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OBSERVATIONS ON THE FLORAL
MORPHOLOGY OF *SASSAFRAS*
RANDAIENSE (LAURACEAE)¹

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ABSTRACT

The floral morphology of *Sassafras randaiense* (Hayata) Rehder (Lauraceae), a rare species endemic to Taiwan, has never been well documented. Consequently, much confusion exists in taxonomic literature regarding its flower structure and reproductive biology. To clarify these matters, we observed 20 flowering individuals of *S. randaiense* in their native habitats in the spring of 2007. The inflorescences of *S. randaiense* are highly reduced panicles to botryoid cymes, with up to 10 such inflorescences clustered subterminally to form an umbel of panicles and/or cymes. Its flowers are bisexual, and its third-whorl anthers are extrorse, structured as a typical hermaphroditic flower of Lauraceae. Our observations also revealed that its flowers are protogynous and flowers in a reproductive shoot alternate their sexual phase synchronously, suggesting the sexual system of synchronous dichogamy. The temporal dioecy imposed by this sexual system may explain why *S. randaiense* has been variously described as a dioecious, androdioecious, or polygamous species in the past.

Key words: Floral morphology, Lauraceae, plant sexual system, *Sassafras*, Taiwan, taxonomy.

Sassafras J. Presl (Lauraceae), comprising *S. albidum* (Nutt.) Nees in eastern North America, *S. tzumu* (Hemsl.) Hemsl. in mainland China, and *S. randaiense* (Hayata) Rehder in Taiwan (Rehder, 1920), is a classic example of eastern North American and East Asian disjunct distribution (Wen, 1999; Nie et al., 2007). This small genus is well circumscribed by a combination of features: deeply fissured bark, deciduous habit, late winter to early spring blossom

before the unfolding of young leaves, and leaves that are often trilobed when young (Rehder, 1920; Keng, 1953). Anatomically, *Sassafras* is the only genus in Lauraceae with typical ring-porous wood (van der Werff & Richter, 1996). The flower structure and sexuality of the three species, however, exhibit considerable variation that in the past was exaggerated as of generic importance, causing much taxonomic controversy (Rehder, 1920; Keng, 1953).

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Nevertheless, the monophyly of the three *Sassafras* species has been confirmed by a recent molecular phylogenetic study (Nie et al., 2007). Results from Nie et al. (2007) also supported the idea that its current intercontinental disjunction reflects a relic status from the Tertiary boreotropical flora (Wolfe, 1975; Denk et al., 2005).

Compared to its North American and mainland Chinese congeners that are commonly found in their native ranges (Rehder, 1920), *Sassafras randaiense* (Taiwan sassafras) is only sparsely found in the mid elevations (900–2500 m) of the island and was ranked as Vulnerable (VU) according to IUCN Red List criteria (Lu & Lin, 1996; IUCN, 2001). In Taiwan, this rare endemic tree species is a prized timber for making high-value furniture (Lu et al., 1982; Wang et al., 1991; Yang et al., 2000) and is well known by the public as the sole host plant of the highly endangered broad-tailed swallowtail butterfly (*Agehana maraho* Shiraki & Sonan) whose caterpillars feed exclusively on the foliage of *S. randaiense* (Hsu et al., 1986). A number of research projects had been devoted to the conservation of this rare and valuable tree in the past several decades (e.g., Hu, 1979; Lu et al., 1982; Chen & Wang, 1985; Wang et al., 1991; Lin, 1992; Yang et al., 2000; Lin et al., 2003; Guan et al., 2006). However, limited by its low and variable annual seed production, deep seed dormancy, and low rate of successful asexual propagation, cultivation of *S. randaiense* remains one of the biggest challenges for forestry in Taiwan.

During the course of preparing the treatment of Lauraceae for *Flora of China*, the second author noticed that, in recent taxonomic literature, *Sassafras randaiense* was almost unanimously described as a polygamous species by local taxonomists (e.g., Liu, 1960; Liu, 1970; Chang, 1976; Liu & Liao, 1980; Ying, 1985; Liao, 1988, 1996). However, Rohwer (1993) suggested that *Sassafras* has apparently hermaphroditic but functionally unisexual flowers. A survey of taxonomic literature also revealed that the inflorescences of *S. randaiense* had been described variously as either racemose (e.g., Hayata, 1911; Rehder, 1920; Kamikoti, 1933; Kanehira, 1936; Liu, 1960; Liu, 1970; Chang, 1976; Li et al., 1982; Lu et al., 1982) or paniculate (e.g., Liu & Liao, 1980; Ying, 1985; Liao, 1988, 1996). Another discrepancy appeared when Kamikoti (1933) described pollen sacs of the third-whorl anthers of *S. randaiense* as open at the sides (latrorse) while introrse stamens had been reported by a majority of the taxonomists (e.g., Hayata, 1911; Kanehira, 1936; Keng, 1953; Liu, 1960; Li, 1963; Chang, 1976; Ying, 1985; Liao, 1988, 1996; Rohwer, 1993). Because inflorescence types and flower structure are important taxonomic characters for Lauraceae, we were prompted to carefully review relevant

taxonomic literature and conduct field observations to clarify the floral morphology of *S. randaiense*.

TAXONOMY OF *SASSAFRAS*

Characterized by distinct staminate and pistillate individuals, the North American *Sassafras albidum* is well documented as a dioecious species (van der Werff, 1997). Its pistillate flowers possess six staminodia surrounding the long-styled gynoecium (van der Werff, 1997). The staminate flowers of *S. albidum* have nine normal stamens in three whorls with a pair of stalked glands attached to the base of each of the third-whorl filaments. All anthers are apparently introrse. The fourth-whorl staminodia and the central gynoecium commonly observed in a typical laurel flower may be lacking in the staminate flowers of the species. For a long time, *S. albidum* was thought to be the only species of the genus *Sassafras* with an isolated distribution in eastern North America (Rehder, 1920).

