Inheritance of the Double-flowered Trait in Decorative Hydrangea Flowers

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Species belonging to the Hydrangea genus, including Hydrangea macrophylla (Thunb.) Ser. and H. serrata (Thunb.) Ser., have inflorescences consisting of decorative and non-decorative flowers. The generation of double-flowered decorative flowers is an important objective for hydrangea breeders. This study aimed to elucidate the inheritance pattern of double flowers in H. macrophylla and H. serrata. Double-flowered progeny were obtained from three out of eleven crosses between double-flowered cultivars as the seed parent and single-flowered cultivars or lines as the pollen parent. When double-flowered progeny were produced using three cross combinations, the progenitor of both double-flowered cultivars and single-flowered lines was the double-flowered cultivar ‘Jogasaki’. In progeny obtained from these crosses, the segregation ratio of double- and single-flowered types was 1:1. Conversely, all progeny obtained from a cross in which the double-flowered cultivar as the seed parent differed from the seed parent of the single-flowered line as the pollen parent bore single flowers, and double-flowered progeny were not produced. Double-flowered progeny were obtained in two out of four crosses among the single-flowered lines; the segregation ratio of double- and single-flowered types was 1:3. The single-flowered lines shared the same seed parents, ‘Jogasaki’ or ‘Sumidanohanabi’. These results indicate that the double-flowered phenotype of decorative hydrangea flowers may be a recessive characteristic controlled by a single major gene. In addition, these results indicate that double-flowered progeny can be obtained when a pair of recessive genes are identical.

Key Words: decorative flower, double flower, Hydrangea macrophylla, inheritance pattern.

Introduction

Hydrangea is an important ornamental plant in Japan, and numerous varieties have been produced by both private breeders and nursery companies. In recent years, there has been a focus on breeding cultivars with double flowers and flowers with marginal variegations as these traits have high ornamental value (Shimizu, 2002).

The inflorescences of Hydrangea species such as Hydrangea macrophylla (Thunb.) Ser. and H. serrata (Thunb.) Ser. have decorative and non-decorative flowers. Uemachi et al. (2006) reported that decorative and non-decorative flowers differ in terms of sepal shape and size, number of floral organs, setting positions on inflorescence axes, and pedicel morphology. The sepal number of decorative flowers are large, and white, blue, purple, pink, or red, whereas the petals are tiny. Sepal number is used to distinguish double- and single-flowered decorative hydrangea flowers. Single-flowered cultivars generally have four sepals per decorative flower (Uemachi et al., 2004), while double-flowered cultivars, such as ‘Jogasaki’ and ‘Sumidanohanabi’, have approximately fourteen sepals per flower (unpublished data).

Most double-flowered H. macrophylla cultivars are derived from H. macrophylla ‘Jogasaki’ or ‘Sumidanohanabi’ (Sakamoto, 2003; Yatabe, 2009). As double-flowered cultivars have few stamens, it is necessary to cross double-flowered cultivars with single-flowered ones in order to breed new double-flowered cultivars. Inheritance of the double-flowered trait in decorative hydrangea flowers has not been clarified.
For efficient breeding, it is important to determine the inheritance pattern of double flowers because it takes more than 18 months to raise the F1 generation (Suyama et al., 2010). Elucidation of the inheritance pattern of double flowers will not only provide useful information for breeding, but also help clarify the molecular mechanism underlying the decorative flower type.

There are several reports concerning the inheritance of double flowers displaying large and showy petals in ornamental plants. Mato et al. (2004) reported that the double-flowered phenotype was a dominant characteristic in *Eustoma grandiflorum* (Raf.) Shinn. Nugent and Snyder (1967) reported that a single dominant gene controlled the double-flowered trait in *Pelargonium hortorum*, and that three modifier genes functioned in the presence of the dominant gene to control petal number. Sampson (1965) reported that the double-flowered trait was a recessive characteristic with irregular expression in *Philadelphus* L., a flowering shrub in the Saxifragaceae.

