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Tricholoma matsutake: an edible mycorrhizal mushroom of high socioeconomic relevance in China

Tricholoma matsutake: **un hongo comestible micorrícico de gran importancia socioeconómica en China**

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Abstract

Background: Almost all world-famous species of edible mycorrhizal mushrooms (EMMs), or closely related species, grow naturally in China. However, China has some outstanding edible mushrooms due to their rare distribution in the rest of the world and because of their great economic importance.

Objective: To review the state of the art in China of one of the EEMs with greatest importance worldwide: *Tricholoma matsutake*.

Results and conclusion: The matsutake is a complex of species closely related which are distributed world-wide and have traditionally been highly demanded in Japan. The growth of matsutake basidiomata starts from a mixture of soil with mycelium and ectomycorrhizas called "shiro". The shiro development is closely correlated with the age of the host plants. In *Pinus densiflora* usually begins when the trees are 10-20 years old. The basidiomata begin to be produced three to four years after the shiro is formed. The harvesting and trading of this species, represents an important source of livelihood for Chinese local farmers, especially in rural mountainous regions where the net income is relatively low. Currently, there are different initiatives to protect and cultivate the matsutake mushroom.

Keywords: matsutake, ectomycorrhizal symbiosis, non-timber forest products, conservation.

Resumen

Antecedentes: Casi todas las especies mundialmente famosas de hongos micorrícicos comestibles (HMC), o especies estrechamente relacionadas, crecen naturalmente en China. Sin embargo, China tiene algunos hongos comestibles con distribución rara en relación al resto del mundo y con gran importancia económica.

Objetivo: Revisar el estado del arte en China de uno de los HMC con mayor importancia a nivel mundial: *Tricholoma matsutake*.

Resultados y conclusión: El matsutake es un complejo de especies que se distribuyen en todo el mundo y que tradicionalmente han sido muy demandadas en Japón. El crecimiento de los basidiomas de matsutake inicia a partir de una mezcla de suelo con micelio y ectomicorrizas llamado "shiro". El desarrollo del shiro está estrechamente relacionado con la edad de las plantas hospedantes. En *Pinus densiflora* generalmente comienza cuando los árboles tienen entre 10 y 20 años de edad. Los basidiomas comienzan a producirse de tres a cuatro años después de la formación del shiro. La recolección y comercialización de esta especie representa una importante fuente de sustento para los agricultores locales chinos, especialmente en las regiones montañosas donde el ingreso neto es relativamente bajo. Actualmente, existen diferentes iniciativas proteger y cultivar el matsutake.

Palabras clave: matsutake, simbiosis ectomicorrícica, productos forestales no maderables, conservación.

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Introduction

Matsutake [*Tricholoma matsutake* (S. Ito et S. Imai) Singer] is a traditional special delicacy in Japan. Since the mid-1970s Japan has annually imported more than 3,000 tons of matsutake from China and other countries (Wang, 1995). Matsutake has become one of the most widely known edible mycorrhizal mushrooms in the world (Ogawa, 1978; Wang, 1995; Hosford *et al*., 1997; Danell, 2002). This is due to its unique flavor, high commercial value, and wide natural distribution. Exploration continues for new matsutake-producing areas, and Mexico, Bhutan, Sweden, and Guatemala are all matsutake exporting countries (Danell, 2002; Hosford *et al*., 1997).

Matsutake (matsu = pine, take = mushroom) is a Japanese common name for *T. matsutake* growing exclusively in pine woods in Japan. In China, matsutake has a variety of names including "song-koumo" (pine-Tricholoma), "song-rong" (pine-mushroom), "song-jun" (pine-fungus), and "qing-gang-jun" (oak-mushroom) (Wang, 1995). Harvesting and trading of matsutake are important economic activities locally in China. This country started exporting *T. matsutake* to Japan from the north-east in the late 1970s (about 10-30 tonnes annually). Since the 1990s another large *T. matsutake*-producing area has been south-western China (Yunnan, Sichuan, and Tibet). China has become the world's largest matsutake exporting country, with more than 1,000 tonnes of matsutake exported to Japan annually (Wang, 1995; Yang *et al*., 2009). Harvesting, processing, and trading of matsutake has become an important industry, and generated multi-million foreign dollars for the Chinese economy. The matsutake-producing areas in China are all remote mountainous regions where agriculture is poor, and hence they provide important income for local communities. In Shangri-La County, Yunnan, 80% of farmers are involved with commercial harvest, processing, and trading of matsutake, generating up to RMB $50,000-60,000 annually per family; 5 to 20 times than a normal farming family's annual income (Figures 1 and 2).

