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RESEARCH ARTICLE

Fruiting pattern of *Tricholoma matsutake* in Southern Finland

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Commercial harvesting of matsutake in Finland has driven the need to understand how fruiting is affected by climate and habitat. A productive site in Finland was studied in this respect. Productivity, duration, and early onset of fruiting were examined in relation to mean air temperature, soil temperature, accumulated degree-days, and precipitation. We monitored the fruiting of matsutake and other macrofungi during 2008–2013. As a pilot study, our results showed the timing and yield of the annual fruiting of *Tricholoma matsutake* varies in Southern Finland and can occur from the middle of July to middle of September; although we did not find a clear and simple correlation between fruiting and rainfall, an average amount of precipitation (i.e. 90–110% of the long-term average precipitation) prior to the first fruiting was associated with high yield; we did not identify any threshold soil temperature associated with the onset of fruiting, however, we found that soil temperature might provide a means to monitor the end of the matsutake fruiting period, and late onset or higher soil temperatures prior to the first fruiting were associated with shorter fruiting periods. These results can be further utilized for developing a model to predict the yield of *T. matsutake* in Nordic regions.

Keywords: *Tricholoma matsutake*; pine mushroom; fruiting pattern; precipitation; soil temperature; productivity

Introduction

Tricholoma matsutake, the pine mushroom, is an ectomycorrhizal (ECM) fungus that is commercially harvested in *Pinus densiflora* forests in the Asia (Ogawa 1978, Wang et al. 1997) Matsutake is regarded as one of the most expensive mushrooms among the world's delicacies (Hall et al. 2003). Although pine mushrooms in Europe were originally described as *Tricholoma nauseosum*, Kytövuori (1988) first recognized (later confirmed by Bergius & Danell 2000) them to be conspecific with *T. matsutake* growing in the Asia. Matsutake forms typical ectomycorrhizas with both Scots pine and Norway spruce, the dominant conifer species in Finland (Vaario et al. 2010). Approximately 76% of Finland (i.e. 23 million hectares) is covered by forest, 90% of which is dominated by either Scots pine (*Pinus sylvestris* L.) or Norway spruce (*Picea abies* [L.] Karst) (Finnish Forest Research Institute 2013). Finland has the potential to develop a significant export of matsutake mushrooms and commercial interest in non-woody forest products has increased in Nordic countries. Recently, a study in Sweden showed that pine forests with highly productive matsutake can yield approximately twice as much profit when maintained for mushroom harvesting rather than cropped for timber (Nagasaka 2013). Understanding the factors that influence fruiting body onset, duration and yield is critical for the successful development of a matsutake export market in Finland and its neighboring countries.

The seasonal timing (or phenology) of fungal fruiting generally depends on climate (Büntgen et al. 2012). Fruiting of *T. matsutake* has been extensively studied in Asian countries for several decades (Kinugawa 1963; Ogawa 1978, Wang et al. 1997; Gong et al. 1999), where the main factors that control productivity are believed to be precipitation and soil temperature (Kinugawa 1963; Wang et al. 1997; Yang et al. 2012). High temperatures and abundant rain in August, when the majority of fruiting bodies emerge, are considered the key factors for high productivity of matsutake in Asia (Wang et al. 1997; Yang et al. 2012). Also, relatively warm and dry conditions during May and June have been suggested to correlate with fruiting delay in China (Yang et al. 2012). While a soil temperature of 19°C has been considered a threshold value for the onset of fruiting in Japan (Kinugawa 1963; Ogawa 1978), other studies have reported that matsutake primordia can develop in a much wider range of soil temperatures (Tominaga & Komeyama 1987; Gong et al. 1999). According to the most recent and frequently cited phenological studies of *T. matsutake* in Asia (Kinugawa 1963; Tominaga & Komeyama 1987; Yang et al. 2012), high rainfall during the fruiting season increases yield, and soil temperature plays an important role in the onset of fruiting body

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emergence. However, statements regarding the fruiting pattern of matsutake in northern Europe remain tentative because this species was poorly known and commercial harvesting only began in 2007. Furthermore, it remains unclear if patterns observed in Asia apply to matsutake growing in northern Europe and if they can be used to predict local fruiting patterns.