In this study, we investigate the inheritance pattern of double flowers in hydrangeas by analyzing progeny from crosses between double-flowered cultivars and single-flowered cultivars or lines, and among single-flowered lines with double-flowered seed parents.

**Materials and Methods**

**Cultivation**

Crosses between double-flowered cultivars and single-flowered cultivars or lines (Experiment 1)

*Hydrangea macrophylla* ‘Jogasaki’, ‘Sumidanohanabi’, and ‘Posy bouquet grace’, which was derived from ‘Jogasaki’, were used as the double-flowered cultivars (Fig. 1). The single-flowered cultivars used were *H. macrophylla* ‘Paris’, ‘Blue diamond’, and ‘Mirai’; *H. serrata* ‘Kiyosumisawa’; interspecific hybrids 03BN4 and 03NB10 derived from reciprocal crosses between ‘Blue diamond’ and *H. serrata* ‘Shichihenge’; and 03NL9, which was derived from a cross between ‘Shichihenge’ and *H. macrophylla* ‘Love you kiss’.

Crosses between the ‘Jogasaki’ seed parent and ‘Paris’, ‘Blue diamond’, and ‘Kiyosumisawa’ pollen parents were conducted in May 2003. The cross between ‘Jogasaki’ and ‘03BN4’ was conducted in May 2005. Crosses were also conducted using ‘Sumidanohanabi’ as the seed parent and 03NB10 or 03NL9 as pollen parents in May 2005. The cross between ‘Posy bouquet grace’ and ‘Mirai’ was conducted in May 2006.

The inflorescences used for cross-pollination were covered with double non-woven fabric to prevent cross-contamination. Capsules formed from crosses in 2006 were harvested in November of the same year. Seedlings were grown as described for Experiment 1.

Culturing of ovules from capsules that formed from crosses in 2007 was as previously described (Suyama et al., 2008). Hybrid individuals acquired were grown in an acclimation room (25°C, 3500 lx, 16-h light/8-h dark photoperiod). When seedlings reached 10 cm in height, they were transplanted into polyethylene pots (9 cm in diameter) filled with the soil mixture described for Experiment 1. The hybrid individuals were then grown in a greenhouse. The decorative flower types and number of sepals per decorative flower were investigated in the spring 2 years after the crosses had been conducted.

**In Vitro Propagation**

These experiments used 05JBN4; 05SNL9, a hybrid obtained from the cross between ‘Sumidanohanabi’ and the interspecific hybrid 03NL9; 05SMAp1, a hybrid obtained from the cross between ‘Sumidanohanabi’ and the single-flowered hybrid 03MaP1 (*H. serrata* ‘Maikoajisai’ × *H. macrophylla* ‘Paris’); and 05SNB10,
a hybrid obtained from the cross between ‘Sumidanohanabi’ and the single-flowered hybrid 03NB10 (Fig. 1). The seed parents of these single-flowered lines were double-flowered cultivars. The cross between 05JBN4 and 05SMaP1 (which share the same seed parent) and artificial self-pollination of 05JBN4 were conducted in May 2007.

Bud pollination and hot-water treatment (45°C, 4 min) to overcome self-incompatibility of 05JBN4 were conducted as previously described (Suyama et al., 2013). Reciprocal crosses were also conducted between 05SNB10 and 05JBN4 with different seed parents. The flowers of hybrids used as the seed parents in these crosses were emasculated the day before anthesis. Culturing of ovules from capsules formed following crossing and investigation of hybrid flower type and number of sepals were as described for Experiment 2.

**Results**

**Experiment 1**

Seven different crosses were conducted between double-flowered cultivars and single-flowered cultivars...
or lines. All 237 progeny obtained from crosses between the double-flowered cultivar ‘Jogasaki’ and the single-flowered cultivars ‘Paris’, ‘Blue diamond’, and ‘Kiyosumisawa’, as well as with the single-flowered line 03BN4, and all 46 progeny obtained from the cross between the double-flowered cultivar ‘Posy bouquet grace’ and the single-flowered cultivar ‘Mirai’ bore single decorative flowers (Table 1). All 139 progeny obtained from crosses between the double-flowered cultivar ‘Sumidanohanabi’ and the single-flowered lines 03NB10 and 03NL9 also bore single decorative flowers.

