Introduction

Biodiversity in Japan

The Japanese archipelago is located on the east coast of the Asian continent. The diversity of its climate, from subarctic to subtropical, with high humidity and precipitation throughout has produced a rich biodiversity (Iwatsuki et al. 1993–2016, Ohwi 1965). The connection with the continent several times before the last glacial maximum may have promoted migration from north and south to produce a flora with mixed subarctic, temperate, and subtropical elements. By contrast, its isolation after the last glacial maximum may have stimulated the phylogenetic differentiation of taxa from the continental mother taxa. However, this biodiversity hotspot (Mittermeier et al. 2004) is also one of the most populous regions in the world. The population pressure poses threats to wild ecosystems both directly via exploitation and indirectly via environmental degradation. More than 2000 species of flora are now threatened (Ministry of Environment of Japan 2012).

Definition of Japanese native fruit trees in this review

Japan has about 5000 species of seed plants (Kajita 2003). About 1000 species are woody, either trees, shrubs, or vines (Satake et al. 1989), and these include many fleshy fruit and nut species. In addition, some species were introduced in the Middle Ages or before. Formerly, some commercial fruit species, including Pyrus pyrifolia (Burm. f.) Nakai and Amygdalus persica L. (=Prunus persica (L.) Batsch), were thought to have originated from native plants (e.g., Kikuchi 1948). Now they are considered to have been introduced in pre-modern times (“archaeophytes”), though empirical confirmation is still rare (e.g., Iketani et al. 2010a, 2012). These introduced plants (listed in Table 1) are excluded from subsequent treatment in this review.

In a broad sense, all non-poisonous fleshy fruits and nuts are edible, and people might have eaten them, especially during times of famine. However, this review covers only plants that were eaten regularly. It excludes plants used only as folk medicine or to produce fruit liquor.

This review covers species supported by archeological evidence (e.g., Terasawa and Terasawa 1981), old historical documents (e.g., Fujiwara et al. 927), or ethnological information (e.g., Sarashina and Sarashina 1976); species that are now commercially grown or marketed even at a minor scale; and species with edible congeners in other regions of the world. In all, 70 genera are included (Table 2).

Usage of scientific names and Romanization of Japanese in this review

As this review lists many species unfamiliar to breeding science and horticulture, a simple standard for the usage of scientific names is necessary. The review uses names adopted in Yonekura (2012), which is a thorough compilation of the scientific names of vascular plants in Japan, including recent nomenclatural changes after Iwatsuki et al. (1993–2016), and which is now the de facto standard. Full details, including updates, are available on line (Yonekura and Kajita 2003–).
Table 1. Fruit trees introduced to Japan in pre-modern times

| Species                      | Period of Introduction | Literature1 (introduced) | Literature1 (native) |
|------------------------------|------------------------|---------------------------|----------------------|
| Ginkgo biloba L.             | 13–14th Century         | Hori and Hori (1997)      |                      |
| Ficus carica L.              | 17th Century?           | Kikuchi (1948)            |                      |
| Eriobotrya japonica (Thunb.) Lindl. | Prehistoric           | Kobayashi (1990)          | Kikuchi (1948)       |
| Malus asiatica Nakai         | 12th Century?           | Kitamura (1979)           |                      |
| Armeniaca vulgaris Lam. (Prunus armeniaca L.) | Prehistoric     | Kikuchi (1948), Kitamura (1979), Kobayashi (1990) | |
| Armeniaca mume (Siebold et Zucc.) de Vriese (Prunus mume Siebold et Zucc.) | Prehistoric | Kitamura (1979), Kobayashi (1990) | Kikuchi (1948) |
| Prunus salicina Lindl.        | Prehistoric             | Kobayashi (1990)          | Kikuchi (1948)       |
| Amygdalus persica L. (Prunus persica (L.) Batsch. | Prehistoric | Kitamura (1979), Kobayashi (1990) | Kikuchi (1948) |
| Pyrus pyrifolia (Burm.f.) Nakai | Prehistoric           | Kobayashi (1990)          | Kikuchi (1948)       |
| Diospyros kaki Thunb.        | 7th Century?            | Kobayashi (1990)          | Kikuchi (1948)       |
| Vitis vinifera L.            | 6–7th Century           | Kobayashi (1990)          |                      |
| Ziziphus jujuba Mill.        | 6–7th Century           | Kobayashi (1990)          |                      |
| Citrus spp.                  | 12th Century?           | Kikuchi (1948)            |                      |
| Punica granatum L.           |                        |                           |                      |

1 Literature supporting the hypothesized origin.

detailed (e.g., using the ranks of subspecies and variety) owing to recent reclassifications based on the broad species concept. This review uses detailed names only when necessary. Otherwise, a simple binomial combination of genus and species is used for convenience and simplicity. Romanized transcriptions of Japanese names mostly follow the Library of Congress and American Library Association (2012), with a few exceptions such as proper nouns.

**Regional usage of fruits and nuts**

Japanese fruit and nut trees grow from the subarctic to the subtropics. The Ainu people, the indigenous inhabitants of subarctic Hokkaidō, ate fruits of *Empetrum nigrum* L. and *Vaccinium oxyccocos* L., which grow in both uplands and lowlands. They also ate fruits of *Phellodendron amurense* Rupr., *Malus baccata* (L.) Borkh. var. mandshurica (Maxim.) C. K. Schneid., *Padus avium* Mill. (=*Prunus padus* L.), *Rosa rugosa* Thunb., *Rubus idaeus* L., and *Sambucus racemosa* L., all of which are distributed in the upper-elevation deciduous forest zone and grow widely in the lowlands of Hokkaidō. Species of *Ribes, Malus, Rubus, Lonicera* and *Vaccinium* might have also been eaten.

