Modification of Sex Expression in *Sagittaria latifolia* by the Application of Gibberellic Acid and Paclobutrazol

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A clear modification of sex expression in *Sagittaria latifolia* from male or trimonoecious to female was induced by a foliar spray of gibberellic acid (GA) at concentrations of 10, 100, and 1000 ppm. This modification began two weeks after the initiation of treatment. The effect was greater at a higher GA concentration. The number of racemes was increased by the treatment. On the other hand, male and perfect flowers were produced in the female line by a foliar spray of paclobutrazol (PBZ) at concentrations of 100 and 1000 ppm two weeks after the initiation of treatment, and a greater number of male flowers was produced in the trimonoecious line by the spray. The number of racemes was decreased by the PBZ application. GA was effective for the internode elongation of rachises and scapes; on the contrary, PBZ was effective in shortening the internodes. Therefore, it was clarified that endogenous GA controlled sex expression, raceme production, and internode length in this species. Female flowers in the male line developed into fruits with a normal seed; further, female flowers that had been pollinated with pollen grains from male flowers of the female line also developed into fruits with a normal seed. These results will be useful for the breeding of *S. latifolia*.

**Key Words:** flowering, GA treatment, paclobutrazol treatment, *Sagittaria latifolia*, sex modification.

**Introduction**

Species belonging to the genus *Sagittaria* (Alismataceae) are distributed in tropical and temperate zones of the world. They grow in rivers, marshes, or shallow areas of lakes. Many species of this genus produce starchy tubers underground. Of these species, *S. latifolia* L., which is a wild species found in North America, produces large edible tubers underground. The natives have gathered these tubers as food and a trade commodity for a long time (Porterfield, 1951; Whitter, 1939). On the other hand, the Chinese arrowhead (*S. trifolia* var. *edulis* (Sieb) Ohwi) has been cultivated for its edible tubers in East Asia and parts of North America. The tubers of *S. latifolia* and *S. trifolia* var. *edulis* are similar to each other in size and taste, and these species propagate both sexually and vegetatively. Furthermore, it has been indicated that *S. latifolia* can become a horticultural crop by conventional breeding techniques (Tanimoto, 1997; Tanimoto and Darby, 1996). In other words, a new variety can be bred by the vegetative propagation of the superior F₁ progeny selected after crossing. *S. latifolia* comprises monoeccious and dioecious plants, and its sex expression is thought to be genetically controlled, although the genetic system responsible for this has not yet been elucidated (Wooten, 1971). It is important to artificially control the sex expression for both clarification of the genetic system and for cross-breeding of the species.

Gibberellins are well known as plant growth regulators that can regulate sex expression in many plant species. They generally promote maleness in species of Cucurbitaceae (Peterson and Anhder, 1960; Rudich et al., 1972; Prakash, 1977) and other families (Atal, 1959; Chailakhyan and Khryanin, 1978; Yin and Quinn, 1994). On the other hand, gibberellins promoted femaleness in *Begonia × cheimantha* (Heide, 1969), *Ricinus communis* (Shifriss, 1961), and *Zea mays* (Krishnamoorthy and Talukdar, 1976).

In this study, gibberellic acid (GA) and paclobutrazol (PBZ), which is an inhibitor of endogenous GA biosynthesis, were applied to the leaves of *S. latifolia*, and I observed a modification of sex expression.

**Materials and Methods**

**Plant materials**

One each of male, female, and monoecious lines of *S. latifolia* was used for the experiments. The three lines
were originated from seeds collected on Sauvie Island in the Columbia River, Oregon State, USA in the autumn of 1995 (Tanimoto and Darby, 1996). The monoecious plants produced not only male and female flowers but also perfect flowers in a raceme and were classified as trimonoecious plants according to Yin and Quinn (1992).

Culture of S. latifolia

Tubers of the three lines were harvested at the Osaka Prefectural Shiroyama Senior High School in Toyono, Osaka, Japan, in November 1999; they were stored to be used as seed tubers at approximately 4°C in a refrigerator until immediately before the experiment was conducted the following year. On April 20, each of the tubers was planted in a plastic container (35 cm in depth) with a capacity of 20 L; this container was filled with approximately 15 L of paddy soil. The water level was maintained at 10 cm from the surface of the soil throughout the experiment. No basal dressing was supplied for the culture of the seed tubers; additional dressing was applied five times during the flowering period, and the total amounts of N, P, and K in the container were 0.9, 0.4, and 0.8 g, respectively.