**Experiment 2**

Four crosses were conducted between double-flowered cultivars and single-flowered lines with double-flowered seed parents. Twenty-seven of the fifty-seven progeny obtained from the cross between the double-flowered cultivar ‘Posy bouquet grace’ and the single-flowered line 03JP1 were double-flowered; the percentage of double-flowered progeny among all progeny was 47% (Table 2). Double flowers were easily distinguished from single ones. The average numbers of sepals per decorative flower in double- and single-flowered progeny were 14.1 and 4.3, respectively. Stamens and petals were absent from decorative flowers of double-flowered progeny, whereas the number of sepals increased (Fig. 2). Thirty-two out of fifty-eight progeny (55%) obtained from the cross between the double-flowered cultivar ‘Posy bouquet suzi’ and the single-flowered line 03JP1 were double-flowered. The average numbers of sepals per decorative flower in double- and single-flowered progeny were 13.3 and 4.2, respectively.

**Table 1. Segregation ratios of decorative flower types in progeny obtained from crosses between double-flowered cultivars and single-flowered cultivars or lines.**

| Parent | No. of plants | No. of doubles | No. of singles | Segregation rate of doubles (%) | χ² value<sup>x</sup> |
|--------|---------------|----------------|----------------|-------------------------------|------------------|
| ‘Posy bouquet grace’ (‘Jogasaki’) | 46 | 0 | 46 | — | — |
| ‘Jogasaki’ | 50 | 0 | 50 | — | — |
| ‘Jogasaki’ | 76 | 0 | 76 | — | — |
| ‘Jogasaki’ | 50 | 0 | 50 | — | — |
| ‘Jogasaki’ 03BN4 (‘Blue diamond’ × ‘Shichihenge’) | 61 | 0 | 61 | — | — |
| ‘Sumidanohanabi’ 03NB10 (‘Shichihenge’ × ‘Blue diamond’) | 72 | 0 | 72 | — | — |
| ‘Sumidanohanabi’ 03NL9 (‘Shichihenge’ × ‘Love you kiss’) | 67 | 0 | 67 | — | — |

<sup>x</sup> Number of plants with double-flowered decorative flowers.

<sup>y</sup> Number of plants with single-flowered decorative flowers.

**Table 2. Segregation ratios of decorative flower types in progeny obtained from crosses between double-flowered cultivars and single-flowered lines with double-flowered seed parents.**

| Parent | No. of plants | No. of doubles | No. of singles | Segregation rate of doubles (%) | χ² value<sup>x</sup> | No. of sepals per decorative flower<sup>v</sup> |
|--------|---------------|----------------|----------------|-------------------------------|------------------|-----------------------------------|
| ‘Posy bouquet grace’ (‘Jogasaki’) 03JP1 (‘Jogasaki’ × ‘Paris’) | 57 | 27 | 30 | 47 | 0.16 | (P = 0.69) | 14.1 ± 0.5<sup>z</sup> | 4.3 ± 0.1<sup>y</sup> |
| ‘Posy bouquet suzi’ (‘Jogasaki’) 03JP1 (‘Jogasaki’ × ‘Paris’) | 58 | 32 | 26 | 55 | 0.62 | (P = 0.43) | 13.3 ± 0.4<sup>z</sup> | 4.2 ± 0.1<sup>y</sup> |
| ‘Posy bouquet kaysey’ (‘Jogasaki’) 05JBN4 (‘Jogasaki’ × ‘03BN4’) | 102 | 55 | 47 | 54 | 0.63 | (P = 0.43) | 13.7 ± 0.3<sup>z</sup> | 4.7 ± 0.1<sup>y</sup> |
| ‘Sumidanohanabi’ 03JP1 (‘Jogasaki’ × ‘Paris’) | 61 | 0 | 61 | 0 | — | — | 4.5 ± 0.1<sup>y</sup> |

<sup>z</sup> Number of plants with double-flowered decorative flowers.