In 1891, Hemsley described two species, *Litsea laxiflora* Hemsl. and *Lindera tzumu* Hemsl., based on flowering and fruiting materials collected by Augustine Henry from Hubei, China. In 1906, E. H. Wilson, prior to his departure for the third botanical exploration to China, suggested to Hemsley that *Litsea laxiflora* and *Lindera tzumu*, together with materials collected by Wilson himself from China, were conspecific with the North American *Sassafras albidum* (Hemsley, 1907a). Inspired by Wilson's proposition, Hemsley reexamined the materials and published an article in which he transferred *Lindera tzumu* to *Sassafras* (as *S. tzumu* (Hemsl.) Hemsl.) and synonymized *Litsea laxiflora* under *S. tzumu* (Hemsley, 1907a). In this and the companion papers, Hemsley described *S. tzumu* as a dioecious species with very similar male and female flowers (Hemsley, 1907a, b), differing from *S. albidum* by the presence of the staminodia and pistillode in both male and female flowers. The flowers of *S. tzumu*, however, were interpreted as being hermaphroditic by Lecomte (1911, 1913). Emphasizing the difference between dioecy and hermaphrodite, Lecomte (1911) established *Pseudosassafras* Lecomte for the plant occurring in China. A few years later, Wilson's observation on the flower sexuality of *S. tzumu* in China was published in *Plantae Wilsonianae* (Gamble, 1916). In this account, Wilson (in Gamble, 1916: 74) suggested that flowers of *S. tzumu* "though apparently hermaphrodite are functionally unisexual and my observations lead me to believe that they are polygamo-dioecious."

The Taiwan endemic *Sassafras randaiense*, uniquely characterized by 2-celled anthers, was first described as *Lindera randaiensis* Hayata (Hayata, 1911). The type specimen (*S. Kusano s.n.*, 1908, TI);

Fig. 2M, N) was interpreted as a staminate individual of the alleged *Lindera* Thunb. species by Hayata (1911). In the fall of 1918, accompanied by R. Kanehira and S. Sasaki, E. H. Wilson collected this species in Alishan (Arishan) in central Taiwan. According to Kanehira's notes (1920, 1936), Wilson collected both fruiting and male flower materials and immediately recognized the close affinity of *L. randaiensis* with *Sassafras*. Wilson's observation and intuition, however, were not accepted by Hayata, whose taxonomy emphasized the importance of anther cell number for the classification of Lauraceae (Kanehira, 1920, 1936). In 1920, based on Wilson's collections in Taiwan, Rehder revised the circumscription of *Sassafras*. Rehder noted the close resemblance between *L. randaiensis* and *S. tzumu*, differing mainly in the 2- versus 4-loculed anthers and the lesser tendency of the lateral lobing in the former species. In this article, *L. randaiensis* was transferred to *Sassafras* and was described as an androdioecious species (Rehder, 1920). In the same article, Rehder (1920) also synonymized *Pseudosassafras* under *Sassafras* and suggested that flowers of *S. tzumu* were hermaphroditic but functionally unisexual. Despite Rehder's treatment, the recognition of *Pseudosassafras* as a separate genus endemic to East Asia was followed by a number of taxonomists (e.g., Handel-Mazzetti, 1931; Liou, 1934; Nakai, 1940). Emphasizing the importance of 2- versus 4-celled anthers, Kamikoti (1933) created *Yushunia* Kamik. to accommodate the 2-celled *Y. randaiensis* (Hayata) Kamik. Although Kamikoti (1933) did not comment on the sexuality of *Y. randaiensis*, he described *Yushunia* as dioecious. *Yushunia* was later criticized as unnatural by Nakai (1940), who instead treated *Y. randaiensis* as a variety of Chinese sassafras (as *P. laxiflorum* (Hemsl.) Nakai var. *randaiensis* (Hayata) Nakai).

In December 1920, Kanehira published an article in Japanese, in which he recorded Wilson's field observations of *Lindera randaiensis* in Alishan and accepted Rehder's (1920) new treatment of Taiwan sassafras. In 1936, the second edition of Kanehira's *Formosan Trees Indigenous to the Islands*, a taxonomic masterpiece in Taiwan, was published. In this work, however, Kanehira did not comment directly on the sexuality of *Sassafras randaiense*. Instead, he briefly described the morphology of male flowers and mentioned that the female flowers were often intermixed with them (Kanehira, 1936). Interestingly, in the illustration, *S. randaiense* was depicted as an androdioecious species, with a hermaphroditic flower and a male flower lacking the fourth-whorl staminodia (Kanehira, 1936), resembling that of *S. albidum*.

In 1953, Keng published a taxonomic revision of *Sassafras* in which he basically followed the generic

concept of Rehder (1920) except for further dividing *Sassafras* into two subgenera. Keng (1953) placed *S. albidum* in subgenus *Sassafras* and the two East Asian species in subgenus *Pseudosassafras* (Lecomte) H. Keng. Keng's (1953) interpretation on the sexuality of the Asian species, however, was somewhat confusing. Although Keng referred to Wilson's comment (Gamble, 1916; see above) on the sexuality of the two Asian species as "the pistillate flowers of the two eastern Asiatic species are apparently hermaphroditic" (Keng, 1953), he concluded his investigations with a series of comparisons between staminate and pistillate flowers of the three *Sassafras* species in the taxonomic key, floral diagrams, and table appended to the paper (Keng, 1953). The differences between the staminate and pistillate flowers of the two Asian species, however, are minor, with staminate flowers characterized by relatively larger androecium and smaller gynoecium in comparison to those of the pistillate flowers (Keng, 1953).

In a monumental dendrology textbook titled *Illustrations of Native and Introduced Ligneous Plants of Taiwan* by T. S. Liu (1960), *Sassafras randaiense* was described as a polygamous species. In that book, the description of the male flowers was basically a Chinese translation of Kanehira's Japanese text (1936). In the illustration of the species, there are two figures each depicting a bisexual flower and a male flower (Fig. 2L), respectively, that are very similar to the line drawings in Kanehira (1936). Subsequent to Liu's treatment (1960), nearly all taxonomic and floristic works of Lauraceae in Taiwan described *S. randaiense* as a polygamous species (Liu, 1970; Chang, 1976; Liu & Liao, 1980; Ying, 1985; Liao, 1988, 1996). However, Chang (1976) and Liao (1988, 1996) did not follow the description of the male flowers in Kanehira (1936) and Liu (1960); instead, their description of the male flowers included fourth-whorl staminodia that were also depicted in Hayata (1911).

In their article titled "Studies on the propagation of Taiwan sassafras," Lu et al. (1982) studied embryology and seed physiology of *Sassafras randaiense*. After examining a considerable numbers of flower buds, Lu et al. (1982) concluded that flowers of Taiwan sassafras are bisexual. Lu et al. (1982) also commented that, although flowers of the type specimen of *S. randaiense* were interpreted as staminate (ovary nonfunctional) by Hayata (1911), they were apparently bisexual. However, the work of Lu et al. (1982) has been rarely cited by recent taxonomic works.

To facilitate the understanding of the complicated taxonomic history of *Sassafras randaiense*, the nomenclature of the species is listed below. Full lists of synonyms of *S. albidum* and *S. tzumu* are available in van der Werff (1997) and Li et al. (2008), respectively.

