁殖器官は時津個体群よりも大きかったが、繁殖成功において有意差はなかった。花の中央部は赤く、蜜標となっており、ポリネーターとしてアゲハ類が重要であるが、周囲が人家や耕作地となっている時津個体群ではセイヨウミツバチの訪花が目立った。種子はカクモンノメイガの食害を受け、果実の虫食い率は高く、特に時津個体群で著しかった。繁殖成功は、ポリネーターと種子捕食者に強い影響を受けるが、それらは個体群周辺の生態的多様性の違いを反映していると考えられる。
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