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The Flower Morphological Characteristics of *Salix caprea*×*Salix gracilistyla*

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Abstract

The interspecific hybrid of *Salix caprea* and *Salix gracilistyla* has never been identified or studied in Korea. Accordingly, this study investigated the flower morphological characteristics of the interspecific hybrid between *S. caprea* and *S. gracilistyla* and compared the interspecific hybrid with *S. caprea* and *S. gracilistyla*, respectively. The female flowers were investigated for 12 characteristics and the male flowers were investigated for nine. For the female flowers, those of the hybrids were larger than those of *S. caprea* and *S. gracilistyla* in terms of catkin length (CL), bract length (BL), and bract width (BW). The hybrids are intermediates between *S. caprea* and *S. gracilistyla* in terms of ovary length, width, and stipitate length as well as gland length (GL). For the male flowers, those of the hybrids were bigger than those of *S. caprea* and *S. gracilistyla* in terms of CL, BL, and BW. The hybrids are intermediates between *S. caprea* and *S. gracilistyla* in terms of catkin width and stamen length (SL). A principal component analysis (PCA) of the female data showed that the first principal component (PC) explained 57.5% of the total variation. The first PC highly correlated the ovary stipitate and pistil style lengths. The analysis was divided into three groups of *S. caprea*, *S. gracilistyla*, and the hybrid by the first PC. The results of a PCA of the male data showed that the first PC explained 35.7% of the total variation. The first PC highly correlated with the adelphous SL and was divided into three groups of *S. caprea*, *S. gracilistyla*, and the hybrid. The results of the discriminant analysis showed that *S. caprea*, *S. gracilistyla*, and the hybrid were distinguishable by flower morphological characteristics. Therefore, the hybrid was distinctly separated from *S. caprea* and *S. gracilistyla* by flower characteristics.

Key Words: interspecific hybrid, discriminant analysis, principal component analysis, *Salix*, paternal

Introduction

Hybridization is used to create plant cultivars (Qu et al. 2018). Hybrids are excellent resources created by combining important characteristics of parent species (Punit 2013) and play a major role in improving ornamental plants (Kuligowska et al. 2016). Additionally, hybrid plants have played an important role in speciation and evolutionary innovation by moving genetic material from one species to another (Mallet 2007). In particular, interspecific hybridization combining the traits of different species can be useful for increasing genetic variation (Kulligowska et al. 2016).

The Salicaceae family is composed of three genera (*Populus, Chosenia*, and *Salix*) and approximately 620 species worldwide, which are widely distributed in the temperate and subtropical regions of the Northern hemisphere (Wu et al. 1999). This family has a great abundance of intra- and inter-specific hybrids. *Populus* species and their hybrids in Salixcaceae is short rotation woody crop (SRWC),

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which is advantageous for rapid biomass production and carbon fixation (Zalesny et al. 2015). It also has advantages such as adaptability and cutting propagation, enabling mass proliferation (Cho et al. 2020). In Korea, *Salix* is the largest genus of Salicaceae and is composed of 61 species (Chang et al. 2017). This genus has many advantages, such as long-distance seed dispersal, high germination percentage, fast initial growth rate, high resistance to flooding (Ishikawa 1980), requires minimum nitrogen fertilizer (Karp et al. 2011), grows multiple stems (Sennerby-Forsse and Zsuffa 1995), and consists of ornamental and flower arrangement material (Kuzovkina 2016). Moreover, the short rotation forest (SRF) consisting of *Salix* species features high productivity (Stolarski et al. 2008). It is suitable for biomass energy sources and has been explored as a biomass for bioethanol production (Kim et al. 2011). Biomass is a promising energy resource that can replace fossil fuels, and among them, wood biomass can contribute to the public functions of forests, such as mountainous revitalization (Cha at el. 2004).

