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Chapter 15
Biogeography of the Japanese Gourmet Fungus, *Tricholoma matsutake*: A Review of the Distribution and Functional Ecology of Matsutake

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15.1 Introduction

Tricholoma matsutake, an ectomycorrhizal (EcM) fungus, is regarded as one of the most desirable mushrooms in the world (Hall et al. 2003). The first research concerning *T. matsutake* was published in Japan over 100 years ago and the field has since grown into a community of researchers in Asia (Ogawa 1978; Yamada et al. 1999; Gong et al. 1999), North America (Hosford et al. 1997; Chapela and Garbelotto 2004) and Europe (Bergius and Danell 2000; Vaario et al. 2010) due to its high value as a non-timber forest product in Japan and the Far East. Recently, global climate change and over-harvesting have raised serious concerns about the resource status and stainability of matsutake populations.

Typically, EcM fungi enhance the nutrient uptake of their host tree and import carbohydrates to the ectomycorrhizosphere through the root–mycelium interface. The ectomycorrhizosphere, which forms a specific interface between the soil and the symbiotic fungi, harbors a large and diverse community of microorganisms that can either inhibit or enhance each other (Smith and Read 2008). The identity of the host-tree and soil characteristics are considered key elements defining the preferred habitat of matsutake and can affect its subsequent productivity. Detailed studies of *T. matsutake* in natural settings led by M. Ogawa during the 1960s and 1970s

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(e.g. The Matsutake Research Association 1964; Ogawa 1978) built the foundation on which modern matsutake research is based (Hosford et al. 1997, see review Wang et al. 2012). Demand for the mushroom as a culinary delicacy has stimulated research that aims to understand the enigmatic role matsutake plays in the forest ecosystem and its highly variable fruiting behavior. Here, we review recent findings from the molecular to ecological scale within the global geographic context, and focus on community structure, biogeography and characterization of the extended shiro and where the mycorrhizae and extraradical mycelium of *T. matsutake* form a whitish mycelium–soil aggregate from which fruiting-bodies develop. The current knowledge base is placed into the context of functional ecology of EcM fungi and forest management.

15.2 Host Diversity of *T. matsutake*

15.2.1 Circumboreal Distribution of T. matsutake *and Related Species*

The taxonomy and phylogeny of matsutake are central to understanding the current distribution of *T. matsutake* and its host associations (Ryman et al. 2000; Ota et al. 2012; Christensen and Heilmann-Clausen 2013). The "Caligata" clade of matsutake mushrooms (Murata et al. 2013b) in the section Caligata (Bon 1991) consists of several *Tricholoma* species associated with conifers, of which the basal member is *T. caligatum* from Europe. According to a phylogeny inferred from retrotransposon elements, the ancestral population of *T. caligatum* shifted host from fagaceous trees to conifers (Murata et al. 2013b). A similar evolutionary shift is also inferred for conifer-associated matsutake in North and Central America, which dispersed through Beringia during the Eocene from a Eurasian ancestor associated with angiosperms (Chapela and Garbelotto 2004). Conifer-associated matsutake also include *T. anatolicum* from the Mediterranean (Intini et al. 2003; Yamada et al. 2010), *T. matsutake* from eastern Asia and central and northern Europe (Kytövuori 1988; Bergius and Danell 2000; Matsushita et al. 2005), and *T. magnivelare* and *Tricholoma* sp. (including *T.* cf. *caligatum* associated with conifers) from North and Central America (Hosford et al. 1997; Amaranthus et al. 2000; Bessette et al. 2013). The occurrence of matsutake in Japan, Korea, China and Fennoscandia suggests that *T. matsutake* is distributed widely throughout Eurasian forests (Yamada 2015), but samples of populations from central Asia and Siberia are currently lacking.

RFLP analyses of the intergenic spacer 1 (IGS1) region of genomic ribosomal RNA gene (rDNA) unfortunately could not resolve the metapopulation structure and dynamics of samples of *T. matsutake* from several locations in Eurasia (Guerin-Laguette et al. 2002; Matsushita et al. 2005). In the analysis of Asian *T. matsutake*, Murata et al. (2008) examined retrotransposon regions in the genome and distinguished local populations of *T. matsutake* in Japan, North Korea, South Korea,

northeast China, and southwest China through Bhutan. In particular, populations at the foot of the Tibetan Plateau and elsewhere in the Far East were highly distinct (Murata et al. 2008; Xu et al. 2010). This suggests isolation and diversification of *T. matsutake* populations during the last ice age (Ray and Adams 2001). One of the main questions to be addressed by future studies concerns the integration and connectivity of *T. matsutake* populations throughout its modern range (Suzuki 2005; Murata et al. 2015a). Although high-resolution genetics can provide evidence of gene flow among populations (Kretzer et al. 2005; Vincenot et al. 2012), it remains difficult to demonstrate the reproductive isolation of any particular one. In an attempt to resolve this issue, monokaryotic cultures of *T. matsutake* populations should be established (Murata et al. 2015a) to determine mating type and interfertility.

Regarding fine population structure, Xu et al. (2008) found a significant positive correlation between genetic distance and geographical distance among populations of *T. matsutake* in southwestern China, which showed significant but low genetic differentiation among populations. Amend et al. (2010) conducted a SNP analysis of *T. matsutake* populations in southwest China that distinguished samples from adjacent watersheds isolated by treeless ridgelines. As a result, they found that high-altitude treeless ridgelines are effective barriers to gene flow, even at distances of less than 65 km. Recently, Zeng and Chen (2015) revealed a clear genetic divergence among *T. matsutake* population from northeastern and southwestern China, two of the main regions producing matsutake for the global market. However, compelling evidence concerning a genetic basis for the host specificity in matsutake is lacking.