GA treatment

Plants of the three lines grew well, and several daughter plants were produced around each mother plant in the containers. These began to flower in late June. After removing all racemes from the leaf sheathes, all leaves were sprayed to run-off with aqueous solutions of GA at concentrations of 10, 100, or 1000 ppm on June 17, 19, and 21. No wetting agent had been added to the solutions. Each treatment comprised 10 plants of each of the three lines. The leaves of another each 10 plants of the three lines were sprayed with pure water as a control on the same days. The sex of each flower was identified on the flowering day, and the number of male, female, and perfect flowers on every raceme was counted until the end of the flowering season. Only the racemes produced on the mother plants were investigated, as was done in 2000.

PBZ treatment

The tubers, which had been stored in a refrigerator, were planted in plastic containers for treatment with PBZ at the school on May 22, 2004. They were cultivated by the same method as that used in the experiment carried out in 2000. Additional dressing was applied three times during the flowering period, and the total amounts of N, P, and K in each container were 1.0, 0.6, and 0.9 g, respectively. After removing all racemes, leaves were sprayed to run-off with aqueous solutions of PBZ (“Bounty SC”, Nihon Nohyaku Co., Ltd., Japan) at concentrations of 10, 100, or 1000 ppm on July 4, 6, and 8. Each treatment comprised 10 plants in the three lines. The leaves of another each 10 plants of the three lines were sprayed with pure water as a control on the same days. The sex of each flower was identified on the flowering day, and the number of male, female, and perfect flowers on every raceme was counted until the end of the flowering season. Only the racemes produced on the mother plants were investigated, as was done in 2000. The pollen stainability rate was examined using an iodine-potassium iodide (I₂-KI) solution. More than 1000 pollen grains per flower were observed with 10 replicates, and diameter of the 20 stainable pollen grains was measured under an optical microscope.

Results

GA treatment

The male, trimonoecious, and female lines produced racemes in the containers after the foliar spray of the GA solutions. The first anthesis in mother plants occurred between June 28 and July 27 in the control treatment and the treatments with three GA concentrations. There was no difference in the day of the first anthesis among the different treatments and lines. Anthesis lasted until late August in all treatments.

In the control treatment, the male line produced only male flowers, and the female line produced only female flowers. The male flowers had many stamens with pale yellow anthers, and the female flowers had many green ovaries containing an ovule (Fig. 1A, C). The trimono-
Female flowers were produced on the upper, middle, and lower nodes of racemes, respectively. Some perfect flowers had many pistils and a few stamens around the pistils, whereas some had a few pistils and many stamens (Fig. 1B).

Table 1 shows the average number of four kinds of flowers on a raceme throughout the flowering season. In the control treatment, the male line produced only male flowers; it produced male, female, and perfect flowers at GA concentrations of 10, 100, and 1000 ppm. This line also produced flowers with abortive pistils (abortive flowers) in the early period after GA application. With an increase in the GA concentration, the number of male flowers on a single raceme decreased, whereas that of female and abortive flowers increased. In this line, the total number of flowers on a raceme was not increased by GA application. The trimonoecious line produced an average of 1.6 male flowers in the control treatment and almost no male flowers at the GA concentration of 10 ppm. This line produced no male flowers and an average of less than two perfect flowers at concentrations of 100 and 1000 ppm. On the other hand, the female line produced female flowers at GA concentrations of 100 and 1000 ppm; however, it produced no male or perfect flowers at any GA concentration.

Table 2 shows the average number of racemes produced on a single plant. Based on the sex tendency, racemes were classified into five types. In the control treatment, the male line produced only male racemes throughout the flowering season. In the GA treatments, it produced, apart from male racemes, andromonoecious, trimonoecious, and gynomonoecious ones. It also produced female racemes at GA concentrations of 100 and 1000 ppm and a few racemes with only abortive flowers at the GA concentration of 1000 ppm. The trimonoecious line produced trimonoecious, gynomonoecious, and female racemes in the control treatment and at the GA concentration of 10 ppm. It produced gynomonoecious and female racemes at the GA concentrations of 100 and 1000 ppm. The number of female racemes was largest at the concentration of 1000 ppm. This line also produced racemes with only abortive flowers at GA concentrations of 100 and 1000 ppm. On the other hand, the female line produced only female racemes both in the control and GA treatments. One plant of this line also produced a raceme with only abortive flowers at the GA concentration of 1000 ppm. In the control treatment, the male, trimonoecious, and female lines produced a total of 4.4, 4.1, and 4.8 racemes, respectively. In the male and female lines, the number of racemes was significantly larger at GA concentrations of 100 and 1000 ppm than in the control treatment. However, in the trimonoecious line, this number was not significantly different among the control and GA treatments.

