Note on the taxonomy, biogeography and conservation of endangered plant species in the Ryukyus

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ABSTRACT: The Ryukyus Archipelago consists of about 200 nearly subtropical islands located between Japan proper and Taiwan. Previous studies have found the Ryukyus to be a region of high biodiversity with many endangered vascular plant taxa, but they are not comprehensive. Here, we discuss the phytogeographic features and circumstances of the endangered plant taxa, make suggestions for effective *in situ* conservation, and highlight endangered plants in the Ryukyus that require further study.

Keywords: Conservation, endangered plants, phytogeography, Ryukyus

The Ryukyu Archipelago

The Ryukyu Archipelago (the Ryukyus) consists of about 200 islands spanning 1300 km between Japanese Kyushu being a western part of Japan proper, and Taiwan. Administratively, the Ryukyus are divided into two prefectures: Kagoshima Prefecture including Yoron Island and other islands in the northeastern part, and Okinawa Prefecture including other islands in the southwestern part (Fig. 1). Biogeographically, on the other hand, the Ryukyus are primarily divided into three major areas by two geographical gaps, namely the Tokara and Kerama gaps. The northern Ryukyus comprise the Osumi Group and most of the Tokara Group; the central Ryukyus consist of the remainder of the Tokara Group, and the Amami and Okinawa Groups; and the southern Ryukyus include the Miyako and Yaeyama Groups (e.g., Tagawa and Miyagi, 1991; Yokota, 1997). The northern Ryukyus belong to the Sino-Japanese floristic area, while the central and southern islands belong to the Southeast Asiatic floristic area (Miyawaki, 1977). Climatically the former is temperate, and the latter is subtropical (Miyawaki, 1977).

The highest mountain in the subtropical region of the Ryukyus, namely without the northern Ryukyu, is Mt. Yuwan-dake on Amami Island (694 m above sea level (a. s. l.); Fig. 2A). There are many endemic and endangered plants near the top of this mountain, for example *Balanophora yuwanensis* Agusawa et Sakuta, nom. nud. (Balanophoraceae; CR; Fig. 2B), *Isachne nipponensis* Ohwi var. *minor* (Honda) Nemoto (Poaceae; CR) and *Ilex dimorphophylla* Koidz. (Aquifoliaceae; CR; Fig. 2C). Also,

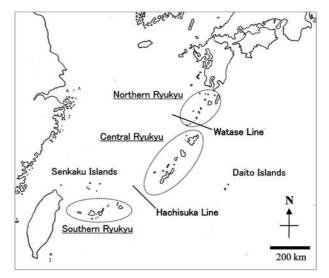


Fig. 1. The three biogeographical areas of the Ryukyu Archipelago.

it is thought that some temperate species, which sparsely populate the mountain with cooler environment, have played a role of refuge after the last glacial period. Thus, Mt. Yuwan-dake is thought to be a local biodiversity hot spot in the Ryukyus (Hotta, 2003). Furthermore, mountain chain including Mt. Yonaha-dake (503 m a.s.l.) in the northern part of Okinawa Island in the central Ryukyus, and Mt. Omoto-dake (526 m a. s. l.) on Ishigaki Island and Mt. Komi-dake (469 m a. s. l.) on Iriomote Island in the southern Ryukyus also has a high level of species diversity (Shimabuku et al., 1991).

The longest river (18.8 km) in the Ryukyus is the Urauchi River on Iriomote Island in the southern Ryukyus (Fig. 3A). Healthy forests including mangroves have been maintained along the river

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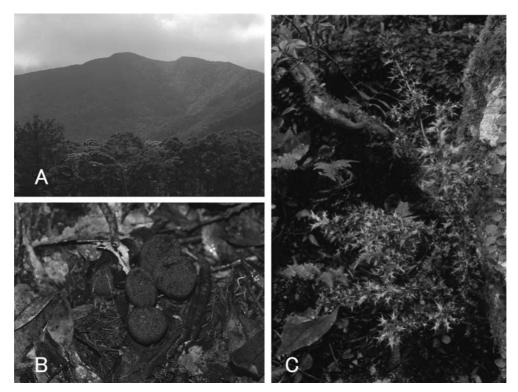


Fig. 2. Mount Yuwan-dake on Amami Island and two endangered plants found there. A. Mt. Yuwan-dake; B. *Balanophora yuwanensis*; C. *Ilex dimorphophylla* (photographed by H. Yamashita).

