



Morphometric analysis of the *Daphne kiusiana* complex (Thymelaeaceae) using digitized herbarium specimens

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ABSTRACT: *Daphne kiusiana* is an evergreen shrub with dense head-like umbels of white flowers distributed in southern Korea, Japan, China, and Taiwan. Plants in China and Taiwan are recognized as var. *atrocaulis* by having a dark purple stem, elliptic leaves, and persistent bracts. Recently, plants on Jeju Island were segregated as a separate species, *D. jejuensis*, given their elliptic leaves with an acuminate apex, a long hypanthium and sepals, and a glabrous hypanthium. Morphological variations of three closely related taxa, the *D. kiusiana* complex, were investigated across the distributional range to clarify the taxonomic delimitation of members of the complex. Twelve characters of the leaf and flower were measured from digitized herbarium specimens using the image analysis program ImageJ and were included in a morphometric analysis, the results of which indicate that the level of variation in the characters is very high. The results of a principal component analysis weakly separated *D. jejuensis* from *D. kiusiana* according to their floral characteristics, such as a longer, glabrous hypanthium, and larger sepals. However, some individuals of *D. kiusiana*, particularly those from Bigeumdo Island, were included in *D. jejuensis*. Recognition of *D. kiusiana* var. *atrocaulis* based on the leaf shape was not supported in the analysis, and *D. jejuensis* may be recognized as a variety of *D. kiusiana*. Our morphometric analysis shows that digitized images of herbarium specimens could be useful and an additional method by which to investigate more diverse specimens.

Keywords: COVID-19, horticulture, hypanthium, morphological variation, multivariate analysis, ornamental plant, virtual herbarium

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INTRODUCTION

The genus *Daphne* L., consisting of about 95 species in Europe, northern Africa, and eastern Asia, belongs to the tribe Daphneae Meissn. in Thymelaeaceae and includes many economically important species (Herber, 2003; White, 2006; Oh and Hong, 2015). Species of *Daphne* are widely cultivated as ornamental plants for their colorful flowers and delicious scent. One such example is *D. odora* Thunb., perhaps the most widely cultivated *Daphne* species in eastern Asia and Europe, with many cultivars. *Daphne kiusiana* Miq. is morphologically closely related to *D. odora* and can be characterized by having glabrous stems, persistent and glabrous leaves, a terminal head-like umbel with caducous bracts on the previous year's branch, and white, tetramerous

flowers with cup-shaped nectary disks (Oh and Hong, 2015). *Daphne odora* is easily distinguished from *D. kiusiana* by having reddish pink flowers (strongly so on the outer surface of the hypanthium). While the native distribution and the origin of *D. odora* are unknown, *D. kiusiana* is distributed in China, Taiwan, Korea, and Japan (Ohwi, 1965; Lee, 2003; Wang et al., 2007).

Two varieties have been recognized in *D. kiusiana*: plants in Korea and Japan are recognized as *D. kiusiana* var. *kiusiana* (Ohwi, 1965; Oh and Hong, 2015) and those in China and Taiwan as *D. kiusiana* var. *atrocaulis* (Rehder) F. Maek. (Wang et al., 2007). In the taxonomic treatment of Thymelaeaceae in China, Rehder (1916) stated that var. *atrocaulis* is similar to var. *kiusiana*, but the former differs by having caducous bracts, thicker leaves, and dark purple stems. In Korea, *D.*

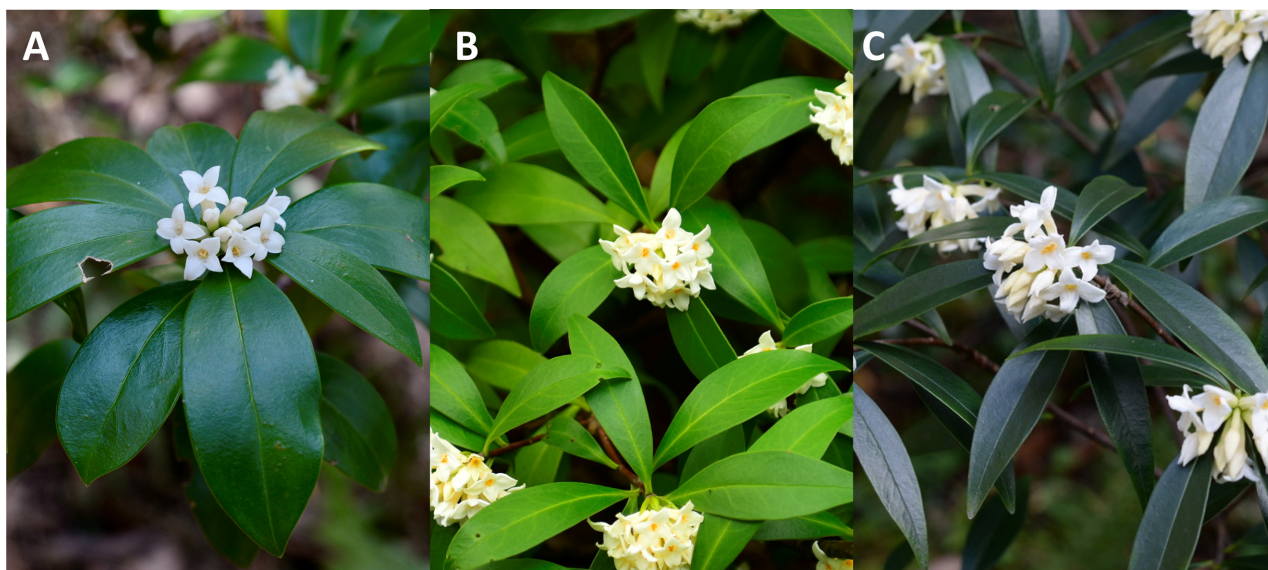


Fig. 1. Photographs of *D. kiusiana* var. *kiusiana* and *D. jejudoensis*. **A.** *D. kiusiana* var. *kiusiana* on Geojedo; **B.** *D. kiusiana* var. *kiusiana* on Bigeumdo; **C.** *D. jejudoensis* on Jejudo. (Photo credit: **A, C:** Sang-Hun Oh, **B:** Dong-Hyuk Lee)

kiusiana var. *kiusiana* is distributed on mountain slopes on offshore islands in the southwest (Bigeumdo and Uido Islands) and in the southeast (Geojedo Island) (Fig. 1A, B). Plants previously identified as *D. kiusiana* var. *kiusiana* in the Gotjawal forest on Jejudo Island have recently been segregated as a distinct species, *D. jejudoensis* M. Kim (Lee et al., 2013) (Fig. 1C). This new species was distinguished from *D. kiusiana* by having elliptic leaves, a glabrous hypanthium, and a long hypanthium and sepals (Lee et al., 2013).

