Production, Uses, and Ancestry of an Oilseed Crop, *Perilla frutescens* (L.) Britton var. *frutescens* in Japan: An Overview

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Summary

Perilla frutescens (L.) Britton var. *frutescens* has been cultivated as a traditional oilseed crop in Japan. Perilla seed oil was once used for industrial products such as fuel for lamps, waterproofing agent, and lacquered wares. Nowadays, it is commonly utilized to add flavor to cooking, and the seeds are also ground and powdered for use in traditional foods as flavoring. Perilla oil has recently received the attention of Japanese consumers because it is a good source of health benefit compounds including unsaturated fatty acids (e.g., α-linolenic acid) and bioactive flavonoids (e.g., luteolin). In the country, however, there has been little effort in improving the production potential of the crop through plant breeding. The present review is an attempt to provide the current information about the production, uses and possible ancestry of *P. frutescens* var. *frutescens* in Japan. The paper also focuses on the problems and prospects of genetic improvement in this crop.

Key words

breeding, cultivation practices, health benefit compounds, landraces, molecular markers

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Received: May 26, 2022 | Accepted: December 5, 2022 | Online first version published: May 15, 2023

Introduction

Perilla frutescens (L.) Britton is an annual, herbaceous species. It belongs to the Lamiaceae family along with a number of aromatic edible plants such as basil, rosemary, sage, oregano, and lemon balm (Kagawa et al., 2019). Two distinct cultivated types (or varieties) are recognized. One, *P. frutescens* var. *frutescens*, is used as an oilseed crop and the other, *P. frutescens* var. *crispa*, as a spicy leafy vegetable (Lee et al., 2002; Nitta et al., 2003). Var. *frutescens* has larger, soft seeds, green leaves and stem, and non-wrinkled leaves (Fig. 1A), whereas var. *crispa* has generally smaller, hard seeds, purple or green leaves and stem, and either wrinkly or non-wrinkly leaves (Lee et al., 2002). The two varieties have traditionally been cultivated in Japan, Korea, China, and other Asian countries since ancient times (Nitta et al., 2003). *P. frutescens* has recently been introduced into Europe, the United States, and Russia as an oilseed crop or an aromatic plant (Nitta et al., 2003).

In Japan, var. *crispa* is more extensively cultivated than var. *frutescens*. Fresh leaves of var. *crispa* are easily available in supermarkets throughout the country, and consumed for food coloring and as a garnish or seasoning served with raw fish or noodles. By contrast, var. *frutescens* is sporadically grown as a traditional folk crop. Its seeds are used like sesame seeds, for oil production and as a condiment for dishes (Anilakumar et al., 2010). In recent years, var. *frutescens* has gained renewed attention because its seed oil contains high amount of unsaturated fatty acids [mainly α-linolenic acid (ω-3 fatty acid)] that are expected to be beneficial to human health (Asif, 2011; Bondioli et al., 2020). The health benefits of var. *frutescens* have also been attributed to its content of bioactive flavonoids and phenolic compounds (Ahmed, 2019).

The objective of this article is to present an up-to-date summary in relation to the production, uses, and cultivation practices of var. *frutescens* in Japan. The paper also focuses on the ancestry of Japanese landraces of var. *frutescens*, as well as the problems and prospects of genetic improvement in this crop.

Ancestry of Japanese Landraces of *P. frutescens* var. *frutescens*

P. frutescens is an allotetraploid species with 2n = 4x = 40 chromosomes (Honda et al., 1994). A wild species, *P. citriodora* (Makino) Nakai (2n = 2x = 20) is thought to be one of diploid genome donors for *P. frutescens* (Honda et al., 1994). However, there is still no definite information about the second diploid genome donor, and neither has the wild ancestor of *P. frutescens* been determined (Nitta et al., 2003; Zhang et al., 2021).

In Japan, seed remains of *Perilla* (either var. *frutescens* or var. *crispa*) were unearthed at several archaeological sites dated ca. 5000 B.P., and these seeds were probably used for flavoring foods (Matsutani, 1983; Minaki, 1991; Nitta et al., 2003). The systematic technique for extracting oil from seeds of var. *frutescens* was devised in Japan in the mid-9th century (Nitta and Ohnishi, 1999), and perilla seed oil was utilized as fuel for lamps until rapeseed oil became widespread in the 17th century (Nishizawa et al., 2010; Masuda et al., 2018). It is also worth mentioning that perilla oil was extensively used as drying oil for waterproofing paper umbrellas and in the manufacture of lacquered wares (Nitta and Ohnishi, 1999; Nitta et al., 2003).