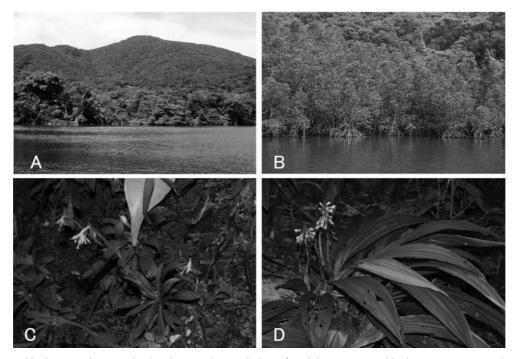


Fig. 3. The Urauchi River on Iriomote Island and two endangered plants found there. A. Urauchi River; B. Mangrove along the river; C. *Heloniopsis kawanoi*; D. *Calanthe formosana*.

(Fig. 3B), and harbor many endangered plant species, for example *Freycinetia williamsii* Merr. (Pandanaceae; EN), *Heloniopsis*

kawanoi (Koidz.) Honda (Liliaceae; VU; Fig. 3C) and *Calanthe formosana* Rolfe (Orchidaceae; EN; Fig. 3D). Moreover, forests

along the Sumiyo River on Amami Island and the Benoki River on Okinawa Island in the central Ryukyus have high levels of vascular-plant species diversity and endemism (Shimabuku et al., 1991).

Species diversity of the Ryukyus

The flora of the Ryukyus has long been studied by numerous botanists (Ito and Matsumura, 1899; Sakaguchi, 1924; Masamune, 1951a, b, 1953, 1954, 1955a, b, c, 1956, 1957, 1964; Takamine, 1952; Hatusima, 1975; Walker, 1976; Hatusima and Amano, 1994; Shimabuku, 1997; Hatusima, 2004). Using some of these taxonomic references, Shimabuku (1984) compared the density of plant species (= species number/area) between the Ryukyus (without the northem Ryukyus) and Japan proper, with a conclusion that the species density of the Ryukyus (0.45 = 1595 species/3540 km²) was 45 times greater than that of Japan proper (0.01 = 3857 species/373,770 km²). It is said that the Japanese Archipelago is one of regions show a high biodiversity in the world (Hara, 1959; Boufford et al., 2004); thus, the results of this density comparison (Shimabuku, 1984) imply that this archipelago is a region of extremely high vascular plant biodiversity.

Possible causes of high biodiversity in the Ryukyus

Flora composed of multiple biogeographical elements

Three factors have been suggested to explain the high vascular plant species diversity in the Ryukyus. The first possible factor is that the flora of the Ryukyus comprises species related to those of different surrounding regions, including Japan proper, Taiwan, the Chinese mainland, and the Malesiana region (Hatusima, 1975; Yokota et al., 2007). Phytogeographically, some plants found in the Ryukyus are thought to relate even to endemics of Australia and New Zealand (Koidzumi, 1928; Ohwi, 1968; Hatusima, 1975; Murata 1992). This is discussed further in Section "Future study of endangered plants in the Ryukyus."

Geographic isolation

The second possible factor is the geographic isolation of terrestrial plants on individual islands. This isolation is thought to strongly contribute to the level of endemism in the Ryukyus (Hatusima, 1975, 1980; Niiro and Miyagi, 1988; Shimabuku et al., 1991; Yokota, 1997; Tateishi, 1998). As mentioned above, two geographical gaps are recognized in the Ryukyus (Fig. 1). The Tokara Gap located along the Tokara Strait between the northerm and central Ryukyus approximately corresponds with a biological

line of the Watase Line, proposed based on the distribution patterns of mammals (Aoki, 1913; Okada and Kiba, 1924; Fig. 1). The Kerama Gap located along the Kerama Trench between the central and southern Ryukyus corresponds with another biological line of the Hachisuka Line, proposed based on avian distribution patterns (Yamashina, 1955; Fig. 1). Although both biological lines were suggested by zoogeological studies, some plant taxa also have distribution patterns defined in part by the two biological lines (e.g., Hatusima, 1975; Shimabuku, 1984).