However, these morphological characteristics delimiting each taxon show a wide range of variation within and among populations (Lee and Oh, 2017). Considering that an assessment of the morphological variations among species and varieties as well as across distributional ranges of temperate evergreen forests has not been conducted, a comprehensive analysis of the morphological variations could help to circumscribe the species. The *D. kiusiana* complex here is defined to include the two varieties of *D. kiusiana* and *D. jejudoensis*.

A virtual herbarium is a herbarium that houses digitized collections and provides various forms of information attached to the collections to broader users (Barkworth and Murrell, 2012; Monfils et al., 2017). The idea of the virtual herbarium was initially advanced in the U.S.A. in the 1990s, and since then individual herbaria and a consortium of multiple herbaria have led to the creation of virtual herbaria that serve as additional portals for botanical research and education. Virtual herbaria are now commonly available in most major herbaria in many regions, i.e., North America, Europe, and Australia (Schmull et al., 2005; Gallego and Sanchez, 2011; Thiers et

al., 2016; Monfils et al., 2017; Cantrill, 2018; Haque et al., 2018; Kovtonyuk et al., 2018; Seregin et al., 2018; Brenskelle et al., 2019). This system has recently been implemented in many institutes in eastern Asiatic countries as well. In Korea, the National Institute of Biological Resources of Korea (<https://species.nibr.go.kr/index.do>) and the Korea Forest Service (<http://www.nature.go.kr/main/Main.do>) provide various types of information on the biodiversity of the country in addition to information about virtual herbaria. In China, a virtual herbarium that contains specimens deposited from various herbaria in China is available to the public from the Institute of Botany of the Chinese Academy of Science (<https://www.cvh.ac.cn>). In Taiwan, a database of the Herbarium of Academia Sinica, Taipei (HAST) with specimen images has been released (<http://www.hast.biodiv.tw/Announce/newsE.aspx>). These virtual herbaria have facilitated the sharing of information easily among researchers and have augmented traditional botanical research (Oh et al., 2010; Dodd et al., 2016; Shalimov et al., 2019; Aguilar-Cano and Hind, 2020).

Difficulties related to the limitation and restriction of specimen loans and travel to herbaria can be overcome by using information from virtual herbaria. During the COVID-19 (coronavirus disease 2019) pandemic, traveling to foreign herbaria was difficult. Specimen loans, though not prohibited, were not readily available due to higher shipping costs and understaffing issues. An analysis of the morphological variation of the *D. kiusiana* complex, which requires materials from China, Taiwan, Korea, and Japan, could be an excellent case study of the use of collections from various virtual herbaria.

Thus, aiming to provide objective evidence of the

morphological and geographic variations of the *D. kiusiana* complex, we (1) investigated the morphological variations among the members of the complex, (2) evaluated the utility of digitalized herbarium specimens, and (3) clarified the taxonomic delimitation of the *D. kiusiana* complex.

MATERIALS AND METHODS

Herbarium specimens of the *D. kiusiana* complex were examined from CNU, KB, TNS, and TUT (herbaria acronyms according to Thiers, 2022). We also investigated the virtual herbaria of HAST and PE, which provide high-resolution specimen images of Taiwanese and Chinese collections, respectively. From these materials, we selected 81 specimens that were morphologically complete and suitable for morphometric measurements (Appendix 1). For an evaluation of the morphological variation within and among the populations, we included multiple specimens. Thirty-three specimens for *D. kiusiana* var. *kiusiana* were selected from accessions from Geojedo Island (17 specimens), Bigeumdo Island (6), and Japan (10). Each of the Japanese specimens represented a different population, but in this study, we regarded them as one large population. The Korean populations are all restricted to offshore islands and are isolated from the Japanese population. Thus, we included as many specimens from the islands as possible in the morphometric analysis to evaluate the range of morphological variation in Korea. Thirty-one specimens for *D. kiusiana* var. *atrocaulis* (14 from mainland China and 17 from Taiwan) were included. For *D. jejuensis*, 17 specimens were investigated. Each specimen was treated as an

operational taxonomic unit (OTU) for the morphometric analysis.

Twelve morphological characters (one qualitative and 11 quantitative) (Fig. 2, Table 1) were analyzed for each specimen that had fully mature leaves and flowers. As the leaf shape has been used to distinguish each taxon of the *D. kiusiana* complex (Lee et al., 2013), seven quantitative traits of shape parameters (C1–C7) (Table 1) were analyzed. Traits representing floral size (C8, C9, C11, and C12) were also included. Pubescence of the outer surface of the hypanthium was treated as a qualitative trait and scored as 0 (glabrous) or 1 (pubescent). The density of the trichome was not considered because there was no gap between

Table 1. Morphological characters used in the morphometric analysis.

Character and definition
C1 Leaf blade length
C2 Maximum leaf width
C3 Leaf width at the one-quarter point of the leaf blade length
C4 Distance from the leaf base to the point of maximum leaf width
C5 Ratio of C4 and C1
C6 Ratio of the leaf width at the three-quarters point of the leaf blade length and C3
C7 Leaf apex angle
C8 Hypanthium length
C9 Hypanthium width
C10 Pubescence on the outer surface of the hypanthium
C11 Sepal length
C12 Sepal width

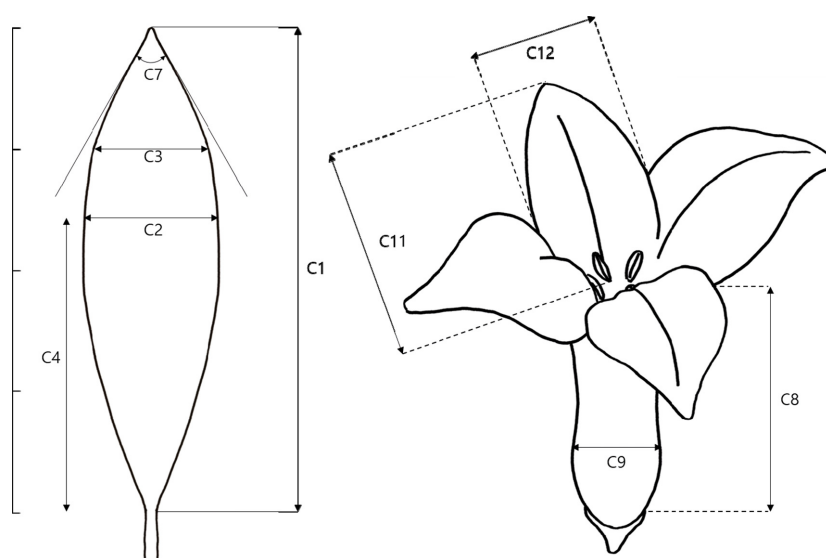


Fig. 2. Diagram showing the morphological characters measured in the morphometric analysis of the *D. kiusiana* complex. Numbers correspond to the character numbers provided in Table 1.

dense pubescence and sparse pubescence.

