



Sexuality of *Aruncus aethusifolius* (Rosaceae)

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ABSTRACT: *Aruncus* L. is a small genus which is distributed in the circumpolar regions of the Northern Hemisphere, including Europe, Asia, and North America. In Korea, there are two taxa, *A. dioicus* var. *kamtschaticus* and *A. aethusifolius*. *Aruncus aethusifolius* is a species endemic to Korea, occurring only on Jeju Island. An important characteristic of *Aruncus* is dioecy. However, there is some controversy regarding the sexuality of this genus, and little is known about *A. aethusifolius*. To characterize the sexuality of *A. aethusifolius* and to provide insight into the evolution of its sexual system, we investigated natural populations and herbarium specimens of *A. aethusifolius*. The results indicate that the species has carpellate, staminate, and bisexual flowers. Carpellate flowers are always borne on separate individuals, and staminate flowers are borne either on separate individuals or mixed with bisexual flowers on the same individuals. The sexuality of *A. aethusifolius* is defined as polygamo-dioecious. The polygamo-dioecious type is also found in *A. dioicus* var. *dioicus* and *A. dioicus* var. *kamtschaticus* and thus may be a general condition in *Aruncus*.

Keywords: Bisexual, dioecious, flower, Jeju Island, polygamo-dioecious

Aruncus L. is a small genus distributed in the circumpolar regions of the Northern Hemisphere, including Europe, Asia, and North America. Number of species in this genus varies depending on the author, with some recognizing one highly polymorphic species of *A. dioicus* (Walter) Fernald (Hara, 1955) or the three species of *A. dioicus*, *A. gombalanus* (Hand.-Mazz.) Hand.-Mazz., and *A. aethusifolius* (H. Lévl.) Nakai (Gu and Alexander, 2003; Lee, 2007). *Aruncus* is easily distinguished from other genera in Rosaceae by several characters, such as dioecious, perennial herbs, 2–3-pinnately or 1–2-ternately compound leaves without stipules, paniculate inflorescences, and follicular fruits (Hutchinson, 1964; Henrickson, 1985; Kalkman, 2004). Recent phylogenetic analyses suggested that *Aruncus* is sister to *Holodiscus* (K. Koch) Maxim., which is a small erect, hermaphroditic shrub in western North America within the tribe Spiraeae (Potter et al., 2007a, 2007b; Xiang et al., 2016). Plants of *Aruncus* are widely cultivated as ornamentals (Hutchinson, 1964) and young leaves, with high antioxidant activities (Shin et al., 2008), are often consumed as vegetables.

In Korea, there are two taxa. *Aruncus dioicus* var. *kamtschaticus* is distributed in the higher elevations of mountains

on the Korean Peninsula and on Ulleung Island, but it has not been reported on Jeju Island. This taxon is widely distributed in East Asia from western China, Korea, to Japan with a wide range of morphological variation (Ikeda, 2001; Gu and Alexander, 2003; Lee, 2003; Lee, 2007). *Aruncus aethusifolius* is an endemic species of Korea, occurring only on Jeju Island. It is usually found in moist places near or crevices of volcanic rocks at elevations ranging from 1,500 to 1,800 m as part of the subalpine vegetation on Mt. Halla, and it occurs as well on moist banks along creeks of the mountain at elevations as low as 400 m. *Aruncus aethusifolius* is occasionally thought of as a variety of *A. dioicus* (Hara, 1955; Lee, 2003), but it is considered to be a distinct species due to several unique morphological characteristics, such as a short plant stature, very short internodes in the stems, highly dissected leaflets, and erect follicles (Nakai, 1912; Lee, 1980; Lee, 2006; Lee, 2007).

One of key characters of *Aruncus* includes the sexuality of the species, in which staminate and carpellate flowers are developed in different individuals in a population, making it dioecious. Dioecious species is very rare among the approximately 90 genera and 3,000 species in Rosaceae,

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occurring only in eight genera and approximately nine species (Table 1). Given that the vast majority of species in Rosaceae are hermaphroditic and considering the phylogeny of Rosaceae (Potter et al., 2007a; Xiang et al., 2016), dioecy in Rosaceae were likely derived independently in each of the species from hermaphroditic ancestors. Dioecy is also rare in angiosperms, found in about 6% of flowering plants (Renner and Ricklefs, 1995), in contrast to the animal system, in which gonochorism with separate males and females is found in 95% of all species (Jarne and Auld, 2006).