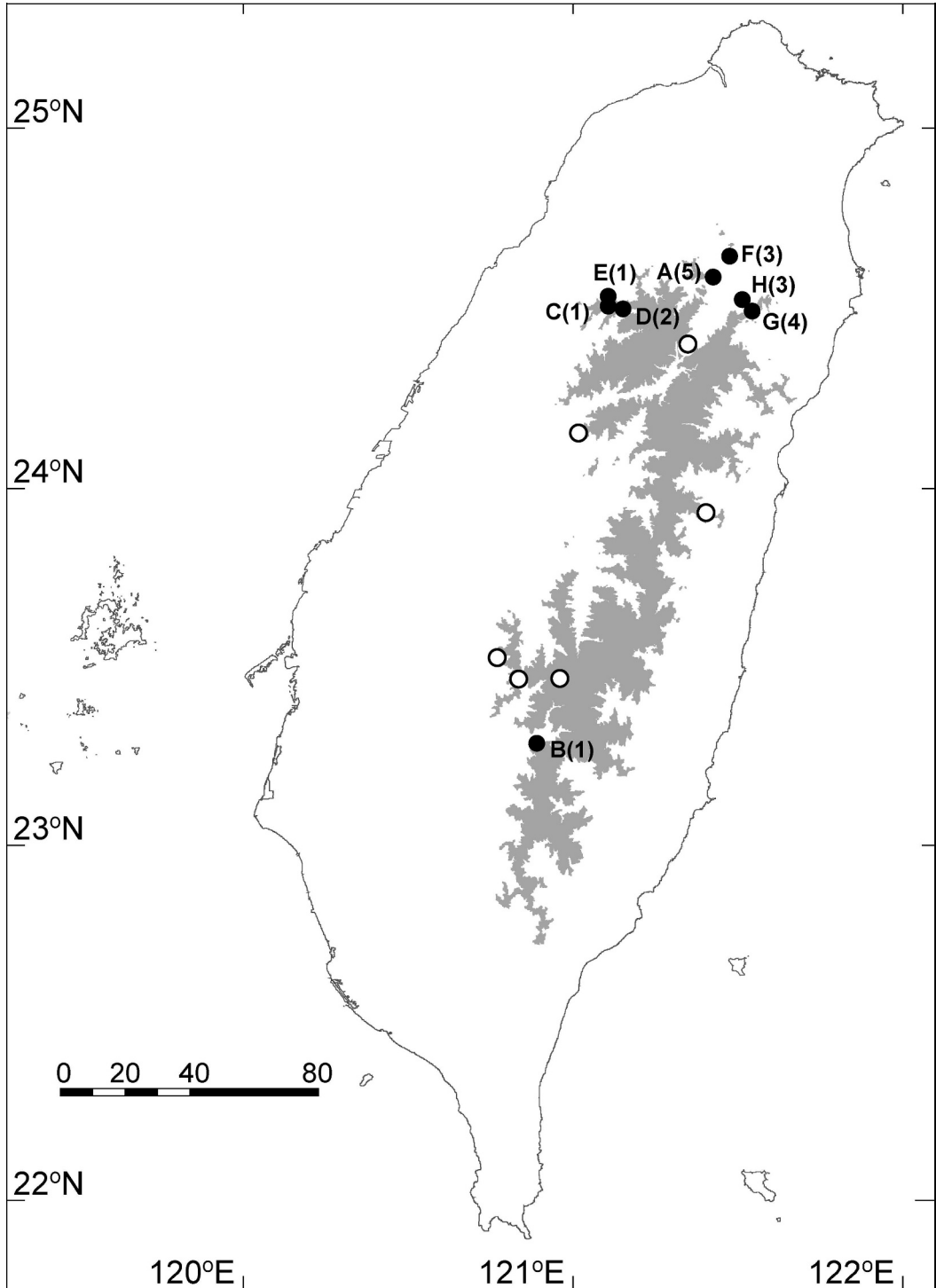


Figure 1. Distribution map of *Sassafras randaiense* (Hayata) Rehder in Taiwan based on specimens at HAST, TAI, and TAI. Black circles (●) indicate localities of field studies in 2007. Open circles (○) indicate localities of the historical collections in the herbarium. The number in parentheses indicates the numbers of individuals studied at each locality. The shaded area delimits mountainous regions above 2000 m. Field study localities (voucher specimens are all deposited at HAST) include A, Litaishenmuyuan (1600 m), 16 Jan. 2007, *Huang 2977*; B, Chungchihkuan (2100 m), 8 Feb. 2007, *Huang 2993*; C, Kuanwu Lodge (2025 m), 9 Feb. 2007, *Huang 3000*; D, Taiwan Sassafras Nature Reserve (1950 m), 9 Feb. 2007, *Huang 3001*; E, Talu Forest Rd. (1550 m), 9 Feb. 2007, *Huang 3006*; F, Mingchih (1200 m), 16 Jan. 2007, *Huang 2977* and 12 Feb. 2007, *Huang 3008*; G, Pingyuan Forest Rd. (1920 m), 13 Feb. 2007, *Huang 3016*; H, Taipingshan Rd. (1600 m), 13 Feb. 2007, *Huang 3017*.

Table 1. Summary of floral morphology of *Sassafras randaiense* (Hayata) Rehder.¹