The image analysis program ImageJ, which is freely downloadable from the ImageJ website (<https://imagej.nih.gov/ij/>), was used to measure the characters from the specimen images. The measurement unit was calibrated in the metric system with the scale provided in each image. To make the measurements consistent, specimens of CNU, KB, TNS, and TUT were digitized on an actual scale before the morphometric measurements.

A data matrix which consists of 81 OTU x 12 characters was constructed and used in the univariate and multivariate analyses (Appendix 2). In the univariate analysis, the range of variation and the mean of eleven quantitative characters were calculated for three groups in var. *kiusiana* (Geojedo Island, Bigeumdo Island, and Japan) as well as var. *atrocaulis* and *D. jejudoensis*. All statistical analyses including the principal component analysis (PCA) were conducted using the IBM SPSS program version 25 (IBM Corp., Armonk, NY, USA).

RESULTS

The variation patterns of the morphological characters

measured here are shown in Fig. 3, and the statistics of the traits are provided in Table 2. In general, the quantitative characters show a wide range of variation within populations or geographic regions (Fig. 3; Table 2). It is difficult to find gaps by which to recognize separate species or varieties (Fig. 3; Table 2). Characters that may represent the leaf shape (C1–C7; see Table 1 for definitions of character abbreviations) also show a range of variations overlapping across taxa (Fig. 3). When the mean values were considered, a few characters exhibited differences among populations or taxa. The mean of C3 in Geojedo is slightly larger than those in other populations. The mean of the angle of the leaf apex (C7) in Geojedo was largest among the five populations, and that of var. *atrocaulis* was smallest, though wide ranges of variation were found within the populations. The hypanthium length (C8) of *D. jejudoensis* is longer than those in *D. kiusiana* (Fig. 3). Likewise, the sepal length (C11) of *D. jejudoensis* is longer than those in *D. kiusiana* (Fig. 3). The length of the hypanthium tends to correlate with the sepal length and width (Fig. 3, Table 2). However, these characters (C8, C11, and C12) varied considerably within *D. kiusiana*. The mean of the Japanese population (var. *kiusiana*) was lowest,

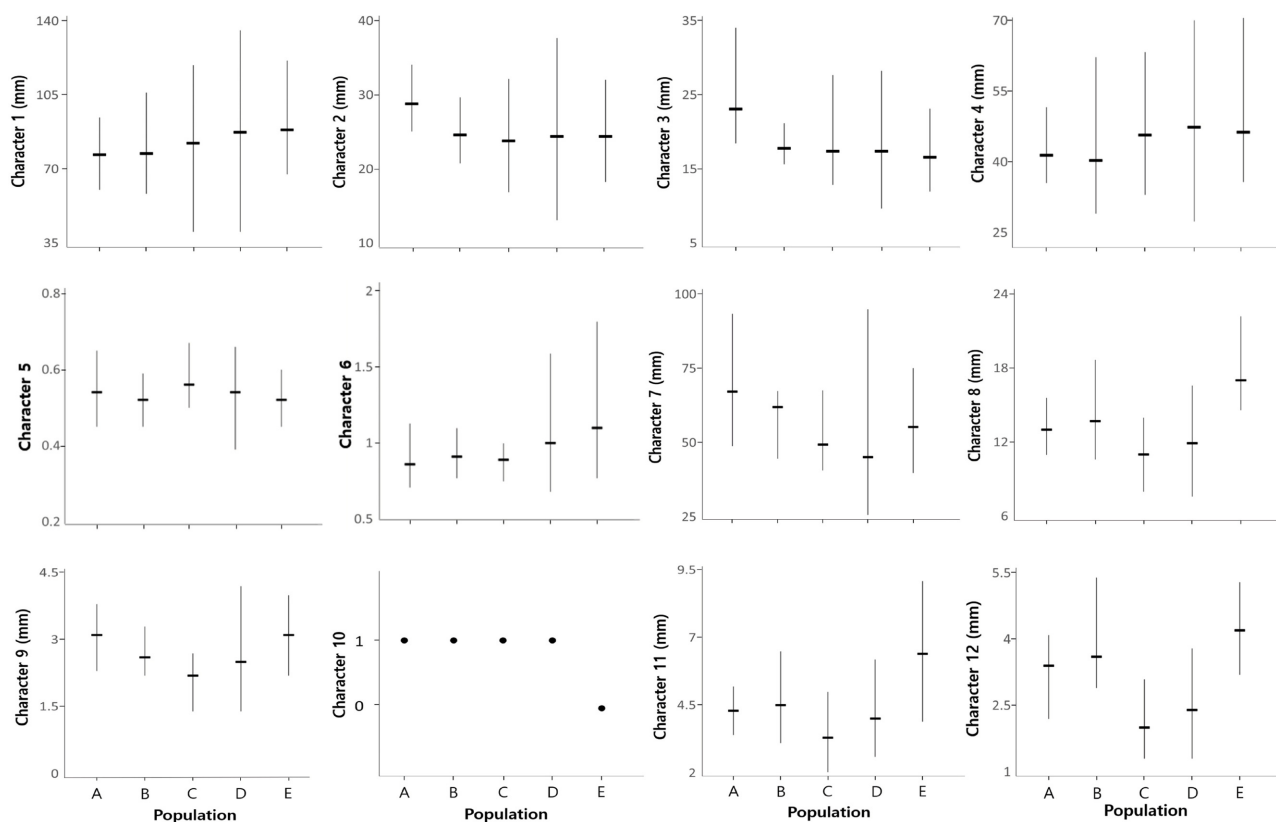


Fig. 3. Maximum, minimum, and mean values for the characters analyzed in this study. Horizontal glyphs represent the mean. Character numbers correspond to those in Table 1. **A–C:** *D. kiusiana* var. *kiusiana* (A=Geojedo, B=Bigeumdo, C=Japan); **D.** *D. kiusiana* var. *atrocaulis* (China and Taiwan); **E:** *D. jejudoensis* (Jeju).