Fungal phenological events include vegetative hyphal growth and fruiting body formation (Kües & Liu 2000), both of which are dependent on climate (Kauserud et al. 2008) and may also be affected by interactions with other fungi (Bruns 1995; Kranabetter & Kroeger 2001). Recent studies have shown that ECM fungi and saprotrophic fungi differ in fruiting phenology (Sato et al. 2012). Many phenological studies of ECM fruiting bodies focused on pooled species and suggested that their productivity was positively correlated with regional cumulative precipitation (Büntgen et al. 2012). Soil characteristics in concert with belowground carbohydrate allocation of the host plant may also influence the amount and timing of ECM fruiting body formation (Straatsma et al. 2001; Egli et al. 2010; Pinna et al. 2010).

In this study, we examined relationships between environmental (i.e. precipitation and mean air and soil temperatures) and fruiting body data from a six-year field survey of *T. matsutake* in Southern Finland. Results were compared with those of earlier studies (Kinugawa 1963; Ogawa 1978; Yang et al. 2012) in order to determine the extent to which relationships observed in Asia concerning temperature, precipitation and yield are applicable to the fruiting pattern of matsutake in Finland. Our overall aim is identifying the environmental factors that might regulate the fruiting pattern of *T. matsutake*. We are aware that a longer period and more sites are needed to explore more firm relationships between fruiting and environmental variables. However, this data-set can give important indications for more extended studies.

Materials and methods

Study area and periods

This study was carried out at a 100 m × 135 m site in a mixed forest containing Scots pine, Norway spruce, and silver birch (*Betula pendula* Roth) in Southern Finland (60°18' N 24°31' E). Fruiting bodies have been found at the site every year since its discovery in 2000. Site characteristics, soil microbial communities, litter cover, and understory vegetation have been described earlier (Vaario et al. 2011, 2013).

Meteorological data

Meteorological data (1970–2013) were spatially interpolated from meteorological observations. Spatial interpolation was made with the grid and auxiliary variables at the Finnish Meteorological Institute (Venäläinen et al. 2005). The spatially interpolated grid has a resolution of 10 × 10 km, and we used the closest grid point for the study site. During the study period (i.e. 2008–2013), accumulated degree-day (ADD, accumulative temperature sum > 5°C) and accumulated precipitation (AP) were calculated from the FMI database for a period spanning from begin of the year to the end of June and July prior to the matsutake fruiting season.

Soil temperature

Soil temperature (T_s) was measured with 21 iButton sensors placed systematically in four fruiting plots at 10 cm depth from the soil surface. T_s was recorded at 4 h intervals starting at the end of May 2009 and from the end of May to the end of September 2013. Soil temperature data were missing for 2008 and for most of the 2012 season. Data through days 102 (10 April) and 282 (12 October) of 2011 formed the longest continuous record of soil temperature and were therefore used in the model estimation procedure. Missing T_s values were inferred with a statistical model using the average T of the previous 30 days (T_{30d}) and previous two days (T_{2d})

$$T_s = aT_{30d} + bT_{2d} + \varepsilon$$

T_{30d} accounts for seasonal variation in soil temperature whereas T_{2d} accounts for short-term variation of upper soil temperature. Parameters a (0.585 ± 0.015, t = 38.8, $p < 10^{-16}$) and b (0.248 ± 0.015, t = 17.1, $p < 10^{-16}$) are fitted coefficients. The model was highly significant ($p < 10^{-16}$, df = 166), with a R^2 of 0.998, and a residual standard error of 0.57°C.