Collection number	No. of inflorescences per reproductive shoot ²	No. of flowers per inflorescence ³	Inflorescence type	Inflorescence length (cm) ³	Sexual phase	No. of anther cells
<i>Huang 2977</i>	10	14–23 (19.4 ± 3.13, N = 10)	P (10)	3–6 (4.4 ± 0.97, N = 10)	Late female	2
<i>Huang 2978-A*</i>	4	7–15 (10.25 ± 3.59, N = 4)	B (2), P (2)	4–4.5 (3.59 ± 0.48, N = 4)	Male	4
	4	10–17 (13.25 ± 2.99, N = 4)	B (1), P (3)	4–4.5 (4.38 ± 0.25, N = 4)	Male	4
<i>Huang 2978-B*</i>	5	7–10 (9.2 ± 1.3, N = 5)	B (5)	3.5–5.5 (4.1 ± 0.82, N = 5)	Female	Most 4, few 2
	6	8–12 (9.33 ± 1.64, N = 6)	B (6)	3–4 (3.75 ± 0.42, N = 6)	Female	4
<i>Huang 2978-C*</i>	6	10–13 (10.83 ± 1.51, N = 6)	B (5), P (1)	3–4 (3.5 ± 0.45, N = 6)	Late female	Most 2, few 4
	6	8–13 (11.17 ± 1.83, N = 6)	B (4), P (2)	2.5–3 (2.75 ± 0.27, N = 6)	Late female	Most 4, few 3
<i>Huang 2978-D</i>	5	10–14 (12 ± 1.58, N = 5)	B (2), P (3)	2.5–3.5 (3.2 ± 0.45, N = 5)	Male	2
<i>Huang 2978-E</i>	3	15, N = 1	P (1)	4.5, N = 1	Male	2
<i>Huang 2993</i>	7	7–12 (10.33 ± 1.97, N = 6)	B (3), P (3)	4.7–5.5 (5.38 ± 0.5, N = 6)	Male	2
<i>Huang 3000</i>	4	11–13 (12.25 ± 0.96, N = 4)	B (2), P (2)	3.7–4.3 (3.95 ± 0.26, N = 4)	Male	2
<i>Huang 3001-A*</i>	5	12–13 (12.67 ± 0.58, N = 3)	B (2), P (1)	3.4–4 (3.7 ± 0.3, N = 3)	Male	2
	6	12–15 (13.6 ± 1.14, N = 5)	B (1), P (5)	3.5–5 (4 ± 0.71, N = 5)	Male	2
<i>Huang 3001-B*</i>	4	15–18 (16.67 ± 1.53, N = 3)	P (3)	3.5–5.7 (4.53 ± 1.11, N = 3)	Male	2
	5	15–19 (16.5 ± 1.73, N = 4)	P (5)	3.5–5.2 (4.55 ± 0.76, N = 4)	Male	2
<i>Huang 3006*</i>	7	10–12 (11 ± 0.84, N = 6)	B (6)	3.1–4.3 (3.65 ± 0.49, N = 6)	Late female	Most 2, few 4
	6	10–12 (11 ± 0.71, N = 5)	B (5)	2.8–4 (3.38 ± 0.57, N = 4)	Late female	2
<i>Huang 3008-A*</i>	4	12–18 (13.75 ± 2.87, N = 4)	B (1), P (3)	6–8 (6.65 ± 0.94, N = 4)	Male	2
	3	10–13 (11.67 ± 1.53, N = 3)	B (2), P (1)	4.1–4.3 (4.2 ± 0.1, N = 3)	Male	2
	6	12–16 (13.67 ± 1.63, N = 6)	B (2), P (4)	6.3–7.6 (6.87 ± 0.73, N = 6)	Male	2
<i>Huang 3008-B</i>	6	12–18 (14.33 ± 2.58, N = 6)	B (2), P (4)	6.5–7 (6.92 ± 0.20, N = 6)	Male	2
<i>Huang 3016-A</i>	8	11–15 (12.75 ± 1.58, N = 8)	P (8)	3–3.5 (3.16 ± 0.23, N = 8)	Male	2
<i>Huang 3016-B</i>	4	9–12 (10.5 ± 1.29, N = 4)	B (2), P (2)	2.8–3.5 (3.15 ± 0.31, N = 4)	Late female	2
<i>Huang 3016-C</i>	6	7–14 (11.33 ± 2.50, N = 6)	B (1), P (5)	2.5–3.5 (3.08 ± 0.38, N = 6)	Female	2
<i>Huang 3016-D</i>	6	9–13 (11 ± 1.55, N = 6)	P (6)	4–5 (4.5 ± 0.55, N = 6)	Late female	2
<i>Huang 3017-A</i>	8	9–13 (11.25 ± 1.75, N = 8)	P (8)	3–4 (3.29 ± 0.38, N = 8)	Male	2
<i>Huang 3017-B</i>	6	14–17 (15.6 ± 1.14, N = 5)	P (6)	3.6–4.5 (4.04 ± 0.38, N = 5)	Male	2
<i>Huang 3017-C</i>	4	16–19 (18 ± 1.73, N = 3)	P (3)	4.00 ± 0.00, N = 3	Male	2
	3–10 (5.54 ± 1.56), N = 28	7–23 (12.68 ± 3.19, N = 142)	B (54, 37.2%); P (91, 62.8%)	2.5–8 (4.18 ± 1.22, N = 141)		

B, botryoid cyme, P, panicle.

* Individuals in which more than one reproductive shoot was observed.

¹ Measurements and observations were based on 28 reproductive shoots of 20 trees of Taiwan *sassafras*.

² Inflorescence number was observed by counting inflorescence axes on a reproductive shoot.

³ Counts and measurements on flowers and inflorescences were made on intact inflorescences only. Range of the measurements, average, standard deviation, and sample size (N) are shown.