Estimates from palaeogeographical studies indicate that a landbridge between the Yaeyama Group in the southern Ryukyus and Taiwan was lost in the late Pleistocene (0.02 MYA; Ujiié, 1990; Kimura, 1996a; Ota, 1998) or the middle to late Pleistocene (0.2 MYA; Kizaki and Oshiro, 1977). However, on the other hand, there have been some different estimates for the establishment of the Tokara and Kerama gaps. The Tokara Gap is thought to have finally formed during the middle to late Pleistocene (0.02 to 0.2 MYA; Kimura, 1996a, b), the early Pleistocene (1.5 MYA) or older (Kizaki and Oshiro 1977; Ota 1998), or the Pliocene (1.7 to 5.2 MYA) (Ujiié, 1990). The Kerama Gap is thought to have finally formed during the late Pleistocene (0.02 MYA; Ujiié, 1990), the middle to late Pleistocene (0.02 to 0.2 MYA; Kimura, 1996a, b; Ota, 1998), or the middle Pleistocene (1 MYA; Kizaki and Oshiro 1977). The palaeogeographical background of the Ryukyus needs to be clarified to better understand the biogeography of the Ryukyus. Recently Nakamura et al. (2009) suggested that the historical barrier effect of the Kerama Gap is rather phytogeographically insignificant, because the floristic differentiation across the gap was no more than could be explained solely by geographical distance. In contrast to traditional conjecture, this suggests that the Kerama Gap may not effectively isolate terrestrial plants.

Diverse environments in the Ryukyus

The third factor that may account for the high diversity of plant species in the Ryukyus is the presence of numerous environments of varying temperature and humidity. As mentioned above, the Ryukyus are primarily subtropical, having temperatures intermediate between temperate and tropical regions; this enables both temperate and tropical plant species to survive there (e.g., Hatusima, 1975). Unlike most subtropical areas around the world, which are relatively dry, the Ryukyus are humid, receiving ample precipitation from typhoons and a regular rainy season (Nioro and Miyagi, 1988). This meteorological characteristic results in moist forest understory environments and xeric environments such as rocky seashores in the Ryukyus. These multiple environments of varying temperature and humidity are thought to contribute to the richness of the vascular plant flora of the Ryukyus.

Endangered plant species in the Ryukyus

Some of the endangered plant taxa in the Ryukyus are rare insular endemics, and the others reach their northern or southern biogeographical extremes in the Archipelago. All of these plant taxa have vulnerable distributions with either small numbers of individuals or few populations in the Ryukyus, and are at risk of extinction due to slight environmental changes. To effectively protect these endangered plants, it is necessary to formulate guidelines for *in situ* conservation based on field surveys, and to perform further field surveys and global distribution comparisons and taxonomic studies.

Areas and environments in the Ryukyus requiring *in situ* conservation

It is not practical to perform field surveys on all 200 islands in the Ryukyus for a short time; such an endeavor would require too much time and effort. Rather, certain areas and environments should be prioritized for in site conservation and investigation. Previously, Shimabuku et al. (1991) suggested that the following areas require strict in situ conservation and need further field surveys because of their concentrations of endangered and endemic plants: Mt. Komi-dake and its vicinity areas on Iriomote Island, Mt. Omoto-dake, and the Sakieda Peninsula on Ishigaki Island in the southern Ryukyus; Mt. Yuwan-dake and the Sumiyo River on Amami Island, and Mt. Inokawa-dake and Mt. Amagidake on Tokunoshima Island in the central Ryukyus. The mountain chain situated at the northern part of Okinawa Island ("Yanbaru") also requires in situ conservation and further field surveys. This mountain chain supports healthy subtropical rain forests, and hosts not only numerous endangered plants but also many endangered animal species. The forests in the "Yanbaru" escaped from developments because they were used for maneuvers by the U.S. military. Carefully considered guidelines are required to conserve all wildlife in the area once these areas are returned to Japan (Tagawa and Miyagi, 1991; Yokota, 1998).

The Ryukyus have few wide lowlands and, consequently few natural bogs or wetlands. However, there are some artificial marshy, such as fallow rice fields, that harbor habitat for some endangered plant species such as *Persicaria tomentosa* Willd. (Polygonaceae) and *Eriocaulon truncatum* Buch.-Ham. ex Mart. (Eriocaulaceae). Unfortunately, marshy reclamation is currently underway in the Ryukyus, and thus some plants growing there are on the edge of extinction. Marshy reclamation on Kita-Daito and Izena Islands, in particular, has become a serious problem (Yokota, 1998).