The rarity of dioecism in angiosperms has led to much attention regarding the evolution and development of separate genders (Darwin, 1877; Westergaard, 1958; Irish and Nelson, 1989; Renner and Ricklefs, 1995; Sakai and Weller, 1999; Charlesworth, 2015; Käfer et al., 2017; Pannell, 2017; Zuluovova et al., 2017). Several characteristics, such as woodiness, wind pollination, and large inflorescences with small white to green flowers, are associated with the evolution of dioecy. With regard to their geographic distribution, dioecious species are more common in the tropics and on oceanic islands, including Hawaii, in angiosperms (Renner and Ricklefs, 1995; Sakai and Weller, 1999; Käfer et al., 2017). *Aruncus* provides an intriguing system with which to study the evolution of dioecy, as it deviates from the general trends in the evolution of the sexual system. However, there is confusion regarding the sexuality of *Aruncus* among authors. While most authors (Radford et al., 1964; Ohwi, 1965; Gleason and Cronquist, 1991; Ikeda, 2001; Lee, 2007; Mellichamp and

Wetherwax, 2012; Mellichamp, 2014) have considered *Aruncus* to be dioecious, Gu and Alexander (2003) have found that *Aruncus* is monoecious, in which staminate and carpellate flowers are borne on the same plant. Tutin (1968) recognized that *Aruncus* is polygamo-dioecious, in which bisexual (or perfect) flowers are developed in some of the male or female plants in a population. Bond (1962) and Robertson (1974) showed that bisexual flowers are occasionally found in staminate inflorescences in *A. dioicus* var. *dioicus* in eastern North America, consistent with Tutin (1968). The occurrence of bisexual flowers is unknown in other varieties of *A. dioicus* and *A. aethusifolius*.

The objectives of this study are to characterize the sexuality of *A. aethusifolius* based on field observations and investigations of herbarium specimens and to provide insights into the evolution of sexual system of this species.

Materials and Methods

Field observations of *A. aethusifolius* were made on Mt. Hallasan on Jeju Island. Fifty-three herbarium specimens of *A. aethusifolius* and 190 specimens of *A. dioicus* var. *kamtschaticus* were examined in KB (the acronyms follow Thiers, 2017), TI, TUT, and Warm-Temperate and Subtropical Forest Research Center. A list of specimens of *Aruncus aethusifolius* examined in this study was provided in Appendix 1.

The sexuality of *A. aethusifolius* in a flower and a plant was determined under a microscope. A Nikon SMZ18 dissecting

Table 1. Genera or species with unisexual flowers in Rosaceae. Most genera with unisexual flowers are monotypic, except for *Spiraea*, *Rubus*, *Fragaria*, and *Sanguisorba*. In the cases of *Spiraea*, *Fragaria*, and *Rubus*, most species produce bisexual flowers. The tribal and supertribal classifications follow Potter et al. (2007b). Data were obtained from Hutchinson (1964), Tutin (1968), Gu et al. (2003), and Kalkman (2004).

Sexuality	Genera (number of species) or species	High-level classification	Distribution
Dioecious	<i>Kageneckia</i> Ruiz & Rav. (1)	Pyreae	South America
	<i>Oemleria</i> Rchb. (1)	Osmaronieae	western North America
	<i>Sibiraea</i> Maxim. (1)	Spiraeaceae	East Asia, Europe
	<i>Spiraea bella</i> Sims	Spiraeaceae	Bhutan, China, India, Nepal
	<i>Spiraea decumbens</i> W. Koch	Spiraeaceae	Europe
	<i>Rubus chamaemorus</i> L.	Rosodae	East Asia, Europe, North America (circumpolar)
	<i>Fragaria virginiana</i> Mill.	Potentilleae	North America
Monoecious	<i>Cliffortia</i> L. (1)	Sanguisorbeae	Africa
	<i>Hagenia</i> J. F. Gmel. (1)	Sanguisorbeae	Africa
	<i>Sanguisorba</i> L. (15)	Sanguisorbeae	Africa, Eurasia, North America
	<i>Sarcopoterium</i> Spach. (1)	Sanguisorbeae	Europe
	<i>Cliffortia</i> (1)	Sanguisorbeae	Africa

stereomicroscope (Nikon, Tokyo, Japan) was used to examine and photograph the flowers. Each specimen was scored as a male or female plant. The proportion of bisexual flowers in a plant was approximated by the length of the inflorescence axis, with bisexual flowers divided by the total length of the inflorescence axis. Flowers of *A. aethusifolius* are very small and borne very tightly along the inflorescence axis. The proportion of bisexual flowers in each gender class was plotted.