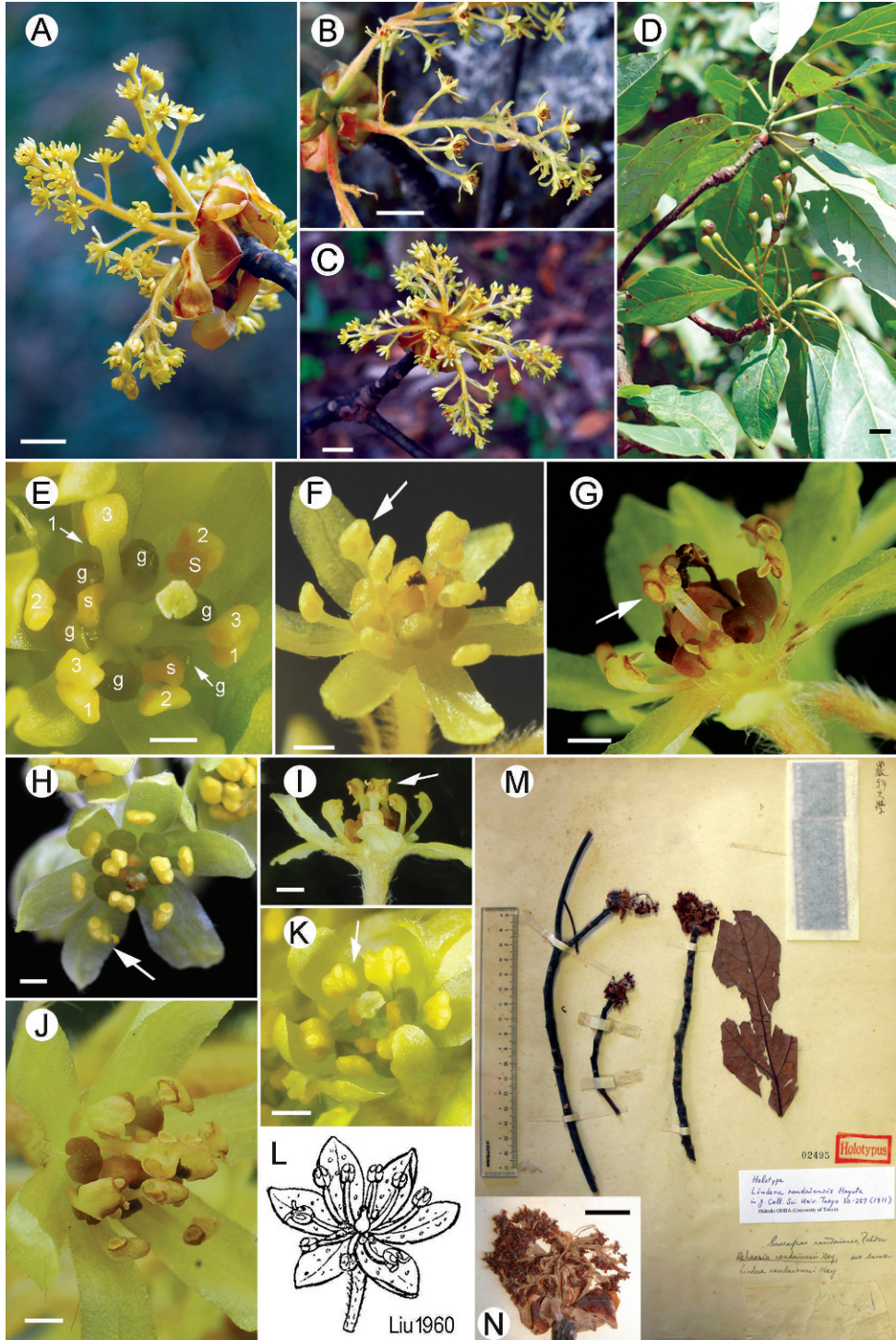


Figure 2. Plate illustrating *Sassaparilla randaiense* (Hayata) Rehder. —A. Botryoid inflorescences (*Huang 3006*). —B. Highly reduced panicle (*Huang 3008*). —C. Umbel of botryoid cymes (*Huang 3006*). —D. Fruiting branch (*Huang 3254* [HAST], 18 July 2007). —E. Flower in female phase; 1 = first whorl of stamens, 2 = second whorl of stamens, 3 = third whorl of stamens, g = gland, s = staminode (*Huang 3016*, 11:50 AM). —F. Flower in late female phase, arrowhead points to a 3-celled anther (*Huang 3006*, 1:51 PM). —G. Flower in male phase, arrowhead points to an extrorse third-whorl anther (*Huang 3008*, 1:56 PM). —H. Flower in late female phase, arrowhead points to a 4-celled anther (*Huang 2978*). —I. Flower in male phase, arrowhead points to a 4-celled anther (*Huang 2978*). —J. Flower in late female phase, arrowhead points to a 4-celled anther (*Huang 2978*). —K. Flower in late female phase, arrowhead points to a 3-celled anther (*Huang 3006*, 1:51 PM). —L. Line drawing of a flower (Liu 1960). —M. Herbarium specimen with ruler, leaf, and flower, with a "Holotypus" label and a handwritten note. —N. Dried flower specimen.

Sassafras randaiense (Hayata) Rehder, J. Arnold Arbor. 1: 244. 1920. Basionym: *Lindera randaiensis* Hayata, J. Coll. Sci. Imp. Univ. Tokyo 30: 257. 1911. *Yushunia randaiensis* (Hayata) Kamik., Annual Rep. Taihoku Bot. Gard. 3: 78. 1933 [1934]. *Pseudosassafras laxiflorum* var. *randaiensis* (Hayata) Nakai, J. Jap. Bot. 16: 126. 1940. TYPE: Taiwan. Mt. Randaizan, 1908, *S. Kusano s.n.* (holotype, TI!).

METHODS

In January and February 2007, we conducted field trips to eight localities in Taiwan (Fig. 1) to collect and observe flowers of *Sassafras randaiense* in their natural habitats. Because Taiwan sassafras trees are tall and often grow on steep mountain slopes, tagging was essentially impossible for the trees we observed. A total of 20 trees were observed. For each of the 20 plants, three to five flowering branches were collected by an extensible (to 40 ft.) pole pruner. One to three flowering shootings were pickled. Pickled flowers and voucher specimens are deposited in the Herbarium of Academia Sinica, Taipei (HAST). Measurements of floral morphology were based on one to three pickled flowering buds. Photographs of flowers and flowering branches were taken in the field. Collecting sites in northern Taiwan (sites A, C–H, Fig. 1) were revisited in June and July 2007. Site B (Fig. 1) was not revisited because of its poor accessibility.

RESULTS

Measurements and observations of floral morphology of the 28 reproductive shoots of 20 *Sassafras randaiense* trees, including the number of inflorescences per reproductive shoot, number of flowers per inflorescence, inflorescence type, inflorescence length, sexual phase, and anther cell number, are summarized in Table 1.

INFLORESCENCE MORPHOLOGY

Young inflorescences of *Sassafras randaiense* are enclosed in a vegetative winter bud (Weberling, 1988, 1989) by four to six decussate bracts (cataphylls, Weberling, 1988, 1989; Fig. 2A), as described by

Rohwer (1993). These bracts have been often misinterpreted as involucre (e.g., Liao, 1996). The inflorescence of *S. randaiense* is determinate, ending with a terminal flower (Fig. 2A–C). On average, about 13 flowers (7–23 [12.68 ± 3.19 , $N = 147$]; Table 1) of Taiwan sassafras are arranged in a highly reduced panicle (62.8%) or raceme-like cyme (37.2%) (Fig. 2A). The determinate racemes are better termed botryoid cymes (e.g., Rohwer, 1993; Li & Christophel, 2000) to distinguish from true racemes, which are indeterminate inflorescences (sensu Weberling, 1988, 1989). In *S. randaiense*, the average length of the inflorescence is 4.18 cm (2.5–8 cm [4.18 ± 1.22 , $N = 145$]), much longer than previously reported (i.e., 3 cm; Hayata, 1911; Keng, 1953; Liao, 1996). Up to 10 (3–10 [5.54 ± 1.56], $N = 28$) panicles and/or botryoid cymes are then tightly clustered around the vegetative terminal bud (pseudoterminal), giving the appearance of an umbel of panicles and/or botryoid cymes (Fig. 2C). After the early spring flowering stage, the vegetative terminal buds turn into a normal leafing branch and elongate (van der Werff, 2001), as shown in Figure 2D. The overall appearance of the inflorescences of *S. randaiense* described above conforms well to the group 1 inflorescence type that is characteristic of the tribe Laureae (sensu van der Werff & Richter, 1996).