Much of the natural vegetation of lowland and coastal areas in the Ryukyus has been lost due to development. However, native peoples in the Ryukyus, especially those of Okinawa Prefecture, are highly religious, and have a custom of protecting certain forests as shrine pleases ("utaki"). Therefore, some natural forests and adjacent coastal vegetation have been conserved in a healthy state as utaki by the local custom. Many endangered-tropical species are found in the forests of the utaki in Okinawa Prefecture, such as Deeringia polysperma (Roxb.) Moq. (Amaranthaceae; CR; Fig. 4A) and Illigera luzonensis (C.Presl) Merr. (Hernandiaceae; CR). On Hateruma Island in the southern Ryukyus, many individuals of Polyalthia liukiuensis Hatus. (Annonaceae; CR; Fig. 4B) have been protected in the utaki (Hatusima, 1979; Tagawa and Miyagi, 1991). In fact, 20 out of 169 sites specified as important areas for in situ conservation of plant communities and plant species include the utaki in Okinawa Prefecture (Environment Agency of Japan, 1978, 1988). Although field surveys of plants in the utaki were conducted by the Okinawa Prefectural Board of Education (1978, 1979, 1980, 1981), the results of the surveys have not been fully incorporated into in situ conservation strategies at the administrative level (Shimabuku et al., 1991).

The open seashores in the Ryukyus can be primarily classified into two typical environments: sandy beaches, and slopes or cliffs of coral limestone. Many endangered and endemic plant species prefer in the latter environment, e.g., *Ligustrum tamakii* Hatus. (Oleaceae; CR; Fig. 4C), *Portulaca okinawensis* E.Walker et Tawada (Portulacaceae; CR; Fig. 4D), and *Solanum miyakojimense* T.Yamaz. et Takushi (Solanaceae; CR; Fig. 4E). However, shore protection and road works have been destroying these environments in the Ryukyus.

Because the islands of the Ryukyus have steep geological configurations and regularly receive large quantities of rainfall, mountain streams flood frequently. Accordingly, rheophilous plants, adapted to fluctuating water-levels with narrow and hairless leaves (van Steenis, 1981; Kato and Imaichi, 1991), are abundant in the Ryukyus, for example, Ainsliaea oblonga Koidz. (Compositae; VU; Fig. 4F) and Farfugium japonicum (L.) Kitam. var. luchuense (Masam.) Kitam. (Compositae; NT). These plants are considered optimal models for evaluating speciation, and some researchers have conducted detailed studies of the rheophytes of the Ryukyus (e.g., Nomura et al., 2006). Most of these rheophilous species are neo-endemic, and are not abundant. However, recent dam construction has completely destroyed stream environments, including the habitats of these rheophytic species in the Ryukyus. In fact, Viola stoloniflora Yokota et Higa being insular endemic species and found in only a certain stream side in "Yanbaru" on Okinawa Island (Violaceae, EW; Fig. 4G) has been thought to be extinct in the wild by dam construction (Yokota et al., 1988; Yokota, 1998; Ministry of Environment of Japan, 2007).

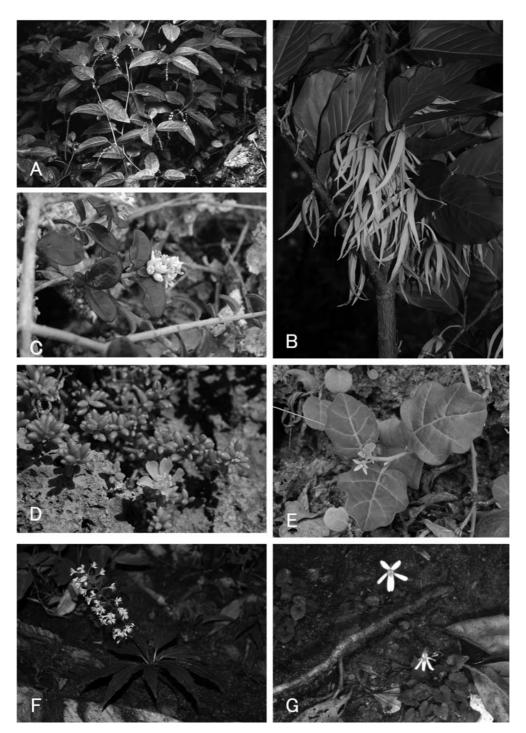


Fig. 4. Endangered plants found in specific environments in the Ryukyus. A. *Deeringia polysperma*; B. *Polyalthia liukiuensis* (photographed by K. Yasuda); C. *Ligustrum tamakii*; D. *Portulaca okinawensis*; E. *Solanum miyakojimense*; F. *Ainsliaea oblonga*; G. *Viola stoloniflora*.