Results and Discussion

Our examination of *A. aethusifolius* indicated that the species has complex patterns of sexuality (Fig. 1). Three types of flowers were found: carpellate (Fig. 1B), staminate (Fig. 1D), and bisexual (Fig. 1F) flowers. The flowers had four basic whorls: sepals, petals, stamens, and carpels. In the carpellate flowers, stamens were not fully developed such that the filaments were very short and the anthers minute (Fig. 1B). In the staminate flowers, rudimentary carpels were located at the center of the flower (Fig. 1D). The bisexual flowers had both stamens and carpels that were fully developed (Fig. 1F). Nectaries on the inner side of the hypanthium were developed in all three types of flowers, which attract pollinators (Fig. 1). The flowers of *A. aethusifolius* are borne in panicles of racemes with 2–9 lateral branches. Carpellate flowers are always borne in separate individuals, making them female (gynoecious) plants (Fig. 1A). There are male (androecious) plants bearing only staminate flowers (Fig. 1C). In some male plants, bisexual flowers were also developed with staminate flowers in an inflorescence (Fig. 1E). Bisexual flowers are located at the lower part of a branch or at the lateral branch of the inflorescence. These andro-polygamous plants have mixed of flowers, staminate and bisexual flowers. The proportion of bisexual flowers in andro-polygamous plants based on herbarium specimens varied, ranging from 22 to 79% (Fig. 2). Thus, the populations of *A. aethusifolius* consist of female, male, and andro-polygamous plants. Of the 53 specimens examined, 14 were female, 23 were male, and 16 were andro-polygamous (Fig. 2). As a result, sexuality of *A. aethusifolius* is defined as polygamo-dioecious.

Polygamo-dioecious may be a general condition in *Aruncus*. An examination of 190 specimens of *A. dioicus* var. *kamtschaticus* collected in Korea, China, and Japan showed that one specimen from Mt. Hwangbyeongsan in Gangwon Province (*Kwon 080727-080*, KB278766) was andro-polygamous. The presence of andro-polygamous plants in *A. dioicus* var. *kamtschaticus*, albeit rare, is consistent with our observations of *A. aethusifolius*. Thus, our investigations of the

sexuality in *A. aethusifolius* and *A. dioicus* var. *kamtschaticus* support previous studies of *A. dioicus* var. *dioicus* (Bond, 1962; Tutin, 1968; Robertson, 1974).

The occurrence of andro-polygamous plants in a dioecious species is occasionally reported in Rosaceae. For example, flowers of *Oemleria cerasiformis* (Torr. & A. Gray ex Hook. & Arn.) J. W. Landon are usually unisexual, developed in separate plants. However, in rare cases, bisexual flowers are also found (Hess, 2014), though the frequency of bisexual flowers is largely unknown.

The frequency of andro-polygamous plants varies across species in *Aruncus*. The occurrence of an andro-polygamous plant is very rare in *A. dioicus* var. *kamtschaticus*, as described above. It is difficult to quantify the frequency of andro-polygamous in the eastern North American *A. dioicus* var. *dioicus*. Robertson (1974) stated that it was 'occasionally' found. However, the frequency of andro-polygamous plants in *A. aethusifolius* is much higher than the frequency in *A. dioicus*. Of the 53 specimens examined, 16 (30%) were andro-polygamous (Fig. 2). The gender frequency based on herbarium specimens may be biased, as female and andro-polygamous plants could be over-represented. Female and andro-polygamous plants bearing flowers or fruits could be prepared for specimens, while male plants may have been neglected when the flowers fell off. Our field study supports the under-representation of male plants in herbarium specimens. Among nearly 60 individuals of nine clumps of *A. aethusifolius* along the Youngsil trail of Mt. Hallasan, male plants were dominant. Plants of *A. aethusifolius* showed a patchy distribution pattern in the population. A clump consisted of two female plants (Fig. 1A), one clump contained three male and four andro-polygamous plants (Fig. 1E), and the remaining clumps included male plants. Our field observation also shows that the frequency of andro-polygamous plants in *A. aethusifolius* is higher than that in *A. dioicus*.