FLOWER MORPHOLOGY

All observed flowers of *Sassafras randaiense* comprise (from the outside inward) six tepals in two whorls, nine stamens in three whorls, and three sagittate staminodia as the fourth whorl, with a central gynoeceum (Figs. 2E–K). The third-whorl stamens possess a pair of globose glands at the base of each filament (g in Fig. 2E). A majority of the anthers are 2-locular (Fig. 2E, G, I, J); however, flowers with 3-celled (Fig. 2F) and 4-celled (Figs. 2H, K) anthers were also observed (Table 1). Specifically, three observed trees in Litaishenmuyuan, Chilanshan area (Huang 2977), have 4-celled or a mixture of 2-celled and 4-celled anthers. While anthers of the first and second stamen whorl are introrse (Fig. 2F, G), those of the third whorl are apparently extrorse or latrorse (Fig. 2F, G, J) but never introrse. When flowers are in the male phase (see below), those of the third whorl are apparently extrorse (Figs. 2G, I, J). The flower

←

phase, arrowhead points to an extrorse third-whorl anther (Huang 3008, 1:56 PM). —J. Flower in male phase (Huang 3008, 2:35 PM). —K. Flower in female phase, arrowhead points to a 4-celled anther (Huang 2978, 16 Jan. 2007). —L. Illustration of a male flower in Liu (1960). —M. Holotype of *Lindera randaiensis* Hayata (*S. Kusano s.n.*, TI). —N. Flowering branch of the holotype. Scale bars: A–D, $N = 1$ cm; E–K = 1 mm.

structure of *S. randaiense* thus fits perfectly with the typical hermaphroditic flowers of Lauraceae (Rohwer, 1993; van der Werff, 2001). In no case have we observed any flower that showed the characteristics of the male flower (Fig. 2L) as depicted in Kanehira (1936) and Liu (1960).

The distinction between introrse and extrorse anthers of the third-whorl stamens of a hermaphroditic laurel flower was considered crucial in the taxonomy of Lauraceae (van der Werff & Richter, 1996) and has been used frequently in taxonomic keys at the generic level (e.g., van der Werff, 1991; Rohwer, 1993). In the taxonomic literature in Taiwan, this character is widely used, and *Sassafras randaiense* has routinely keyed out by the introrse anthers of its third-whorl stamens (e.g., Li, 1963; Liu & Liao, 1980; Ying, 1985; Liao, 1988, 1996; Liu et al., 1994; Yang et al., 1997). However, because filaments of many laurel species are long and become twisted after desiccation, this character is difficult to observe correctly and its application in taxonomic identification is problematic (van der Werff, 2001). Our differing observations on this subject therefore necessitate a revision of such taxonomic keys for the Lauraceae.

FLOWER BEHAVIOR AND POSSIBLE SEXUAL SYSTEM OF *SASSAFRAS RANDAIENSE*

In addition to being apparently hermaphroditic, flowers of *Sassafras randaiense* are clearly protogynous and alternate their sexual phase synchronously within a reproductive shoot (Table 1). Figures 2E and 2K show a female-phase flower, as indicated by the bright and apparently receptive stigma (Kubitzki & Kurz, 1984) and closed anther cells. At this phase, all anthers are well positioned away from the stigma and the third-whorl stamens bend further toward the first-whorl stamens (Fig. 2E). In Figure 2F and H, the stigma is wilted and the third-whorl stamens are no longer in close contact with the first-whorl stamens. In Figure 2G and J, the three third-whorl stamens bend further inward, exposing the extrorse anthers and enclosing the gynoecium. If the third-whorl anthers of *S. randaiense* were introrse as described by a majority of previous authors, pollen of these innermost anthers would not be dispersed away from the flower.

The protogyny and sexual phase synchrony in a reproductive shoot (Table 1) in *Sassafras randaiense* suggest the possibility of a sexual system of synchronous (or synchronized, see Kubitzki & Kurz, 1984) dichogamy, a mechanism well documented in *Persea americana* Mill. and other hermaphroditic Lauraceae species (Kubitzki & Kurz, 1984; Renner, 2001). Species with synchronous dichogamy comprise two flower morphs that differ in the timing of flower opening. It is called

synchronous because all flowers within an individual plant alter their sexual phases synchronously. In *P. americana*, for example, flowers of the first morph enter the female phase in the morning, wilt and close at noon to emerge as male phase in the afternoon, and close again in the evening. The second-morph individuals, on the contrary, start the same cycle in the afternoon, resulting in a temporal dioecy for the species (Stout, 1927; Kubitzki & Kurz, 1984). However, to confirm the existence of synchronous dichogamy in *S. randaiense*, it would be necessary to tag and to follow a population of individuals in the field (McDade, 1986; Renner, 2001; Utteridge & Saunders, 2001). Although we were unable to perform such investigations in 2007 due to the difficulty of accessing the tall Taiwan sassafras trees in their natural habitats, we have recently located other populations that are suitable for pursuing more sophisticated studies on the reproductive biology of *S. randaiense* in the next flowering season.

The protogynous and possibly synchronous dichogamy of *Sassafras randaiense* also explains why this species had been associated with several kinds of sexual systems (e.g., androdioecy, Rehder, 1920; dioecy, Kamikoti, 1933; polygamy, Liu, 1960). When flowers of Taiwan sassafras are found in their female phase (e.g., Fig. 2E, K), the flowers are usually described as hermaphroditic. However, when flowers on the plant are found in the male stage, the wilted gynoecia are likely to be interpreted as nonfunctional and the plant likely to be interpreted as a staminate individual. Although the condition of the holotype (Fig. 2M, N) did not allow us to closely examine its flowering stage, the type specimen is likely to represent a male-phased individual of *S. randaiense*.