<sup>y</sup> Number of plants with single-flowered decorative flowers.

<sup>x</sup> Test for one locus segregation (1:1).

<sup>v</sup> The number of sepals of the decorative flower with the most sepals was investigated in each progeny.

<sup>y</sup> Mean ± SE.
numbers of sepals per decorative flower in double- and single-flowered progeny were 13.3 and 4.2, respectively. Regarding the cross between the double-flowered cultivar ‘Posy bouquet kaysey’ and the single-flowered line 05JBN4, 55 out of 102 progeny (54%) were double-flowered. The average numbers of sepals per decorative flower in double- and single-flowered progeny were 13.7 and 4.7, respectively. Chi square testing confirmed that the segregation ratios of double- and single-flowered types in these crosses fitted the expected 1:1 ratio. All 61 progeny obtained from the cross between the double-flowered cultivar ‘Sumidanohanabi’ and the single-flowered line 03JP1 bore single decorative flowers (Table 2).

Table 3. Segregation ratios of decorative flower types in progeny obtained from crosses among single-flowered lines with double-flowered seed parents.

| Parent | Single-flowered line (origin) | Single-flowered line (origin) | No. of plants | No. of doubles | No. of singles | Segregation rate of doubles (%) | \( \chi^2 \) value | No. of sepals per decorative flower |
|--------|------------------|------------------|--------------|---------------|---------------|-------------------------------|----------------|-----------------------------|
| 05SNL9 ('Sumidanohanabi' × 03NL9) | 05SMaP1 ('Sumidanohanabi' × 03MaP1) | 172 | 46 | 126 | 27 | 0.28 \((P=0.60)\) | 12.2 ± 2.4\* | 4.4 ± 0.1 |
| 05JBN4 ('Jogasaki' × 03BN4) | 05JBN4 ('Jogasaki' × 03BN4) | 38 | 9 | 29 | 24 | 0.04 \((P=0.85)\) | 11.7 ± 0.9 | 4.9 ± 0.1 |
| 05SNB10 ('Sumidanohanabi' × 03NB10) | 05JBN4 ('Jogasaki' × 03BN4) | 83 | 1 | 82 | 1 | 0.60 | 8.0 | 4.4 ± 0.1 |
| 05JBN4 ('Jogasaki' × 03BN4) | 05SNB10 ('Sumidanohanabi' × 03NB10) | 93 | 0 | 93 | 0 | 0.85 | — | — 4.6 ± 0.1 |

\* Number of plants with double-flowered decorative flowers.
\* Number of plants with single-flowered decorative flowers.
\* Test for one locus segregation (1:3).
\* The number of sepals of the decorative flower with the most sepals was investigated in each progeny.
\* Mean ± SE.

Experiment 3

Four crosses were conducted among single-flowered lines with double-flowered seed parents. In the four crosses, most progeny acquired by ovule culture grew smoothly, allowing successful investigation of the decorative flower type to be performed.

Of 172 progeny obtained from the cross between 05SNL9 and 05SMaP1, 46 (27%) were double-flowered (Table 3). The average numbers of sepals per decorative flower in the double- and single-flowered progeny were 12.2 and 4.4, respectively. Of the 38 progeny obtained from the artificial self-pollination of 05JBN4, nine (24%) were double-flowered. The average numbers of sepals per decorative flower in the double- and single-flowered progeny were 11.7 and 4.9, respectively. Chi square testing revealed that the segregation ratios of double- and single-flowered types in these crosses fitted the expected ratio of 1:3. The numbers of double-flowered progeny from the reciprocal crosses between 05SNB10 and 05JBN4 were 1 and 0, respectively.

Discussion

All progeny obtained from the seven crosses between double-flowered cultivars as the seed parent and single-flowered cultivars or lines as the pollen parent were single-flowered in Experiment 1. Therefore, the single-flowered decorative flower trait is likely to be dominant in hydrangeas.