Hybridization is used to maximize advantages. The hybrid of *Salix* is used as a resource for bio-energy and ornamentals in many countries, including the USA and Europe. Hybridization is studied for various strategies to obtain resources with excellent productivity, such as interspecific hybrids (Kopp et al. 1997; Aylott et al. 2008; Serapiglia et al. 2014). Studies of interspecific hybridization in Salicaceae include the study of interspecific hybrids between *Populus caspica* and *P. deltoids* (Ali et al. 2017), as well as the study of the stamen and pistil morphological characteristics of interspecific hybrids between *Salix alba* and *Salix fragilis* (Triest 2001). Another study conducted cytological analysis of an interspecific hybrid of four *Populus* and *Salix viminalis* species (Bagniewska-Zadworna et al. 2010). Additionally, various hybrid species of *Salix* have been developed in both China and Japan (Wu et al. 1999; Ohashi 2000). The study of hybrid in *Salix* have been mentioned in many countries but the hybrid between *S. caprea* and *S. gracilistyla* have never been studied in Korea.

Salix is a tree with remarkable ornamental value. Their hairy catkins of early blooms are highly utilized for decoration (Kuzovkina et al. 2016). Most species of *Salix* are known to be difficult to classify because catkins appear before leaves appear in spring (Park 1995). The catkins are an important key in the classification of *Salix* (Wu et al. 1999). *S. caprea* and *S. gracilistyla* can also be distinguished by their flower morphological characteristics. Accordingly, this study investigated the flower morphological characteristics of the interspecific hybrid between *S. caprea* and *S. gracilistyla* and compared the interspecific hybrid to both *S. caprea* and *S. gracilistyla*.

Materials and Methods

Plant material

The interspecific hybrids of *S. caprea* (♀) and *S. gracilistyla* (♂) in the National Institute of Forest Science were developed by the National Institute of Forest Science in 2015. This study used the 50 female and 50 male trees of hybrid. It was selected among the 5-year-old hybrid seedling. The 30 female and 30 male trees of *S. caprea* were selected in Chuncheon-si, Gangwon-do, and 30 female and 30 male trees of *S. gracilistyla* were selected in Gangneung-si,

Table 1. List of flower morphological characteristics of *Salix caprea, Salix gracilistyla,* and *Salix caprea*×*Salix gracilistyla*

Abbreviation	Characteristics
Female flower	
CL	Catkin length (mm)
CW	Catkin width (mm)
CS	Catkin stalk length (mm)
PSL	Pistil style length (mm)
BL	Bract length (mm)
BW	Bract width (mm)
BHL/ BW	Bract hair length (mm)/bract width (mm)
OL	Ovary length (mm)
OW	Ovary width (mm)
OS	Ovary stipitate length (mm)
GL	Gland length (mm)
NOS	No. of stigma(ea)
Male flower	
CL	Catkin length (mm)
CW	Catkin width (mm)
SL	Stamen length (mm)
ASL	Adelphouse stamen length (mm)
BL	Bract length (mm)
BW	Bract width (mm)
BHL	Bract hair length (mm)
GL	Gland length (mm)
AC	Anther color

Gangwon-do. They are dioecious plants. The flowers in fully blooming catkins were collected per tree. Flowers bloomed at the end of February (*S. gracilistyla*), in early March (*S. caprea*×*S. gracilistyla*), and in mid-March (*S. caprea*). The location of the flowers is second at the apical on the current-year branch.

Flower morphological characteristics extraction

The morphological characteristics of female flowers measured were: quantitative characteristics of catkin length (CL), catkin width (CW), catkin stalk (CS), pistil style length (PSL), bract length (BL), bract width (BW), bract hair length /BW (BHL/BW), ovary length (OL), ovary width (OW), ovary stipitate length (OS), and gland length (GL), and qualitative characteristics of no. of stigma (NOS) (Table 1, Fig. 1A, C, E). The morphological characteristics of male flowers measured were: quantitative characteristics of CL, CW, stamen length (SL), adelphous SL (ASL), BL, BW, BHL/BW, and GL, and qualitative characteristics of anther color (AC) (Table 1, Fig. 1B, D, F). Each value was determined using Vernier calipers (Absolute Digital, CD-15DP, USA) and Digital Microscope (Hirox MXB-2016Z, Europe).