These plants also grow at high altitudes in temperate Honshū but were rarely or never used there, possibly because their habitats were remote from settlements. One exception is *Vaccinium uliginosum* L., which grows wild above 1500 m a.s.l. in volcanic desert vegetation on Mount Asama and surrounding areas, where local people gathered wild fruits for decades after World War II (Koike and Miyagawa 1974). This practice is now prohibited, because most of the habitat is protected. Another exception is *Pyrus ussuriensis* var. *ussuriensis* in the upper deciduous forest zone in northern Honshū (Iwate Prefecture). Trees introgressed with archaeophytic *P. pyrifolia* grow wild in this area as well as in cultivation (Iketani *et al.* 2010a, Katayama and Uematsu 2006). Whether this species began to be used before or after introgression is still unknown. This is discussed in more detail by Katayama (2016) in this issue.

Archaeological studies of the utilization of plants in the subtropical Ryūkyū Islands were limited until recent reports of the remains of seeds or stones of many species (e.g., Omatsu and Tsuji 2001). On the other hand, ethnological studies are abundant (e.g., Amano 1982, Sato and Nohara 1997, Tawada 1982). According to these studies, people may have eaten many tree fruits, especially during times of famine (Table 2).

Nut species have been more generally utilized than fleshy fruit species since the hunting-and-gathering age (Taneishi 2014). The most important reason is that nuts are rich in carbohydrates or fats and are thus highly nutritious. Hatakeyama (1989) estimated that wild nuts might have supplied about one-third of the daily energy intake during winter in mountainous settlements of the Kitakami Mountains, where the harvest of cereal crops had been always insufficient. Another reason is that nut genera such as *Quercus* and *Castanea* are usually dominant in vegetation, and people can easily gather nuts in abundance. Although *Aesculus* species contain saponins and most *Quercus* species contain tannins, people have used them for food by leaching out these components. Nuts have been utilized in almost all areas from Hokkaidō to the Ryūkyū Islands. The Ainu people used only nuts of *Quercus*, although *Aesculus* is common in southern Hokkaidō (Watanabe 1975). People continued to eat wild nuts until the 1940s in some regions (Hatakeyama 1989, in the Kitakami Mountains; Sato and Nohara 1997, in...
Table 2. List of Japanese native fruit and nut species. The arrangement of families and scientific names follows Yonekura (2012)