Future study of endangered plants in the Ryukyus

Taxonomic study

Taxonomic data of the Ryukyu plants have been accumulated

by numerous botanists. However, new plant taxa and newly recorded plants are still being discovered, and taxonomic problems, including lack of consensus treatments, remain for some of the plants (e.g., Yokota, 1997; Tateishi, 1998).

Many plant species in the Ryukyus are common, or have related

species in other regions. Some species, such as *Disporum sessile* D.Don (Liliaceae; Fig. 5A), are thought to have migrated southward from Kyushu and other regions of Japan proper. Others, such as *Aeschynanthus acuminatus* Wall. ex DC. (Gesneriaceae; CR;

Fig. 5B) and *Ajuga pygmaea* A.Gray (Labiatae; Fig. 5C), have migrated northward through Taiwan. *Cyrtandra cumingii* C.B.Clarke (Gesneriaceae; Fig. 5E) is thought to have been derived from the Philippines, and *Phyllanthus liukiuensis* Matsum.

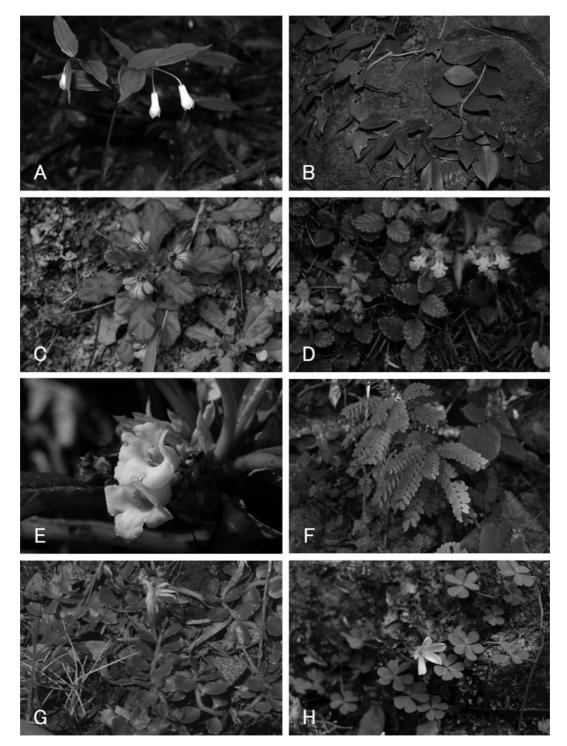


Fig. 5. Endangered Ryukyus plant species common to other regions. A. *Disporum sessile*; B. *Aeschynanthus acuminatus*; C. *Ajuga pygmaea*; D. *Suzukia luchuensis*; E. *Cyrtandra cumingii*; F. *Phyllanthus liukiuensis*; G. *Lobelia loochooensi*; H. *Oxalis exilis*.

ex Hayata (Euphorbiaceae; EN; Fig. 5F) is thought to have come from China (Hatusima, 1975). Taxonomic treatments, being generally accepted at present, of these species common to the Ryukyus and other regions may not always be correct. For example, *Phyllanthus liukiuensis* (Fig. 5F) has been treated as a common species between the Ryukyus and China (*P. leptoclados* Matsum. ex Hayata) before detail taxonomic reconsideration based on morphological comparisons performed by Kurosawa (1999).

A few plant species, such as *Lobelia loochooensis* Koidz. (Campanulaceae; Fig. 5G) and *Oxalis exilis* A.Cunn. (Oxalidaceae; Fig. 5H), are thought to be disjunctively distributed between the Ryukyus and Oceania at generic and species levels (Koidzumi, 1928; Ohwi, 1968; Hatusima, 1975; Murata 1992). However, detail taxonomic comparisons have little applied for plant taxa hypothesized to be disjunctively distributed between the Ryukyus and Oceania. Therefore, to better understand these endangered species, further global taxonomic comparison is required.