15.2.2 Host-Tree Associations of T. matsutake *in Japan*

In Japanese, *matsu-take* means pine mushroom, denoting the well-known association between *T. matsutake* and its main host there—the Japanese red pine (*Pinus densiflora*). Japanese red pine occurs naturally 0–2000 m a.s.l. from Yakushima in the south (30° N) to Hokkaido (42.5° N) in the north (Satake et al. 1989). In Japan, *T. matsutake* can be found in conifer forests from Hokkaido in the north to Kyushu in the south and west (ca. 31° N) (Hamada 1964; Ogawa 1978; Murata and Minamide 1989; Murata et al. 2001; Guerin-Laguette et al. 2002). Matsutake productivity has been monitored in Japan for several decades (Fig. 15.1), and the highest domestic harvests of recent years have come from Japanese red pine forests. In the deep mountainous terrain of Honshu, *Tsuga siebordii* and *T. diversfolia* are the main ectomycorrhizal hosts of *T. matsutake* in temperate and subalpine climates, respectively (Hamada 1964; Ogawa 1976b, 1977a, b; Endo et al. 2015). At the edge of the range of *P. densiflora* in Hokkaido, *P. pumila*, *Picea glehnii*, and *Abies sachalinensis* serve as hosts of *T. matsutake* in alpine, alpine-subalpine, and subalpine climates, respectively (Hamada 1964; Ogawa 1976a, b; Murata and Minamide 1989; Endo et al. 2015). Japanese subalpine forests are quite diverse in terms of

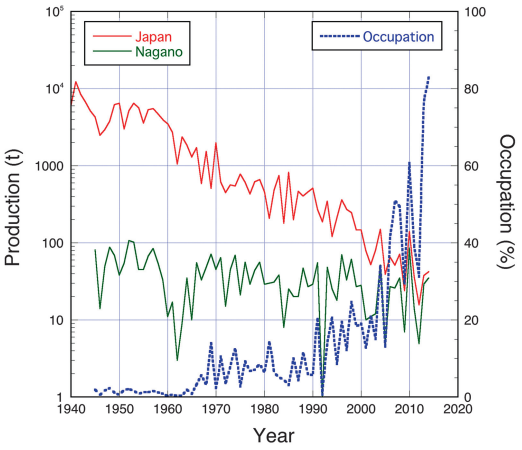

Fig. 15.1 Production of *T. matsuake* in Japan and Nagano Prefecture

conifers, especially on Honshu where pines, firs, spruces, hemlocks, a larch, and a false hemlock can be found. Unfortunately, little is known of their respective roles as host trees for *T. matsutake*, although *Abies veitchii* was recently confirmed as an alternative host (Endo et al. 2015). Given that the association between firs and *T. matsutake* has been confirmed in Japan, a comprehensive survey of host-tree use for populations in China and Fennoscandia should be performed.

15.2.3 Host Associations of T. matsutake *in Other Regions*

In China, *T. matsutake* has been reported in two separate areas: southwest including Yunnan, Tibet, Guizhou, Gangsu, Guangxi and Sichuan provinces, and northeast including Jilin and Heilongjiang provinces (Zang 1990). It is interesting to note that *T. matsutake* populations in China are believed to be naturally associated with both conifers and fagaceous trees (Amend et al. 2010; Yamanaka et al. 2011; Wan et al. 2012), whereas in Japan and northern Europe matsutake appears restricted to the roots of conifers. If a relationship between *T. matsutake* and fagaceous trees (oaks and beeches) is accurate, the evolutionary scenario of host use in this clade must be reconsidered in light of a phylogeny based on retrotransposon data (Murata et al. 2013b). To date, three genera in Fagaceae (i.e., *Quercus*, *Lithocarpus*, and *Pasania*) are listed as EcM hosts of *T. matsutake* in China (Yamanaka et al. 2011). However, these associations should be confirmed with molecular analyses of both partners in conjunction with morphological and ecological observations of EcM and fruiting-body formation in oak-dominated woodlands. Another important point concerning *T. matsutake* populations in China is that an annual mushroom harvest of $>$1000 tons represents ca. 70% of matsutake imported to Japan (Table 15.1). The Chinese harvest has been 20–50 times larger than that in Japan over recent years. If

Table 15.1 Matsutake import to Japan from abroad in the recent 5 years[a]

	China		USA		Canada		Turkey		Mexico		Morocco		World	
Year	Ton[b]	Yen[c]	Ton	Yen	Ton	Yen	Ton	Yen	Ton	Yen	Ton	Yen	Ton	Yen
2015	497	33	72	3.7	253	10	58	1.7	5	0.3	7	0.3	897	50.3
2014	669	35.3	212	9.7	87	4.2	88	2.1	7	0.4	–	–	1073	54.3
2013	775	39.7	214	7.9	173	6.2	27	0.7	17	0.9	3	0.1	1222	58.4
2012	1132	44.1	79	3.7	54	2.7	111	2.6	7	0.3	33	2.4	1436	56.2
2011	875	42.2	99	4.6	147	6.1	64	1.3	17	0.7	–	–	1215	57.1

The data was extracted from Database of Ministry of Agriculture, Forestry and Fisheries in 2016 (http://www.maff.go.jp/j/tokei/kouhyou/kokusai/index.html)

[a]This list includes *T. matsutake* and other related matsutake mushrooms: China import is mostly *T. matsutake* but included a small amount of *T. bakamatsutake* and potentially *T. fulvocastaneum*, USA and Canada imports are mostly *T. magnivelare*, Turkey and Morocco imports are mostly *T. anatolicum*, and Mexico import is Mexico import is mostly *Tricholoma sp.* (Yamada et al. 2010)

[b]The volume of import is indicated as metric ton

[c]The value means Japanese yen with $\times 10^8$

the host-species identity explains this difference in productivity, matsutake forests could be managed to maximize fruiting through the planting or selection of suitable tree species, controlling tree age and density, and careful harvesting to protect the industry and genetic diversity of the population.