| Family            | Genus         | Edible part | Growth Form | Life Form | Vegetation Zone | Floristic Region | Beginning of Cultivatation | Congeneric cultivated species | Number of species | Number of threatened taxon | Representative (possibly) utilized species | Literature |
|-------------------|---------------|-------------|-------------|-----------|----------------|------------------|--------------------------|----------------------------|-----------------|---------------------------|-------------------------------------------|------------|
| Cycadaceae        | Cycas         | N           | S           | E         | ST             | A, Oc            | +                        | 1                          | 7              | 1                         | C. revoluta Thunb.                           | Sa, Ta     |
| Pinaceae          | Pinus         | N           | S, T        | E         | Sa-ST          | N                | +                        | 7                          | 1              | 1                         | P. koraiensis Siebold et Zucc.               |            |
| Cephalotaxaceae   | Cephalotaxis  | N           | S, T        | E         | Tm-W           | EA               |                         | 8                          |                |                           | C. harringtonia (Knight ex Forbes) K.Koch    | W          |
| Taxaceae          | Torreya       | N           | S, T        | E         | Tm-W           | W                |                          | 1                          |                |                           | T. nucifera (L.) Siebold et Zucc.            | T, W       |
| Lauraceae         | Cinnameum     | F           | S, T        | E         | ST             | T                |                          | 7                          | 2              | 1                         | C. yahnakkei H.Ohba                           | Sa         |
|                  | Litsea        | F           | S, T        | E         | W-T            | A                |                          | 9                          | 1              | 1                         | L. coreanii H.Lév.                            | Sa         |
| Pandanaceae       | Pandanus      | F           | T           | E         | ST             | OW               |                          | 1                          | 1              |                           | P. odoratissumus L.f.                         |            |
| Lardizabalaceae   | Akebia        | F           | V           | D         | Tm-W           | EA               | R                        | 2                          |                |                           | A. quinata (Houtt.) Deeene.                  | F, Ma      |
|                   | Stauntonia    | F           | V           | E         | W               | EA               | R                        | 1                          |                |                           | S. hexaphylla (Thunb.) Deeene.               | F          |
| Grossulariaceae   | Ribes         | F           | S           | D         | Tm             | N                |                          | + 9 3                      |                |                           | R. japonicum Maxim., Ma, S                   |            |
| Vitaceae          | Ampelopsis    | F           | V           | D         | E              | Tm-W             | AA                       | 4                          |                |                           | A. glandulosa (Wall.) Momiyi.                | W          |
|                   | Vitis         | F           | V           | D         | Tm-ST          | N                | R                        | + 5 2                      |                |                           | V. coignetiae Pulliat ez Planch.             | Hk, Om, S, T, Ta |
| Rosaceae          | Amelanchier   | F           | S           | T         | D              | Tm             | N                        | + 1                        |                |                           | A. asiatica (Siebold et Zucc.)               | Endl. ex Walp. |
|                   | Cerasus       | F           | T           | D         | Tm             | W                | EU                       | + 10 4                     |                |                           | C. jasminiflora Siebold ex Koidz. H. Ohba    |            |
|                   | Rhododendron  | F           | T           | D         | Tm             | N                |                          | + 2 2                      |                |                           | C. hirsuta Maxim.                            | S          |
|                   | Rubus         | F           | S           | D         | Tm             | N                |                          | + 5 2                      |                |                           | M. toringo Borkh.                            |            |
| Padus             | F             | T           | D         | Tm        | N                |                          | + 4                        |                            |                |                           | P. avium Mill.                               | Ai         |
| Pyrus             | F             | T           | D         | Tm        | N                |                          | + 2                        |                            |                |                           | P. ussuriensis Maxim.                         | Ma         |
| Rhododendron      | N             | S           | E         | W         | EA              |                 |                          | 1                          |                            |                           | R. indica (L.) Lindl.                         | Sa, Ta, W |
| Rosa              | F             | S           | D         | Tm         | W               | N                |                          | 12 2                       |                            |                           | R. rugosa Thunb.                             | Fu, Hk, S |
| Rubus             | F             | S           | D         | Tm         | N                |                          | + 44                       |                            |                |                           | R. idaeus L.                                 | F, S, Sa, T, Ta |
| Sorbus            | F             | S           | T         | D         | Tm             | N                |                          | + 4                        |                            |                           | S. commixta Hedl.                             |            |
| Elaeagnaceae      | Elaeagnus     | F           | S, T, V    | D         | E              | Tm-W             | N                | + 16 5                     |                            |                           | E. multiflora Thunb.                          | Ma, S, T, Sa, Ta |
| Rhamnaceae        | Berchemia     | F           | S           | T         | D              | Tm-W             | W                | 5                          |                            |                           | B. linearis (L.) DC.                          | Ta         |
| Sageretia         | F           | S           | T         | D         | E              | W-ST             | W                | 1                          |                            |                           | S. thou (Osbeck) M.C. Johnst.                | Ta         |
| Moraceae          | Bloussonetia  | F           | S           | T         | D              | Tm-W             | EA               | 3                          |                            |                           | B. papyrifera (L.) f. Hér. ex. Vent.         | Om, W       |
| Morus             | F           | S           | T         | D         | Tm             | W                | AA               | + 4 1                      |                            |                           | F. erecta Thunb.                             | F, T, Ta, W |
| Fagaceae          | Castanopsis   | N           | T           | D         | Tm-W           | N                |                          | 1                          |                            |                           | C. sieboldii (Makino) Hatus. ex Om, M, Ta, W |            |
|                   | Castanea      | N           | T           | E         | W              | EA               | 2                            |                           |                           | T.Yamaz. et Mashiba                   |            |
| Fagus             | F             | T           | D         | Tm        | N                |                          | 2                            |                           |                           | F. crenata Thunb.                            | M, W       |
| Lithocarpus       | F             | T           | E         | W-T       | AA               |                          | 2                            |                           |                           | L. edulis (Makino) Nakai                    | F, M, Om, Ta, W |
| Quercus           | N             | T           | D         | Tm         | W               | N                | 15 1                        |                           |                           | C. crispis Blume, C. serrata                | Fu, Ht, M, Om, S, T, Ta, W                   |
| Myricaceae        | Myrica        | F           | T           | E         | W              | N                |                          | + 2                        |                            |                           | M. rubra Laut.                                | Om, S, Ta, T, W |
| Juglandaceae      | Juglans       | N           | T           | D         | Tm              | N                |                          | + 1                        |                            |                           | J. manchurica Maxim.                          | Fu, Hk, Ma, M, S, T, W |
| Betulaceae        | Corylus       | N           | S           | D         | Tm              | N                | + 2                        |                            |                           | C. heterophylla Fisch. ex Besser             | F, W       |
| Celastraceae      | Euonymus      | N           | S, T, V    | D         | Tm             | W               | 19 6                       |                            |                           |                           | E. carnosus Hems.                             | Ta         |
| Gymnosporia       | N             | S           | E         | ST-T      | W               | 1                            | 1                            |                           |                           | G. diversifolia Maxim.                      | Sa         |
**Table 2. (continued)**