The question then arises as to from where *P. frutescens* reached Japan. *Perilla* crops most likely originated in China because China has been assumed to be the primary center of biodiversity of *Perilla* (Zeven and de Wet, 1982; Nitta et al., 2003). Var. *frutescens* and var. *crispa* have been recognized as distinct crops in China for a long time (Li, 1969), and with this in mind, Nitta and Ohnishi (1999) supposed that these two crops were introduced into Japan from China in their present forms, namely two as distinct crops.

In addition to the two *Perilla* crops, weedy plants of these crops occur in Japan, Korea, and China (Nitta et al., 2003); weedy plants grow along roadsides and riverbanks, in wastelands, and around farmers' fields. RAPD (Random Amplified Polymorphic DNA) and AFLP (Amplified Fragment Length Polymorphism) analyses were carried out to assess genetic relationships among

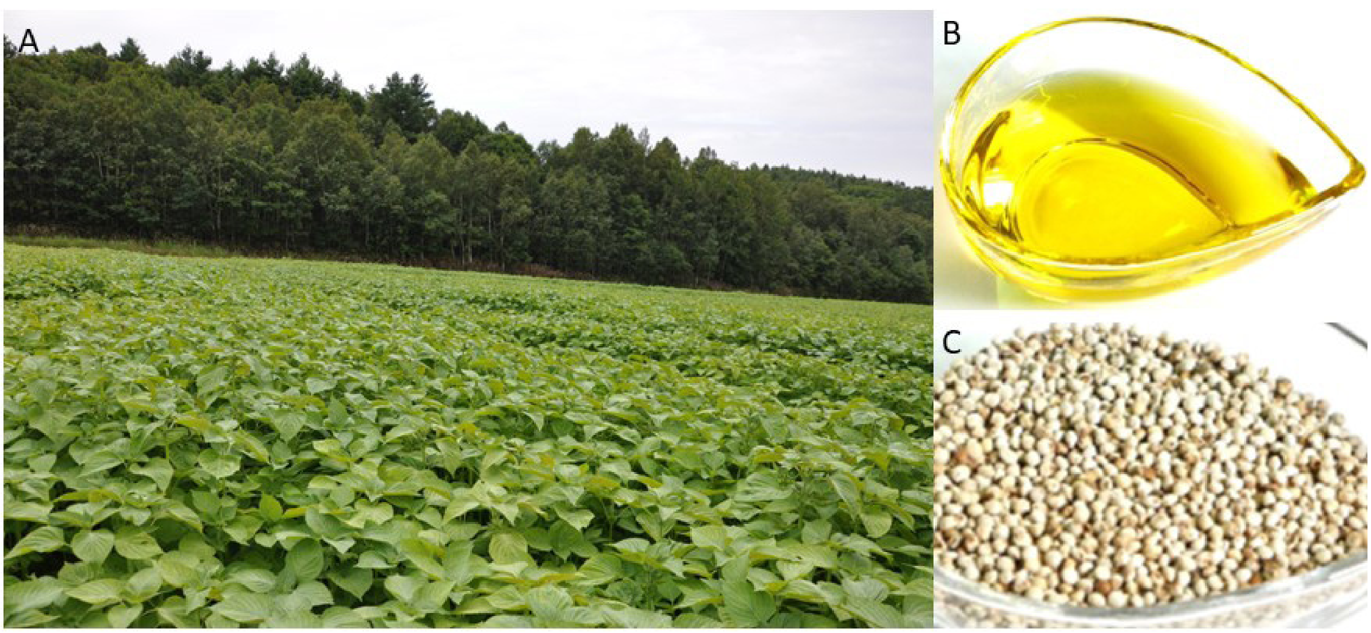

Figure 1. *Perilla frutescens* var. *frutescens* cultivated in a field (A), its seed oil (B), and seeds (C)

two *Perilla* crops and their weedy types collected from Japan, Korea, and China (Nitta and Ohnishi, 1999; Nitta et al., 2003; Lee and Ohnishi, 2003).