Statistical analysis

The 11 characteristics of the female flowers (CL, CW, CS, PSL, BL, BW, BHL/BW, OL, OW, OS, and GL) and the eight characteristics of the male flowers (CL, CW, SL, ASL, BL, BW, BHL/BW, and GL) were used for analysis. Statistical analysis was carried out with the R program (4.0.0 for Windows). Analysis of variance (ANOVA) was conducted on the flower morphological characteristics extraction. Mean comparison was conducted by Duncan's test at $p \leq 0.05$ using the agricolae package. The principal component analysis (PCA) using the prcomp package was performed to compare the flower morphological characteristics between *S. caprea*, *S. gracilistyla*, and the hybrid. Through analysis, distances between the three groups were calculated and the contribution of each principal component (PC) was obtained. The score of the first and second PCs was arranged on the x- and y-axis. The discriminant analysis was performed to classify *S. caprea*, *S. gracilistyla*, and the hybrid. This was performed using the MASS package. Overall, 70% of the data were used as a training set, and the remaining 30% of data were used as the testing set.

Results

Results of flower morphological characteristics extraction

The mean and standard deviation of the flower morphological characteristics of the three groups are presented in Table 2. Significant differences between the groups were found in these characteristics, excluding the CL, BL, and BHL/BW of male flowers. In the female flowers, the CL of the hybrid (31.5±4.8 mm) was bigger than those of *S. caprea* (30.3±6.3 mm) and *S. gracilistyla* (24.8±3.0 mm).

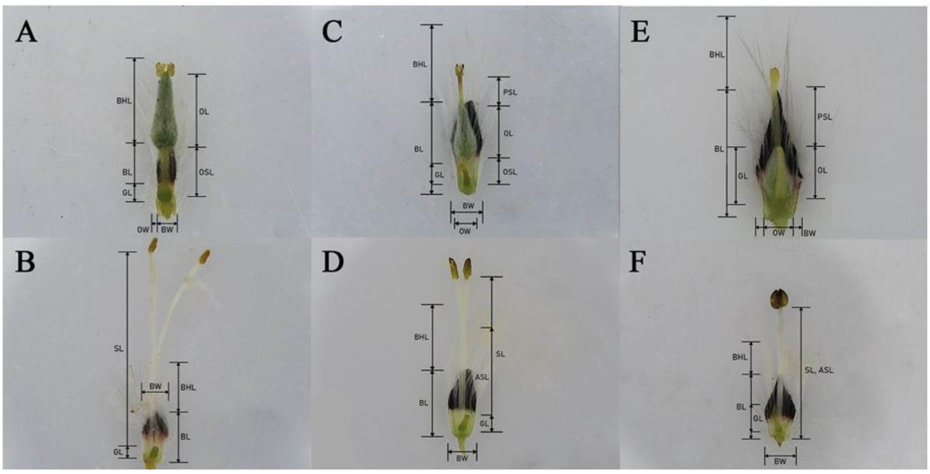

Fig. 1. Flower morphological characteristics of *Salix caprea* female flower (A), *S. caprea* male flower (B), *S. caprea*×*S. gracilistyla* female flower (C), *S. caprea*× *S. gracilistyla* male flower (D), *S. gracilistyla* female flower (E), and *S. gracilistyla* male flower (F). Abbreviations of characteristics are the same as those shown in Table 1.