QUESTIONS OF MALE FLOWERS

The apparent hermaphroditic condition of *Sassafras randaiense* led us to question the identity and authenticity of the particular male flower (Fig. 2L) depicted in Kanehira (1936) and Liu (1960). Similar to the line drawing (e.g., Fig. 2L), Kanehira's description on the male flower did not include staminodia (Kanehira, 1936), nor did the description in Liu (1960). Although Hayata (1911) probably misinterpreted the male-phased bisexual flowers as male flowers, the fourth-whorl staminodia are clearly present in the type specimen and precisely described by Hayata (1911). According to the notes in Kanehira (1920, 1936) that Wilson collected fruiting and male flower materials in Arishan in October 1918, the line drawings of Kanehira (1936) and Liu (1960) were likely based on specimens collected during that trip. However, Kanehira's notes on the phenology of Taiwan sassafras are problematic because *S. ran-*

daiense normally blooms in the late winter to early spring (mid December to late March). To trace the source of the male flower depicted in Kanehira (1936) and Liu (1960) and validate the accuracy of these two illustrations, we examined the specimens collected by Wilson and Kanehira currently housed in A and TAIF, respectively. Interestingly, we found no flowering material among Wilson's collections (*E. H. Wilson 10800* and *E. H. Wilson 10800a* at A) that had been examined by Rehder (1920) as well as specimens collected by R. Kanehira and S. Sasaki on the same trip with E. H. Wilson (*R. K. Kanehira & S. Sasaki 10682–10688* at TAIF; Sasaki, 1930). Without a credible voucher specimen, it is reasonable to question the authenticity of the line drawing in Kanehira (1936) and Liu (1960) as well as Wilson's observation recorded by Kanehira (1920, 1936).

SUMMARY

Our field observations on *Sassafras randaiense* clarify its inflorescence and flower morphology and suggest that its sexual system is likely synchronous dichogamy. Given the significant publicity and economic interest of *S. randaiense* in Taiwan, it is rather unusual that, except for Lu et al. (1982) and possibly Kamikoti (1933), very few botanists had critically examined the flowers and reproductive biology of this species. One possible explanation is that, because this easily recognized species poses no difficulty in the taxonomy of Lauraceae in Taiwan, there is no demanding need for a critical study of its flower morphology. Our findings on protogyny and possibly synchronous dichogamy of *S. randaiense* can also explain, at least in part, why its seed production is low and variable. As is well documented in *Persea americana*, whose sexual system is synchronous dichogamy, in the absence of the two morphs of avocados growing in close proximity, the crop yield of avocado is extremely low (Stout, 1927). Our subsequent investigation in July 2007 found low or no seed production in populations of *S. randaiense* where the distribution of trees was scattered, with the closest trees more than 1 km away from each other (localities C–E in Fig. 1). By contrast, in localities where individual trees are less than 100 m apart (G, H in Fig. 1), abundant seed production was observed (e.g., Fig. 2D). However, further field studies are needed to confirm the existence of synchronous dichogamy in *S. randaiense* and its influence on its seed production.

Literature Cited

Chang, C.-E. 1976. Lauraceae. Pp. 406–468 in H. L. Li, T.-S. Liu, T.-C. Huang, T. Koyama & C. E. DeVol (editors), *Flora of Taiwan*, Vol. 2. Epoch Publishing Co., Taipei.

Chen, M.-H. & P.-J. Wang. 1985. Somatic embryogenesis and plant regeneration on *Sassafras randaiense* (Hay.) Redh. Bot. Bull. Acad. Sin. 26: 1–12.

Denk, T., F. Grímsson & Z. Kvaček. 2005. The Miocene floras of Iceland and their significance for late Cretaceous North Atlantic biogeography. Bot. J. Linn. Soc. 149: 369–417.

Gamble, J. G. 1916. Lauraceae. Pp. 66–86 in C. S. Sargent (editor), *Plantae Wilsonianae*, Vol. 2. The University Press, Cambridge.

Guan, B. T., W.-C. Kuo, S.-T. Lin & C.-F. Yu. 2006. Short-distance dispersal of intact Taiwan sassafras fruits in a temperate montane rain forest of northeastern Taiwan. Bot. Stud. 47: 427–434.

Handel-Mazzetti, H. 1931. *Symbolae Sinicae*, Vol. 7. Julius Springer, Vienna.

Hayata, B. 1911. Materials for the flora of Formosa. J. Coll. Sci. Imp. Univ. Tokyo 30: 1–471.

Hemsley, W. B. 1891. Laurineae. J. Linn. Soc., Bot. 26: 370–393.

———. 1907a. *Sassafras* in China. Bull. Misc. Inform. Kew 2: 55–56.

———. 1907b. *Sassafras tzumu*. Hooker's Icon. Pl. 29: tab. 2833.

Hsu, Y.-F., C.-C. Chen & P.-S. Yang. 1986. The tentative review on the endemic butterflies in Taiwan. Mem. Coll. Agric. Natl. Taiwan Univ. 26: 55–69 (In Chinese, with English summary).

Hu, C.-Y. 1979. Introduction to the research project on *Sassafras* propagation. Taiwan Forest. 5: 30–31 (In Chinese).

IUCN. 2001. IUCN Red List Categories and Criteria, Version 3.1. Prepared by the IUCN Species Survival Commission. IUCN, Gland, Switzerland, and Cambridge, United Kingdom.

Kamikoti, S. 1933. Neue und kritische Lauraceen aus Taiwan. I. Ann. Rep. Taihoku Bot. Gard. 3: 77–80.

Kanehira, R. 1920. On sassafras in Taiwan. Trans. Nat. Hist. Soc. Formosa 10: 270–272 (In Japanese).

———. 1936. *Formosan Trees Indigenous to the Islands*, 2nd ed. Department of Forestry, Government Research Institute, Taihoku (In Japanese, with English notes).

Keng, H. 1953. A taxonomic revision of *Sassafras* (Lauraceae). Quart. J. Taiwan Mus. 6: 78–85.

Kubitzki, K. & H. Kurz. 1984. Synchronized dichogamy and dioecy in Neotropical Lauraceae. Pl. Syst. Evol. 147: 253–266.

Lecomte, H. 1911. Sur un *Pseudosassafras* de Chine. Notul. Syst. (Paris) 2: 266–270.

———. 1913. *Pseudosassafras* H. Lec. Nouv. Arch. Mus. Hist. Nat. sér. 5, 5: 108.

Li, H.-L. 1963. *Woody Flora of Taiwan*. Livingston Publishing Co., Narberth, Pennsylvania.

Li, H.-W., P.-Y. Pai, S.-K. Lee, F.-N. Wei, Y.-T. Wei, Y.-C. Yang, P.-H. Huang, H.-P. Tsui, Z.-D. Shia & J.-L. Li. 1982. Lauraceae. In H. W. Li (editor), *Flora Reipublicae Popularis Sinicae*, Vol. 31. Science Press, Beijing (In Chinese).

Li, J. & D. C. Christophel. 2000. Systematic relationships within the *Litsea* complex (Lauraceae): A cladistic analysis on the basis of morphological and leaf cuticle data. Austral. Syst. Bot. 13: 1–13.