Matsutake was known as *T. nauseosum* in northern Europe until molecular techniques revealed its conspecificity with *T. matsutake* (Bergius and Danell 2000; Matsushita et al. 2005). Unfortunately, studies dealing with its host-species, distribution and productivity there remain sporadic, most likely because matsutake mushrooms are not eaten by north Europeans. During the past 20 years, mapping of harvest data has shown that matsutake can be found at 350–400 localities in Fennoscandia, and the real number may be 10 times higher (The Global Fungal Red List Initiative 2015). In Finland and Sweden, *T. matsutake* has only been found in pine forests of at least 50 years old (Risberg et al. 2004). Among the three major forest tree species in Finland, *T. matsutake* has a confirmed association with *Pinus sylvestris* and *Picea abies* (Vaario et al. 2010), but no symbiotic relationship was found with *Betula pendula*.

15.2.4 Host Specificity

In general, host-plant genotype is believed to determine root colonization, ecological fitness, and metabolic activity of EcM fungi as well as the outcome of competitive interactions between two or more EcM fungi colonizing the same host (Bryla and Koide 1990; Tagu et al. 2005; Courty et al. 2011). In line with natural observations, in vitro trials have shown that matsutake can form root symbioses with conifers such as *Pinus*, *Picea*, *Abies* and *Tsuga* (Yamada et al. 1999, 2014; Gill et al. 2000; Vaario et al. 2010; Endo et al. 2015), as well as form partial associations with other plants (e.g., *Larix kaempferi, Cedrela odorata*, *Prunus* spp., *Betula platyphylla* var. *japonica* and *Populus tremula* × *tremuloides*), but these have not been confirmed in natural settings (Murata et al. 2013a, 2014a, b, 2015b, 2016; Yamada et al. 2014). Although associations based on in vitro trials can help us to understand the genetic basis of EcM specificity, the extent to which results reflect natural phenomena with ecological significance is unclear. By using cloned material of *P. sylvestris*, it has been shown that those individuals containing high concentrations of phenolics and bear thick epidermal cell walls have more limited or no association with matsutake mycelium (Vaario et al. 2015a). Additional studies using genetically-uniform material should be undertaken to understand the factors regulating the compatibility of EcM fungi with their host plants.

15.3 Microbial Diversity in the *T. matsutake* Shiro

In the forest ecosystem, above- and below-ground communities are inextricably linked. Plant species can influence the soil, rhizosphere, and forest-floor microbial community structure through root exudates and leaf litter quality (Grayston et al. 1997; Westover et al. 1997). Similarly, soil microbial activities directly affect plant growth, survival, productivity and can influence plant community composition and ecosystem function (van der Heijden et al. 1998; Zak et al. 2003). The ectomycorrhizosphere, which forms a highly specific interface between the soil and EcM fungi, harbors a large and diverse microbial community capable of self (positive and negative) regulation (Rudnick et al. 2015). A detailed in vitro study of non-EcM microbes in the shiro concluded that the density of fungi and actinomycetes adjacent to actively-growing matsutake mycelium decreased and the overall microflora in the shiro exhibited an annual cycle of deterioration and recovery (Ogawa 1977b). However, in vitro culture methods tend to over-represent the importance of those microbes that lend themselves to artificial culture, and may mislead our understanding of the natural community and its ecology. Recent metagenomic studies emphasize the narrow window through which culture methods view microbial ecology (Amann et al. 1995; Lombard et al. 2011). It should be mentioned that metagenomic analyses are also prone to a systematic bias in the form of primer performance during amplification and the generation of chimeric sequences may similarly over- or underestimate the abundance and importance of certain taxa (Morales and Holben 2011). A summary of recent molecular and culture-based studies is provided in Table 15.2.

15.3.1 Fungal Diversity in the Shiro

A study of seven sampling sites in Japan showed that 96% of mycorrhizal root tips in the shiro belonged to *T. matsutake*, the remaining 4% ascribed to *Rhizopogon* sp., *Russula* sp. and *Tomentellopsis* sp. (Lian et al. 2006). Matsutake usually forms a whitish mycelium–soil aggregate and mycorrhizae in the mineral soil layer. In an analysis of soil microflora above and below the shiro, some EcM fungi (e.g., *Tomentellopsis* sp. and *Tylospora* sp.) above the shiro were identified as potential indicator species, i.e., were significantly and positively correlated with matsutake occurring below them (Vaario et al. 2011). According to an analysis of root tips in the shiro, only a small number of EcM fungi with low abundance were detected, but it should be stressed that the EcM community is dynamic and may recover relatively quickly (Lian et al. 2006). This is consistent with observations of moderately diverse EcM fungi in the shiro (Vaario et al. 2011; Kim et al. 2013). A 3-year fruiting-body survey in southern Finland revealed that only ca. 20% of other macrofungal species fruited during the peak season for *T. matsutake*, with the

Table 15.2 Summary of recent studies of microbial community in *T. matsutake* shiro

