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Relationship between climate, expansion rate, and fruiting in fairy rings ('*shiro*') of an ectomycorrhizal fungus *Tricholoma matsutake* in a *Pinus densiflora* forest

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ABSTRACT

Tricholoma matsutake is an economically important fungus in Japan. Its basidiocarps occur in groups called *shiro*. Little is known about the relationship between the expansion rate of *shiro* and the number of basidiocarps or meteorological factors. When data from an 18-yr survey were analyzed using a hierarchical Bayesian framework, the expansion rate was estimated to be 0.17 ± 0.01 m yr^{-1}. Positive correlations were found between the expansion rate and the number of basidiocarps, mean air and soil temperature, and total precipitation. Similarly, there was a positive correlation with an index of accumulated warmth, termed WI_{20}, especially in the pre-emergence season. The Akaike information criterion (AIC) of linear models decreased when precipitation was excluded as an explanatory variable. Furthermore, mean air temperature and WI_{20} showed positive correlations with the number of basidiocarps. These results suggest that the effect of temperature in the pre-emergence season is greater than that of precipitation with respect to the expansion rate of *shiro*, which in turn affects the numbers of basidiocarps.

Introduction

Tricholoma matsutake (Matsutake) is usually found in forests of *Pinus densiflora* (Japanese red pine), *Pinus pumila var. yezoalpina* (Dwarf stone pine), and *Tsuga siebordii* (Tsuga) in Japan (Ogawa, 1975, 1976, 1977). The mycelia of the Matsutake form ectomycorrhizas with the fine roots of these trees (Yamada et al., 1999). Together with vegetative hyphae, these ectomycorrhizas form massive structures, and basidiocarps (fruit bodies) of the Matsutake are derived from the edge of the mass

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(Ogawa, 1975; Yamada et al., 1999), similar to fairy rings (Dix and Webster, 1995; Carlile et al., 2001). These rings of Matsutake are often termed *shiros* (Ogawa, 1975).

The basidiocarps of Matsutake have been consumed for food by the Japanese for centuries (Arioka, 1997). A culture method for ectomycorrhizas has been developed (Guerin-Laguette et al., 2000; Yamada et al., 2006; Kobayashi et al., 2007). However, Matsutake fruit bodies must be collected from natural forests, because Matsutake production is unreliable and annual variations in basidiocarp numbers are evident, rendering the mushroom economically valuable (Suzuki, 2005). Some methods of collection can damage the underground mycelia (Hosford et al., 1997; Carlile et al., 2001). Identification of factors that influence the annual variations in basidiocarp numbers is, therefore, essential to establish reliable production methods for Matsutake.

The quantity of mushrooms produced in the wild, including Matsutake, is affected by environmental factors such as temperature and precipitation (Luoma et al., 1991; Kawakami, 1994; Aragon et al., 2007; Yang et al., 2012), but the relationships are not well understood. With regard to saprotrophic fungi, the quantity of mushrooms produced is also affected by the biomass of mycelia, which is affected by environmental conditions during cultivation (Tokimoto, 2010). Despite the importance of any possible correlation between ectomycorrhizal fungal biomass and environmental conditions, few data are available, as the mycelia usually grow underground (Smith and Read, 1997). Moreover, the distribution patterns of basidiocarps and mycelia are not always consistent among ectomycorrhizal fungi (Zhou et al., 2000; Linde et al., 2009). In contrast, the mycelia and mycorrhizas of the Matsutake are primarily observed directly beneath the basidiocarps (Lian et al., 2006). In addition, as described above, some ectomycorrhizal fungi, including the Matsutake, form basidiocarps in a rings or arc formations (Hamada, 1970; Ogawa, 1985), in contrast to other fungi, such as *Suillus grevillei* (Zhou et al., 2000). Thus, the expansion rate of *shiro*, which is based on the distribution of basidiocarps, has been used as an alternative method of estimating the biomass of mycelia (Kawakami, 1994). The distribution pattern of Matsutake basidiocarps has been examined previously (Hamada, 1970; Ogawa, 1975; Etoh et al., 1999), as has the expansion rate (Hamada, 1953; Kawakami, 1994; Murata et al., 2001). However, the data available regarding annual expansion rates are insufficient to determine the influence of meteorological factors on this parameter. One reason for such paucity of data may be a lack of methods that allow quantitative estimation of expansion rates, as well as the relatively brief descriptions of such methods provided in previous studies. To estimate an expansion rate, it can be useful to approximate the *shiro* as a full circle. However, the distribution of basidiocarps may not always form a full circle in nature (Ogawa, 1975). Therefore, quantitative estimation of the expansion rate is deemed to be difficult. In the present study, we estimated the expansion rate of *shiro* of the Matsutake using a hierarchical Bayesian framework based on 18 yr of observations, which was then used to examine the correlation between expansion rate and meteorological factors as well as the occurrence of *T. matsutake* basidiocarps.