In order to avoid snowpack and freeze–thaw effects on T_s and to minimize the effects of initial T_s, we ran the model for an initialization period from 10 April until 15 May before generating estimates for analysis. Testing the model with T_s data from 2009 and 2010 (15 May–1 October) showed that the residual standard error of predictions were 1.1 and 0.9, and biases (i.e. means of measured-predicted during the period) were –0.8°C and –0.1°C, for years 2009 and 2010, respectively. The larger negative bias generated an underestimate of cumulative T_s (–72°C), which we considered to be due to uncertainty of the used T_s sum for 2008 and 2012. Note that this uncertainty is by definition 0°C at the start of the season and increases to 72°C by season's end.

Monitoring of the fruiting pattern and productivity of **T. matsutake** *and other macrofungi*

The new matsutake fruiting bodies were counted, picked, and mapped two to three times per week during the fruiting season from the middle of July to the end of September. Other macrofungi were recorded once a week in the same way. We scored the final results on a weekly basis. Systematic and continuous observations

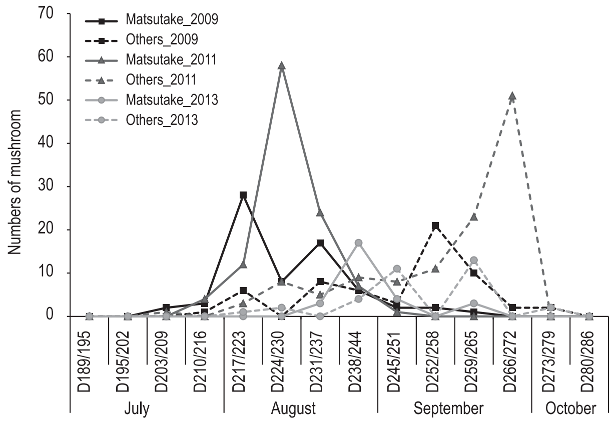

Figure 1. Fruiting pattern of *T. matsutake* and other macrofungi in the study site during 2008–2013.

took place on calendar days 200–266 (18–19 July to 22–23 September), which corresponds to the mushroom fruiting season observed during the 2008–2013 sampling period. The fruiting bodies of other macrofungi were inventoried every other year during the study period for two weeks prior, during, and two weeks after the matsutake monitoring period. Based on the distribution of fruiting bodies, we estimated there to be five separate *T. matsutake* fruiting patches in the Southern Finland site (see Figure 1 in Vaario et al. 2012). All other macrofungal fruiting bodies within each patch were counted and the limits of the patches were based on observations over several years.

Statistical analyses

Differences in mean T_s four weeks before or after the first fruiting date across study years were examined with an analysis of variance ($p < 0.05$). Backward multiple regressions were conducted to evaluate whether ADD, AP (the accumulated data from the begin of the year to the first fruiting date), T, and T_s on the first fruiting date were necessary to predict productivity; to evaluate whether AP on the first fruiting date and/or mean T_s four weeks before and after the first fruiting affect duration; to evaluate whether onset day and T_s were necessary to predict duration. Normality and homogeneity of variance were examined using Kolmogorov–Smirnov, Shapiro–Wilk, and Levene's tests. All statistical analyses were performed with SPSS (version 20.0; SPSS Inc., Chicago, Illinois).

Results

Fruiting pattern of T. matsutake *and other macrofungi*

The results of detail observation were summarized in Table 1. Matsutake fruiting in the study site was highly variable among years. During the six consecutive years of the study period, first fruiting dates varied from day

Table 1. Selected meteorological features during *T. matsutake* fruiting in the study site during 2008–2013.