Internode elongation was found in racemes at GA concentrations of 100 and 1000 ppm in the three lines. The scapes and rachises of racemes curved and bent down in the GA treatments. However, the leaf morphology was not clearly modified by these treatments.

The female flowers that were produced on the male line after the GA treatments developed into fruits after both an open pollination and an artificial one. The fruits were globose in shape and composed of achenes. The achenes

| Line            | GA concentration (ppm) | Number of racemes observed | Number of flowers observed | Number of flowers observed |
|-----------------|------------------------|-----------------------------|----------------------------|---------------------------|
| Male            | 0                      | 43                          | 25.1 ± 1.5¹                 | 0.0 ± 0.0                 | 0.0 ± 0.0                 | 25.1 ± 1.5                 |
|                 | 10                     | 54                          | 20.8 ± 1.4                  | 1.6 ± 0.6                 | 2.9 ± 1.0                 | 2.0 ± 0.6                 | 21.3 ± 1.6                 |
|                 | 100                    | 59                          | 9.3 ± 1.2                   | 2.7 ± 0.6                 | 7.3 ± 1.2                 | 2.0 ± 0.6                 | 21.3 ± 1.6                 |
|                 | 1000                   | 56                          | 2.1 ± 0.6                   | 1.1 ± 0.4                 | 13.6 ± 1.4                | 7.3 ± 1.6                 | 24.1 ± 1.5                 |
| Trimonoeious    | 0                      | 40                          | 1.6 ± 0.6                   | 5.5 ± 0.9                 | 9.6 ± 0.7                 | 0.0 ± 0.0                 | 16.8 ± 1.2                 |
|                 | 10                     | 38                          | 0.2 ± 0.1                   | 6.1 ± 0.9                 | 13.1 ± 1.0                | 0.0 ± 0.0                 | 19.4 ± 1.4                 |
|                 | 100                    | 46                          | 0.0 ± 0.0                   | 1.9 ± 0.5                 | 17.9 ± 1.8                | 6.7 ± 1.6                 | 26.5 ± 1.9                 |
|                 | 1000                   | 45                          | 0.0 ± 0.0                   | 0.4 ± 0.4                 | 16.9 ± 2.5                | 15.4 ± 3.0                | 32.8 ± 2.8                 |
| Female          | 0                      | 48                          | 0.0 ± 0.0                   | 0.0 ± 0.0                 | 20.8 ± 0.9                | 0.0 ± 0.0                 | 20.8 ± 0.9                 |
|                 | 10                     | 52                          | 0.0 ± 0.0                   | 0.0 ± 0.0                 | 22.1 ± 1.3                | 0.0 ± 0.0                 | 22.1 ± 1.3                 |
|                 | 100                    | 63                          | 0.0 ± 0.0                   | 0.0 ± 0.0                 | 21.4 ± 1.4                | 0.1 ± 0.1                 | 21.5 ± 1.4                 |
|                 | 1000                   | 66                          | 0.0 ± 0.0                   | 0.0 ± 0.0                 | 25.0 ± 1.6                | 0.9 ± 0.3                 | 25.9 ± 1.6                 |

¹ Mean ± SE.
had wings on both margins and a beak. They contained a U-shaped seed. The achenes and seeds were normal in size and shape.

**PBZ treatment**

After spraying with the PBZ solutions, the first anthesis in the mother plants of the male and female lines occurred between July 16 and August 3 in the control and PBZ treatments. On the other hand, in the trimonoecious line, it occurred between July 22 and August 8 in both control and PBZ treatments. There was no difference in the day of the first anthesis among the control and PBZ treatments in the three lines, and anthesis lasted until late August.