The analyses led to four intriguing observations regarding the ancestry of Japanese landraces of var. *frutescens*. (1) Var. *frutescens* and var. *crispa* cultivated in Japan were clearly separated by RAPD markers, which implies that gene flow between the two crops has been limited though they are crossable with each other. (2) On the whole, Japanese and Korean accessions of cultivated var. *frutescens* were closely related to each other, suggesting that most of the Japanese accessions of var. *frutescens* are migrants from Korea. (3) Japanese *Perilla* accessions collected from the same geographic areas were not always closely related, both in var. *frutescens* and var. *crispa*. *Perilla* crops were likely introduced into Japan through multiple routes. (4) The weedy type of var. *frutescens* in Japan, Korea, and China seems to have multiple origins: some weedy accessions may be an escaped form from cultivation or a relic form of the var. *frutescens* crop that has been abandoned, and some probably have originated from intervarietal hybrids.

Production

P. frutescens var. *frutescens* has been cultivated on a small scale around Japan (Fig. 1A), particularly in hilly and mountainous areas. After World War II, its production continuously declined until the 2000s, with the change in Japanese dietary habits and shrinkage in the farming population. In 2005, for example, Japan produced only 76.7 metric tons of var. *frutescens* on 130.3 ha (MAFF, 2007).

In recent years, however, the acreage and yield of this crop have started to increase; the crop was harvested from 429.1 ha with a total yield of 137.9 tons in 2019 (JSAPA, 2021). It seems certain that this recovery tendency is mainly due to community building efforts in hilly and mountainous areas. These areas have seen significant change over the past decades. A declining and aging population has led to a shortage of agricultural labor, which in turn has accelerated the abandonment of farmland (Su et al., 2018; Kitano, 2021). In hilly and mountainous areas, cultivation of var. *frutescens* has been encouraged with the hope of preventing the abandonment of cultivated land and revitalizing local communities (Ito et al., 2006; Sodegaki et al., 2014; JSAPA, 2021). This is largely because perilla seed oil has been in the limelight as health food and its consumption has been expected to gradually grow. Moreover, these areas are vulnerable to damage from wild animals such as deer, wild boars, and Japanese macaques (Sodegaki et al., 2014; Yasue et al., 2020). Var. *frutescens* is known to give off a characteristic fragrance that can repel wild animals in question (Sodegaki et al., 2014). This may also help to explain the increase in the cultivation of var. *frutescens*.

Uses and Cultivars

As mentioned above, perilla seed oil was once widely utilized in industrial purposes in Japan. Nowadays, perilla oil is commonly used to add flavor to cooking thanks to its mild aroma and refreshing taste. As shown in Fig. 1B, it is a kind of light yellow, clear, and transparent liquid. Traditional method for extracting perilla oil involves squeezing the oil out of seeds by applying pressure without heating them up or at low temperature (JETRO, 2021). Although the oil yield obtained by this mechanical pressing method is lower than that by other methods (e.g., solvent extraction and aqueous enzymatic extraction), the loss of active ingredients including linolenic acid can be avoided in the mechanical pressing process (Zhao et al., 2021; JETRO, 2021). We would also like to add that the oil press residue (oil cake) is used as feed for livestock and poultry and as crop fertilizer.

In Japan, a variety of vegetables and mushrooms have been dressed with ground seeds of var. *frutescens* since the distant past (Tachibana, 1989; Ehara, 2010). The ground seeds are also mixed with fermented soybean paste for use in traditional foods as flavoring.

Based on the flowering time, Japanese var. *frutescens* cultivars are typically classified into early (days from seeding to flowering: <100 days), late (>130 days) and intermediate maturing types (Lee and Ohnishi, 2001). Early maturing type is mostly cultivated in high-latitude regions such as Hokkaido Island (41°N-46°N) and Iwate Prefecture (38°N-40°N), whereas var. *frutescens* grown in low-latitude regions [e.g., Hiroshima Prefecture (34°N-35°N)] is late or intermediate maturing type. Seeds of Japanese var. *frutescens* genotypes are almost round in shape (Fig. 1C), and 1000 seed weight was reported to range from 2.8 to 5.3 g among the genotypes (Akimoto et al., 2020). Seed coat comes in a variety of colors, grayish white to dark brown (Fig. 1C) (Nakamura, 2009). Despite a very long history of cultivation of var. *frutescens* in Japan, there has been very little effort in improving the agronomic characteristics of this crop through plant breeding. In fact, most farmers still cultivate landraces of their own regions (Nitta and Ohnishi, 1999; Nakamura, 2009).