| Family               | Genus            | Representative (possibly) utilized species | Literature 10 |
|----------------------|------------------|--------------------------------------------|---------------|
| Elaeocarpaceae       | Elaeocarpus      | E. japonicus Siebold et Zucc. Om, Ta       |                |
| Euphorbiaceae        | Mallotus         | M. japonicus (L.f.) Müll.Arg. W           |                |
| Phyllanthaceae       | Antidesma       | A. japonicum Siebold et Zucc. Ta          |                |
| Bischofia            | Bischofia        | B. javanica Blume Sa, Ta                  |                |
| Salicaceae           | Idesia           | I. poplycarpa Maxim. L, Om, Ta            |                |
| Calophyllaceae       | Calophyllum      | C. inophyllum L. Ta                        |                |
| Combretaceae         | Terminalia       | T. catappa L. Ta                          |                |
| Myrtaceae            | Syzgium         | S. buxifolium Hook. et Arn. Ta            |                |
| Anacardiaceae        | Choerospondias   | C. axillaris (Roxb.) B.L.Burtt et A.W.Hill |                |
| Sapindaceae          | Aesculus         | A. turbinata Blume Ht, M, W               |                |
| Rutaceae             | Phellodendron    | P. amurense Rupr. Fu, Hk                  |                |
| Toddalia             | Toddalia         | T. asiatica (L.) Lam. Ta                  |                |
| Malvaceae            | Firmiana         | F. simplex (L.) W.F.Wight                 |                |
| Santalaceae          | Buckleya         | B. lanceolata (Siebold et Zucc.) Miq.     |                |
| Cornaceae            | Cornus           | C. kousa Buerger ex Hance                 |                |
| Sapotaceae           | Planchonella     | P. obovata (R.Br.) Pierre                 |                |
| Adinandra            | Adinandra        | A. ryukuensis Masam. Ta                   |                |
| Ebenaceae            | Diospyros        | D. japonica Siebold et Zucc. Ma, Sa, Ta   |                |
| Primulaceae          | Ardisia          | A. quinquegona Blume, A. sieboldii Miq.   |                |
| Theaceae             | Camellia         | C. japonica L. Sa, W                      |                |
| Symplocaceae         | Symplocos        | S. sp. (undetermined) Hook. et Arn.       |                |
| Actinidiaceae        | Actinicia        | A. arguta (Siebold et Zucc.) Planch. ex Miq.|            |
| Sauraria             | Sauraria         | S. tristyla DC. Ta                        |                |
| Ericaceae            | Empetrum         | E. nigrum L. Fu, Hk                       |                |
| Vaccinium            | Vaccinium        | V. oxycoccos L., V. oldhamii Miq., V. uliginosum L. |          |
| Boraginaceae         | Ehretia          | E. dicksonii (Yonekura 2012).            |                |
| Goodeniaceae         | Scaevola         | S. taccada (Gaertn.) Roxb. Ta             |                |
| Adoxaceae            | Sambucus         | S. racemosa L. Ai                         |                |
| Viburnum             | Viburnum         | V. suspensum Lind.                        |                |
| Caprifoliaceae       | Lonicera         | L. caerulea (Yonekura 2012).             |                |
| total                |                  |                                            |               |

1: F, fleshy part; N, nut. 2: S, shrub; T, tree; V, vine. 3: D, deciduous; E, evergreen. 4: A, subartic; T, temperate; W, warm temperate; ST, subtropical; T, tropical. 5: A, Asian; AA, Asian-American; EA, East Asian; EU, Eurasian; N, Northern Hemisphere; OW, Old world; Oc, Oceania; T, Tropical. 6: O, Old (prehistoric); R, recently. 7: Presence of congeners cultivated in other countries. 8: Number of species in the germplasm of the Japan Institute of Plant Breeding (2012). 9: Ministry of Environment of Japan (2012). 10: Ai, Ainu Museum (2015); Am, Amano (1982); A, Fujiwara et al. (927); Fu, Fukuoka (1995); Hk, Hokkaido Institute of Public Health (2015); Ht, Hatakeyama (1989); L, Liu (1988); M, Matsuyama (1982); Om, Omatsu and Tsuji (2001); S, Sarashina and Sarashina (1976); Sa, Sato and Nohara (1997); T, Terasawa and Terasawa (1981); Ta, Tawada (1982); W, Watanabe (1975).
the Ryūkyū Islands).

Large seeds of some non-amentiferous species such as *Terminalia* and *Euonymus* have been used in the Ryūkyū Islands but their dietary use is almost unknown in mainland Japan (Table 2). It is perhaps because they commonly grow in that Islands. Other large-seeded species in addition to the Fagaceae, *Juglans*, and *Aesculus* may also have been eaten in Honshū and Hokkaidō if thinking the high dietary value of seeds.

### Domestication of Japanese native wild fruit trees

#### Domestication in pre-modern times

Humans arrived in Japan around 35,000 years BP or later (Hudson 2007, Keally 2009). During the hunting-and-gathering age, people gathered and ate native fruits, as well as other wild plant and animal foods. These wild plants continued to be utilized after the beginning of agriculture (Terasawa and Terasawa 1981), but only a few became domesticated, such as the vegetable species *Cryptotaenia canadensis* (L.) DC. subsp. *japonica* (Hassk.) Hand.-Mazz., *Petasites japonicus* (Siebold et Zucc.) Maxim., and *Dioscorea japonica* Thunb. Although not important vegetables now, they might have been eaten before the modern age.

Among the native species listed (Table 2), *Castanea crenata* is the only one to become a major cultivated crop. It is also one of the few species domesticated in pre-modern times, along with *Myrica rubra* and *Pyrus ussuriensis* var. *ussurienensis*. Cultivation of *C. crenata* may have begun in prehistoric times, and its utilization for timber was also important in ancient times (Amino 2001). *Myrica rubra* grows wild in evergreen forests in middle and western Japan and has long been used as firewood. Its cultivation as a fruit tree may have begun in the late Edo period (19th century). However, the present leading cultivars are said to have been introduced from China (Wada 2000).

This paucity of cultivated native species was perhaps influenced by the presence of many introduced fruit trees. Large fleshy fruits are lacking among Japanese native species. Mammal-dispersed fruits, which are usually larger than bird-dispersed fruits, are rare among Japanese temperate species, occurring only in *Akebia*, *Stauntonia*, *Actinidia*, *Pyrus*, *Chaenomeles*, and *Cornus kousa*. The first three have been locally commercialized in modern times, as described below. Subtropical genera with mammal-dispersed fruits, such as *Syzygium* and *Toddalia*, have not been cultivated.

#### Recent domestication

High economic growth and cultural westernization after World War II increased the diversity of diet and foodstuffs in Japan. The consumption of fruits increased in both quantity and quality (such as jams, juices, and confectioneries). However, consumption stagnated and fell after the high economic growth ended, and some production areas tried to convert existing crops into new products (Uchiyama 1996). In areas depopulated by the high economic growth, various projects for reactivation of the local economy have been attempted since the 1960s. In the agricultural sector, fruit crops were developed as specialty products and matched with tourism strategies. Fruits and nuts are produced not only as regular products, but also as value-added products for gifts and souvenirs.