Table 3 shows the average number of the four kinds of flowers on a raceme throughout the flowering season. The male line produced only male flowers in the control treatment and at the PBZ concentrations of 10 and 100 ppm. It produced male flowers at the PBZ concentration of 1000 ppm. Some of the abortive flowers had abnormal stamens, whereas some had no stamens or pistils. In this line, the total number of flowers on a raceme was smaller at the PBZ concentration of 1000 ppm than that in the control treatment and the treatments with other PBZ concentrations; this was because some flower buds died before anthesis at the PBZ concentration of 1000 ppm. Therefore, there was no difference in the number of buds produced among the control and PBZ treatments. On average, in the trimonoecious line, a single plant produced 2.0 male, 6.6 perfect, and 8.9 female flowers on a raceme in the control treatment. Further, on average, the total number of flowers on a raceme was 17.5 in the control treatment. This line produced an increased number of racemes with only abortive flowers at the PBZ concentrations of 1000 ppm. Some of the abortive flowers had abnormal stamens, whereas some had no stamens or pistils. In this line, the total number of flowers on a raceme was smaller at the PBZ concentration of 1000 ppm than that in the control treatment and the treatments with other PBZ concentrations; this was because some flower buds died before anthesis at the PBZ concentration of 1000 ppm. Therefore, there was no difference in the number of buds produced among the control and PBZ treatments. On average, in the trimonoecious line, a single plant produced 2.0 male, 6.6 perfect, and 8.9 female flowers on a raceme in the control treatment. Further, on average, the total number of flowers on a raceme was 17.5 in the control treatment. This line produced an increased number of racemes with only abortive flowers at the PBZ concentrations of 1000 ppm. Some of the abortive flowers had abnormal stamens, whereas some had no stamens or pistils. In this line, the total number of flowers on a raceme was smaller at the PBZ concentration of 1000 ppm than that in the control treatment and the treatments with other PBZ concentrations; this was because some flower buds died before anthesis at the PBZ concentration of 1000 ppm. Therefore, there was no difference in the number of buds produced among the control and PBZ treatments. On average, in the trimonoecious line, a single plant produced 2.0 male, 6.6 perfect, and 8.9 female flowers on a raceme in the control treatment. Further, on average, the total number of flowers on a raceme was 17.5 in the control treatment. This line produced an increased number of racemes with only abortive flowers at the PBZ concentrations of 1000 ppm. Some of the abortive flowers had abnormal stamens, whereas some had no stamens or pistils. In this line, the total number of flowers on a raceme was smaller at the PBZ concentration of 1000 ppm than that in the control treatment and the treatments with other PBZ concentrations; this was because some flower buds died before anthesis at the PBZ concentration of 1000 ppm. Therefore, there was no difference in the number of buds produced among the control and PBZ treatments. On average, in the trimonoecious line, a single plant produced 2.0 male, 6.6 perfect, and 8.9 female flowers on a raceme in the control treatment. Further, on average, the total number of flowers on a raceme was 17.5 in the control treatment. This line produced an increased number of racemes with only abortive flowers at the PBZ concentrations of 1000 ppm. Some of the abortive flowers had abnormal stamens, whereas some had no stamens or pistils. In this line, the total number of flowers on a raceme was smaller at the PBZ concentration of 1000 ppm than that in the control treatment and the treatments with other PBZ concentrations; this was because some flower buds died before anthesis at the PBZ concentration of 1000 ppm. Therefore, there was no difference in the number of buds produced among the control and PBZ treatments. On average, in the trimonoecious line, a single plant produced 2.0 male, 6.6 perfect, and 8.9 female flowers on a raceme in the control treatment. Further, on average, the total number of flowers on a raceme was 17.5 in the control treatment. This line produced an increased
number of male flowers with an increase in the PBZ concentration, and produced an average of 7.2 male flowers at the PBZ concentration of 1000 ppm. A greater number of perfect flowers was produced at the PBZ concentrations of 100 and 1000 ppm than that in the control treatment and at the PBZ concentration of 10 ppm. The number of female flowers decreased with an increase in the PBZ concentration, and no female flowers were produced at the PBZ concentration of 1000 ppm. Only one abortive flower was observed at the PBZ concentration of 10 ppm. The total number of flowers on a raceme was not visibly different among the control and PBZ treatments. The female line produced only female flowers in the control treatment and male, perfect, and female flowers in the PBZ treatments. In particular, it produced a considerably higher number of male and perfect flowers and comparatively fewer female flowers at the PBZ concentration of 1000 ppm than those produced in the control and the PBZ treatments with other concentrations. The total number of flowers on a raceme was not clearly different among the control and PBZ treatments.