	Country	Study location	Sample type	Major host species	Isolation method	Type of analysis	Phylum[a]	Key results[b]	References
Bacterial community	Finland	62°10′N, 22°50′E; 60°18′N, 24°31′E	Soil	*Pinus sylvestris, Picea abies*	Non-culturable	PCR-DGGE-direct DNA sequence	Only Act was studied	37 Act OTUs found in shiro + *Thermomonosporaceae, Nocardia* sp. *Streptomyces* sp. were positively correlated with the presence of *T. matsutake*	Vaario et al. (2011)
	Japan	35°11′N, 135°20′E	Soil	*Pinus densiflora*	Culturable	PCR-RFLP-direct DNA sequence	Pro, Fir, Act	The most frequent bacteria belong to *Stretomyces* sp.	Kataoka et al. (2012)
	China	26°36′N, 102°32′E	Fruiting-body	Pine and oak	Non-culturable	PCR-DGGE-Direct sequencing	Pro, Fir, Act	The dominated bacteria were from Pro and Fim phylum	Li et al. (2014)
	Korea		Soil	NR	Non-culturable	Pyrosequencing	Pro, Aci, Act	More Act in shiro + than Shiro + In and Shiro + Out	Kim et al. (2014)
	China	Yunnan	Soil	Pine and oak	Culturable	PCR-direct sequencing	Pro, Fir, Bac, Act	Pro was the dominated phylum, Act had the lowest percentage (<5%)	Jiang et al. (2015)
Fungal community	Japan	39°56′N, 141°14′E	EcM root tips	*Pinus densiflora*		Morphytyping and PCR-RELP-direct DNA sequence		Matsutake was the dominated species in shiro+, only 4% was other ECM in shiro+	Lian et al. (2006)
	Finland	62°10′N, 22°50′E; 60°18′N, 24°31′E	Soil	*Pinus sylvestris, Picea abies*		PCR-DGGE-direct DNA sequence		Matsutake dominated in shiro soil; *Tomentollopsis* sp. (shiro + abv), *Piloderma sp.* (shiro+) positively correlated with matsutake presenting	Vaario et al. (2011)

	Korea		Soil	NR		Pyrosequencing		Total fungal OTUs was 1.5–2 times lower in Shiro + than Shiro + In, Shiro + Out. 88.57% OTUs in Shiro + accounted for Trichoomataceae	Kim et al. (2013)

[a]*Aci* Acidobacteria, *Act* Actinobacteria, *Bac* Bacteroidetes, *Fir* Firmicutes, *Pro* Proteobacteria
[b]*Shiro+* shiro area, *Shiro + In* inside direction of shiro, *Shiro + Out* outside direction of shiro

majority fruiting thereafter (Vaario et al. 2015c); a phenomemon reflected by fungal diversity and community dynamics in the shiro.

15.3.2 Bacterial Diversity in the Shiro

Ohara and Hamada (1967) investigated the bacterial community inner, within and outer the shiro using dilution plating. They found that *T. matsutake* had antagonistic effects on soil bacteria, which accounts for the rather rare occurrence of actinomycetes and other bacteria in shiro soil. Ohara (1980) isolated *Sarcina* and *Micrococcus* and *Streptomyces* from the shiro, but it should be stressed that an artificial and homogenous culture medium typically supports only a small fraction of the microbes present in the inoculum. Although bacterial diversity appears to be rather low in the shiro (Kataoka et al. 2012), recent molecular analyses have detected Proteobacteria, Firmicutes and Actinobacteria commonly represented in shiro samples from different continents (Vaario et al. 2011; Kataoka et al. 2012; Kim et al. 2014; Li et al. 2014; Jiang et al. 2015).

Species of *Streptomyces* are the most common actinomycetes detected in shiro soil samples screened with traditional culture-plate techniques (Kataoka et al. 2012). PCR-DGGE and direct sequencing revealed that one of these OTUs correlated positively with the presence of matsutake in shiro soil (Vaario et al. 2011). By using barcoded pyrosequencing, Kim et al. (2014) found that the relative abundance of Actinobacteria peaked beneath the fairy ring, agreeing with the earlier results, but Actinobacteria were not detected in fruiting-body samples (Li et al. 2014). Some Actinobacteria, especially *Streptomyces,* are able to facilitate development of mycorrhizae and root nodulation (Schrey et al. 2005; Frey-Klett et al. 2007; Tarkka et al. 2008).

Knowledge concerning the bacterial community and its function in the shiro remains limited and largely outside of the EcM and the process of fruiting-body formation. Recently, a study of soil bacteria during the development of *Tuber melanosporum* fruiting-bodies showed how EcM became significantly enriched with actinobacterial sequences similar to species of *Streptomyces* and *Thermoleophilum* (Antony-Babu et al. 2014). The role played by *Streptomyces* as a plant symbiont has been recently explored in terms of inhibiting the growth of fungal phytopathogens, inducing plant-defence pathways, and even promoting the growth of rhizosphere fungi (Maier et al. 2004; Seipke et al. 2012). These studies have raised the question to what extent do EcM fungi support or encourage the growth of certain bacteria that enhance their symbiosis with the host plant? Compared to the limited fungal diversity in the shiro, bacteria seem to be more diverse. In vitro culture-based studies are required to determine, which taxa inhabiting the EcM and/or fruiting-body participate in nutrient mobilization and other physiological responses of the host plant and fungus.

15.4 Fruiting Pattern of Matsutake in Relation to Climate and Weather

Logistic difficulties of monitoring the variable phenology of a fungus, especially fruiting itself, still limit our understanding of the phenomenon. We must also consider the extent to which phenology is affected by geography (i.e., latitude), how climate varies within the natural distribution area of matsutake, and how the fruiting period is influenced by weather. Herbarium records of European fungi demonstrate a rapid change in phenology in terms of the first fruiting date, last fruiting date, mean fruiting date and duration, all of which are believed to be a response to climate change (Buntgen et al. 2013, 2015; Gange et al. 2007; Kauserud et al. 2010).