Species complex

Tricholoma matsutake is considered to be the true ("hong" in Japanese) matsutake in Japan. It grows in many parts of Asia (Japan, China, North Korea, South Korea, Russia, and Bhutan), Europe (Turkey, Sweden, Finland, Norway, Germany, Czechoslovakia, Austria, Switzerland, and Italy), and North Africa (Algeria and Morocco). There are closely related species in China. *Tricholoma bakamatsutake* Hongo (false matsutake) is mainly found in oak forests and has a stronger matsutake-like aroma but less commercial value. *Tricholoma fulvocastaneum* Hongo is another related species with lower commercial value. Three new species were recently discovered in China; *T. lavendulophyllum* F. Q. Yu, *T. longicystidium* F. Q. Yu, and *T. pseudomatsutake* F. Q. Yu. These belong genetically and morphologically to the matsutake group (Yu, 2007). *T. matsu-*

Figure 1. Local Tibetan famers selling *Tricholoma matsutake* to a middle-man at a wild mushroom market, Zhongdian, Yunnan.

Figure 2. *Tricholoma matsutake* at a wild mushroom market, Zhongdian, Yunnan.

take (S. Ito et S. Imai) Singer var. *formosana* Sawada was described by Sawada (1931), based on collections of matsutake from Taiwan, and is now considered synonymous with *T. matsutake*.

Tricholoma magnivelare (Peck) Redhead (pine mushroom or white matsutake) is a closely related species with good commercial value, found in Canada, the USA, and Mexico (Hosford *et al.,* 1997). *Tricholoma caligatum* is another closely related species, mainly found in southern Europe (Kytövuori, 1989), with no commercial value due to its bitter taste. These two species are not found in China.

Matsutake and related species are found mainly in north-eastern and south-western China. In the north-east, matsutake is found in pine forests along the eastern mountain ranges; the Xiaoxingan-ling and Changbai Mountains, between 200 m and 1,500 m a.s.l. In south-western China matsutake is found under pine and oak forests at high elevations between (1,200-) 2,000 and 3,500 (-4,200) m a.s.l. in Yunnan, Sichuan, and Tibet. Matsutake is also found on Mt. Yushan, in Taiwan.

Based on molecular analysis (Murata *et al*., 2008), *T. matsutake* can be divided into two genotypes; genotype A refers to the mushrooms in Japan, the Korean Peninsula, and north-eastern China, and genotype B refers to those in south-western China. Genotype A may be further divided into three sub-genotypes: sub-genotypes 1 and 2 refer to the mushrooms in Japan, sub-genotype 3 to those on the Korean Peninsula, and sub-genotype 4 to those in south-western China. We believe that the biogeography of matsutake genotypes can be satisfactorily explained by the vicariance model. It can also be related to their different host associations. The matsutake mushrooms of genotype A are mainly associated with *Pinus densiflora* while those of genotype B are associated with a diversity of species in *Pinus*, *Quercus*, *Lithocarpus*, and *Castanopsis* (Wang, 1995; Yu, 2007).

Shiro: cradle of matsutake

Tricholoma matsutake and related species form distinctive fungal colonies in the soil called shiro (= white, castle or place) in Japanese. These colonies are white in pine forests, to pale grey in oak forests, and consist of a compact mass of mycelia which colonizes everything in the shiro soil including plant roots (fine rootlets and thick mother roots, soil granules and rocks, and gaps between soil granules (Figure 3). The shiro can be divided into a few zones, including a zone of maximum mycelial growth and root infection where fruit bodies are produced. After fructification, roots collapse and die, and the soil becomes extremely hydrophilic. Fruit bodies and primordia are only found in shiros. The shiro is the matsutake mushroom birth-place.

Figure 3. *Tricholoma matsutake* shiro in a P*inus yunnanensis* forest, Huize, Yunnan.