Double-flowered progeny were obtained from three crosses in Experiment 2: these used the double-flowered cultivars ‘Posy bouquet grace’ and ‘Posy bouquet suzi’ as seed parents and the single-flowered line 03JP1 as the pollen parent, and the double-flowered cultivar ‘Posy bouquet kaysey’ as the seed parent and the single-flowered line 05JBN4 as the pollen parent. Stamens and petals disappeared from the decorative flowers of double-flowered progeny, whereas the sepal number increased. These phenomena were the same as reported for decorative flowers of double-flowered cultivars by Uemachi et al. (2012). The segregation ratios of double- and single-flowered types fitted the expected ratio of 1:1. The experimental results allow consideration of whether the double-flowered decorative flower trait is controlled by a single recessive gene. On the basis of this hypothesis, the genotype of double flowers in the three double-flowered cultivars will be recessive homozygote “ss”, while the two single-flowered lines will be the heterozygote “Ss”.

However, all progeny obtained from the cross between the double-flowered cultivar ‘Sumidanohanabi’ and the single-flowered line 03JP1 bore single decorative flowers. This result contradicts the theory that a single recessive gene controls the double-flowered decorative flower trait. There is a good explanation for this; the double-flowered cultivars (‘Posy bouquet grace’, ‘Posy bouquet suzi’, and ‘Posy bouquet kaysey’) used as seed parents in the crosses bearing double-flowered progeny were derived from ‘Jogasaki’. Both single-
flowered lines (03JP1 and 05JBN4) used as pollen parents in the crosses have the seed parent ‘Jogasaki’ in common. On the other hand, 03JP1 crossed with ‘Sumidanohanabi’ did not bear double-flowered progeny, and has ‘Jogasaki’ as the seed parent. In this cross, the double-flowered progenitors of the seed and pollen parent were different. Therefore, we consider that double-flowered progeny are only obtained when the seed and the pollen parents in the cross have the same double-flowered progenitor.

If the double-flowered genotype of ‘Jogasaki’ is assumed to be “s₁s₁”, then the genotype of ‘Sumidanohanabi’ can be assumed to be “s₂s₂”. Using this hypothesis, the genotypes of the double-flowered cultivars ‘Posy bouquet grace’, ‘Posy bouquet suzi’, and ‘Posy bouquet kaysey’ are “s₁s₁” as ‘Jogasaki’ is their progenitor (Sakamoto, 2003). The genotype of the single-flowered lines 03JP1 and 05JBN4 is “Ss₁” as these lines have ‘Jogasaki’ as their seed parent. Therefore, progeny obtained from crosses between the double-flowered cultivars and the single-flowered lines can have two genotypes: “Ss₁” and “s₁s₁”. The segregation ratio of these two genotypes is approximately 1:1. Progeny with the “s₁s₁” genotype have double flowers (Fig. 3). On the other hand, progeny obtained from the cross between ‘Sumidanohanabi’ with genotype “s₂s₂” and 03JP1 with genotype “Ss₁” have two genotypes: “Ss₂” and “s₁s₂”. Their segregation ratio is approximately 1:1. Progeny with the genotype “s₁s₂” do not have double flowers. Double-flowered progeny can be obtained when a pair of recessive genes, such as “s₁s₁” and “s₂s₂”, are identical. Conversely, double-flowered progeny are not obtained when a pair of recessive genes, such as “s₁s₂”, are different.

The cross between single-flowered lines 05SNL9 and 05SMaP1, as well as the self-pollination of 05JBN4, produced double-flowered progeny in Experiment 3. The segregation ratios of double- and single-flowered types in the crosses fitted the expected ratio of 1:3. These results support the above hypothesis for the