Observations of the fruiting phenology of *T. matsutake* date back to the 1940s, when Japanese scholars described the spatial arrangement of fruiting-bodies as a fairy ring with an outward progression of the shiro of 0.1–0.2 m per year (Narimatsu et al. 2015; Ogawa 1978). In Nagano Prefecture, first fruiting date and productivity have been recorded for over 30 years (Furukawa et al. 2016; Fig. 15.2). Similar long-term studies have recently been established in China and Finland (Chen et al. 2011; Yang et al. 2012; Vaario et al. 2015c). Based on field observations, fruiting phenology and production of *T. matsutake* is highly variable among years and across the natural distribution (Table 17.3). In this review, we focus on temperature and precipitation to summarize the main findings of a recently published paper in this area (Furukawa et al. 2016; Table 17.3) with a view towards understanding the fruiting pattern of matsutake in relation to climate and geography.

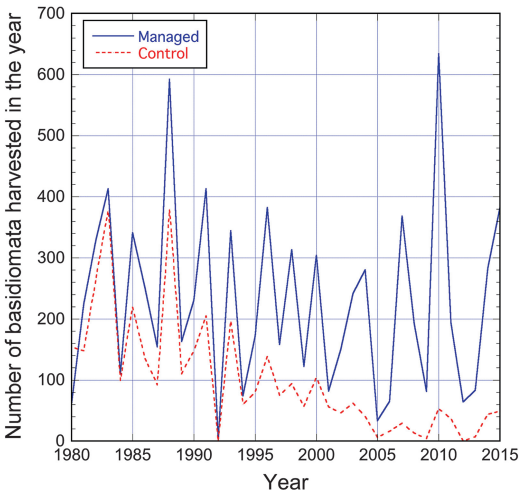

Fig. 15.2 Harvest of *T. matsuake* at Toyooka experimental forest site in Nagano Prefecture (Japan). **Solid line* indicates the harvest in the plot (ca. 0.5 h) which has been managed for sustainable fruiting (e.g., removal of shrubs and litter layer every few years), and the *dotted line* indicates the harvest at the neighboring plot that did not receive such treatment. Redrawn from the data of Furukawa et al. (2016)

15.4.1 Temperature

Matsutake is found in temperate and boreal coniferous forests and mixed woodlands with an annual mean temperature of 4–14 °C, and annual mean precipitation ranging from 600 to 2300 mm (Table 15.3). First fruiting can occur from early summer to late autumn and varies in duration from 15 to 150 days depending on local geographic (i.e., topography and altitude) and climatic factors (Table 17.3). Eleven years of continuous observation from Baoshan (China) revealed a significant delay in the first fruiting date. Comparing similar studies from three countries, the production of *T. matsutake* varies greatly among shiros within a site, among locations and from year to year (Fig. 15.3, Table 15.3). The most productive area occurs in Diqing (China) with an estimated annual harvest of 75–105 kg/ha.

A comparison of climate and weather among sites during the fruiting period in China (Chen et al. 2011) showed that the only factor that significantly differed among sites was maximum temperature. This suggests that the fruiting of *T. matsutake* requires a specific temperature treatment to trigger fruiting, and soil temperatures of 16–16.5 °C at 20–30 cm depth were consistent across sites. In Japan, the fruiting temperature for *T. matsutake* was first determined to be 19 °C at 10 cm depth in a *P. densiflora* forest (Kinugawa 1963). In western Honshu, this temperature was shown to be a good indicator of fruiting (Ogawa 1978). However, in Nagano and Iwate Prefectures, some populations were believed to fruit at lower temperatures (Narimatsu et al. 2015; Endo et al. 2015) because the cool temperate and subalpine forests experience lower soil temperatures. Similarly, soil temperature at first fruiting is much lower based on a 6-year survey in southern Finland (Vaario et al. 2015c). This suggests that some variation, perhaps local adaptation, exists in the fruiting temperature for populations of *T. matsutake*. Some studies have also shown that fruiting could cease soon after soil temperature falls 2–4 °C below that at which it began (Vaario et al. 2015c; Wang et al. 1997). As such, soil temperature may offer a way to remotely monitor fruiting in matsutake and optimize harvesting activity. It is well known that commercially-cultivated saprobic mushrooms such as shiitake (*Lentinula edodes*) vary greatly in terms of the induction temperature for fruiting. Mushroom farmers manipulate this property to create strains suitable for a given location or climate (Hasebe et al. 1998).

Productive areas of *T. matsutake* in Japan are limited to established forests with annual mean temperatures below 13 °C and which expand to a boreal or subalpine climate (Yamada 2015). Higher summer temperatures due to recent global warming will likely have a negative impact on the wild populations of matsutake in these areas (Yamada and Kobayashi 2008; Yamada 2015). Matsutake mycelium cultured on nutrient agar exhibits maximum growth at 20–25 °C but slows to almost zero at 30 °C (Hamada 1953). In the warm temperate forests of Japan, soil temperatures 5–10 cm depth may reach over 25 °C during prolonged hot spells in summer. It remains unclear how soil temperature affects mycelial growth and survival of *T. matsutake* in natural settings. Furthermore, studies from Japanese researchers suggest that a thin litter layer above the shiro could influence soil temperature

Table 15.3 Site information of studies concerning *T. matsutake* fruiting pattern