Observation		Year					
		2008	2009	2010	2011	2012	2013
Number of matsutake		17	69	38	106	7	27
Day of first fruiting (day of year)		D211	D205	D232	D213	D221	D234
Duration of fruiting (days)		44	58	18	33	23	22
Temperature (°C)	at first fruiting	16.8	18.4	14.9	16.3	15.1	15.6
	at last fruiting	7.7	13.9	14.3	13.9	14.3	14.7
Soil temperature (°C)	at first fruiting	13.9	13.8	14.4	15.6	14	14.6
	at last fruiting	9.8	10.1	11.9	13.2	12.5	12.5
	four weeks prior to first fruiting[a]	13.04 ± 0.16 e[b]	12.55 ± 0.17 e	16.67 ± 0.17 a	15.77 ± 0.20 b	14.65 ± 0.14 d	14.26 ± 0.18 c
	four weeks post to first fruiting	13.40 ± 0.11 b	13.37 ± 0.23 b	12.50 ± 0.24 c	14.70 ± 0.11 a	13.06 ± 0.13 bc	13.76 ± 0.20 b
Accumulated degree-day (d.d.)	at first fruiting	842	748	1298	1066	950	1304
	at last fruiting	1238	1342	1429	1424	1174	1518
Accumulated precipitation (mm)	at first fruiting	423	334	367	289	452	315
	at last fruiting	585	443	409	392	484	339

[a]Means ± SE; [b]common letter indicates no significant difference among the study years.

204 (23 July) to 234 (22 August), and the last fruiting dates varied from day 243 (31 August) to 262 (19 September). The highest productivity recorded was 106 fruiting bodies in 2011; the lowest was seven in 2012 (Table 1), with 20–120 g fresh weight per fruiting body. Almost three quarters (>73%) of fruiting took place in August and lasted 18–58 days (mean of 33 days; Table 1). With respect to other macrofungal fruiting bodies, 59 (2009), 119 (2011), and 33 (2013) were detected in the study site. More than 77% of these macrofungi appeared in September, immediately after the peak fruiting period of *T. matsutake* (Figure 1).

ADD, AP, and soil temperatures during the fruiting periods

During the six-year study period, ADDs on the first and last fruiting days varied from 748 to 1304 degree day (d.d.) and 1174 to 1519 d.d.; APs ranged from 289 to 452 mm and 339 to 585 mm, respectively (Table 1). T decreased from 0.6°C to 9.1°C from the first to the last fruiting day, respectively. However, the ranges of T_s from the first to the last fruiting day were much narrower increasing from 1.5°C to 4.2°C (Table 1). Four weeks prior to the onset of fruiting, a significantly higher mean T_s was recorded in 2010; mean T_s four weeks after the first fruiting was significantly higher in 2011 (Table 1).

ADD of the long-term average (LTA: 970–2013) in the study site was 464 d.d. in June, 839 d.d. in July, and ADD values in 2011 and 2013 were both higher than mean values of LTA. AP values in 2009 and 2011, which were good fruiting years, were 92–110% of the LTA (LTA 236 mm in June, 301 mm in July); but the values in the poor fruiting years of 2008 and 2012 were wet (AP 143–164% of LTA). AP in 2013 was 72–79% of LTA (Figure 2).

The mean T_s four weeks prior to first fruiting during 2008–2013 ranged from 12.6°C to 16.7°C was significantly higher in 2010, and negatively correlated with the fruiting duration (p = 0.046). This suggests that a higher soil temperature prior to the onset of fruiting may result in a short fruiting period (Table 1). The mean T_s four weeks after first fruiting was from 12.5°C to 14.7°C, the highest was in 2011 (Table 1).

Relationship between matsutake fruiting and weather

A multiple regression analysis showed that the yield of *T. matsutake* in the study site was affected by AP almost significantly (p = 0.055, R^2 = 0.64). The model explaining the duration of fruiting in terms of onset and mean T_s four weeks prior to first fruiting had R^2 of 0.67 (p = 0.057). Within this model, T_s of four weeks prior to first fruiting was significantly and negatively correlated with fruiting duration, which means that higher soil temperature before the initial fruiting shortens the fruiting duration (p = 0.026). Similarly, timing of first fruiting significantly and negatively affected duration; R^2 was 0.87 (p = 0.048), showing that fruiting periods that start earlier tend to remain productive for longer.