Although major fruits such as citrus, apple, and table grape are grown for product differentiation strategy, some minor fruits such as introduced berry and tropical fruit species also have a role. The most specialized products are newly domesticated native fruit trees. Among 8 genera with 11 species (Table 3), *Vitis coignetiae* and *Actinidia* spp. (*A. arguta*, *A. polygama* and *A. rufa*) have congeneric major fruit species, *V. vinifera* and *A. delicosa*, respectively. *Vaccinium* also has many cultivated species, including blueberry and cranberry, in temperate and subarctic climate zones in other countries. *Lonicera caerulea* is also cultivated in

### Table 3. New commercial cultivation of Japanese native fruit trees

| Species | Production (t) | Representative Regions | Source |
|---------|---------------|------------------------|--------|
|         | 2003 | 2012 |                      |        |
| Akebia quinata and *A. trifoliata* | 25.7 | 8.9 | Yamagata, Ehime, Akita | 1) |
| *Stauntonia hexaphylla* | 135.6 | 186.7 | Iwate, Yamagata, Hokkaidō | 2), 3) |
| *Vitis coignetiae* | | | Hokkaidō, Aomori | 4) |
| *Rosa rugosa* | | | Aomori | 4) |
| *Elaeagnus multiflora* | | | Fukushima, Nagano, Nara | 5), 6), 7) |
| *Vaccinium oldhamii* | | | Fukushima, Kagawa, Yamagata | |
| *Actinidia arguta* | 13.1 | 10.6 | Akita | 8) |
| *A. polygama* | 1.9 | — | Miyazaki | 8) |
| *A. rufa* | 60.0 | 90.2 | Hokkaidō, Aomori | 8) |

Production data were drawn from the website of the Ministry of Agriculture, Forestry, and Fisheries (http://www.e-stat.go.jp/SG1/estat/List.do?id=00001129267). Information on other plants was based on the following websites: 1) http://www.nube.jp/mube.html, 2) http://www.n-slow.com/item_detail/itemCode.su-1591/, 3) http://www.umai-aomori.jp/know/sanchi-report/146.phtml, 4) http://www.morikaju.jp/kudamono-natu.html, 5) http://www.nico2farm.jp?page_id=21, 6) http://www.iijan.or.jp/oishii/products/fruit/post-1424.php, 7) http://natsuhaze.com/index.html, 8) http://www.yappamiyazaki.jp/store/search.php?codeNumber=1265765213
Russia and North America. Recently, Japanese cultivars were introduced into the USA and their adaptability to the climate was evaluated (Hummer et al. 2012, Thompson and Chavanalikit 2002). The other five genera do not have any other major species grown for food in other countries. The most notable are *Akebia* (*A. quinata* and *A. trifoliata*) and *Stauntonia* (*S. hexaphylla*), both endemic to East Asia (Takhtajan 1986), and thus almost unknown in the West as fruit.

As these native species have a niche market, both their area and quantity of production are limited, and production has fluctuated. Except for *Vitis* *coignetiae* and *Lonicera caerulea*, the commercial cultivation of these native plants is extremely limited, possibly with as few as half a dozen growers at the fewest.

Although species of *Pinus*, *Amelanchier*, *Cornus*, *Crataegus*, and *Sorbus* are cultivated in other parts of the world, Japanese species are not utilized. They may have been eaten by indigenous people, but archaeological or ethnological evidence is lacking. The rarity of *Crataegus* and *Sorbus* (except for *S. commixta*) in Honshū and further south may be a reason. Seed of *Pinus* has been imported from Korea since the Middle Ages (von Verschuer 2006). However, there is no evidence for the utilization of Japanese species. Only imported seeds might have been consumed, and historical references (e.g., Minamoto 930s) might have been nothing more than citations from the Chinese literature. Although *Pinus* is common in the Japanese flora, *P. koreensis*, which is the main edible species, is rare and may have been neither cultivated nor collected in the wild.

**Future conservation**

Horticultural and breeding studies have included Japanese wild species of *Vitis*, *Malus*, *Pyrus*, and *Actinidia*, which are congeneric with major fruit tree species, along with other wild species (e.g., Janick and Moore 1996, Moore and Ballington 1990). However, the conservation of these wild species, both *in situ* and *ex situ*, is inadequate: 84 taxa in *Table 2* are nominated in the Japanese National Red List (Ministry of Environment of Japan 2012), including two species of *Vitis* (*V. amurensis* and *V. romanetii*), two of *Malus* (*M. hupehensis* and *M. spontanea*), and two of *Pyrus* (*P. calleryana* and *P. ussuriensis*). The Red List only contains threatened plants and has no legal standing for the prohibition of picking and selling. *Ex situ* conservation is also precarious. Until recently, the NIAS Genebank, which is the Japanese national genebank for agricultural crops, has held few or no germplasm accessions of these native species. Other facilities such as botanical gardens are in a similar situation. To address this lack, extensive explorations have been performed for *Pyrus* (Iketani et al. 2005, 2006, 2008, Iketani and Mase 2009), *Malus* (Iketani et al. 2006, 2007, 2008, Iketani and Mase 2009, 2013, 2016), and *Vitis* (Iketani et al. 2014) in the past 10 years.