Table 2. Quantitative flower morphological characteristics of *Salix caprea, Salix gracilistyla*, and *Salix caprea*×*Salix gracilistyla*

Flower characteristics[Z]	*S. caprea*	*S. caprea*×*S. gracilistyla*	*S. gracilistyla*
Female flower			
CL***[Y]	30.3±6.3[X]a [W]	31.5±4.8a	24.8±3.0b
CW***	13.9±2.1a	8.8±0.9b	5.3±0.7c
CS***	5.3±2.1a	-b	-b
PSL***	0.2±0.2c	1.2±0.2b	1.4±0.3a
BL**	2.1±0.4c	3.1±0.4a	2.5±0.3b
BW***	0.6±0.2b	1.0±0.2a	0.9±0.1a
BHL/BW**	2.6±0.8b	3.2±0.7a	2.0±0.5c
OL***	3.4±0.7a	2.1±0.3b	1.1±0.2c
OW***	1.0±0.2a	0.9±0.1b	0.7±0.1c
OS***	2.6±0.5a	0.8±0.1b	-c
GL***	0.6±0.1c	0.9±0.1b	1.1±0.2a
Male flower			
CL[ns]	30.2±4.6b	44.8±5.8a	33.8±4.2b
CW***	20.5±4.0a	15.9±1.7b	10.4±1.5c
SL***	9.8±1.8a	6.5±1.6b	4.6±0.8c
ASL***	-b	4.4±2.0a	4.6±0.8a
BL[ns]	2.8±0.6b	3.3±0.7a	2.9±0.4b
BW*	0.8±0.3b	1.0±0.2a	1.0±0.2a
BHL/BW[ns]	2.2±0.9b	3.0±0.8a	2.5±0.8b
GL***	0.7±0.1c	0.8±0.2b	1.1±0.2a

[Z]Abbreviations of flower characteristics are the same as those in Table 1.
[Y]ANOVA test (Significant at non-significant 'ns', $p<0.05$'*', $p<0.01$'**', $p<0.001$'***').
[X]Mean±standard deviation (mm).
[W]Duncan's multiple range test (Significant at $p<0.05$).

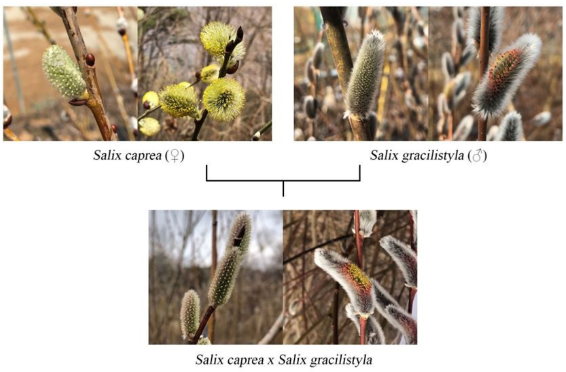

Fig. 2. Flower shape and color of female and male flowers of *Salix caprea*, *Salix gracilistyla* and *S. caprea*×*S. gracilistyla.*

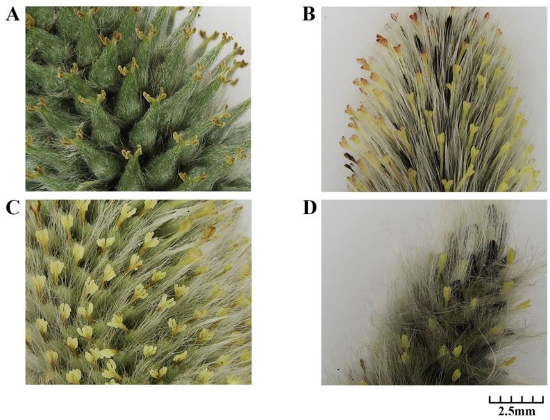

Fig. 3. No. of stigmas of female flowers in *Salix caprea* (A), *Salix gracilistyla* (B), and *S. caprea*×*S. gracilistyla* (C, D).