Table 4 shows the average number of five raceme types produced on a single plant after PBZ application. The male line produced only male racemes until the end of the experiment in the control and PBZ treatments. The trimonoecious line produced andromonoecious, trimonoecious, and gynomonoecious racemes in the control treatment and at the PBZ concentration of 10 ppm. At the PBZ concentration of 10 ppm, this line also produced female racemes. It produced male and andromonoecious racemes at the PBZ concentrations of 100 and 1000 ppm as well as trimonoecious racemes at the PBZ concentration of 100 ppm. The number of male and andromonoecious racemes increased with an increase in the PBZ concentration, and that of trimonoecious and gynomonoecious racemes decreased with this increase. The female line produced only female racemes in the control treatment. It produced trimonoecious, gynomonoecious, and female racemes at the PBZ concentration of 10 ppm. At the PBZ concentration of 100 ppm, it produced andromonoecious racemes as well. It produced andromonoecious, trimonoecious, and gynomonoecious racemes at the PBZ concentration of 1000 ppm. In this line, the highest number of andromonoecious racemes was produced at the PBZ concentration of 1000 ppm. In the control treatment, the male, trimonoecious, and female lines produced a total of 3.5, 2.9, and 4.0 racemes, respectively. The number of racemes decreased with an increase in the PBZ concentration.

At the PBZ concentrations of 100 and 1000 ppm, the petioles and scapes in these lines were shorter than those in the control treatment; at that of 1000 ppm, the length of racemes was 20% to 30% of that in the control treatment. The morphology of the leaf blade was not visibly modified by the PBZ treatments in these lines.

Many pollen grains were produced by the male and perfect flowers in the female line after PBZ treatment, as in the case of flowers in the male and trimonoecious lines in the control treatment. The pollen stainability rates and stainable pollen diameters are shown in Table 5. In the male line, the pollen stainability rates were 93.1% and 91.2% in the control treatment and at the PBZ concentration of 1000 ppm, respectively. On the other hand, this rate was 78.7% at the PBZ concentration of 1000 ppm in the female line. In the male line, the pollen diameters were 29.1 and 29.4 µm in the control treatment and at the PBZ concentration of 1000 ppm, respectively. It was 27.7 µm at the PBZ concentration of 1000 ppm in the female line. The diameter was significantly smaller in the PBZ-treated female line than in the male line.

In the female line, the female flowers in the control treatment were artificially pollinated with the pollen

| Line         | PBZ concentration (ppm) | Sex type of racemes | Racemes with only abortive flowers | Racemes whereby the type was not identified | Total§ |
|--------------|-------------------------|---------------------|-----------------------------------|---------------------------------------------|--------|
| Male         |                         | Male                | Andromonoecious                   | Trimonoecious                              | Gynomonoecious | Female |
|              | 0                       | 3.5                 | 0.0                               | 0.0                                         | 0.0                     | 0.0   | 0.0 | 3.5 a |
|              | 10                      | 3.4                 | 0.0                               | 0.0                                         | 0.0                     | 0.0   | 0.0 | 3.4 a |
|              | 100                     | 3.1                 | 0.0                               | 0.0                                         | 0.0                     | 0.0   | 0.0 | 3.1 a |
|              | 1000                    | 2.2                 | 0.0                               | 0.0                                         | 0.0                     | 0.0   | 0.0 | 2.2 b |
| Trimonoecious|                         | 0                   | 0.0                               | 0.1                                         | 2.0                     | 0.8   | 0.0 | 2.9 a |
|              | 10                      | 0.0                 | 0.0                               | 0.3                                         | 2.0                     | 0.3   | 0.4 | 3.0 a |
|              | 100                     | 0.1                 | 1.1                               | 1.0                                         | 0.0                     | 0.0   | 0.0 | 2.2 b |
|              | 1000                    | 0.3                 | 1.3                               | 0.0                                         | 0.0                     | 0.0   | 0.0 | 1.6 c |
| Female       |                         | 0                   | 0.0                               | 0.0                                         | 0.0                     | 4.0   | 0.0 | 4.0 a |
|              | 10                      | 0.0                 | 0.0                               | 0.1                                         | 0.2                     | 3.4   | 0.0 | 3.7 a |
|              | 100                     | 0.0                 | 0.1                               | 0.5                                         | 1.2                     | 1.7   | 0.0 | 3.5 a |
|              | 1000                    | 0.0                 | 1.4                               | 0.6                                         | 0.1                     | 0.0   | 0.0 | 2.1 b |