Table 2. Comparison of the quantitative characters of *D. kiusiana* and *D. jejudoensis*

Character	<i>D. kiusiana</i>				<i>D. jejudoensis</i>
	var. <i>kiusiana</i>			var. <i>atrocaulis</i>	
	Geojedo	Biguemdo	Japan		
C1 (cm)	6.0–(7.7)–9.5	5.8–(7.7)–10.6	4.0–(8.2)–11.9	4.0–(8.7)–13.6	6.8–(8.9)–12.2
C2 (cm)	2.5–(2.9)–3.4	2.1–(2.5)–3.0	1.7–(2.4)–3.2	1.3–(2.4)–3.8	1.8–(2.4)–3.2
C3 (cm)	1.9–(2.3)–3.0	1.6–(1.8)–2.1	1.3–(1.7)–2.8	1.0–(1.7)–2.8	1.2–(1.7)–2.3
C4 (cm)	3.6–(4.1)–5.2	2.9–(4.0)–6.2	3.3–(4.6)–6.3	2.7–(4.7)–7.0	3.6–(4.6)–7.1
C5	0.5–(0.5)–0.7	0.5–(0.5)–0.6	0.5–(0.6)–0.7	0.4–(0.5)–0.7	0.5–(0.5)–0.6
C6	0.71–(0.86)–1.13	0.77–(0.91)–1.1	0.75–(0.89)–1	0.68–(1.0)–1.59	0.77–(1.1)–1.8
C7 (degree)	48.9–(67.2)–93.5	44.7–(62.0)–67.5	40.8–(49.3)–67.7	25.7–(45.1)–95.0	39.8–(55.3)–75.2
C8 (mm)	11.0–(13.0)–15.6	10.6–(13.7)–18.7	8.0–(11.0)–14.0	7.6–(11.9)–16.6	14.6–(17.0)–22.2
C9 (mm)	2.3–(3.1)–3.8	2.2–(2.6)–3.3	1.4–(2.2)–2.7	1.4–(2.5)–4.2	2.2–(3.1)–4.0
C11 (mm)	3.4–(4.3)–5.2	3.1–(4.5)–6.5	2.0–(3.3)–5.0	2.6–(4.0)–6.2	3.9–(6.4)–9.1
C12 (mm)	2.2–(3.4)–4.1	2.9–(3.6)–5.4	1.3–(2.0)–3.1	1.3–(2.4)–3.8	3.2–(4.2)–5.3

Minimum and maximum values with the mean in parenthesis are provided. Character numbers correspond to those in Table 1.

Table 3. Loading of the first three principal components for 12 characters from the analysis of 81 individuals of *D. kiusiana* and *D. jejudoensis*

Character	Components		
	1	2	3
C1	0.111	0.039	0.960
C2	0.117	0.699	0.546
C3	0.017	0.888	0.356
C4	0.001	0.238	0.921
C5	–0.194	0.417	0.102
C6	0.312	–0.729	–0.23
C7	0.264	0.756	–0.426
C8	0.926	–0.142	–0.006
C9	0.705	0.103	–0.022
C10	–0.745	0.227	–0.081
C11	0.878	–0.146	0.196
C12	0.893	0.041	–0.059
Eigenvalue	3.709	2.716	2.437
Cumulative % of eigenvalue	30.9	53.5	73.8

followed by the mean of var. *atrocaulis*. The qualitative character (C10) was the only trait that distinguished *D. jejudoensis* from *D. kiusiana*.

The PCA results revealed that the first three principal components (PC1, PC2, and PC3) account for 73.8% of the total variation. PC1, PC2, and PC3 explain 30.9%, 22.6%,

and 20.3% of the variation, respectively (Table 3). Characters heavily loaded in PC1 were all floral traits (C8–C12) and those heavily loaded in PC2 and PC3 were leaf shape parameters (Table 3). Traits corresponding to the leaf width (C2, C3, and C6) and leaf apex angle (C7) strongly contributed to PC2, while characters of the leaf length (C1) and distance from the base to the point of maximum width (C4) were loaded heavily in PC3 (Table 3).

A scatter plot of the first two principal components showed that most individuals of *D. jejudoensis* were located on the positive axis of PC1, weakly separated from most individuals of *D. kiusiana* (Fig. 4). This trend is consistent with the univariate analysis (Fig. 3, Table 2), in which the hypanthium and sepals of *D. jejudoensis* are larger, on average, than those of *D. kiusiana*. However, two plants from Biguemdo were nested within a group that consisted of individuals of *D. jejudoensis*. Three plants from Geojedo and one from China overlap in the *D. jejudoensis* group. The Japanese individuals tend to be on the negative axis, consistent with the results of the univariate analysis (Fig. 3; Table 2), in which the means of the characters representing the flower size were small (C8, C9, C11, and C12). There were no significant patterns between the Chinese and Taiwanese plants, which showed a wide range of variation across the PC1 axis.

PC2 did not place the OTUs into any taxonomic group or any discernible geographic grouping. The individuals of Geojedo tend to be located on the positive axis, while those of Jeju (*D. jejudoensis*) are on the negative axis (Fig. 4).

A scatter plot of PC1 and PC3 (Fig. 5) showed patterns

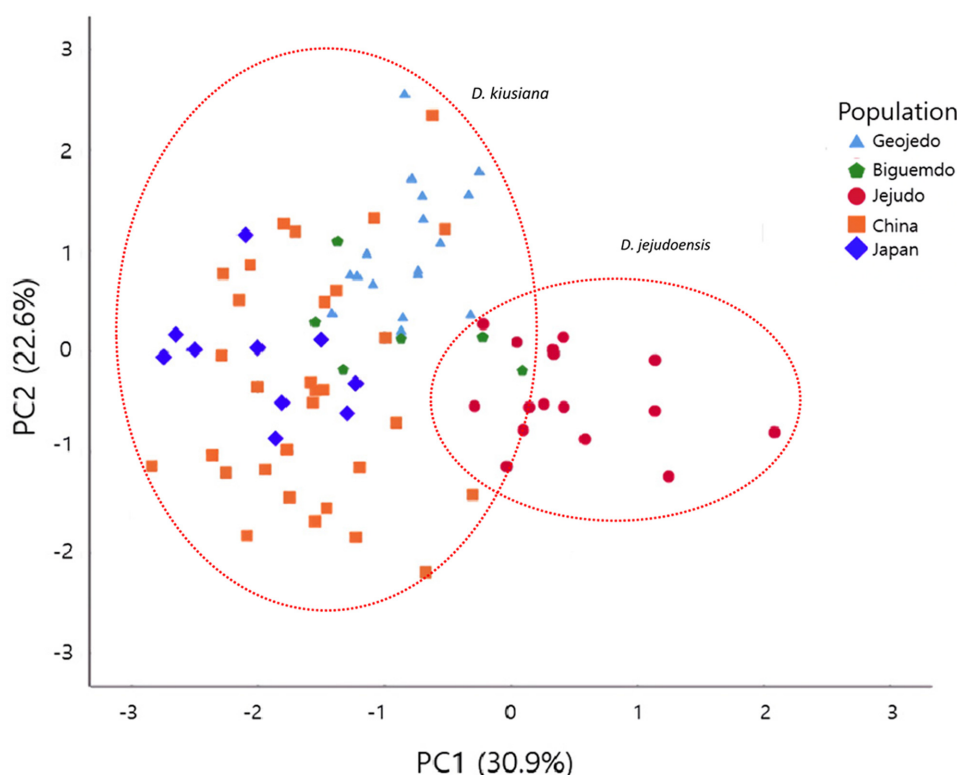


Fig. 4. Scatter plot of the first two principal components in the principal component analysis from the 81 specimens of the *D. kiusiana* complex using 12 morphological characters (see Table 1). Some individuals are hidden due to identical values.

similar to the plot of PC1 and PC2 (Fig. 3). Individuals of *D. kiusiana* and *D. jejudoensis* show a wide range of variation along PC3, resulting in no clear groupings. PC2 and PC3 are highly correlated in terms of their leaf characters (C1–C4, C6, and C7), as stated previously, and the leaf characters (size and shape) may not be useful taxonomically in the *D. kiusiana* complex.