Cultivation Practices

Var. *frutescens* grows well under comparatively cool and humid climate (Fujime, 2017). It may be direct-seeded or transplanted. In Japan, transplanting has been widely practiced because this method generally results in better yield and reduces the need for weed control as compared with direct seeding. The seeds are sown in nursery beds during mid-May through late June in the country. Seedlings become ready for transplanting within 30 to 40 days when they attain the height of 15 to 20 cm. This crop can grow on most soil types, but prefers a well-drained loam or sandy-loam soil that has good moisture retention (Fujime, 2017).

Var. *frutescens* is a short-day crop and typically begins flowering in August to September (Nakamura, 2009). Harvesting should be started when two thirds of the leaves turn yellow in color, around one month after flowering (Nakamura, 2009). Seeds of var. *frutescens* tend to fall off soon after they mature, and therefore missing the right time to harvest causes severe yield loss. The crop suffers relatively little damage from diseases or insects. The representative diseases are Perilla rust (caused by *Coleosporium plectranthi*), anthracnose (caused by *Colletotrichum yoshinoi*), and bacterial wilt (caused by *Ralstonia solanacearum*) (NARO Genebank, 2022). The insect pests such as *Pyrausta panopealis* and *Spodoptera litura* occasionally attack this crop.

Concluding Remarks

Crop yield and quality can be improved through pest and disease control, fertilizer application, and cultural manipulations, but all these have to be repeated each time the crop is grown (dela Peña, 1990). In this regard, development of new cultivars through conventional plant breeding is the most stable method of crop improvement. There are three general approaches to obtain improved cultivars suited to needs of farmers and consumers, and these are (1) introduction of new genotypes from other source, (2) selection of naturally occurring variants which appear in nature or within local landraces, and (3) generation of expanded variation by controlled crossing or mutagenesis, and subsequent selection of desirable variants.

Recently, two cultivars of var. *frutescens* ('Hikei alps 1 go' and 'Hida osaka ontake 1 go'), which are rich in functional ingredients such as α-linolenic acid and the flavonoid luteolin, have been released in Japan (Sodegaki et al., 2014; Yasue et al., 2020). These cultivars have been developed from selection within locally grown landraces, and are not the products of controlled crosses.

As stated by Breseghello and Coelho (2013), simply applying selection on pre-existing genetic diversity is an eroding process that eventually comes to a limit. The creative power of plant breeding certainly resides in promoting homologous recombination between chromosomes via controlled crossing to generate novel genetic diversity. Before cross-breeding programs can be initiated, germplasm accessions or foundation stocks must be evaluated and available as parent materials for hybridization. The germplasm of var. *frutescens* has been augmented both through collections made within Japan and introduced from abroad (NARO Genebank, 2021). Nevertheless, significant genetic erosion of diversity may occur in the areas where var. *frutescens* cultivation has declined substantially (Nitta et al., 2004; Yasumoto et al., 2004). More emphasis needs to be laid on the germplasm collection of local landraces from such areas.

Molecular markers and more recently, high-throughput genome sequencing efforts, have dramatically increased knowledge of and ability to characterize genetic diversity in the germplasm pool (Moose and Mumm, 2008; Khosa et al., 2016). Genomic applications will facilitate the selective incorporation and utilization of diverse germplasm into var. *frutescens* breeding programs. In var. *frutescens*, studies have been performed to develop such markers as RAPD, AFLP, and SSR (Simple Sequence Repeat) markers (Lee et al., 2002; Lee and Ohnishi, 2003; Nitta et al., 2003; Sa et al., 2018; Kim et al., 2021). Among these markers, SSR markers have been widely used for the analysis of genetic diversity and relationships, genetic mapping and association mapping in many crop species, because of high reproducibility, multi-allelic nature, co-dominant inheritance, and abundance in crop genomes (Powell et al., 1996; Baldwin et al., 2012; Oh et al., 2021).