Distribution comparison

Some plants species are commonly endangered between the Ryukyus and its adjacent regions, for instance *Suzukia luchuensis* (Fig. 5D) are commonly endangered in Japan (VU) and Taiwan (VU). However, it is not necessary that all of endangered plant species in the Ryukyus are on the edge of extinction in other regions. For example, *Aeschynanthus acuminatus* (Fig. 5B) is recorded in only one place on Iriomote Island in Japan (Kobayashi and Kokubugata, 2004), but is relatively common in moist highland areas of Taiwan. In contrast, *Ajuga pygmaea* (Labiatae; Fig. 5E) is abundant in the Ryukyus but is treated as endangered in Taiwan (NT; Lu et al., 2000). This may indicate that isolated-marginal populations are easy to be threatened by human impacts. Therefore, global comparison at population and even genetic levels is also essential to better understand the biological nature of endangered species.

In conclusion, to improve our biological understanding of endangered species, further global taxonomic studies and distribution comparisons are needed. Also these studies should contribute to global natural history such as the Floristic Survey of the Earth (Iwatsuki, 1993).

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Literature Cited

- Aoki, B. 1913. A hand-list of Japanese and Formosan mammals. Annotationes Zool. Jpn. 8: 261-353.
- Boufford, D. E., Y. Hibi and H. Tada. 2004. Japan. *In* Hot Spots (rev.). Mittermeier, R. A., P. R. Gil, M. Hoffmann, J. Pilgrim, T. Brooks, C. G. Mittermeier, J. Lamooreux and G. A.B. da Fonseca (eds.), Cemex, Mexico City. Pp. 333-346.
- Environment Agency of Japan. 1978. The 2nd Basic Survey for Conservation of Natural Environments. Report on Special Plant Communities, Important Plant Communities in Japan. Envir. Agency Jpn., Tokyo (in Japanese).
- Environment Agency of Japan. 1988. The 3rd Basic Survey for Conservation of Natural Environments. Report on Special Plant Communities, "Important Plant Communities in Japan". Envir. Agency Jpn., Tokyo. (in Japanese).
- Hara, H. 1959. An outline of the phytogeography of Japan. *In* Distribution Maps of Flowering Plants. Hara, H. and H. Kanai (eds.), Inoue Book Co., Tokyo. Pp. 1-94.
- Hatusima, S. 1975. Flora of the Ryukyus (additions, corrections). Okinawa Assoc. Biol. Educ., Naha (in Japanese).
- Hatusima, S. 1979. A new species of *Polyalthia* (Annonaceae). Hokuriku J. Bot. 26: 86-87.
- Hatusima, S. 1980. The origin of flora in the Ryukyus. *In* History of Nature of Ryukyu. Kizaki, K. (ed.), Tsukiji Shokan, Tokyo. Pp. 113-123 (in Japanese).
- Hatusima, S. 2004. Flora of Kyushu. A list of ferns and flowering plants from Kyushu including the Amami Islands. Kagoshima Univ. Mus. Monogr. 1: 1-343 (in Japanese).
- Hatusima, S. and T. Amano. 1994. Flora of the Ryukyus, South of Amami Island (2nd edition). Biol. Soc. Okinawa, Nishihara (in Japanese).
- Hotta, M. 2003. Why there are many endangered plants in the area ranging from southern Kyushu to southwest islands. *In* Kagoshima Red Data Book (Plants). Kagoshima Pref. (ed.), Kagoshima Pref. Pp. 589-596 (in Japanese).
- Ito, A. and G. Matsumura. 1899. Tentamen Florae Lutchuensis. J. Sci. Coll. Imp. Univ. Tokyo 12: 261-541.
- Iwatsuki, K. 1993. Biology of Diversity. Iwanami Shoten Publ., Tokyo (in Japanese).
- Kato, M. and R. Imaichi. 1991. Leaf anatomy of tropical fern rheophytes, with its evolutionary and ecological implications. Can. J. Bot. 70:165-174.
- Kimura, M. 1996a. Quaternary paleogeography of the Ryukyu Arc. J.

Geography 105: 259-285 (in Japanese with English abstract). Kimura, M. 1996b. Paleogeography of the Ryukyu Arc. Chikyu

Monthly 18: 488-494 (in Japanese). Kizaki, K. and I. Oshiro. 1977. Palaeogeography of the Ryukyu Islands.