	China			Japan		Finland
Monitoring site	Chuxiong, Yunnan	Baoshan, Yunnan	Diqing, Yunnan	Toyooka, Nagao[d]	Yokkaichi, Iwate	Nuuksio, Espoo
Location (latitude/longitude)	25°10′N, 99°0′E	25°16′N, 99°18′E	28°23′N, 99°8′E	35°33′N, 137°57′E	39°56′N, 141°14′E	60°18′N, 24°31′E
Elevation (m.s.l)	2450	2350	3300	720–750	360–380	n/a[a]
AMT(°C)	14	12.2	4.7	9.9–11.3–12.2[c]	9.3	4.4–6.7[b]
P(mm)	1140	1200	633.7	1000–1650–2300[c]	1145	596–932[b]
Vegetation	Mixture of *Pinus yunnanensis* and *Castanopsis* spp.	Mixture of *Pinus yunnanensis* and *Castanopsis delavayi*	Mixture of *Pinus densata* and *Quercus semecarpifolia*	*Pinus densiflora*	*Pinus densiflora*	Mixture of *Pinus sylvestris* and *Picea abeis*
# of plots and/or shiros	10	56	10	20–30	5	5
Area	n/a	1 ha	0.1 ha	0.25 ha	n/a	1.35 ha
Observation duration	2009	2000–2011	2009	1982–2014	1994–2011	2008–2013
Years observed	1	11	1	33	18	6
First fruiting day	Jul 14	Jun 7–Jun 19–Jul 19[b]	Jul 25	Aug 29–Oct 18[b]	First 10 days in Sep-first 10 days in Oct	Jul 23–Aug 22[b]
Last fruiting date	Oct 10	Oct 20–Oct 30–Nov 22[b]	Sep 14	Oct 1–Nov 10[b]	n/a	Aug 31–Sep 19[b]
Duration	105	125–136–148[c]	51	15–30[b]	n/a	18–58[b]
Peak of fruiting	Aug–Sep	Aug–Sep	Aug	Oct	Oct	Aug
Multi-year fruiting bodies variation	n/a	233–416–810[b]	n/a	3–231–634[c]	12.5–48.4[b]	7–44–106[c]

(continued)

Table 15.3 (continued)

	China			Japan		Finland
Monitoring site	Chuxiong, Yunnan	Baoshan, Yunnan	Diqing, Yunnan	Toyooka, Nagao[d]	Yokkaichi, Iwate	Nuuksio, Espoo
Productivity (kg/ha)	45–75	30–45[b]	75–105[b]	0.1–25–80[c]	n/a	n/a
Fairy expansion rate	n/a	n/a	n/a	10–20 cm/yr	17 ± 1 cm/yr	n/a
Literature	Chen et al. (2011)	Chen et al. (2011), Yang et al. (2012)	Chen et al. (2011)	Furukawa et al. (2016)	Narimatsu et al. (2015)	Vaario et al. (2015b, c)

[a]No answer
[b]Showing the earliest related date or min value, the latest related date or max value
[c]Showing the earliest related date or min value, the mean related date or value and the latest related date or max value
[d]The values are only the post mid-summer data in this site. Limited natural fruiting occurs prior to the mid-summer season, but this is not recorded in the commercial harvest data

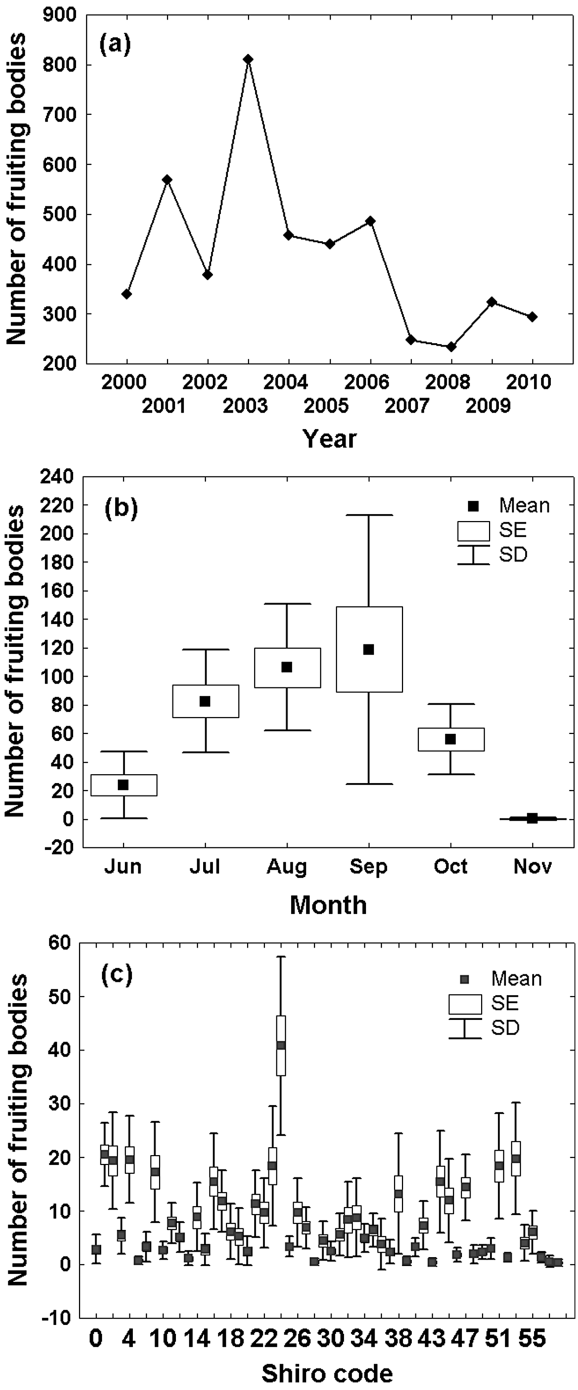

Fig. 15.3 Variation in productivity between years (**a**), months (**b**) and among shiros (**c**) in Baoshan (China). In (**b**) and (**c**), SE is the standard error and SD is the standard deviation from the mean

sufficiently to cause early fruiting (The Matsutake Research Association 1964; Ogawa 1978).