DISCUSSION

Daphne jejudoensis is a recently recognized species from Jeju based on elliptic leaves with an acuminate apex, a glabrous hypanthium, and a longer hypanthium and sepals (Lee et al., 2013). PCA results here show that the OTUs of *D. jejudoensis* tend to be separate from those of *D. kiusiana* by PC1 (Figs. 4, 5), which is correlated with the size of the hypanthium (C8, C9) and sepals (C11, C12), as well as the pubescence of the hypanthium (C10). However, *D. kiusiana* and *D. jejudoensis* are not clearly separable. Six individuals of *D. kiusiana* from Biguemdo, Geogedo, and China overlap with *D. jejudoensis* (Figs. 4, 5). This pattern suggests that the floral characteristics found in those individuals of *D. kiusiana* may be similar to those in *D. jejudoensis*. Some plants of *D. kiusiana* var. *kiusiana* on Biguemdo, such as accession

numbers 7878 and 7879 (Appendix 2), show relatively long hypanthia and sepals (Fig. 3), not clearly distinguished from *D. jejudoensis*. All of the materials of *D. jejudoensis* included in our morphometric analysis show a glabrous hypanthium (Fig. 3). However, individuals with a pubescent hypanthium were occasionally found in the investigation of the specimens in *D. jejudoensis*, suggesting that this qualitative characteristic may be incompletely fixed within the Jeju population.

Leaf shape is not an accurate indicator to support *D. jejudoensis*. Variables that represent the leaf shape (C3–C6) and apex (C7) are loaded in PC2, which does not have the resolution to separate *D. jejudoensis* from *D. kiusiana*. Our examination of specimens indicates that the leaf shape is highly variable in the *D. kiusiana* complex, in which elliptic, elliptic-oblong, lanceolate, and oblanceolate leaves are found. It appears that the leaves of Geojedo and Japan are oblanceolate, with the widest point located above the middle of the leaf blade (Ohwi, 1965; Murata, 1999). The character C5 quantifies the relative position of the widest point of a leaf blade (Fig. 2, Table 1). Our measurements indicate that the means and ranges of the Geojedo and Japan populations are similar to those of other populations (Fig. 2; Table 2). Plants on Geojedo tend to have an acute apex, but this varies within the population, and specimens of other populations

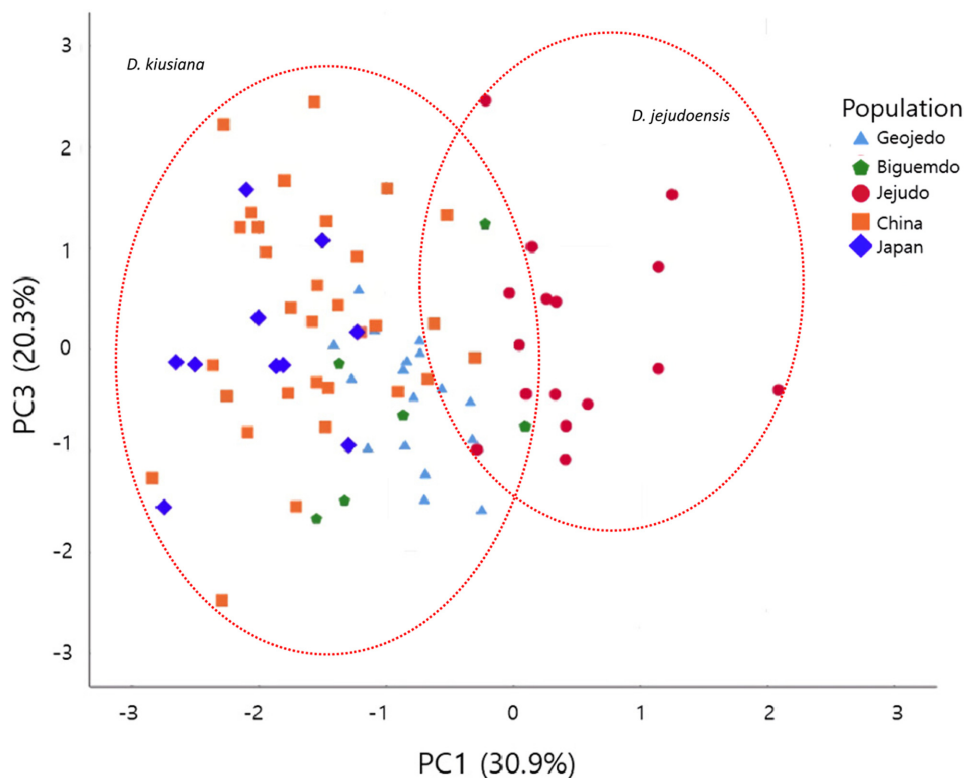


Fig. 5. Scatter plot of principal component 1 and principal component 2 in the principal component analysis from the 81 specimens of the *D. kiusiana* complex using 12 morphological characters (see Table 1). Some individuals are hidden due to identical values.

show a wide range of variation from an acute to an acuminate apex.

Lee et al. (2013) also highlighted that *D. jejudoensis* is distributed in forests in the interior areas of Jejudo, whereas *D. kiusiana* occurs in the coastal region. This may be valid when only the specimens of Korea are considered. As plants in Japan, China, and Taiwan are distributed in forests in various regions at low elevations based on information on the specimen labels examined in this study and from the literature (Ohwi, 1965; Wang et al., 2007), there is no differentiated habitat preference among the taxa.