Why does *A. aethusifolius* show a high frequency of andro-polygamous plants? It may be that the fitness of bisexual flowers, the population size, the genetic mechanism of sex determination, or a combination of these factors is associated with the frequent development of bisexual flowers. The occurrence of the same pattern of sexuality in all taxa of *Aruncus*, including *A. dioicus* and *A. aethusifolius*, suggests that polygamo-dioecious is genetically determined. Given that its sister group, *Holodiscus*, and most other members of Spiraeaceae are hermaphroditic (Table 1), the gender polymorphism and underlying genetic network in *A. aethusifolius* should have evolved in the most recent common ancestor of *Aruncus*. It is interesting to note that seeds produced

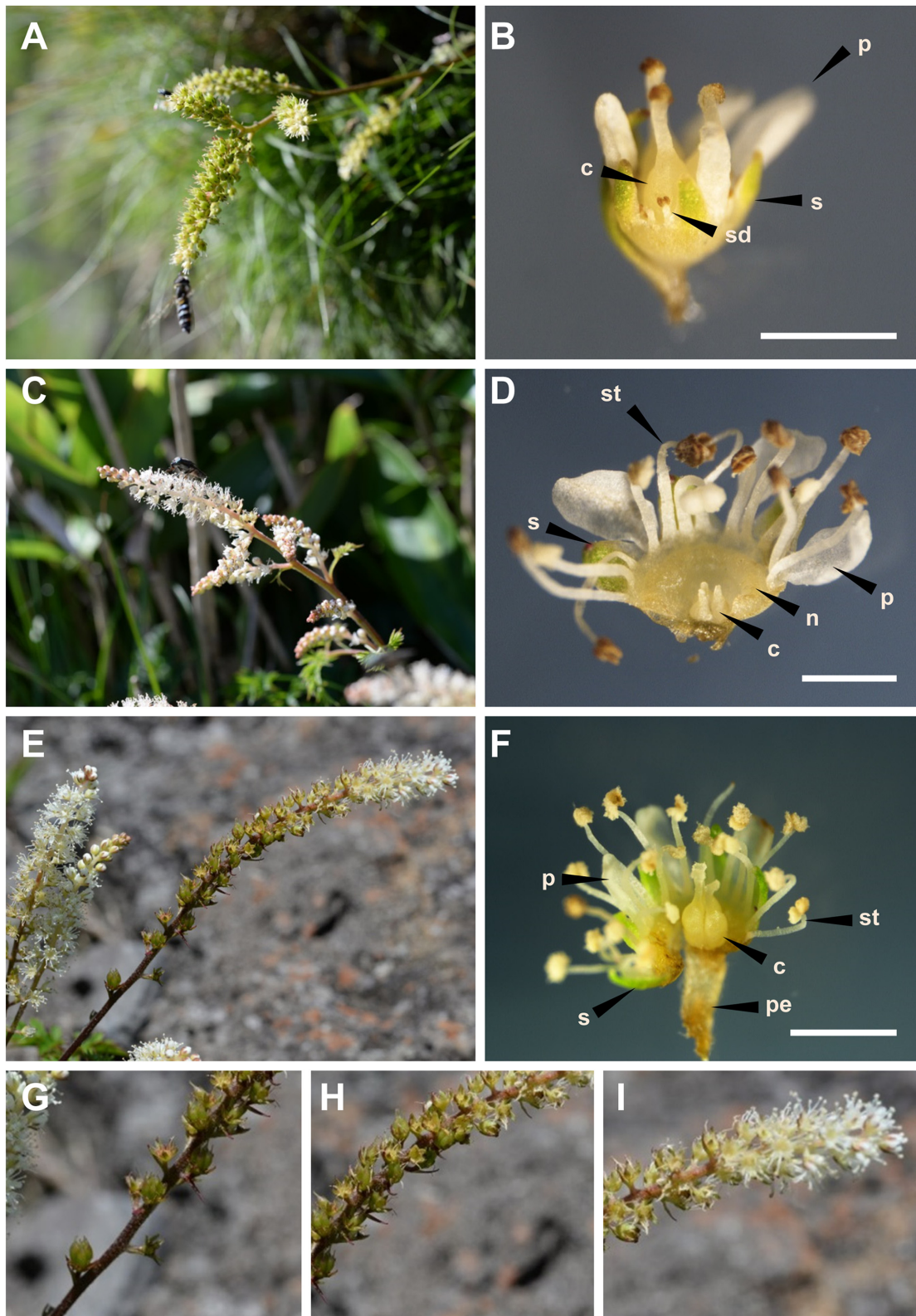


Fig. 1. Photographs of *A. aethusifolius*. **A.** Inflorescence of carpellate flowers. **B.** Carpellate flower. **C.** Inflorescence of staminate flowers. **D.** Staminate flowers. Parts of the hypanthium, stamens, and perianth were removed. **E.** Inflorescence mixed with bisexual and staminate flowers. **F.** Bisexual flowers. Parts of the hypanthium, stamens, and perianth were removed. **G–I.** Close-up of the inflorescence shown in **E.** c, carpel; n, nectary; p, petal; pe, pedicel; s, sepal; sd, staminode or rudimentary stamen; st, stamen. Scale bars = 1 mm.

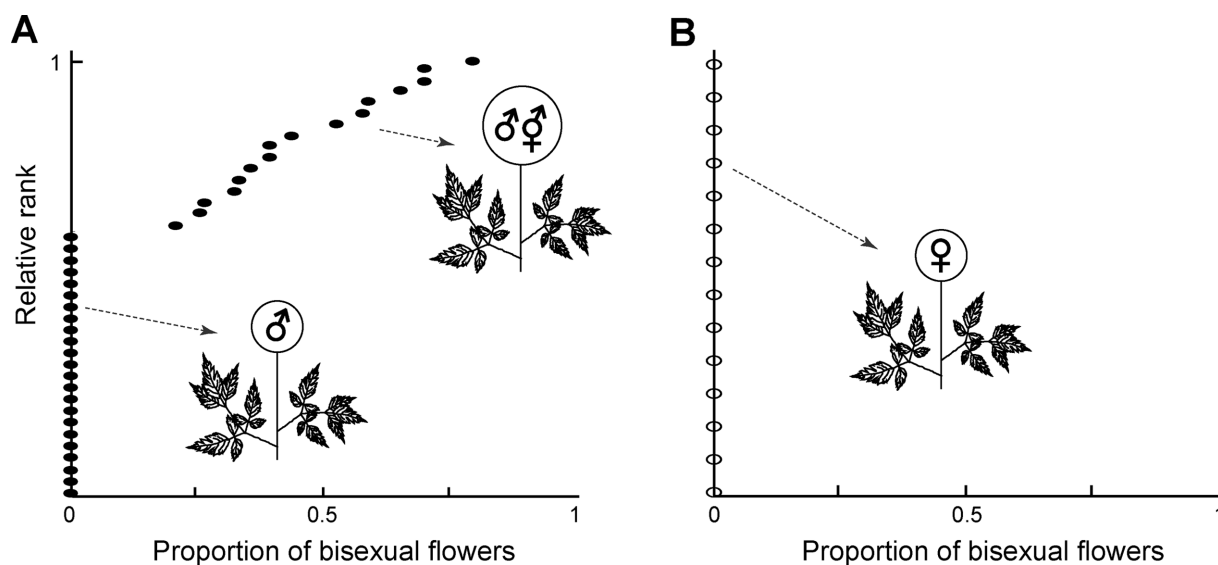


Fig. 2. Plot of the proportion of bisexual flowers. **A.** Male and andro-polygamous plants. **B.** female plants. Each circle represents one individual. For andro-polygamous plants, each plant was ranked according to the proportion of bisexual flowers and was plotted.