§ Mean separation within each of the lines by Tukey’s test, 5% level.
produced at the PBZ concentration of 1000 ppm. The flowers developed into fruits; these consisted of many achenes containing a seed. The fruits, achenes, and seeds were not different in size and shape from those that were produced by pollination with the pollen in the control treatment in the male line.

**Discussion**

The male line of *S. latifolia* produced female and perfect flowers after foliar spraying of GA. The trimonoecious line produced almost no male flowers, a few perfect ones, and many female ones after the treatments. These two lines produced more female flowers at a higher GA concentration. Therefore, they produced gynomonoecious and female racemes in response to the treatments. On the other hand, the female line of this species produced male and perfect flowers in addition to female flowers following foliar spraying of PBZ. The trimonoecious line produced almost no male flowers, a few perfect ones, and many female ones following the treatment. They produced a greater number of male flowers at a higher PBZ concentration. Therefore, the female and trimonoecious lines produced andromonoecious and male racemes, respectively, at a higher PBZ concentration. The trimonoecious line produced a greater number of andromonoecious racemes following the PBZ treatment than in the control treatment.

These results indicate that the primordia develop into perfect and male flowers at a low GA concentration in the female line and that they develop into perfect and female flowers at a high GA concentration in the male line. Consequently, the sex of flowers may be determined after flowers at a high GA concentration in the male line and that they develop into perfect and female lines. It is believed that there is a gradient of GA content along the rachis in the trimonoecious racemes; that is, the content may be lowest at the top and highest at the base in the rachis, resulting in the production of the three kinds of flowers.

Yin and Quinn (1995) showed that GA promoted maleness in *Buchloe dactyloides* and that only GA regulated sex expression. Subsequently, they suggested that a hormone could induce the expression of one sex and inhibit that of the other independently. GA promoted the reverse effect on the sex tendency in *S. latifolia*. Nonetheless, the results in this experiment appear to agree with their hypothesis.

The GA treatment did not clearly promote flower production on a raceme in *S. latifolia* in this experiment; however, it promoted raceme production. The PBZ treatment suppressed raceme production in the species, although it did not noticeably decrease flower production on a raceme under the conditions in this experiment. Hence, endogenous GA is thought to control raceme production.

Tanimoto (1989) treated seed tubers of *S. trifolia var. edulis* with GA directly before planting and found that raceme production was promoted by this treatment. Kuramochi et al. (1996) reported the promotion of raceme production on adding GA or a solution containing an artificial analogue to irrigation water after transplanting the juvenile plants of *S. pygmaea*. On the whole, exogenous GA may increase the number of racemes in *Sagittaria* species regardless of the differences in the methods of its application. On the other hand, they did not report a modification of sex expression following the treatments in these species. These differences in sex expression may be due to the differences in the methods of GA application and to the physiological conditions of plants.

Shiffriss (1961) suggested a delay in anthesis, decrease in leaf size, and increase in internode elongation following GA treatment in many herbaceous plants. In this experiment, the first anthesis was not delayed and the leaf size was not decreased by the GA treatments in the three lines. However, treatment promoted the internode elongation of the racemes and scapes in *S. latifolia*. On the contrary, PBZ shortened the internodes of racemes, scapes, and petioles in this species. Hence, endogenous GA evidently controls the internode length, as has been shown by Shiffriss (1961) and many others. However, the other effects of exogenous GA are thought to differ among plant species.

The female flowers in the male line developed into fruits with a normal seed, and those that had been pollinated with pollen grains on the male flowers of the species would become gynomonoecious and female racemes.
female line developed into fruits with a normal seed. These results will enable future crossing between plants belonging to lines of the same sex for the breeding of *S. latifolia*. Moreover, they are useful in clarifying the genetic mechanism of sex determination in this species.

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