Most recently, Park et al. (2021) have detected several SSR markers related to the content of fatty acids including linolenic acid and oleic acid in var. *frutescens*. These SSR markers are expected to be useful for improving the seed oil quality of var. *frutescens* through marker-assisted selection. As far as we know, however, the progress of molecular marker applications in this crop is still at its early stage when compared to other important crops. Efforts need to be directed towards developing effective molecular marker resources and generating high-density linkage maps that can assist breeders in QTL (Quantitative Trait Loci) dissection and marker-assisted breeding.

Acknowledgements

We are grateful to Mr. Hidetoshi Nakajima (LLC OMEGA Farmers) for support throughout this work.

References

Ahmed H. M. (2019). Ethnomedicinal, Phytochemical and Pharmacological Investigations of *Perilla frutescens* (L.) Britt. Molecules 24: 102. doi: 10.3390/molecules24010102

Akimoto M., Takagi K., Konishi Y. (2020). Comparative Study of the Growth and Yields in the Native Varieties of Perilla (*Perilla frutescens*) Grown in Tokachi Region. Res Bull Obihiro Univ 41: 30-39. doi: 10.24556/00004687 (in Japanese)

Anilakumar K. R., Pal A., Khanum F., Bawa A. S. (2010). Nutritional, Medicinal and Industrial Uses of Sesame (*Sesamum indicum* L.) seeds – An Overview. Agric Conspec Sci 75 (4): 159-168

Asif M. (2011). Health Effects of Omega-3,6,9 Fatty Acids: *Perilla frutescens* Is a Good Example of plant Oils. Orient Pharm Exp Med. 11 (1): 51-59. doi: 10.1007/s13596-011-0002-x

Baldwin S., Pither-Joyce M., Wright K., Chen L., McCallum J. (2012). Development of Robust Genomic Simple Sequence Repeat Markers for Estimation of Genetic Diversity within and among Bulb Onion (*Allium cepa* L.) Populations. Mol Breed 30 (3): 1401-1411. doi: 10.1007/s11032-012-9727-6

Bondioli P., Folegatti L., Rovellini P. (2020). Oils Rich in Alpha Linolenic Acid: Chemical Composition of Perilla (*Perilla frutescens*) Seed Oil. OCL 27: 67. doi: 10.1051/ocl/2020066

Breseghello F., Coelho A. S. G. (2013). Traditional and Modern Plant Breeding Methods with Examples in Rice (*Oryza sativa* L.). J Agric Food Chem 61 (3): 8277-8286. doi: 10.1021/jf305531j

dela Peña R. S. (1990). Development of New Taro Varieties through Breeding. In: Proceedings of Taking Taro into the 1990s: A Taro Conference (Hollyer J. R., Sato D. M., eds), University of Hawaii, Hilo, HI, USA, pp. 32-36

Ehara A. (2010). Vegetables and the Diet of the Edo Period, Part 2, Vegetable Production and the Diet in Rural Villages. Food Culture 19&20: 2-8

Fujime Y. (2017). *Perilla frutescens* var. *frutescens*: Cultivation Practices. In: A Compendium of Agricultural Technology, vol. 11, Nobunkyo, Tokyo, Japan, pp. 57-59 (in Japanese)

Honda G., Yuba A., Kojima T., Tabata M. (1994). Chemotaxonomic and Cytogenetic Studies on *Perilla frutescens* var. *citriodora* ("Lemon Egoma"). Nat Med 48: 185-190

Ito H., Yamada R., Iida T. (2006). Studies on Growth and Flowering Characters and Development of the High Production Methods of Extremely Early Variety in *Perilla*. Res Bull Aichi Agric Res Ctr 38: 73-79 (in Japanese)

JETRO (Japanese External Trade Organization) (2021). Highlighted Japanese Ingredients. Perilla (Egoma). Available at: http://www.jetro.go.jp/en/trends/foods/ingredients/egoma.html [Accessed 11 December, 2021] (in Japanese)

JSAPA (Japanese Specialty Agriculture Products Association) (2021). Local Specialty Crops - Industrial and Medicinal Crops, and the Material Plants of Japanese Paper. Available at: www.jsapa.or.jp/Acrop_Jpaper/nousakumotuchousar1.pdf [Accessed 11 December, 2021] (in Japanese)

Kagawa N., Iguchi H., Henzan M., Hanaoka M. (2019). Drying the Leaves of *Perilla frutescens* Increases Their Content of Anticancer Nutraceuticals. Food Sci Nutr 7 (4): 1494-1501. doi: 10.1002/fsn3.993