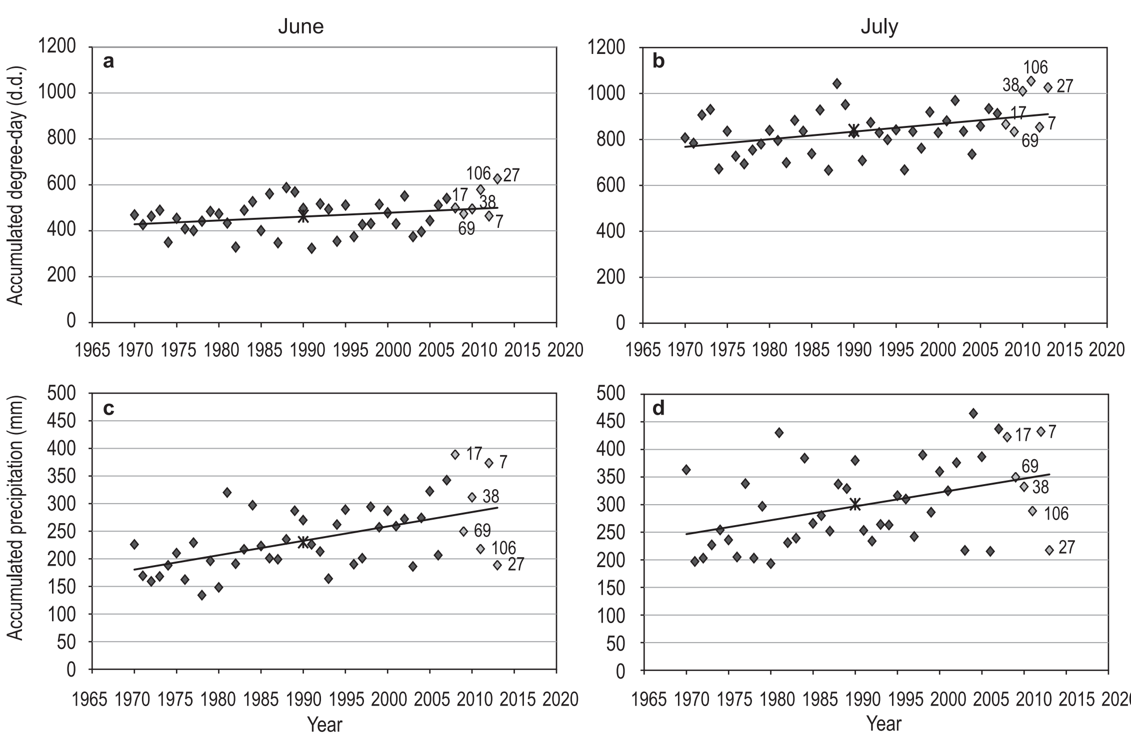

Figure 2. ADDs and APs in the end of June and July during 1970–2013 in the study site. Numbers indicate the number of matsutake fruiting bodies for each year during the studying period.
Note: An asterisk indicates the mean value over 44 years.

Discussion

The present study is the first to describe the fruiting situation of *T. matsutake* as it occurred in a productive forest site in Southern Finland during 2008–2013. The following findings were obtained: (1) start and end dates of the fruiting period varied among years and ranged from the middle of July to the middle of September; (2) we did not find a significant relationship between productivity and rainfall during the fruiting season but we observed that productivity was highest when the AP prior to first fruiting was close to the LTA, whereas dry or wet deviations from LTA resulted in low fruiting body production; (3) *T. matsutake* fruiting might be more sensitive to soil temperature than to air temperature, but a threshold value for the onset of fruiting was not found in our study; (4) later start of fruiting or a relatively higher soil temperature prior to first fruiting was associated with a shorter fruiting period; (5) only ca. 20% of the other fungal species present at the same site fruited during August, the peak period for *T. matsutake* at the study site.