Moreover, the CW of the hybrid (8.8±0.9 mm) was intermediate between *S. caprea* (13.9±2.1 mm) and *S. gracilistyla* (5.3±0.7 mm). The CS of the hybrid was the same as the CS of *S. gracilistyla.* The hybrid was bigger than both *S. caprea* and *S. gracilistyla* in terms of BL and BHL/BW. The hybrid was an intermediate between *S. caprea* and *S. gracilistyla* in terms of PSL, OL, OW, OS, and GL. The hybrid catkin shape was more similar shaped to the oblong-shaped *S. gracilistyla* than the ellipse-shaped *S. caprea* (Fig. 2). The female hybrid NOS showed both the characteristics of *S. caprea* (four-lobed stigma) and *S. gracilistyla* (two-lobed stigma), with 86% of characteristics similar to *S. caprea* (Fig. 3).

In the male flowers, the CL of the hybrid (44.8±5.8 mm) was bigger than that of *S. caprea* (30.2±4.6 mm) and *S. gracilistyla* (33.8±4.2 mm). Moreover, the CW of the hybrid (15.9±1.7 mm) was an intermediate between *S. caprea* (20.5±4.0 mm) and *S. gracilistyla* (10.4±1.5 mm). The SL of the hybrid (6.5±1.6 mm) was an intermediate between *S. caprea* (9.8±1.8 mm) and *S. gracilistyla* (4.6±0.8 mm), and the ASL of the hybrid (4.4±2.0 mm) was an intermediate between *S. caprea* (did not exist) than *S. gracilistyla* (4.6±0.8 mm). The hybrid adelphous stamen shape was an intermediate between *S. gracilistyla* (completely connate into one stamen) and *S. caprea* (completely free). The hybrid was bigger than *S. caprea* and *S. gracilistyla* in terms of BL, BW, and BHL/BW. Moreover, the hybrid was intermediate between *S. caprea* than *S. gracilistyla* in terms of GL. The catkin shape of the hybrid was more similar to *S. gracilistyla*, and was between the ellipse-shaped *S. caprea* and the oblong-shaped *S. gracilistyla* in terms of shape (Fig. 2). The AC of the hybrid was similar to that of *S. gracilistyla* where that of *S. caprea* appears yellow before blooming and that of *S. gracilistyla* appears red before blooming (Fig. 2). Principal component analysis and discriminant analysis

As a result of the female flower PCA, the first and second PCs explained 57.5% and 17.9% of the total variation, respectively (Table 3). The first PC indicated that the highest correlation with OS was 0. 0.3839, followed by CW (0.3713), OL (0.3660) and PSL (-0.3626). OS showed a (+) correlation and PSL showed a (-) correlation in the first PC. The first PC was divided into three groups; *S. caprea* (the ovary was stipitate and the style was very short), *S. gracilistyla* (the ovary was sessile and the style was long), and the hybrid (the ovary was stipitate and the style was long). The second PC indicated that the highest correlation with the female BL was 0.5480 and CL was 0.5413.

As a result of the male flower PCA, the first and second PCs explained 35.7% and 23.9% of the total variation, respectively (Table 4). The first PC indicated that the highest correlation with ASL was 0.5058, followed by CW (-0.4738) and SL (-0.4344). ASL was divided into three groups; *S. caprea* (two stamens, completely free), *S. gracilistyla* (two stamens, completely connate into one stamen), and the hybrid (two stamens, filaments partly connate). The second highest correlation with the male CW was -0.3946. The second PC indicated that the highest correlation with

Table 3. Results of principal component analysis for 11 female flower morphological characteristics of *Salix caprea, Salix gracilistyla* and *Salix caprea*×*Salix gracilistyla*

Morphological characters	Principal 1	Principal 2	Principal 3
CL	0.1269	0.5413	0.1237
CW	0.3713	0.1572	-0.0791
CS	0.3529	-0.1082	-0.1807
PSL	-0.3626	0.1557	0.0166
BL	-0.1976	0.5480	-0.0561
BW	-0.2781	0.3791	-0.2777
BHL/BW	0.0589	0.1494	0.9093
OL	0.3660	0.1964	-0.0847
OW	0.2931	0.3615	-0.1317
OS	0.3839	0.0579	-0.0572
GL	-0.3208	0.0859	-0.1034
Eigenvalue	6.3197	1.9722	1.0799
Standard deviation	2.5139	1.4044	1.0392
Proportion	0.5745	0.1793	0.0982
Cumulative	0.5745	0.7538	0.8520