Shiro development is closely correlated with the age of the host plants and usually begins when *Pinus densiflora* trees are 10 to 20 years old. The fruit bodies begin to be productive three to four years after the shiro is formed. The shiro advances between 100 and 200 mm per year. Matsutake production reaches its peak when shiros become circles, arcs, or other irregular shapes. Finally the shiro collapses and disappears, and production of fruit bodies declines to nothing. Shiros can survive and still produce fruit bodies for several years even if host trees are clear-felled (Ogawa, 1978; Wang, 1995).

Shiro occurrence is related to environmental conditions, including topography, vegetation, and soils. Shiros usually occur on the middle to upper parts of hills, on sunny and semi-sunny slopes (Wang, 1995; Gong *et al*., 1999), where plant canopy provides only 50 to 80% cover and the shrub layer is relatively sparse. Suitable soils are well-drained, poor, rocky-sandy or sandy loam, dry-moist and not wet, with pH 4.5 to 5.5, and a thick litter layer. In general, shiros occur in very harsh environments, probably with reduced competition from other fungi, microorganisms, insects and other natural enemies.

In north-eastern China, matsutake always occurs in pure stands of *Pinus densiflora* or where these trees are mixed with a few individuals of *Quercus mongolica*, and with bush and herb layers containing fewer than 20 species, including *Rhododendron* species, *Lespedeza bicolor, Atractilis japonica, Atractylodes japonica, Artemisia* species, *Imperata cylindrica, Peucedanum terebinthaceum, Pedicularis* sp., *Platycodon grandiflorus, Polygonatum odoratum,* and *Carex callitrichos*. These are considered indicator plants for matsutake-producing areas (Wang and Xie, 1982; Sun *et al*., 1989; Fu *et al*., 1996). In eastern China (Anhui Province) and Taiwan, matsutake is found under *Pinus taiwanensis* (Chen, 1983). In south-western China, matsutake forests can be divided into two kinds; pure pine stands or pine mixed with oak and other broadleaf trees, and pure oak forests or oak mixed with pines. The pine species in this area are *P. densata, P. yunnanensis,* and *P. armandii*. The oak species include *Q. semicarpifolia* (Figure 4), *Q. aquifoliodes, Q. senescens, Q. panosa, Q. gillilana,* and *Q. spinnosa*, and other common trees within these forests are *Castanopsis delavayi, Cyclobalanopsis delavayi, Lithocarpus sphaerocapus,* and *L. dealbatus*. The bush and herb layers are less developed and include *Rhododendron* species, grasses such as *Carex* and *Festuca*, and fern species. Canopy density ranges from 0.6–0.7. *Rhododendron* species are always found in matsutake-producing areas in China, indicating that soils are acidic and poor.

Tricholomauber matsutake is also rarely found associated with other tree species. It is sometimes found under Pinus pumila and *P. koraiensis,* for example, in north-eastern China (Figure 5), under *Picea meyeri i*n Shanxi Province, China (Liu, 1991), under *Pinus yunnanensis* var. *pygmaea i*n south-western China, and under *Tsuga chinensis* in Taiwan (Hu, 1994).

Fruiting

Matsutake primordia develop just below the surface layer of the shiro, and take 10 to 20 days to open into mushrooms depending on soil temperature, moisture, and other factors. Matsutake fruits between July and early September in north-eastern China and July to October in south-western China, and yields are closely tied to weather patterns, especially rainfall and temperature. Generally, *T. matsutake* yields are highest when there is plentiful rain in spring, a relatively hot and dry summer, and a moist cool autumn. According to Sun (personal communication) in Heilongjiang Province, north-eastern China, good harvests can be expected if the 100 mm soil temperature is between 16 and 19 °C, and 70 to 100 mm of rain falls in around 10 showers between the last 10 days of July and the first 10 days of August. Alternatively if the soil temperature is between 19 and 22 °C, good production will follow if there is a rainfall of no more than 100 mm, spread over eight showers. However, if the soil temperature has a conspicuous increase (over 19 °C) or

Figure 4. *Tricholoma matsutake* growing under *Quercus semicarpifolia* trees (3000 m a.s.l), Zhongdian, Yunnan.