15.4.2 Precipitation

In addition to temperature, precipitation is linked to the productivity of *T. matsutake*. In the prevalent climate in Nagano Prefecture (i.e., Cfa–Dfa boundary of the Köppen climate classification (Peel et al. 2007), *T. matsutake* harvests show a strong and positive correlation with precipitation in August and September prior to fruiting (Furukawa et al. 2016). Precipitation during the fruiting period (i.e., October) does not appear to affect yield. It is worth noting that accumulated precipitation prior to fruiting seems to be negatively related to productivity, i.e., a wet spring-summer typically means a poor matsutake crop in the boreal forest (Vaario et al. 2015c). In contrast, other groups (Furukawa et al. 2016; Yang et al. 2012) observed that abundant rain in August preceded a good matsutake crop in Yunnan and Toyooka, but high rainfall from November/December to May was associated with few fruiting bodies the following season in Yunnan (Yang et al. 2012). Taking into account that the fruiting of *T. matsutake* in Yunnan begins in early June and ends in November (Yang et al. 2012), it seems that the pattern observed in China is inconsistent with that in southern Finland (Vaario et al. 2015c). Furthermore, given that the fruiting phenology of *T. matsutake* differs from other fungi in the shiro (Vaario et al. 2015c), this might reflect the growth of matsutake mycelium in response to soil moisture rather than being tied to temperature (Narimatsu et al. 2015). To understand the relationship between matsutake fruiting pattern and meteorological factors, long-term phenological data from distant and varied locations throughout the range are required.

In addition to variation in climate and geography, two basic issues remain poorly understood but could shed considerable light on fruiting dynamics: (1) the relationship between fruit-body biomass and that of soil mycelia, and (2) the relationship between mycorrhizal biomass and climate. Regarding the first relationship, a recent study in Japan applied a novel method to measure the amount of *T. matsutake* mycelia in a soil sample by quantifying a single-copy DNA element that is uniquely conserved within *T. matsutake* but absent from other fungi present in the shiro (Yamaguchi et al. 2016). Although widely accepted, it has yet to be confirmed that the summer and early autumn is an important period during which matsutake mycelium increases due to an optimal growth temperature. As such, higher precipitation during this time enhances mycelial biomass, which in turn can support a higher biomass of fruiting-bodies (Ogawa 1978). On the other hand, EcM fruiting-body formation exhibits a close relationship with the host plant condition, which is often improved by higher soil moisture and temperature during the growing season, which leads to a richer supply of carbohydrates supplied to the roots where they are used in the formation of fruiting-bodies (Sato et al. 2012). Although experimental evidence is lacking, this provides a mechanistic explanation for why higher

precipitation prior to the fruiting season is associated with higher sporocarp production. Regarding the latter relationship, we still know relatively little about general EcM ecology as few environmental determinants have so far been identified (Smith and Read 2008). In *P. densiflora* forest, annual mean EcM biomass fluctuates significantly, and high precipitation in late autumn is associated with a lower yield the following year (Okada et al. 2011).

15.5 Ecological Strategies of Matsutake

EcM symbiosis is a widespread and important component of the forest soil ecosystem and the fungi involved may occupy one or more positions along the biotrophy–saprotrophy continuum (Taylor and Alexander 2005). The hypothesis that matsutake mushrooms are true EcM mutualists has garnered the attention of many mycologists and mycorrhizologists. Ogawa and coworkers have studied the ecological strategy of matsutake in detail through a soil-sectioning approach and direct observation of shiro structure (Ogawa 1978). Since that pioneering work, research has sought to explain field observations with controlled microcosm experiments in the laboratory. We will now discuss the main findings from recently published studies with the aim of providing a more complete synthesis of the ecological strategy of the fungus.

T. matsutake is a typical EcM fungus in terms of its morphology. Basically, *T. matsutake* shows a typical EcM structure when associated with a compatible host plant, i.e. a Hartig net and mantle (Yamada et al. 1999; Gill et al. 2000). In addition, in vitro inoculation of *T. matsutake* generates a typical EcM structure with a mutualistic effect on the pine host (Guerin-Laguette et al. 2004; Yamada et al. 2006; Murata et al. 2013a). However, in comparison to other EcM fungi such as *Rhizopogon roseolus*, pine seedlings infected with *T. matsutake* may be not a good symbiont for pine seedlings in vitro (Yamada et al. 2010). It is generally accepted that late-stage fungi represent poor inoculum for young seedlings, because hyphae of those fungi have slow growth rates and higher carbon demand (Deacon and Fleming 1992; Cairney and Chambers 1999; Smith and Read 2008).

15.5.1 Functional Diversity and Nutrient Acquisition

A detailed morphological study of *T. matsutake* mycorrhiza recognized four developmental stages of mycorrhizal root tips (Gill et al. 2000). Briefly, whitish ectomycorrhizae gradually turn darker similar to the root cortical cell and finally become black with a thin mantle (Agerer 1987–1998; Yamada et al. 1999). Although data are limited, an in vitro developmental study showed that this sequence can be completed within several months in a granite-based natural soil substrate (Yamada et al. 2006; Kobayashi et al. 2007). Enzyme activities linked with the degradation of organic matter in the shiro (Vaario et al. 2011) have been

identified; *T. matsutake* produces a range of extracellular enzymes including amylases, β-glucosidase, xylosidase and proteinases in vitro (Terashita et al. 1995; Hur et al. 2001; Vaario et al. 2002, 2012; Kusuda et al. 2006, 2008). The growth of *T. matsutake* mycelium in a forest-litter extract containing organic carbon (Vaario et al. 2013) could be explained by relatively high concentrations of hemicellulose occurring in root and leaf litter (Kiikkilä et al. 2011). However, the relative growth of *T. matsutake* and true saprotrophic fungi on this and other organic carbon sources has yet to be studied and compared.