Table 4. Results of principal component analysis for 8 male flower morphological characteristics of *Salix caprea, Salix gracilistyla* and *Salix caprea*×*Salix gracilistyla*

Morphological characters	Principal 1	Principal 2	Principal 3
CL	0.2677	-0.2246	0.5689
CW	-0.4738	-0.3060	0.2283
SL	-0.4344	-0.3737	0.0873
ASL	0.5058	-0.0575	0.1805
BL	0.2191	-0.5749	0.1495
BW	0.2539	-0.5044	-0.2115
BHL/BW	0.1020	0.3579	0.6125
GL	0.3694	-0.0018	-0.3764
Eigenvalue	2.8537	1.9108	1.5130
Standard deviation	1.6893	1.3823	1.2300
Proportion	0.3567	0.2388	0.1891
Cumulative	0.3567	0.5956	0.7847

the male BL was -0.5749. The PCA graph in the plot of PC1 versus PC2 showed that the hybrid was situated between *S. caprea* and *S. gracilistyla*. The hybrid more closely resembled *S. gracilistyla* than *S. caprea* (Fig. 4). The locations of the hybrid were closer to *S. gracilistyla* than *S. caprea*.

As a result of the discriminant analysis, *S. caprea*, *S. gracilistyla*, and the hybrid were distinguishable (Fig. 5). The misclassification was 0% in female flowers (Fig. 5A) and male flowers (Fig. 5B).

Key to the identification of S. caprea, S. gracilistyla, and S. caprea×S. gracilistyla

The characteristics of female flower to classify *S. caprea*, *S. gracilistyla*, and the hybrid were OS and PSL, which were highly correlated with first PC in female flowers. The graph with OS as the x-axis and PSL as the y-axis showed that the hybrid was separated from *S. caprea* and *S. gracilistyla* (Fig. 6A). OS and PSL of the hybrid are intermediate characteristics between *S. caprea* and *S. gracilistyla*. The characteristics of male flower to classify *S. caprea*, *S. gracilistyla*, and the hybrid were ASL and CW, which were highly correlated with first PC in male flowers. The graph with the male ASL as the x-axis and CW as the y-axis showed that the hybrid was separated from *S. caprea* and *S. gracilistyla* (Fig. 6B). The ASL of the hybrid was the intermediate characteristic between *S. caprea* and *S. gracilistyla*.

In summary, the results showed that the hybrid can be separated from *S. caprea* and *S. gracilistyla* by its flower morphological characteristics. This study presents the iden-

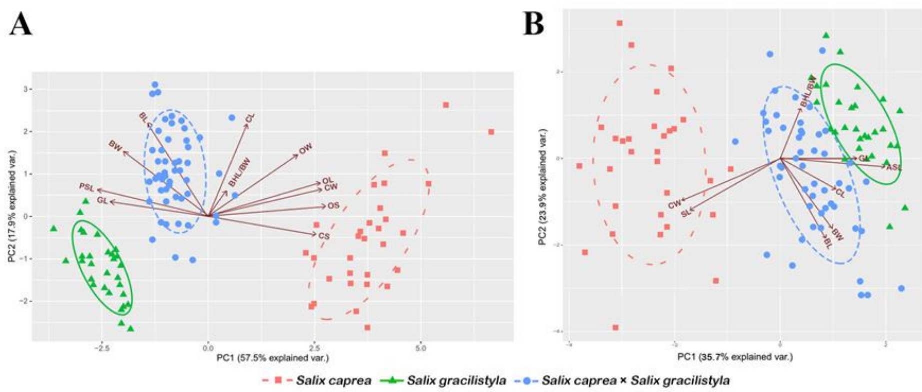

Fig. 4. Principal component analysis of females (A) and males (B) based on flower morphological characteristics of *Salix caprea, Salix gracilistyla*, and *S. caprea*× *S. gracilistyla*. Abbreviations of characteristics are the same as those shown in Table 1.