Figure 5. *Tricholoma matsutake* growing under *Pinus koraensis* trees, Yichun, Heilongjiang.

drops too low (below 15 °C) for several days after the primordia have been formed, the primordia will abort and there will be no fruiting that year.

In Japan and Korea, matsutake production starts when *P. densiflora* trees are around 20 years old and reaches a maximum in 40 to 50 year old forests, gradually declining over the following 30 to 40 years as the litter layer builds up and the pines grow old; finally being replaced by other plant species such as deciduous oaks. In China, matsutake production starts when pine trees are 45 to 45 years old and ends when they are around 120 years old (Sun *et al*., 1989; Wang, 1995).

Matsutake: not a normal ectomycorrhizal fungus

Following over 100 years of research history of matsutake in Japan, the symbiotic association of *T. matsutake* and *P. densiflora* has been recognized as a parasitic ectomycorrhiza or an ectomycorrhiza with a parasitic nature (Masui, 1927; Ogawa, 1982; Tomonaga and Komeyama, 1987). Mycologists working recently in Japan (Gill *et al*., 2000; Guerin-Laguette *et al*., 2002; Yamada *et al*., 1999a; Yamada *et al*., 1999b; Vaario *et al*., 2002) have reexamined mycorrhizal roots formed by this association in situ and in vitro, and concluded that they are typical ectomycorrhizae, although atypical behaviors do exist (Gill *et al*., 2000; Hur *et al*., 2001; Vaario *et al*., 2002; Yamada *et al*., 1999a). The saprophytic nature of *T. matsutake* was discovered and studied by Hiromoto (1963 a, b) and others (Terashita and Kono, 1987; Terashita *et al*., 1995; Wang, 1995; Hur *et al*., 2001; Vaario *et al*., 2002, 2011; Wang and Hall, 2006; Yamada *et al*., 2006, 2010). However, all attempts to grow *T. matsutake* using typical methods for cultivating saprotrophic mushrooms have failed (Ogawa, 1978; Wang, 1995).

Our research suggests that matsutake is not a typical ectomycorrhizal fungus and her biotrophy involves mutualism, parasitism, and saprophytism. We have previously discussed this in detail (Wang, 1995, Wang *et al*., 1997; Wang and Hall, 2006).

Conservation and cultivation

Increasing commercial harvest of matsutake from natural forests has damaged matsutake environments and populations in China to the extent that harvests have dramatically decreased over the past 20 years. The Shangri-La region is the most important matsutake producing region in China. Production in this area dropped from over 700 tonnes in 1999 to around 500 tonnes after 2010 (Yang *et al*., 2009). The issue of the conservation and cultivation of matsutake has been raised previously. Attempts at production of matsutake-infected seedlings for the establishment of plantations have had little success in or outside China (Ogawa, 1978; Wang, 1995; Hu, 1994; Gong *et al*., 1999; Guerin-Laguette *et al*., 2000; Yamada *et al*., 2002), even though the technology for the infection of matsutake seedlings has made good progress in Japan and other countries (Yamada *et al*., 2006, 2010; Park *et al*., 2007). Research of *T. matsutake* in China has concentrated on its conservation and ways of stimulating fruiting in forests (Wang and Xie, 1982; Wei *et al*., 1985; Fu *et al*., 1996; Gong *et al*., 1999), and similarly in Japan and Korea (Ogawa, 1978; Park *et al*., 1997; Koo and Milek, 1998) it has been reported that the number of shiros increased by 9.8%, and fruit bodies increased by 44.7%, in experimental plots in Yunnan following three years of management of matsutake forests. The contracting of matsutake forests to individuals is an effective way of managing matsutake resources in Yunnan (Su, 2002). Recently, local regulations have been issued and a few matsutake reserves have been established in Jilin, Helongjiang, and Yunnan Provinces (Zhou, 2002). However, the protection and management of matsutake forests are still big challenges in China, due to a variety of social, cultural, and institutional factors (Yang *et al*., 2009).

The recent application of molecular technology has considerably progressed our understanding of the biology of matsutake (Lian *et al*., 2003; Yu, 2007; Xu *et al*., 2008, 2010; Wang *et al*., 2013; Wang and Chen, 2014). Hopefully, advances in molecular technology will help to provide better ways of protecting and cultivating the matsutake mushroom.

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