Daphne kiusiana var. *atrocaulis* was established as a new variety based on a collection in eastern Sichuan, China, and is distinguished from var. *kiusiana* by having caducous bracts, thicker leaves, and dark purple branchlets (Rehder, 1916). Since then, plants distributed in China and Taiwan have been classified in var. *atrocaulis* (Li, 1977; Wang et al., 2007). However, our examination of specimens of the *D. kiusiana* complex shows that these characteristics do not have diagnostic value. Bracts of var. *kiusiana* are caducous, as in var. *atrocaulis*. The color of the branchlets also varies, ranging from light brown to dark purple in specimens of the *D. kiusiana* complex. The holotype of var. *atrocaulis* (Henry 7119 housed in GH) is a sterile material and has persistent leaves

developed in previous years. The material shows that the youngest branchlet is darker in color tone than branches developed in previous years, suggesting that the type material may have had a dark purple branchlet. The thickness of the leaves is a complex character to be determined in herbarium specimens.

Wang et al. (2007) noted that var. *kiusiana* differs from var. *atrocaulis* by oblanceolate leaf blades and smaller flowers with the hypanthium 7–8 mm long. Our morphometric analysis shows that the hypanthium of var. *atrocaulis* is not significantly longer than that of var. *kiusiana* (Fig. 3, C8). As discussed previously, the leaf shape in var. *kiusiana* is variable.

Thus, our morphometric analysis suggests that recognition of var. *atrocaulis* is not supported. Recognition of *D. jejudoensis* as a distinct species needs further investigations using molecular data. Our morphometric analysis, which shows that *D. jejudoensis* is not clearly separable (Figs. 3–5), suggests the possibility of the recognition of *D. jejudoensis* as a variety of *D. kiusiana*. The *D. kiusiana* complex is distributed in lowlands of warm temperate regions of eastern Asia, referring to areas that have been connected and disconnected during the last glaciation and deglaciation period over the past 20,000 years. It is likely that current populations of the *D. kiusiana* complex are fragmented and isolated across

the region. The flowers of *Daphne*, including those of the *D. kiusiana* complex, have a nectary disk at the base of the carpel, and the fruits when mature are bright red in color, implying that animals may be involved in pollination and dispersal (Oh and Hong, 2015). Further studies are needed to reveal the genetic diversity within and among populations and the relationships and structures of the populations of the *D. kiusiana* complex.

Our morphometric analysis showed that digitized images of herbarium specimens can be useful for morphological analyses (Figs. 3–5). An image analysis program like the one used in this study, ImageJ developed as an open-resource project (<https://imagej.net>), can be a valuable tool for handling digitized herbarium specimens. Traditionally, morphological characters are usually scored based on an examination of actual specimens (Lee and Park, 1994; Lee et al., 2021; Islas-Hernández et al., 2022). In most cases, researchers borrow specimens from herbaria to examine and measure the characters or visit herbaria to obtain morphological data. Recently, digital images of herbarium specimens and associated information have become available on herbarium websites (Barkworth and Murrell, 2012). Although limitations exist with regard to the complete replacement of actual specimens, as some characters, particularly those of anatomical features, are difficult to examine, the use of a virtual herbarium provides an additional method for investigating more diverse specimens and taxa.

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CONFLICTS OF INTEREST

Sang-Hun OH, the Editor-in-Chief of the Korean Journal of Plant Taxonomy, was not involved in the editorial evaluation or decision to publish this article. The authors have declared no conflicts of interest.

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Appendix 1. Specimens of the *Daphne kiusiana* complex analyzed for the morphometric analysis.

***D. jejuensis* M. Kim:** KOREA. Jeju-do: Jeju-si, Hangyeong-myeon, Cheongsu-ri, Cheongsugotjawal, 13 Feb 2020, *S. H. Oh & H. J. Suh* 7843, 7844, 7845, 7846, 7847, 7848, 7849, 7850, 7851 (TUT); Jeju-si, Hangyeong-myeon, Cheongsu-ri, Cheongsugotjawal, 30 Mar 2020, *S. H. Oh* 7883 (TUT); Jeju-si, Hangyeong-myeon, Jeoji-ri, Jeojigotjawal, 13 Feb 2020, *S. H. Oh & H. J. Suh* 7852, 7853, 7854, 7855 (TUT); Jeju-si, Hangyeong-myeon, Jeoji-ri, Jeojigotjawal, 13 Feb 2020, *D. H. Lee* 7882 (TUT); Jeju-si, Hangyeong-myeon, Cheongsu-ri, Sanyanggotjawal, 27 Mar 2014, *G. H. Nam et al.* 467671 (KB); Jeju-si, Jocheon-eup, Seonheul-ri, Seonheulgotjawal, 25 Mar 2013, *M. H. Kwak et al.* 428151 (KB); Jeju-si, Jocheon-eup, Seonheul-ri, Seonheulgotjawal, 2 Mar 2018, *G. P. Song et al.* 718968 (KB).

***D. kiusiana* Miq. var. *kiusiana*:** KOREA. Gyeongsangnam-do: Geoje-si, Dapo-ri, 20 Feb 2020, *S. H. Oh et al.* 7862, 7863, 7864, 7865, 7866, 7867, 7868, 7869, 7870, 7871 (TUT); Geoje-si, Geogu-ri, 20 Feb 2020, *S. H. Oh et al.* 7856, 7857, 7858, 7859, 7860, 7861 (TUT). Jeollanam-do: Sinan-gun, Bigeumdo, 14 Mar 2020, *D. H. Lee*, 7875, 7876, 7877, 7878, 7879, 7880 (TUT).

JAPAN. Honshu: Chiba Pref.: Awapgun, Amatsu, Todaichiba, 23 Mar 1968, *S. Uehara* 223542 (TNS); Koutou, Kiyosumi, 27 Mar 1963, *T. Wakana* 155810 (TNS); 27 Feb 1966, *H. Georges* 996574 (TNS). Hyogo Pref.: Tanba-gun, Sasagamine, 26 Apr 1936, *S. Hosomi* 56748 (TNS). Mie Pref.: Watarai-gun, Kajiya-dani Valley, 4 Apr 1996, *Fujii et al.* 678564 (TNS). Tottori Pref.: Iwami-gun, 5 Apr 1975, *K. Iwatsuki et al.* 335713 (TNS). Yamaguchi Pref.: Nagato, Abu-gun, Kasekajaka, 18 Mar 1919, *J. Nikai* 47295 (TNS). Shikoku: Kagawa Pref.: Shodoshima, Kankakei, 28 Mar 1962, *N. Soromu* 19573 (TNS). Kyushu: Miyazaki Pref.: Kobayshi, 8 Jan 2019, *J. H. Lee*. 8238 (CNU); Noveokashi, 9 Jan 2019, *J. H. Lee*. 8239 (CNU).