Recent advances in molecular population genetics have revealed that a species can be genetically differentiated when a genetic barrier among subpopulations exists. Therefore, a widely distributed species is likely to be differentiated where geographical barriers to gene flow, such as seas or high mountains, intervene, unless long-distance dispersal is possible. For example, *Pyrus ussuriensis* (*sensu lato*) is widely distributed in northeastern China, eastern Russia (Amur to Primorsky), the Korean Peninsula, and central and northern Honshū. Iketani et al. (2010a, 2012) revealed that native populations on the Asian continent, in central Honshū, and in northern Honshū are highly differentiated. Thus, it will be necessary to evaluate genetic differentiation within taxa to maximize the collection of genetic diversity.

Conservation of minor plants is more problematic, especially for the purpose of agricultural genetic resources. Their economic importance is limited. Basic information such as past ethnological utilization is necessary, as well as research for agricultural and industrial utilization. For example, Matsushima et al. (2013) newly reported several edible uses of plants on the basis of interviews in a mountain village in central Honshū. For the conservation of these species, several explorations have been performed (Iketani et al. 2010b, Ito 2011, 2012, Ito and Sugawara 2006, 2007, 2008, 2009, 2010). The collected germplasm is conserved in NIAS Genebank (http://www.gene.affrc.go.jp/index_en.php), along with the abovementioned *Pyrus*, *Malus*, and *Vitis* germplasm.

Preservation of collected germplasm also has difficulty because most of fruit trees have to be stored in the form of living plants. As it costs enormously, only national or international organizations have been capable to preserve fruit tree genetic resources. However, smaller organizations such as local governments and communities, private companies, non-governmental organizations and farmers could have a role (Frese et al. 2014, Maxted et al. 2011). We have to seek a new way that enables their participation. In Japan, on farm conservation of local vegetables can be cited as examples (Nishikawa 2012). Similar approaches in minor fruits and local fruit landraces could be possible by combining various potential benefits of germplasm collections such as local culture, education and tourism, not only economic ones.

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**Literature Cited**

Ainu Museum (2015) Ainu to Shizen Digital Museum (Digital Museum of the Ainu and Nature). (http://www.ainu-museum.or.jp/si/siror/).

Amano, T. (1982) Ryūkyū Rettō Yūyō Jumokushi (Useful Woody Plants of the Ryūkyū Peninsula). Ryūkyū Rettō Yūyō Jumokushi Kankōkai, Naha, 255 pp.

Amino, Y. (2001) Chūsei Minshū no Seigyō to Gijutsu (The Development of Crafts and Industries in Japan’s Medieval Society). University of Tokyo Press, Tokyo, 285 pp.
Fresc, L., A. Palmc and C. Kik (2014) On the sustainable use and conservation of plant genetic resources in Europe. Report from Work Package 5 “Engaging the user Community” of the PGR Secure project “Novel characterization of crop wild relative and landrace resources as a basis for improved crop breeding” (http://www.nordgen.org/index.php/en/Plants/Innehaal/Workshops-Conferences/Plant-Genetic-Resource-Workshop-2013-Final-report-and-policy-paper).

Fujiwara, T., T. Fujiwara et al. (Names of other authors are unknown) (eds.) (927) English ski (Procedures of the Engi Era). English translation by F.G. Bock is available at the Japanese Historical Text Initiative of the University of California at Berkeley (http://pnc-ecal.ouc.ac.jp/jhti/Engi Shiki editions and copyrights.html).

Fukuoka, I. (1995) Ainu Shokubutsushi (Folkloric Flora of the Ainu People). Sôfûkan, Tokyo, 241 pp.

Hatakeyama, T. (1989) Jomonjin no Matsuei Tachi, Hie to Ki no Mi no Seikatsu (Descendants of Jûmon People, Food Style with Japanese Millet and Nuts). Sairiyûsha, Tokyo, 333 pp.

Hokkaido Institute of Public Health (2015). Ainu Minzoku no Yûyô—A Global Treatise from Biology to Medicine. Springer, Berlin, pp. 385–411.

Hudson, M.J. (2007) Japanese Beginnings. In: Tsutsui, W.M. (ed.) A Companion to Japanese History, Blackwell, Oxford, pp. 13–29.

Hummer, K.E., K.W. Pomper, J. Postman, C.J. Graham, E. Stover, E.W. Mercure, M. Aradhya, C.H. Crisosto, L. Ferguson, M.M. Thompson et al. (2012) Emerging Fruit Crops. In: Badenes, M.L. and D.H. Byrne (eds.) Fruit Breeding, Handbook of Plant Breeding 8, Springer, Berlin, pp. 97–147.

Iketani, H., N. Mase and Y. Sato (2005) Exploration and collection of Pyrus ussuriensis var. hondoensis in Yamanashi and Nagano Prefectures. Annu. Rep. Explor. Introd. Plant Genet. Res. 21: 37–43.

Iketani, H., N. Mase and Y. Sato (2006) Exploration and collection of Pyrus and Malus genetic resources in Northern Tohoku region. Annu. Rep. Explor. Introd. Plant Genet. Res. 22: 13–21.

Iketani, H., N. Mase and Y. Sato (2007) Exploration and collection of Malus genetic resources in Nagano and Yamanashi Prefectures. Annu. Rep. Explor. Introd. Plant Genet. Res. 23: 55–61.

Iketani, H., N. Mase and Y. Sato (2008) Exploration and collection of rosaceous fruit tree genetic resources in Toyama and Ishikawa Prefectures. Annu. Rep. Explor. Introd. Plant Genet. Res. 24: 55–61.

Iketani, H. and N. Mase (2009) Exploration and collection of Malus and Pyrus genetic resources in Tochigi Prefecture. Annu. Rep. Explor. Introd. Plant Genet. Res. 25: 61–69.