Li, X. W., J. Li & H. van der Werff. 2008. *Sassafras* J. Presl. Pp. 159–161 in Z. Y. Wu, P. H. Raven & D. Y. Hung (editors), *Flora of China*, Vol. 7 (Menispermaceae through Capparaceae). Science Press, Beijing, and Missouri Botanical Garden, St. Louis.

- Liao, J.-C. 1988. The Taxonomic Revisions of the Family Lauraceae in Taiwan. Department of Forestry, National Taiwan University, Taipei.
- . 1996. Lauraceae. Pp. 433–499 in Editorial Committee of the Flora of Taiwan (editor), Flora of Taiwan, 2nd ed., Vol. 2. Editorial Committee of the Flora of Taiwan, Taipei.
- Lin, J.-H., B. T. Guan, S.-T. Lin & C.-F. Yu. 2003. Attributes of leaves on reproductive shoots of Taiwan sassafras (*Sassafras randaiense* (Hay.) Rehder) at Chilan Shan, northeastern Taiwan. *J. Exp. Forest Natl. Taiwan Univ.* 17: 25–32 (In Chinese, with English abstract).
- Lin, T.-P. 1992. A method of breaking the deep dormancy of *Sassafras randaiense* (Hay.) Rehd. seed. Pp. 365–368 in S.-C. Huang, S.-C. Hsieh & D.-J. Liu (editors), The Impact of Biological Research on Agricultural Productivity: Proceedings of the Society for the Advancement of Breeding Research in Asian and Oceania International Symposium. Society for the Advancement of Breeding Research in Asian and Oceania, Changhua.
- Liou, H. 1934. Lauracées de Chine et d'Indochine. Hermann & Cie, Paris.
- Liu, T.-S. 1960. Illustrations of Native and Introduced Ligneous Plants of Taiwan, Vol. 1. College of Agriculture, National Taiwan University, Taipei (In Chinese).
- & C.-J. Liao. 1980. Dendrology, Vol. 1. The Commercial Press, Ltd., Taipei (In Chinese).
- Liu, Y.-C. 1970. Colored Illustrations of Important Trees in Taiwan. National Chung-Hsing University, Taichung (In Chinese).
- , F.-Y. Lu & C.-H. Ou. 1994. Trees of Taiwan. College of Agriculture, National Chung-Shing University, Taichung (In Chinese).
- Lu, F.-Y., C.-H. Ou & C.-C. Liao. 1982. Studies on the propagation of Taiwan sassafras (I). *Quart. J. Chin. Forest.* 15: 73–86 (In Chinese, with English summary).
- Lu, S.-Y. & M.-C. Lin (editors). 1996. Rare and Endangered Plants in Taiwan, Vol. 1. Council of Agriculture, Executive Yuan, Taipei (In Chinese).
- McDade, L. A. 1986. Protandry, synchronized flowering and sequential phenotypic unisexuality in neotropical *Pentagonia macrophylla* (Rubiaceae). *Oecologia* 68: 218–223.
- Nakai, T. 1940. Notulae ad plantas Asiae orientalis (XIV). *Jap. J. Bot.* 16: 121–138.
- Nie, Z.-L., J. Wen & H. Sun. 2007. Phylogeny and biogeography of *Sassafras* (Lauraceae) disjunct between eastern Asia and eastern North America. *Pl. Syst. Evol.* 267: 191–203.
- Rehder, A. 1920. The American and Asiatic species of *Sassafras*. *J. Arnold Arbor.* 1: 242–245.
- Renner, S. S. 2001. How common is heterodichogamy? *Trends Ecol. Evol.* 15: 595–597.
- Rohwer, J. G. 1993. Lauraceae. Pp. 366–391 in K. Kubitzki, J. G. Rohwer & V. Bittrich (editors), The Families and Genera of Vascular Plants, Vol. 2: Flowering Plants. Dicotyledons—Magnoliid, Hamamelid, and Caryophyllid Families. Springer-Verlag, Berlin.
- Sasaki, S. 1930. A Catalogue of the Government Herbarium. Department of Forestry, Government Research Institute, Taihoku.
- Stout, A. B. 1927. The flower behavior of avocados. *Mem. New York Bot. Gard.* 7: 145–203.
- Utteridge, T. M. A. & R. M. K. Saunders. 2001. Sexual dimorphism and functional dioecy in *Maesa perlaris* and *M. japonica* (Maesaceae/Myrsinaceae). *Biotropica* 33: 368–374.
- van der Werff, H. 1997. Lauraceae. Pp. 26–36 in Flora of North America Editorial Committee (editor), Flora of North America North of Mexico, Vol. 3. Oxford University Press, New York.
- . 2001. An annotated key to the genera of Lauraceae in the flora Malesiana region. *Blumea* 46: 125–140.
- & H. G. Richter. 1996. Toward an improved classification of Lauraceae. *Ann. Missouri Bot. Gard.* 83: 409–418.
- Wang, P. J., C. Y. Hu & M. H. Chen. 1991. Taiwan sassafras [*Sassafras randaiense* (Hay.) Rehd.]. Pp. 180–190 in Y. P. S. Bajaj (editor), Biotechnology in Agriculture and Forestry, Vol. 16, Trees III. Springer-Verlag, Berlin.
- Weberling, F. 1988. Inflorescence structure in primitive angiosperms. *Taxon* 37: 657–690.
- . 1989. Morphology of Flowers and Inflorescences. Cambridge University Press, Cambridge.
- Wen, J. 1999. Evolution of eastern Asian and eastern North American disjunct pattern in flowering plants. *Annual Rev. Ecol. Syst.* 30: 421–455.
- Wolfe, J. A. 1975. Some aspects of plant geography of the Northern Hemisphere during the late Cretaceous and Tertiary. *Ann. Missouri Bot. Gard.* 62: 264–279.
- Yang, J.-C., J.-Y. Tsay, J.-D. Chung & Z.-Z. Chen. 2000. Multiple shoot proliferation and plantlet establishment in shoot tip and nodal culture of Taiwan Sassafras (*Sassafras randaiense* (Hay.) Rehd.). *Taiwan J. Forest. Sci.* 15: 31–39.
- Yang, Y.-P., H.-Y. Liu & S.-Y. Lu. 1997. Manual of Taiwan Vascular Plants, Vol 2. Council of Agriculture, The Executive Yuan, Taipei (In Chinese).
- Ying, S.-S. 1985. A revision of the family Lauraceae in Taiwan. *Mem. Coll. Agric. Natl. Taiwan Univ.* 25: 83–117 (In Chinese, with English summary).