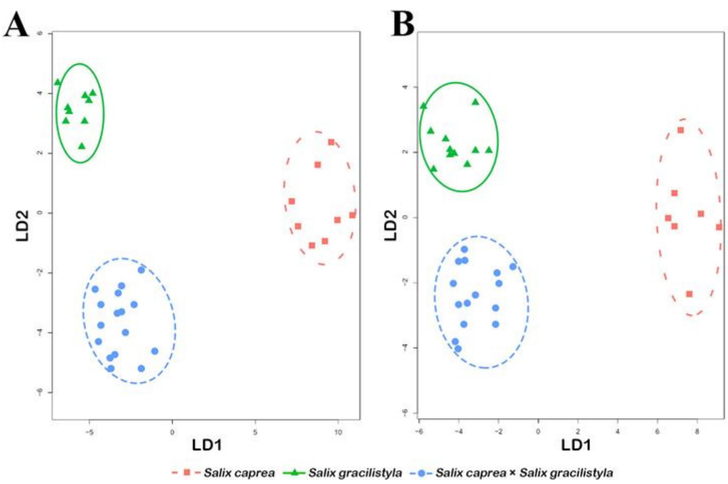

Fig. 5. Multiple discriminant analysis of females (A) and males (B) based on flower morphological characteristics of *Salix caprea*, *Salix gracilistyla*, and *S. caprea*× *S. gracilistyla*.

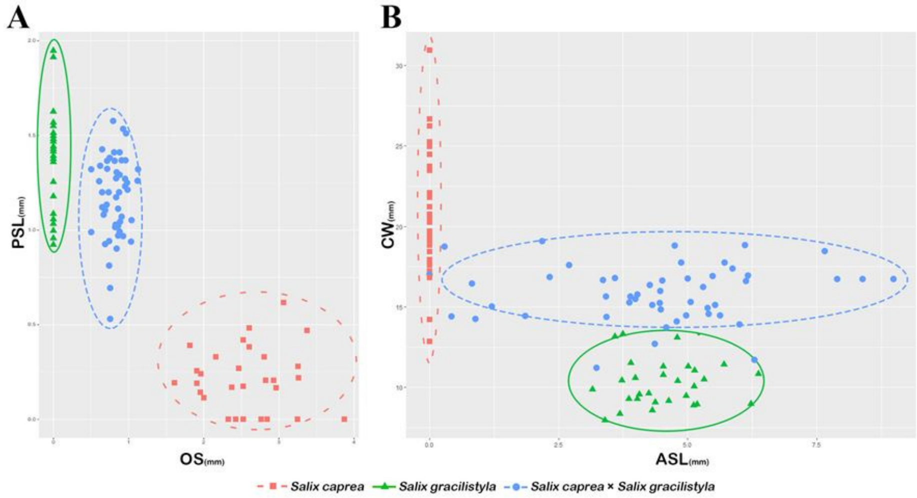

Fig. 6. Combination graph of female OS-PSL (A) and male ASL-CW (B) based on flower morphological characteristics of *Salix caprea*, *Salix gracilistyla*, and *S. caprea*×*S. gracilistyla*. Abbreviations of characteristics are the same as those shown in Table 1.

tification key of *S. caprea*, *S. gracilistyla*, and the hybrid. The identification key is the OS of female flower and ASL of male flower. This will provide the basis for classifying this hybrid if *S. caprea*×*S. gracilistyla* is found in nature.