Iketani, H., T. Yamamoto, H. Katayama, C. Uematsu, N. Mase and Y. Sato (2010a) Introggression between native and prehistorically naturalized (archaeophytic) wild pear (Pyrus spp.) populations in northern Tohoku, northeast Japan. Conserv. Genet. 11: 115–126.

Iketani, H., K.E. Hummer, J.D. Postman, H. Imanishi and N. Mase (2010b) Collaborative exploration between NIAS Genebank and USDA ARS (U.S. Department of Agriculture, Agricultural Research Service) for the collection of genetic resources of fruit and nut species in Hokkaido and the northern Tôhoku Region. Annu. Rep. Explor. Introd. Plant Genet. Res. 26: 13–26.

Iketani, H., H. Katayama, C. Uematsu, N. Mase, Y. Sato and T. Yamamoto (2012) Genetic structure of East Asian cultivated pears (Pyrus spp.) and their reclassification in accordance with the nomenclature of cultivated plants. Plant Syst. Evol. 298: 1689–1700.

Iketani, H. and N. Mase (2013) Exploration and collection of two crabapple species, Malus spontanea Makino and “Takanabe kaidô,” in Southern Kyûshû, Japan. Annu. Rep. Explor. Introd. Plant Genet. Res. 29: 119–125.

Iketani, H., A. Kono, Y. Ban, S. Yamamoto and N. Mase (2014) Collection of a rare and endangered wild grapevine species, Vitis kiusiana Momiyama, in Southern Kyûshû, Japan. Annu. Rep. Explor. Introd. Plant Genet. Res. 30: 101–107.

Iketani, H. and N. Mase (2016) Collection of wild and cultivated rare Malus genetic resources in Northern Kyûshû, Japan. Annu. Rep. Explor. Introd. Plant Genet. Res. 31 (in press).

Ito, Y. and Y. Sugawara (2006) Exploration and collection of akushibamodoki (Vaccinium yakuishimense Makino) in Yakushima. Annu. Rep. Explor. Introd. Plant Genet. Res. 22: 33–35.

Ito, Y. and Y. Sugawara (2007) Exploration and collection of nagobonshobo (Vaccinium sieboldii Miq.) in Aichi Prefecture and arage-natsuhaze (Vaccinium ciliatum Thunb.) in Hiroshima Prefecture. Annu. Rep. Explor. Introd. Plant Genet. Res. 23: 63–67.

Ito, Y. and Y. Sugawara (2008) Exploration and collection of tsurukoke-momono (Vaccinium oxyccoccus L.) and kurokamonomon (Vaccinium uliginosum L.) in Nemuro City in Hokkaido. Annu. Rep. Explor. Introd. Plant Genet. Res. 24: 79–83.

Ito, Y. and Y. Sugawara (2009) Exploration and collection of munin-shashanbo (Vaccinium boninense Nakai) in Chichijima Island, the Ogasawara Islands in Tokyo Metropolitan Prefecture. Annu. Rep. Explor. Introd. Plant Genet. Res. 25: 53–59.

Ito, Y. and Y. Sugawara (2010) Exploration and collection of keyononi (Lonicera caerulea L. subsp. edulis (Regal) Hultén) and kuroninouguisukagura (Lonicera caerulea L. subsp. edulis (Regal) Hultén var. emphylolocalyx (Maxim.) Nakai) in the Yufutsu Wilderness in Hokkaido. Annu. Rep. Explor. Introd. Plant Genet. Res. 26: 7–12.

Ito, Y. (2011) Exploration and collection of kurokamonomon (Lonicera caerulea L. subsp. edulis (Regal) Hultén var. emphylolocalyx (Maxim.) Nakai) in three wetlands in eastern Hokkaido. Annu. Rep. Explor. Introd. Plant Genet. Res. 27: 35–39.

Ito, Y. (2012) Exploration and collection of shashanbo (Vaccinium bracteatum Thunb.) on Yakushima island, Kagoshima prefecture. Annu. Rep. Explor. Introd. Plant Genet. Res. 28: 105–111.

Iwatsuki, K., T. Yamazaki, D.E. Boufford and H. Ohta (eds.). (1993–2016). Flora of Japan Vol. 1–4, Kodansha Scientific, Tokyo.

Janick, J. and J.N. Moore (eds.) (1996) Fruit Breeding Vol. I–III, Wiley, New York.

Kajita, T. (2003) Cycadophyta, Ginkgophyta, Coniferophyta and Magnoliophyta. In: Union of Japanese Societies for Systematic Biology (ed.) Japanese Biota Species Number Survey, 1st Edition. (http://ujssb.org/biospnum/search.php).

Katayama, H. and C. Uematsu (2006) Pear (Pyrus species) genetic resources in Iwate, Japan. Genet. Resour. Crop Evol. 53: 483–498.

Katayama, H., H. Amo, T. Wuyun, C. Uematsu and H. Iketani (2016) Genetic structure and diversity of the wild Ussurian pear in East Asia. Breed. Sci. 66: 90–99.

Keally, C.T. (2009) Japanese Archaeology. (http://www.t-net.ne.jp/~keally/index.htm).

Kikuchi, A. (1948) Kaju Engeigaku Jôkan (Horticulture of Fruit Trees, Vol. 1). Yokendo, Tokyo, 528 pp.

Kobayashi, A. (1990) Bunka to Kudamono (Culture and Fruits). Yokendo, Tokyo, 198 pp.
Koike, H. and K. Miyagawa (1974) Studies on the blueberries, 1: On characteristics and propagations of the wild blueberry (*Vaccinium uliginosum*) in Japan. Nagano Hort. Exp. Sta. 1: 1–10.