Khosa J. S., McCallum J., Dhatt A. S., Macknight R. C. (2016). Enhancing Onion Breeding Using Molecular Tools. Plant Breed 135 (1): 9-20. doi: 10.1111/pbr.12330

Kim J. Y., Sa K. J., Ha Y. J., Lee J. K. (2021). Genetic Variation and Association Mapping in the F2 Population of the Perilla Crop (*Perilla frutescens* L.) Using New Developed *Perilla* SSR Markers. Euphytica 217 (7): 135. doi: 10.1007/s10681-021-02867-z

Kitano S. (2021). Estimation of Determinants of Farmland Abandonment and Its Data Problems. Land 10 (6): 596. doi: 10.3390/land10060596

Lee J. K., Ohnishi O. (2001). Geographic Differentiation of Morphological Characters among *Perilla* Crops and Their Weedy Types in East Asia. Breed Sci 51 (4): 247-255. doi: 10.1270/jsbbs.51.247

Lee J. K., Ohnishi O. (2003). Genetic Relationships among Cultivated types of *Perilla frutescens* and Their Weedy Types in East Asia Revealed by AFLP Markers. Genet Resour Crop Evol 50 (1): 65-74. doi: 10.1023/A.1022951002271

Lee J. K., Nitta M., Kim N. S., Park C. H., Yoon K. M., Shin Y. B., Ohnishi O. (2002). Genetic Diversity of *Perilla* and Related Weedy Types in Korea Determined by AFLP Analysis. Crop Sci 42 (6): 2161-2166. doi: 10.2135/cropsci2002.2161

Li H. L. (1969). The Vegetables of Ancient China. Econ Bot 23 (3): 253-260. doi: 10.1007/BF02860457

MAFF (Ministry of Agriculture, Forestry and Fisheries, Japan) (2007). Statistics of Production and Cropping Acreage of Specialty Crops. Available at: http://www.maff.go.jp/j/tokei/kouhyou/tokusan_nousaku/index.html [Accessed 22 December, 2021] (in Japanese)

Masuda A., Hidaka K., Honda S., Taniguchi A., Doi S., Masuda T. (2018). Radical Scavenging Properties of Roasted Egoma (*Perilla frutescens* var. *frutescens*) Oils and Identification of Their Characteristic Scavengers. J Nutr Sci Vitaminol 64 (6): 466-472. doi: 10.3177/jnsv.64.466

Matsutani A. (1983). *Perilla frutescens* var. *frutescens* – *P. frutescens* var. *crispa*. In: Research on the Jomon Culture, vol. 2, Occupations. (Katoh S., Kobayashi T., Fujimoto T., eds), Yuzankaku, Tokyo, Japan, pp. 50-62 (in Japanese)

Minaki M. (1991). Large-Size Plant Remains and Their Transition. Report on Gohdo Site in Chiba City, Chiba Prefecture, Japan, pp. 167-177 (in Japanese)

Moose S. P., Mumm R. H. (2008). Molecular Plant Breeding as the Foundation for 21st Century Crop Improvement. Plant Physiol 147 (3): 969-977. doi: 10.1104/pp.108.118232

Nakamura S. (2009). *Perilla frutescens* var. *frutescens*: Cultivars and Farming Practices. Tokusansubyou 5: 32-33 (in Japanese)

NARO (National Agriculture and Food Research Organization) Genebank (2021). Plant Genetic Resources. Available at: www.gene.affrc.go.jp/databases.php [Accessed 22 December, 2021] (in Japanese)

NARO (National Agriculture and Food Research Organization) Genebank (2022). Database of Plant Diseases in Japan. Available at: www.gene.affrc.go.jp/databases-micro_pl_diseases-list [Accessed 30 April, 2022] (in Japanese)

Nishizawa T., Tamaoki M., Aono M., Kubo A., Saji H., Nakajima N. (2010). Rapeseed Species and Environmental Concerns Related to Loss of Seeds of Genetically Modified Oilseed Rape in Japan. GM Crops 1 (3): 143-156. doi: 10.4161/gmcr/1.3.12761