Key based on female plants

1a. Ovary stipitate length 1.62-3.87 mm, Style length 0-0.62 mm·································· *Sailx caprea*

1b. Ovary sessile or very shortly stipitate less than 1.13 mm

2a. Ovary sessile························· *Sailx gracilistyla*

2b. Ovary stipitate length 0.49-1.12 mm ························ *Sailx caprea*×*Sailx gracilistyla*

Key based on male plants

1a. Anthers yellow before blooming, Stamens 2, completely free····································· *Sailx caprea*

1b. Anthers reddish-purple before blooming, Stamens 2, completely connate or partly connate

2a. Filaments completely connate······ *Salix gracilistyla*

2b. Filaments partly connate ························ *Salix caprea*×*Salix gracilistyla*

Discussion

According to previous studies, *S.*×*leucopithecia* of Japanese taxa was discovered in a natural state in both 1926 and 1946 and was recorded as a new species (Tokyo Botanical Society 1926; 1946). It was then treated as a hybrid between *Salix bakko* and *Salix gracilistyla* by Ohwi and Nakaike (1978). Later, *S.*×*leucopithecia* was introduced as an ornamental plant in the USA (Kuzovkina et al. 2016). *S.*×*leucopithecia* and the hybrid show the same range of CL, CS, BL, BW, OS, and GL in female flowers (Tokyo Botanical Society 1926). Additionally, *S.*×*leucopithecia* and the hybrid showed the same range of CL, BW, GL, ASL, and AC in the male flowers (Tokyo Botanical Society 1946). As a result, most flower characteristics of the hybrid are similar to *S.*×*leucopithecia*. For more accurate comparisons with *S.*×*leucopithecia*, it is necessary to further study the morphological characteristics of the vegetative organs, such as leaves.

Salix species are ornamental resources in many countries. In particular, *S.*×*leucopithecia* and various cultivars made through *S.*×*leucopithecia* are cultivated for ornamental purposes in early spring. It has very large catkins. In this study, the CL and bract size of the hybrid were bigger than those of *S. caprea* and *S. gracilistyla*. Therefore, this hybrid is also expected to be used as an ornament in Korea.

In this study, most flower characteristics of the hybrid were more similar to *S. gracilistyla* than *S. caprea*. Additionally, the PCA results indicated that the flower characteristics of the hybrid were closer to *S. gracilistyla* (paternal parent) than *S. caprea* (maternal parent). In general, interspecific hybrid characteristics more closely resembled maternal than paternal characteristics. According to Lee et al. (2005), the interspecies hybrid between *Dianthus giganteus* and *Dianthus carthusianorum* resembles the maternal characteristics rather than the paternal characteristics. Additionally, in a study by Kim et al. (2015), the interspecies hybrid between *Brassica napus*, *Brassica campestris*, and *Brassica rapa* resembles maternal rather than paternal characteristics. According to previous studies, this maternal effect is affected by cytoplasmic genetics, endosperm nuclei, and maternal phenotypes (Roach and Wulff 1987). The cytoplasm components, such as plastids and mitochondria, can be directly moved from the maternal plant to the offspring, and this movement is independent of the nucleus. The endosperm always contains greater amounts of maternal than paternal genes. Moreover, the tissues surrounding a developing embryo and endosperm are maternal. These tissues can influence the phenotype by forming the seed coat, fruit, and accessory seed structures. Previous studies have shown that maternal effects can contribute to the phenotype of a hybrid.

The hybrids of *Salix* are also affected by maternal effects. The results of a study by Orians (2000) involving the concentration of condensed tannin in a hybrid between *Salix sericea* and *Salix eriocephala* were not correlated with *S. eriocephala* (paternal parent), but with S. sericea (maternal parent), the maternal taxon that produces low concentrations. In addition, a study by Aravanopoulos (2010) showed that a hybrid sharing the same maternal parent is more similar in terms of leaf morphometry than a hybrid sharing the same paternal parent.

On the other hand, the present study found that the hybrid characteristics resembled those of *S. gracilistyla* (paternal tree) to a greater degree than those of *S. caprea* (maternal parent). According to Simon (1977), the amount and origin of the callus in the stamen culture of *Solanum* hybrids indicate a substantial paternal influence. However, there is currently a lack of studies regarding the paternal effect on hybrid characteristics. Additional studies, such as a reciprocal study, are required to determine the effects of parents in hybrids.

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