by bisexual flowers grow into andro-polygamous plants in *A. dioicus* var. *dioicus* (Bond, 1962). If we assume that this system applies to *A. aethusifolius*, the genotype of the andro-polygamous plant is inherited and maintained in a population. The frequency of the genotype in *A. aethusifolius* may be high due to the large population size on Mt. Hallasan and indeed on Jeju Island. The large population size compared to *A. dioicus* may have played a role in the preservation of the genotype of the andro-polygamous plant.

The fitness of the andro-polygamous plants in *A. aethusifolius* may be greater than the fitness of andro-polygamous plants in *A. dioicus*. Bisexual flowers are borne on the part of the male inflorescence, as described above (Fig. 2). Thus, the proportion of seeds from andro-polygamous plants in a population would decrease as the size of the inflorescence increases. The size of the panicles of female plants in *A. dioicus* is very large (11–27.8 cm in length [mean = 17.5 cm]), producing numerous follicles. In contrast, the size of the inflorescence of female plants in *A. aethusifolius* is small, ranging from 7.7 to 12.5 cm in length (mean = 9.4 cm). This suggests that the magnitude of the difference in the number of seeds produced between carpellate and bisexual flowers in *A. aethusifolius* is smaller compared to that in *A. dioicus*. This would result in a higher proportion of seeds from bisexual flowers in a seed pool or bank in a population of *A. aethusifolius*. Further study of the gender specificity of these seeds is therefore necessary.