Nitta M., Ohnishi O. (1999). Genetic Relationships among Two *Perilla* Crops, Shiso and Egoma, and the Weedy Type Revealed by RAPD Markers. Genes Genet Syst 74 (2): 43-48. doi: 10.1266/ggs.74.43

Nitta M., Lee J. K., Ohnishi O. (2003). Asian *Perilla* Crops and Their Weedy Forms: Their Cultivation, Utilization and Genetic Relationships. Econ Bot 57 (2): 245-253. doi: 10.1663/0013-0001(2003)057[0245:APCATW]2.0.CO;2

Nitta M., Hirashima S., Nagamine T. (2004). Exploration for Collecting *Perilla* Crops in Shikoku. In: Annual Report on Exploration and Introduction of Plant Genetic Resources, vol. 20 (Kawase M., Ebara K., Fukuoka S., Uga Y., eds), NARO Genebank, Tsukuba, Japan, pp. 27-37 (in Japanese)

Oh J. S., Sa K. J., Park H., Hyun D. Y., Lee S., Rhee J. H., Lee J. K. (2021). Genetic Variation of Native *Perilla* Germplasms Collected from South Korea Using Simple Sequence Repeat (SSR) Markers and Morphological Characteristics. Plants 10 (9): 1764. doi: 10.3390/plants10091764

Park H., Sa K. J., Hyun D. Y., Lee S., Lee J. K. (2021). Identifying SSR Markers Related to Seed Fatty Acid Content in *Perilla* Crop (*Perilla frutescens* L.). Plants 10 (7): 1404. doi: 10.3390/plants10071404

Powell W., Machray G. C., Provan J. (1996). Polymorphism Revealed by Simple Sequence Repeats. Trends Plant Sci 1 (7): 215-222. doi: 10.1016/1360-1385(96)86898-1

Sa K. J., Choi I. Y., Park K. C., Lee J. K. (2018). Genetic Diversity and Population Structure among Accessions of *Perilla frutescens* (L.) Britton in East Asia Using New Developed Microsatellite Markers. Genes Genomics 40 (12): 1319-1329. doi: 10.1007/s13258-018-0727-8

Sodegaki K., Kawase A., Maeda T., Kagiya T. (2014). A New Cultivar of *Perilla*, a Local Specialty in Hida Region, Gifu Prefecture, and Its Production Yielding High Functional Ingredients. Bull Gifu Prefect Res Inst Agric Tech Hill Mt Areas 9: 19-24 (in Japanese)

Su G., Okahashi H., Chen L. (2018). Spatial Pattern of Farmland Abandonment in Japan: Identification and Determinants. Sustainability 10 (10): 3676. doi: 10.3390/su10103676

Tachibana R. (1989). The Cultivation of "Egoma" by "Yakihata" in the Mt. Hakusan Area. Annu Rep Hakusan Nature Conserv Center 16: 73-93. (in Japanese)

Yasue T., Tanaka Y., Kagiya T. (2020). Breeding a new Cultivar 'Hida Osaka Ontake 1 Go' and Its Characteristics. Bull Gifu Prefect Res Inst Agric Tech Hill Mt Areas 15: 9-13. (in Japanese)

Yasumoto S., Tokushuku T., Yokota I. (2004). Exploration for Collecting Local Varieties of *Perilla frutescens* and *Sesamum indicum* in Gifu Prefecture and Northern Region of Aichi Prefecture. In: Annual Report on Exploration and Introduction of Plant Genetic Resources, vol. 20 (Kawase M., Ebara K., Fukuoka S., Uga Y., eds), NARO Genebank, Tsukuba, Japan, pp. 19-25 (in Japanese)

Zeven A. C., de Wet J. M. J. (1982). Dictionary of Cultivated Plants and Their Regions of Diversity. Centre for Agricultural Publishing and Documentation, Wageningen, Netherlands

Zhang Y., Shen Q., Leng L., Zhang D., Chen S., Shi Y., Ning Z., Chen S. (2021). Incipient Diploidization of the Medicinal Plant *Perilla* within 10,000 Years. Nat Commun 12 (1): 5508. doi: 10.1038/s41467-021-25681-6

Zhao B., Fu S., Li H., Chen Z. (2021). Chemical Characterization of Chinese *Perilla* Seed Oil. J Oleo Sci 70 (11): 1575-1583. doi: 10.5650/jos.ess21076

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