Library of Congress and American Library Association (2012) The ALA-LA Romanization Tables. (http://www.loc.gov/catdir/cpso/roman.html).

Liu, M.-J. (1998) Zhong guo ye sheng guo shu (Wild fruit trees of China), Agricultural Press of China, Beijing, 418 pp.

Matsushima, K., K. Nemoto, A. Tsurukawa, Y. Kato, S. Ohsaki, Y. Nishida and M. Minami (2013) Investigation on wild edible plants in Ohshika, Simo Ina, Nagano, Japan. J. Fac. Agric. Shinshu Univ. 49: 43–50.

Matsuyama, T. (1982) Ki no Mi (Ethnology of Tree Nuts). Hosei University Press, Tokyo, 371 pp.

Maxted, N., M.E. Dulloo, B.V. Ford-Lloyd, L. Frese, J. Iriondo and M.A.A.P. de Carvalho (eds.) (2011) Agrobiodiversity Conservation: Securing the Diversity of Crop Wild Relatives and Landraces. CABI, Wallingford, 392 pp.

Minamoto, S. (930s) Wamyō Ruijushō (Japanese Names, Classified and Annotated). (Digital images of a later publication (Nawa, D. (ed.) 1617) are available at http://dl.ndl.go.jp/info:ndljp/pid/2606770).

Ministry of the Environment of Japan (2012) The Fourth Red List, Plant I, II. (http://www.biodic.go.jp/rdb/rdb_f.html).

Mittermeier, R.A, P.R. Gil, M. Hoffman, J. Pilgrim, T. Brooks, C.G. Mittermeier, J. Lamoreux and G.A.B. da Fonseca (eds.) (2004) Hotspots Revisited: Earth’s Biologically Richest and Most Threatened Terrestrial Ecoregions, University of Chicago, Chicago, 390 pp.

Moore, J.N. and J.R. Ballington, Jr. (eds.) (1990) Genetic Resources of Temperate Fruit and Crops Vol. 1–2. International Society for Horticultural Science, Wageningen, 975 pp.

Nishikawa, Y. (ed.) (2012) Seibu tsu Tayōsei wo hagukumu Shoku to Nō (Food and Agriculture nurturing the Biodiversity). Commons, 240 pp.

Ohwi, J. (1965) Flora of Japan, Smithsonian Institution, Washington DC. 1067 pp.

Omatsu, S. and S. Tsuji (2001) Early Jomon plant macroremains from the Ireibaru C Site in south Okinawa, southwestern Japan. Jpn. J. Histor. Bot. 10: 17–32.

Sarashina, G. and K. Sarashina (1976) Kotan Seibutsuki I, Jumoku Zassō hen (Biota of Ainu Settlements I, Woody and Herbaceous Plants). Hosei University Press, Tokyo, 265 pp.

Satake, Y., H. Hara, S. Watari and T. Tominari (eds.) (1989) Wild Flowers of Japan, Woody Plants Vol. 1–2, Heibonsha, Tokyo.

Sato, H. and T. Nohara (1997) Nansei shotō ni okeru kyūkōshoku to shiteno yasei dōshokubutsu shigen no riyō (Use of wild plant and animal resources during famine in Nansei Islands). Okinawa Minzoku Kenkyū 17: 41–59.

Takhtajan, A. (1986) Floristic Regions of the World (Transl. by T.J. Crovello). Univ. Calif. Press, Berkeley, 522 pp.

Taneishi, Y. (2014) Kodai Shokuryō Kakutoku no Kōkogaku (The Archaeology of Food Acquisition in the Ancient Japan). Dōseisha, Tokyo, 325 pp.

Tawada, S. (1982) Shushoku no Hensen (History of Staple Diets) Shin-okinawabungaku 54: 40–48.

Terasawa, K. and T. Terasawa (1981) Yayoi Jidai Shokubutsushitsu Shokuryō no Kisoteki Kenkyū (Basic Research on Plant-Based Diets in the Yayoi Period). Studies in Archaeology: Proc. Kashiwara Archaeol. Inst. 5: 1–129.

Thompson, M.M. and A. Chaovanalikit (2002) Preliminary observations on adaptation and nutraceutical values of blue honeysuckle (*Lonicera caerulea*) in Oregon, USA. Acta Hortic. 626: 65–72.

Uchiyama, Y. (1996) Kaju Seisan Chiiki no Kōsei (Structure of Fruit Production Area). Taimeido, Tokyo, 229 pp.

von Verschuer, C. (2006) Across the Perilous Sea. Japanese Trade with China and Korea from the Seventh to the Sixteenth Centuries. Cornell Univ., N.Y., 226 pp.

Wada, H. (2000) Yamamomo (Bayberry) In: Rural Culture Association Japan (ed.) Kaju Engei Dai Hyakka 15, Jōryoku Tokusan Kaju (Encyclopedia of Fruit Trees 15, Evergreen Local Fruits), Rural Culture Association Japan, Tokyo. pp. 335–345.

Watanabe, M. (1975) Jōmon Jidai no Shokubutsushoku (Plant-Based Diets of the Jōmon Period). Yuzankaku, Tokyo, 187 pp.

Yonekura, K. (2012) An Enumeration of the Vascular Plants of Japan. Hokuryukan, Tokyo, 379 pp.

Yonekura, K. and T. Kajita (2003–) YList, Index of Common Names and Scientific Names of Japanese Plants. (http://ylist.info/index.html).