The genetic mechanisms which determine gender in plants are diverse (Pannell, 2017) because dioecy evolved multiple

times from hermaphroditism. A genetic network for sex determination controlled by environmental signals was shown in *Ceratopteris richardii* Brongn. (Tanurdzic and Banks, 2004). Chromosomal sex determination has been widely studied in several angiosperms, such as *Fragaria virginiana* Mill. (Spigler et al., 2008), *Sagittaria latifolia* Willd. (Dorken and Barret, 2004), and *Silene latifolia* Poir. (Fujita et al., 2012). In monoecious plants such as melons and maize, the sexual identity of flowers as either male or female is determined by different genetic networks that react to hormones (Irish, 1999; Boualem et al., 2015). These case studies suggest that there is no general model of gender determination in plants. It would be interesting and important to study the sex determination mechanism in *A. aethusifolius*.

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Appendix 1. A list of specimens of *Aruncus aethusifolius* examined in this study.

KOREA. Jeju-do. Jeju-si: Yeon-dong, elev. 180 m, 18 Aug 2014, *Cho M. S. et al. 140818008* (KB 519644); Yeongpyeong-dong, elev. 450 m, 13 Aug 2008, *Gyu Y. C. ANH_en_080813_005* (KB 197921); Mt. Hallasan, 24 Nov 2009, *Kim C. S. et al. 28845* (WTFRC 100011016); Mt. Hallasan, 1 Nov 2011, *Kim G. R. 33568* (WTFRC 10017850); Mt. Hallasan, 20 Aug 2009, *Kim J. 27610* (WTFRC 100011029); Mt. Hallasan, 24 Jul 2011, *Kim J. 32119* (WTFRC 10016400 [2 plants]); Mt. Hallasan, 29 Jul 2011, *Kim J. 32152* (WTFRC 10016433 [2 plants]); Mt. Hallasan, 23 Jul 1924, *Saito s. n.* (KB 543926, 544381, 547728); Mt. Hallasan, 27 Jul 2008, *Song G. M. et al. 26142* (WTFRC 100011017); Mt. Hallasan, 20 Jul 2001, without collector and number (WTFRC 100011005). Seogwipo-si: Sanghyo-dong, elev. 570 m, 30 Aug 2011, *Im H. T. 336112_0049* (KB 388519); Sanghyo-dong, Donnaeko Valley, elev. 550 m, 23 Oct 2011, *Im H. T. Im61305* (KB 382410); Sanghyo-dong, elev. 506 m, 7 Aug 2010, *Kim C. H. et al. 50733* (KB 329762 [3 plants], 463109); Sanghyo-dong, 26 Jul 2005, *Kim C. S. 3872* (KB 208594 [2 plants]); Namwon-eup, 15 Jul 2011, *Kim G. R. 32072* (WTFRC 10016352 [2 plants]); Sanghyo-dong, 26 Jul 2005, *Kim J. et al. 20764* (WTFRC 100011013); Yeongnam-dong, Mt. Hallasan, 7 Aug 2008, *Kim J. et al. 26183* (WTFRC 100010985); Namwon-eup, 3 Aug 2006, *Kim J. E. et al. 22785* (WTFRC 100011008–100011011); Namwon-eup, 3 Aug 2010, *Kim J. E. 29971* (WTFRC 10014220 [4 plants]); Namwon-eup, elev. 597 m, 3 Aug 2010, *Kim J. E. et al. 29971* (KB 318083); Mt. Hallasan, 19 Jun 2009, *Lee C. S. et al. leecs090987* (KB 256006); Namwon-eup, 21 Aug 2003, *Moon M. O. et al. s. n.* (WTFRC 100010986–100010991, 100010993, 100010994); Hawon-dong, Mt. Hallasan, 15 Jul 2014, *Song J. H. & OK M. K. sok201407_37* (KB 491953); Sanghyo-dong, Donnaeko Valley, 2 Aug 2001, without collector and number (WTFRC 100010998, 100011000, 100011001, 100011003, 100011004); Namwon-eup, 28 Sep 2002, without collector and number (WTFRC 100010995).