T. matsutake prefers forest sites on soil derived from an acidic parent rock such as granite (Hamada 1964; Ogawa 1978). It has been observed that *T. matsutake* mycelium tightly adheres to the surfaces of small rocks in the shiro. It has been confirmed in vitro how these interfaces enable the fungus to mobilize and absorb many important minerals and trace elements (e.g., Al, Fe, Mn, Zn) directly from the rock fragments. Furthermore, X-ray powder diffraction identified a uniform mineralogical profile containing major phases of quartz, microcline, orthoclase and albite in 14 shiro samples collected in southern Finland (Vaario et al. 2015b). Yet, it remains challenging to draw any firm conclusions concerning a preferred mineralogical profile of the matsutake shiro as a comparison between shiro and non-shiro soil is currently lacking. In relation to this issue, a recent study showed how matsutake mycorrhizae secrete oxalic acid and obtained the soluble phosphoric acid from insoluble aluminum phosphate in the shiro to form the antimicrobial substance as the (oxalate)aluminate complex released into the shiro (Nishino et al. 2016a, b). The extent to which sandy soil over granite bedrock is a prerequisite for *T. matsutake* is an interesting topic for future research.

To date, there are no convincing data that clearly define the relationship of *T. matsutake* with its host plant along a mutualistic-parasitic scale (Yamada 2015). However, evidence is accumulating to suggest that EcM fungi produce degrading enzymes and are able to decompose organic matter (Taylor and Alexander 2005; Cullings and Courty 2009), especially when the carbon supply from the host is experimentally limited (Buée et al. 2005; Mosca et al. 2007). Talbot and colleagues (2008) proposed a hypothetical model of saprotrophic events in the life cycle of EcM fungi when the supply of photosynthate from the host plant is low, or when photosynthate is available but mycelial growth is limited by another resource. A more recent study (Lindahl and Tunlid 2015) proposed that EcM fungi benefit from organic matter decomposition primarily through increased nitrogen mobilization rather than the direct release of metabolic carbon.

15.5.2 Forest Management and T. matsutake *Productivity*

In forest ecosystems, *T. matsutake* can be categorized as a late-stage EcM fungus (Deacon and Fleming 1992), because fruiting occurs in forests where *P. densiflora* dominates the canopy or in climax stands of hemlock (Hamada 1964; Ogawa 1977a, b). In *P. densiflora* forests, it is generally accepted that *T. matsutake* is

more productive when associated with trees that are 40–60 years-old. Forest management measures such as clearing of shrubs and broadleaves and removal of the litter layer is generally thought to prolong the productive period (Ogawa 1978). However, carbon derived from litter seems to have a positive effect on *T. matsutake* fruiting-body formation (Vaario et al. 2013). This suggests that pine root dominance as well as specific and stable physio-chemical properties and soil microbial community is necessary to sustain the shiro over long periods (Suzuki 2005; Yamada 2015). Although the forest management described above has been widely applied in *P. densiflora* forests of Japan, data from other geographic regions are limited, making any comparisons difficult. As the shiro of *T. matsutake* is primarily sustained by the carbon input from the host root system, the mycorrhizal biomass in the forest may be a critical factor for *T. matsutake* mushroom production at the stand level. Therefore, we should seek to develop a theoretical model incorporating mycorrhizal biomass, tree density, tree age and soil chemical and mineralogical properties. It is generally believed in Japan that *T. matsutake* prefer habitats typical of mountain ridges or rocky areas in forests, both of which are well drained, but similar studies from other locations are lacking and prevent more general observations from being made at this time.

Some areas have witnessed a marked decline in matsutake productivity due to various reasons. Unfortunately, in spite of considerable effort, the artificial cultivation of this mushroom remains in its infancy. Outplanting of mycorrhizal seedlings and directly inoculating mature host trees with *T. matsutake* in forest sites has been attempted for a long time in Asia (Ogawa 1978; Guerin-Laguette et al. 2005; Park et al. 2007; Ka et al. 2008; Kobayashi et al. 2015). The only encouraging result in the public domain concerns outplanted mycorrhizal pine seedlings that were grown for at least 2 years following in vitro inoculation (Kobayashi et al. 2015). So far, the majority of data from the in vitro culture of *T. matsutake* with seedlings offer some limited insights into the nutritional and ecological function of *T. matsutake* in association with mature trees. A transcriptome analysis of mycorrhizal root tips and sporocarp samples taken at different stages of development coupled with stable isotope fractionation analysis constitute an ideal approach to clarify the ecophysiology of this species.

15.6 Conclusions

Recent studies have focused on determining the extent to which fungal diversity and its geographical variation play a role in ecosystem processes (Põlme et al. 2013; Tedersoo et al. 2014). *Tricholoma matsutake* is distributed widely in temperate and boreal forests of Eurasia, where it inhabits a diversity of coniferous and fagaceous host tree species in a variety of climates and natural settings. As a late-stage EcM fungus, *T. matsutake* co-exists with several soil microbes in the shiro, and some evidence supports the notion of microbial cooperation in nutrient acquisition and mediation of the host–tree response. In this review, we have seen that the use of

molecular identification and quantification techniques has removed many of the barriers that existed for studying above- and below-ground microbial communities associated with the matsutake shiro. However, systematic surveys over a broad geographic scale are lacking and which prevent general statements from being made about the habitat preferences of this enigmatic and highly sought-after mushroom.

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