Temperature and precipitation

Although the initial fruiting date varied among years, *T. matsutake* formed fruiting bodies from July to September every year in our study site. The initial fruiting date was earlier and the fruiting period was shorter in Finland compared to observations of the fungus in Japan and China (Ogawa 1978; Gong et al. 1999), probably due to the different climates of these regions. From 1991 to 2012, the mean monthly temperatures in Southern Finland ranged from –4°C in January to 14.4°C in June. The same values for Nagano province in Japan during 1967–2000 ranged from −1.5°C in January to 20.1°C in June (Takeuchi et al. 2004), and from 8°C in January to 22°C in June in Yunnan based on data from 1971–2000 (Yang et al. 2012). We did not find a clear relationship between air temperature and fruiting pattern or productivity in this study, which is consistent with previous reports from Asia (Yang et al. 2012).

Earlier reports (see review by Wang et al. 1997) emphasized a positive relationship between temperature, precipitation, and productivity. More specifically, matsutake yield was suggested to be positively related to plentiful rain in spring, a relatively hot and dry summer, and a moist, cool autumn (Wang et al. 1997). We could not confirm a similar pattern in this study and, in contrast, observed that high AP prior to first fruiting correlated negatively with productivity. A one-year study of inventory wildwood mushrooms in Norway also did not find clear relationship between rainfall and mushroom fruiting, but did find a positive correlation between cloud cover and fruiting body formation which explained by increasing soil humidity via cloud cover (Dahl et al. 2008). However, Ohenoja (1993) reported that high precipitation in one year was predictive of a poor yield of mycorrhizal fungi next autumn based on 12-year inventory in northern Finland at different forest sites. Yang et al. (2012) reported that abundant rain in August preceded a good matsutake crop in Yunnan, and noted that high humidity from November/December to May was associated with few fruiting bodies the following season. 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 consistent with that described in our study. Our result was also partly consistent with the results of 12-year inventory in northern Finland. It should be emphasized that in relatively good harvest years, APs observed during June and July were only slightly lower or close to the LTA, which may mean that soil was slightly dry or typical for the site.

Results presented here together with those of our previous study of the same location (Vaario et al. 2011) reveal that *T. matsutake* prefers a relatively dry forest. Also, *T. matsutake* mycelium mainly grows under the organic humus in the mineral soil layer, which is usually sandy and well drained. High AP will increase the wetness of the mineral soil layer. Soil moisture at the Finnish site was lower than that in Japan (ca. 15%; Ogawa 1978) and in southwest China (20–25%; Gong et al. 1999). We have investigated the influence of soil moisture on the growth of *T. matsutake* mycorrhizal seedlings and found an optimal level of ca. 15% (unpublished data). In general, mycorrhizal 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. Good host plant condition ensures the carbohydrate supply to roots, and thereby supports the formation of fungal fruiting bodies. However, in contrast to most ECM fungi, *T. matsutake* is a facultative saprotroph (Vaario et al. 2002, 2012; Kusuda et al. 2006) and we suggest that it can also obtain organic carbon from other sources in the soil (Vaario et al. 2012, 2013). In other words, mycelial growth of matsutake may enjoy a level of independence from the host plant during the fruiting season. Lastly, we found that the fruiting phenology of *T. matsutake* differs from other fungi. Being able to initiate fruiting in relatively dry conditions may be an adaptation to take advantage of the reduced activity of other soil microbes under such conditions and the increased availability of organic carbon sources (Schimel et al. 1999; Williams 2007; Castro et al. 2010).

Matsutake is a dominant species of mycorrhizal root tips and mycelium in the shiro (Lian et al. 2006; Vaario et al. 2011). The occurrence of most other fungi was negatively correlated with the presence of *T. matsutake* mycelium in the mineral layer, and only a few species (e.g. *Tomentellopsis* sp., *Tylospora* sp.) were positively correlated with the presence of *T. matsutake* in the organic layer (Vaario et al. 2011). In general, emergence of fungal fruiting bodies has been reported to correspond to warmer and wetter conditions (Pinna et al. 2010; Büntgen et al. 2012). Furthermore, growth of ECM fungi reflects temperature-dependent and drought-induced changes of photosynthetic activity of the host plants rather than changes in growth conditions of the fungal mycelium itself during the summer (Sato et al. 2012). Notably, only ca. 20% of the other macrofungi present at the same site fruited during the peak season for *T. matsutake* in August. This fruiting pattern was observed in three subsequent years in the study site. We suggest that *T. matsutake* fruits under conditions that do not favor the fruiting of other macrofungal species. The fruiting of *T. matsutake* may reflect growth of the mycelium in response to soil moisture rather than a temperature-dependent increase.