- Marine Sci. Month. 9: 542-549 (in Japanese with English abstract).
- Koidzumi, G. 1928. Plantae novae Amami-Ohsimensis nec non insularum adjacentium. Kagoshima.
- Kobayashi, S. and G. Kokubugata. 2005. Rediscovery of *Aeschynanthus* in Japan. Bunrui 5: 43-44 (in Japanese with English abstract).
- Kurosawa, T. 1999. Genus *Phyllanthus*. In Flora of Japan vol. IIC, Iwatsuki, K., D. E. Boufford and H. Ohba (eds.), Kodansha, Tokyo. Pp. 4-7.
- Lu, S.-Y., S.-J. Moore, C.-I Peng and T.-H. Hsieh. 2000. Rare and endangered plants in Taiwan. vol. 5. Twn. Council Agricul. Taipei (in Chinese with Latin name).
- Masamune, G. 1951a. Enumeratio Tracheophytarum Ryukyu Insularum I. Sci. Rep. Kanazawa Univ. 1: 22-54.
- Masamune, G. 1951b. Enumeratio Tracheophytarum Ryukyu Insularum II. Sci. Rep. Kanazawa Univ. 1: 167-199.
- Masamune, G 1953. Enumeratio Tracheophytarum Ryukyu Insularum III. Sci. Rep. Kanazawa Univ. 2: 87-114.
- Masamune, G 1954. Enumeratio Tracheophytarum Ryukyu Insularum IV. Sci. Rep. Kanazawa Univ. 2: 1-59.
- Masamune, G 1955a. Enumeratio Tracheophytarum Ryukyu Insularum V. Sci. Rep. Kanazawa Univ. 3: 101-182.
- Masamune, G. 1955b. Enumeratio Tracheophytarum Ryukyu Insularum VI. Sci. Rep. Kanazawa Univ. 3: 253-338.
- Masamune, G 1955c. Enumeratio Tracheophytarum Ryukyu Insularum VII. Sci. Rep. Kanazawa Univ. 4: 45-134.
- Masamune, G 1956. Enumeratio Tracheophytarum Ryukyu Insularum VIII. Sci. Rep. Kanazawa Univ. 4: 201-280.
- Masamune, G 1957. Enumeratio Tracheophytarum Ryukyu Insularum IX. Sci. Rep. Kanazawa Univ. 5: 85-121.
- Masamune, G 1964. Enumeratio Tracheophytarum Ryukyu Insularum X. Sci. Rep. Kanazawa Univ. 9: 119-154, pls 1.
- Ministry of the Environment of Japan. 2007. Red Data List (Plants). http://www.biodic.go.jp/rdb/rdb_f.html. Accessed on 18 February 2010 (in Japanese with Latin names).
- Miyawaki, A. 1977. Nature and Plants in Japan. *In* Flora of Japan. Miyawaki, A. (ed.), Gakken, Tokyo. Pp. 1-32 (in Japanese).
- Murata, J. 1992. Morphology and chromosome number of *Lobelia* loochooensis Koidz. J. Jpn. Bot. 67, 292-285.
- Nakamura, K., R. Suwa, T. Denda and M. Yokota. 2009. Geohistorical and current environmental influences on floristic differentiation in the Ryukyu Archipelago, Japan. J. Biogeography 36: 919-928.
- Niiro, Y. and Y. Miyagi. 1988. Forest of Yanbaru, now and old time. *In* Islands in Nirai and Kanai, Nature of Okinawa is now. Ikehara, S. and Y. Kato (eds.), Tsukiji Shokan, Tokyo. Pp. 127-148 (in

Japanese).