***D. kiusiana* var. *atrocaulis* (Rehder) F. Maek.:** CHINA. Fujian: Fuzhou, 1943, *L. Yong* 5475 (KW 02135789); Fuzhou, Nanping, 22 Nov 1981, *K. W. Heo* 1610 (PE 1270226). Guangdong: 11 Dec 1957, *J. Huang* 44396 (PE 724105); 2 Dec 1978, *H. F. Chow* 13764-1 (KW 227068); Lecheng, 22 Dec 1936, *L. Yao* 2185 (KW 515031). Guangxi: Zhuangzu, 24 Nov 1978, *Chow* 358709 (PE). Hunnan: 30 Jan 1996, without collector's name (PE 1469159); Zhanguha, 10 Nov 1975, *Manchowae* 1166492 (PE). Zhejiang: 15 Oct 1927, *Chun* 02135791, 227054, 227055 (KW); Hangzhou 18 Mar 1957, *Zhang* 0552192 (PE); Hangzhou 25 Feb 1963, *Yang* 0945737 (PE). Without specific locality, 11 Feb 1993, *Lin et al.* 28150 (HAST).

TAIWAN. Chilan: 7 Jan 1996, *Lu* 59337 (HAST). Hualien: 29 Nov 2008, *Lu* 123919 (HAST). Ilan: Mingchih, 30 Jan 1996, *Lu* 69614 (HAST). Nantou: 15 Jan 1993, *Chen* 24227 (HAST); 23 Feb 2002, *Wang & Lin* 2345927 (PE). Shihlu: 19 Feb 2002, *Huang* 90323 (HAST); 21 Feb 2002, *Huang* 89200 (HAST). Taipei: 22 Feb 1987, *Ryu* 16443 (HAST); 7 Mar 1996, *Kuo* 70168 (HAST); 15 Mar 1997, *Chiang* 69995 (HAST); Mt. Yangming, 9 Feb 1987, *Peng et al.* 8845 (HAST); 24 Feb 1997, *Kuo* 70143 (HAST); 24 Feb 2005, *Huang* 112788 (HAST). Yaoyuan: 4 Jan 1996, *Wang* 64360 (HAST). Without specific locality, 15 Jun 2015, *Liang* 245233, 2455343, 2455344 (HAST).

Appendix 2. Data matrix used in the Principal Component Analysis.

Accession No.	Population	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12
7843	Korea, Jejudo	9.5	2.3	1.4	4.7	0.5	1.1	30.4	16.1	2.4	0	6.0	4.0
7844	Korea, Jejudo	7.0	2.4	1.7	3.6	0.5	1.0	70.0	16.6	3.0	0	5.5	4.1
7845	Korea, Jejudo	9.2	2.7	1.9	5.2	0.6	1.1	49.2	17.1	3.2	0	5.7	3.8
7846	Korea, Jejudo	6.8	1.8	1.2	3.9	0.6	1.0	39.7	15.2	3.2	0	3.9	3.6
7847	Korea, Jejudo	12.1	3.2	2.3	7.1	0.6	0.8	38.0	14.6	2.6	0	6.5	3.4
7848	Korea, Jejudo	9.8	2.3	1.6	5.8	0.6	1.0	38.0	16.2	3.3	0	7.0	3.2
7849	Korea, Jejudo	10.6	2.9	2.1	4.8	0.5	0.9	42.8	19.1	3.0	0	7.3	5.2
7850	Korea, Jejudo	7.7	2.3	1.6	3.6	0.5	1.1	40.1	15.4	2.9	0	6.2	3.5
7851	Korea, Jejudo	7.3	2.0	1.4	3.9	0.5	1.1	35.4	17.7	2.0	0	5.9	5.3
7852	Korea, Jejudo	12.2	3.1	1.4	5.7	0.5	1.8	33.7	19.2	3.7	0	6.6	4.1
7853	Korea, Jejudo	7.9	2.2	1.5	4.7	0.6	1.0	43.1	16.0	2.8	0	6.0	4.5
7854	Korea, Jejudo	8.5	2.2	1.3	4.1	0.5	1.3	37.8	22.2	4.0	0	9.1	5.2
718968	Korea, Jejudo	8.9	2.7	1.9	4.6	0.5	1.1	44.5	16.9	2.7	0	6.5	3.8
428151	Korea, Jejudo	7.3	2.4	1.5	3.6	0.5	1.3	46.5	16.0	4.0	0	5.8	4.1
7882	Korea, Jejudo	8.2	2.3	1.9	4.1	0.5	1.3	52.0	16.8	4.0	0	7.0	5.0
7883	Korea, Jejudo	11.1	2.7	1.5	5.1	0.5	1.2	31.3	16.1	1.7	0	5.7	3.1
7856	Korea, Geojedo	8.6	2.3	1.9	4.7	0.5	0.8	48.2	16.2	2.2	0	6.8	3.8
7857	Korea, Geojedo	7.4	2.8	2.5	4.8	0.7	0.7	68.8	13.7	2.9	1	4.7	3.3
7858	Korea, Geojedo	7.6	2.9	2.4	3.9	0.5	0.8	58.7	11.8	2.3	1	4.5	3.1
7859	Korea, Geojedo	6.9	2.6	2.1	3.7	0.5	0.7	71.0	13.4	3.1	1	4.4	3.4
7860	Korea, Geojedo	9.4	3.0	2.4	4.3	0.5	0.8	59.5	12.4	2.5	1	4.7	2.7
7861	Korea, Geojedo	8.2	2.9	2.1	4.8	0.6	0.9	53.7	12.5	2.9	1	4.9	3.8
7862	Korea, Geojedo	8.2	2.8	2.1	3.9	0.5	1.0	54.8	12.9	2.5	1	4.9	3.6
7863	Korea, Geojedo	8.1	3.1	2.3	4.2	0.5	0.9	58.4	12.6	3.6	1	3.9	3.8
7864	Korea, Geojedo	9.3	3.2	2.5	4.8	0.5	0.9	51.7	11.5	2.9	1	3.7	3.2
7865	Korea, Geojedo	8.4	3.1	2.3	4.2	0.5	1.1	51.2	11.0	2.6	1	3.4	2.6
7866	Korea, Geojedo	7.5	2.8	2.5	4.6	0.6	0.8	72.0	14.5	3.8	1	4.5	3.7
7867	Korea, Geojedo	6.0	2.8	2.3	3.6	0.6	0.9	89.1	13.9	3.4	1	5.2	3.6
7868	Korea, Geojedo	6.3	2.7	2.2	3.6	0.6	0.7	73.6	12.7	3.4	1	3.6	3.8
7868	Korea, Geojedo	6.8	3.0	2.4	3.2	0.5	0.8	58.0	12.9	2.9	1	3.9	2.2
7869	Korea, Geojedo	8.4	3.1	2.4	4.3	0.5	0.9	48.1	15.6	3.4	1	3.7	3.0
7870	Korea, Geojedo	6.4	2.5	1.8	3.6	0.6	0.9	55.5	13.4	3.1	1	4.1	3.7
7871	Korea, Geojedo	8.6	3.4	3.0	5.2	0.6	0.7	71.9	11.2	3.0	1	3.9	3.5
7881	Korea, Geojedo	7.0	2.4	1.9	3.7	0.5	0.9	55.2	15.4	3.6	1	4.5	4.1
7875	Korea, Biguemdo	5.8	2.1	1.6	3.0	0.5	0.8	62.9	12.3	2.2	1	3.1	2.9
7876	Korea, Biguemdo	7.7	2.7	1.9	3.6	0.5	1.0	55.4	13.8	2.4	1	4.7	3.2
7877	Korea, Biguemdo	6.1	2.3	1.6	2.9	0.5	1.1	53.6	12.6	2.3	1	3.7	2.6
7878	Korea, Biguemdo	8.2	2.2	1.6	3.7	0.5	0.9	44.0	18.7	2.2	1	5.5	5.4
7879	Korea, Biguemdo	10.6	2.5	1.9	6.2	0.6	0.8	38.9	14.2	3.3	1	6.5	4.6
7880	Korea, Biguemdo	8.1	3.0	2.1	4.7	0.6	0.8	63.1	10.6	2.9	1	3.3	3.2