The six-year data-set from the study site is limited to inferences concerning the relationship between AP and productivity of matsutake mushrooms in Southern Finland. However, our findings emphasize the need to study the phenology of this species further and to consider forest management strategies from the perspective of encouraging matsutake, at least in Nordic countries.

Soil temperature

The dependency of matsutake fruiting on soil temperature has been emphasized in several studies (Ogawa 1978; Kinugawa 1963) and many Japanese reports (A. Yamada pers. comm.). Although a wide range of soil temperatures (9–19°C at <10 cm depth) has been reported in southwest China (Gong et al. 1999), studies based in Western Japan claim that a more narrow optimal soil temperature of 19°C is necessary for fruiting body formation. Such a threshold temperature is unreasonable for Finnish matsutake due to the fact that soil temperatures are rarely this high. In this study, we did not find a threshold soil temperature for the onset of fruiting and we question the importance of this factor in matsutake phenology. However, we note that soil temperature on the last fruiting day was usually 2–4°C cooler than the first fruiting day. According to Chen et al. (2011), mean air temperature, mean soil moisture, and maximum temperature during the fruiting season differed among years, whereas soil temperature remained a consistent 16.0–16.5°C in southwest China. Soil temperature is affected by air temperature, soil type, and vegetation covers. In Southern Finland, limited vegetation but high litter cover was reported in our previous study (Vaario et al. 2013). Bare soil receives maximum solar radiation which leads to higher soil temperature and lower soil moisture (Liddle 1997). Our results together with other studies suggest that the onset of fruiting is dependent on several factors related to site vegetation.

In this study, we focused on the conditions around the first fruiting date and compared mean soil temperatures among survey years. A higher soil temperature prior to initial fruiting seemed to accelerate mycelial growth and shorten the fruiting period. Matsutake grows very slowly in nature, does not form rhizomorphs to transport nutrients over long distances to developing fruiting bodies, and *in vitro* extension is rather limited compared to that for other ECM fungi (Ogawa 1978; Vaario et al. unpublished data). Mycelium may require a certain amount of time to accumulate sufficient resources to form and support fruiting bodies (Krebs et al. 2008). Echoing Wang et al. (1997), we noticed that fruiting soon ceased after soil temperature dropped 2–4°C below that at which it began. As such, soil temperature may offer a way to remotely monitor the fruiting period and optimize harvesting activity. We accept that soil temperature plays a role in matsutake fruiting, but so far we do not have any evidence for an “initiation temperature” or “switch” as suggested by Kinugawa (1963). We did not find a significant correlation between productivity or length of the fruiting period and the number of degree days accumulated at the end of June, July, or August, although this factor has been reported to relate to the onset and duration of morel fruiting (Mihail et al. 2007).

In conclusion, the fruiting pattern of *T. matsutake* in Finland during the studied years did not fully match those reported earlier in China or Japan. Although six-year time scale is still too short to make confident conclusion of matsutake fruiting pattern, our results indicated potential relationships between fruiting and environmental factors, that can contribute to further detail studies in the related regions. The first suggests that a closer (i.e. 90–110%) to average amount of AP prior to the fruiting season may ensure the good productivity. The second suggests that later start of fruiting or a relatively high soil temperature prior to the first fruiting date may shorten the fruiting period. Overall, matsutake is living in a complex ecosystem in which aboveground and belowground factors affect growth and fruiting body formation. We agree with the suggestion made by Yang et al. (2012) that we still lack the depth of understanding necessary to draw the fruiting pattern of matsutake mushrooms. More systematic information concerning the phenology of *T. matsutake* together with accurate climatic data from distinct geographic regions is needed to better understand this complex ecosystem and the factors that influence it.

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Disclosure statement

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