![Fig. 3](image-url) Segregation of decorative flower types and assumption of genotypes in progeny obtained from crosses between double-flowered cultivars and single-flowered cultivars or lines, and among single-flowered lines with double-flowered seed parents.
expression of double-flowered progeny. The genotype of single-flowered line 05SNL9 used as the seed parent is “Ss”, as 05SNL9 is progeny obtained from the cross between the double-flowered cultivar ‘Sumidanohanabi’ and the single-flowered line 03NL9. The genotype of the single-flowered line 05SMaP1 used as the pollen parent is also “Ss”, as 05SMaP1 is progeny obtained from the cross between the double-flowered cultivar ‘Sumidanohanabi’ and the single-flowered line 03MaP1. The genotypes of progeny obtained from the cross between 05SNL9 and 05SMaP1 are “SS”, “Ss”, and “sS”. The segregation ratio of these genotypes is 1:2:1, with the ratio of double-flowered progeny obtained from the cross being one-quarter of the total (Fig. 3). The genotype of the single-flowered line 05JBN4 used for artificial self-pollination is “Ss”; 05JBN4 is obtained from the cross between the double-flowered cultivar ‘Jogasaki’ and the single-flowered line 03BN4. The genotypes of progeny obtained from artificial self-pollination of 05JBN4 are “SS”, “Ss”, and “sS”. Their segregation ratio is 1:2:1. The ratio of double-flowered progeny obtained from the cross was also one-quarter of the total. Thus, the segregation ratios reported in Experiment 3 matched the expected ratio of 1:3.

The numbers of double-flowered progeny from reciprocal crosses between 05SNB10 and 05JBN4 were 1 and 0, respectively. Using the hypothesis developed above, the genotypes of progeny obtained from reciprocal crosses between 05SNB10 and 05JBN4 are “SS”, “Ss”, and “sS” because the genotypes of the single-flowered lines 05SNB10 and 05JBN4 are “SS”, and “Ss”, respectively. The segregation ratio of these genotypes is 1:1:1:1. All progeny with these genotypes have single flowers (Fig. 3). The segregation ratios reported in Experiment 3 almost fitted the expected ratio. It is necessary to test whether the double-flowered progeny were truly obtained from the cross between 05SNB10 and 05JBN4 through DNA marker analysis; double-flowered progeny were not expected from this cross. The result that all progeny obtained from the cross between the double-flowered cultivar H. serrata ‘Yaeamacha’ and the single-flowered line 05SNL9 with double-flowered seed parent ‘Sumidanohanabi’ bore single flowers (unpublished data) also supports the possibility that genes controlling decorative flower types in hydrangeas differ among double-flowered cultivars.

In many ornamental plants, such as Dianthus caryophyllus and E. grandiflorum, genes controlling the double-flowered trait and the segregation ratios of flower types are generally the same within a species (Mato et al., 2004; Saunders, 1917). In Matthiola incana (L.) R. BR, the segregation ratio of flower types differs among lines of the same species (Frost, 1915). The single-flowered trait is a dominant characteristic controlled by a single major gene in a stock line. The populations obtained from self-pollination of single-flowered individuals with a heterozygous genotype segregated into two types: double- or single-flowered. The segregation ratio of these types was approximately 1:3. Conversely, in populations obtained from self-pollination of eversporting lines with a heterozygous genotype, the segregation ratio was 1:1. This phenomenon can be explained by the presence of a lethal gene linked to the dominant gene for the single-flowered trait (Waddington, 1929). However, a lethal gene is not considered to exist in hydrangeas because the ratio of double-flowered progeny obtained from crosses between single-flowered lines with the same seed parents was constant.

Uemachi and Okumura (2012) reported that the lacecap phenotype was dominant over the mophead phenotype in hydrangea inflorescences, and that a single major gene controlled inflorescence type. Insertion of a long terminal repeat retrotransposon into the locus controlling inflorescence type in H. macrophylla ‘Blue sky’ with the lacecap phenotype caused the mutation resulting in the mophead phenotype. Therefore, the insertion of a retrotransposon or the occurrence of a point mutation in the locus controlling decorative flower types may have caused the change from the single-flowered to the double-flowered trait.

This study revealed the inheritance patterns of decorative flower types in cultivars or lines derived from H. macrophylla ‘Jogasaki’ or ‘Sumidanohanabi’. These findings will be useful for efficient breeding of hydrangeas and for clarifying the molecular mechanism underlying decorative flower-type determination. Future research is required to determine the inheritance pattern of the double-flowered trait in other members of Hydrangea, and to identify the gene controlling decorative flower types.

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