Table 2. Continued

Accession No.	Population	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12
8238	Japan	7.9	2.3	1.6	4.1	0.5	1.0	42.2	11.9	2.7	1	3.0	2.0
8239	Japan	8.4	2.3	1.6	4.7	0.6	0.9	39.3	14.0	2.5	1	5.0	2.6
335713	Japan	11.9	3.2	2.8	6.3	0.5	0.8	61.1	10.7	2.2	1	2.1	1.5
56748	Japan	8.0	2.5	2.0	4.4	0.5	0.9	57.5	9.1	1.4	1	2.5	1.3
996574	Japan	10.1	3.0	2.0	5.6	0.6	1.0	49.9	12.5	2.7	1	3.7	2.2
678564	Japan	8.0	2.0	1.3	4.3	0.5	1.0	36.2	11.9	2.1	1	3.9	2.1
155810	Japan	6.3	1.8	1.3	3.6	0.6	0.9	49.5	12.7	2.4	1	5.0	3.1
223542	Japan	9.1	2.8	1.9	4.5	0.5	0.9	53.0	8.8	1.9	1	3.8	2.4
370892	Japan	5.3	1.7	1.3	3.3	0.6	0.7	48.4	8.0	2.2	1	2.0	1.3
47295	Japan	7.3	2.2	1.6	4.9	0.7	0.9	46.0	10.2	1.8	1	2.6	1.8
90323	Taiwan	11.5	3.1	2.8	7.0	0.6	0.7	52.3	9.7	1.7	1	3.9	1.7
89200	Taiwan	7.1	1.8	1.3	2.7	0.4	1.3	35.4	10.3	1.9	1	3.4	1.9
112788	Taiwan	9.2	2.8	2.3	5.1	0.6	0.9	58.8	12.9	2.7	1	4.3	1.9
59337	Taiwan	8.9	2.6	1.7	5.9	0.7	1.0	28.1	9.9	2.0	1	4.6	2.5
69614	Taiwan	9.9	1.9	1.1	5.4	0.5	1.4	25.8	13.4	3.3	1	3.9	2.9
69995	Taiwan	9.7	2.7	2.3	5.9	0.6	0.7	41.1	8.4	2.7	1	3.7	1.9
123919	Taiwan	6.3	1.3	1.0	3.2	0.5	0.8	43.7	7.6	1.4	1	2.8	1.6
8845	Taiwan	9.1	3.1	2.8	5.7	0.6	0.6	82.6	12.8	2.9	1	6.0	3.0
16443	Taiwan	4.0	1.7	1.3	2.3	0.6	1.0	67.7	11.1	2.0	1	2.0	1.3
24227	Taiwan	9.8	2.4	1.8	4.9	0.5	0.9	41.2	12.1	2.6	1	4.8	1.9
64360	Taiwan	7.6	1.7	1.2	4.2	0.6	1.0	39.9	12.0	2.7	1	3.5	2.1
70143	Taiwan	6.6	2.6	2.0	3.4	0.5	0.9	100.4	10.7	2.5	1	2.6	1.6
70168	Taiwan	10.7	3.5	2.8	6.5	0.6	0.8	52.1	11.6	3.0	1	2.6	1.6
2455343	Taiwan	7.7	2.1	1.0	3.4	0.4	1.6	27.4	14.7	3.3	1	4.9	3.2
2455344	Taiwan	8.1	1.8	1.3	4.7	0.6	1.1	29.5	14.2	2.6	1	5.0	3.1
2455233	Taiwan	7.8	1.7	1.0	4.5	0.6	1.2	31.0	16.6	4.2	1	6.2	2.7
28150	China	8.7	3.1	2.5	5.0	0.6	0.7	61.8	14.4	2.1	1	4.0	3.5
0945737	China	8.9	2.2	1.2	4.6	0.5	1.3	33.2	12.4	2.4	1	3.5	2.2
1469159	China	10.2	3.8	2.8	5.7	0.6	0.9	52.5	15.0	3.4	1	5.0	3.0
811335	China	10.8	3.0	2.4	5.9	0.5	1.0	57.4	13.2	2.2	1	3.7	2.4
0552192	China	8.7	1.7	1.2	3.6	0.4	1.2	39.5	11.1	2.5	1	3.9	2.8
1270226	China	7.8	2.0	1.1	4.3	0.5	0.9	35.9	10.3	2.0	1	3.1	1.7
515031	China	11.4	3.2	2.2	5.6	0.5	0.8	34.9	12.3	3.2	1	4.7	3.3
116492	China	9.1	2.6	1.5	5.2	0.6	1.3	28.7	9.8	2.1	1	3.8	2.5
02135789	China	8.1	2.7	1.8	4.6	0.6	1.0	37.6	13.2	2.3	1	3.7	2.6
227054	China	7.3	2.0	1.4	4.3	0.6	1.2	46.7	12.2	2.9	1	5.1	3.8
227055	China	7.6	1.7	1.0	4.1	0.5	1.3	40.7	13.6	2.6	1	4.1	2.2
02135791	China	6.6	2.7	1.7	3.3	0.5	1.3	51.4	11.1	2.6	1	3.5	2.4
358709	China	7.5	1.9	1.0	3.7	0.5	0.8	30.5	11.0	2.1	1	3.2	1.9
227068	China	13.6	3.3	2.0	5.8	0.4	0.8	28.1	12.1	2.2	1	4.5	2.5
2345927	China	10.7	3.0	2.3	6.5	0.6	0.8	61.6	8.4	2.0	1	3.5	2.4