- Nomura, N., H. Setoguchi and T. Takaso. 2006. Functional consequences of stenophylly for leaf productivity: comparison of the anatomy and physiology of a rheophyte, *Farfugium japonicum* var. *luchuense*, and a related non-rheophyte, *F. japonicum* (Asteraceae). J. Plant Res. 119: 645-656.
- Ohwi, J. 1968. A new species of *Eriachne* from the Ryukyus Islands. J. Jpn. Bot. 43: 137-138.
- Okada, Y. and K. Kiba. 1924. Study on distribution of animals in Japan. Zool. Mag. 43: 320-351.
- Okinawa Prefectural Board of Education (ed.). 1978. Report on Forests of Shrines, Temples and Utakis in Okinawa Prefecture I. Okinawa Pref. Board Educ., Naha.
- Okinawa Prefectural Board of Education (ed.). 1979. Report on Forests of Shrines, Temples and Utakis in Okinawa Prefecture II. Okinawa Pref. Board Educ., Naha.
- Okinawa Prefectural Board of Education (ed.). 1980. Report on Forests of Shrines, Temples and Utakis in Okinawa Prefecture III. Okinawa Pref. Board Educ., Naha.
- Okinawa Prefectural Board of Education (ed.). 1981. Report on Forests of Shrines, Temples and Utakis in Okinawa Prefecture IV. Okinawa Pref. Board Educ., Naha.
- Ota, H. 1998. Geographic patterns of endemism and speciation in amphibians and reptiles of the Ryukyu Archipelago, Japan, with special reference to their paleogeographical implications. Res. Popul. Ecol. 40: 189-204.
- Sakaguchi, S. 1924. Comprehensive List of Plants of Okinawa. Ishizuka Shoten, Naha.
- Shimabuku, K. 1984. History of flora in Okinawa Prefecture. *In* Plants, Minutes of the National Conference. Soc. Biol. Sci. Educ. Jpn. (ed.), Soc. Biol. Sci. Educ. Jpn, Tokyo. Pp. 23-32.
- Shimabuku, K. 1997. Check List Vascular Flora of the Ryukyu Islands. Kyushu Univ. Press, Fukuoka.
- Shimabuku, K., K. Shinjo and M. Yokota. 1991. Flora in Southwest Islands. *In* Report on Essential Conditions for Conservation of Wild Species in Southwest Islands in Fiscal 1990. Nat. Conserv. Bureau, Envir. Agency Jpn. (ed.), WWF Japan, Tokyo. Pp. 39-50.
- Tagawa, H. and Y. Miyagi. 1991. Vegetation of the southwest islands and its features and conservation. *In* Report on Essential Conditions for Conservation of Wild Species in Southwest Islands in Fiscal 1990. Nat. Conserv. Bureau, Envir. Agency Jpn. (ed.), WWF Japan, Tokyo. Pp. 122-183.
- Takamine, H. 1952. Flora of the Yaeyama Islands. Ryukyu Forest. Res. Inst., Naha.
- Tateishi, Y. 1998. Flora of Okinawa. Planta (Tokyo) 55: 4-9 (in Japanese).
- Ujiié, H. 1990. Geological history of the Ryukyu Island Arc. *In* Nature of Okinawa, Geomorphology and Geology. Ujiié, H. (ed),

Hirugisha, Naha. Pp. 251-255 (in Japanese).

- van Steenis, C. G. G. J. 1981. Rheophytes of the World. Sijthoff and Noordhoff, Alpen aan den Rijn, the Netherlands.
- Walker, E. H. 1976. Flora of Okinawa and the Southern Ryukyu Islands. Smithsonian Inst. Press, Washington, D.C.
- Yamashina, Y. 1955. Border Lines of Distribution of Birds in the Ryukyu Islands. Rep. Jpn. Biogeogr. Assoc. 16-19: 371-375.
- Yokota, M. 1997. Small plants in Okinawa. *In* Knowing Nature of Okinawa. Ikehara, S. and Y. Katoh (eds.), Tsukiji Shokan, Tokyo. Pp. 139-155.

Yokota, M. 1998. Endangered plant species in Okinawa. Planta (Tokyo)

55: 10-18 (in Japanese).

- Yokota, M., S. Higa, H. Yoshioka and K. Shimabuku. 1988. *Viola stoloniflora* (Violaceae), a new species from the Ryukyus. Bot. Mag. Tokyo 101: 1-8.
- Yokota M. T. Kanemoto and G Kokubugata. 2007. Endangered plant species in the Ryukyu Archipelago I What is endangered species in the Ryukyus. *In* Conservation of Plant Diversity in Japanese Botanic Gardens. Ishida, G, T. Iwashina, T. Konishi, Y. Kurashige, J. Oikawa and T. Yukawa (eds.), Jpn. Assoc. Bot. Gard., Tokyo; Tsukuba Bot. Gard.; Bot. Gard. Conservation Intl., Richmond. Pp. 220-225.