Materials and methods

Study site

The study was conducted in the research forest of the Iwate Prefectural Forestry Technology Center (39°56′ N, 141°14′ E), in northeastern Japan. The study site was established in a natural Japanese red pine forest where basidiocarps of Matsutake occur annually. Three ridges were included in the site, which faces southwest with a gradient of almost 20° at altitudes between 360 and 380 m above sea level. The ridges were located approximately 200–300 m apart. Mean annual temperature and precipitation were 9.3 °C and 1 145 mm, respectively. Monthly mean temperatures were lowest in Jan. (-2.9 ± 1.3 °C) and highest in Aug. (22.8 ± 1.4 °C), based on data from the nearest meteorological survey station (Japan Meteorological Agency).

The vegetation at the study site is dominated by Japanese red pine ca. 90 yr old, reflecting natural regeneration after timber harvesting. The mean diameter at breast height, mean tree density, and basal area of the pine trees at the study site were 24.8 cm, 1 729.2 ha^{-1}, and 114.06 m^2 ha^{-1}, respectively (Narimatsu, 2004). *Fraxinus sieboldiana*, *Quercus serrata*, *Prunus sargentii*, *Aria alnifolia*, and *Lyonia ovalifolia* ssp. *neziki* are also present in the shrub layer. *Rhus ambigua*, *Oplismenus undulatifolius*, and *Pyrola japonica* are frequently present on the forest floor. Ectomycorrhizal fungi other than Matsutake detected at the study site included *Cenococcum geophilum*, *Tomentella* sp., and *Russula* sp. (Lian et al., 2006). No management protocols, such as thinning or cutting, were conducted at the site during the study period.

Discrimination of the 'shiro' *and survey of basidiocarps*

Five replicate groups of basidiocarps present on the three ridges at all times during the study period were designated '*shiro*'. *Shiros* 1, 2 and 5 lay distant from *shiros* 3 and 4, which were contiguous. All *shiros* were less than 500 m apart and all were almost totally covered by the canopy layer of the *P. densiflora* forest, as described above.

Within these *shiros*, the numbers of Matsutake basidiocarps were counted annually in the 18 yr between 1994 and 2011. The basidiocarp surveys were conducted at intervals of several days during periods of fruiting in Sep. and Oct.. All basidiocarps were collected after the pileus had completely opened for the dispersal of basidiospores. In addition, the first day of basidiocarp collection in each year was recorded; this date was used to define the beginning of the fruiting season in further analyses. However, basidiocarp formation did not occur in 1996; thus, the beginning of the fruiting season in 1996 was defined as the middle 10 d of Sep., based on mean data from the remaining 17 yr. Concurrent with basidiocarp counts, their positions were marked using fiberglass poles (Nittoh Denko, Osaka). The tops of the poles were painted annually using different colors each year, and numbers were written on the poles to identify individual basidiocarps. These indicator poles were surveyed using total stations (CS-20A, Topcon, Tokyo) in the winter. Based on the survey results, the coordinates of basidiocarp positions were calculated within each *shiro*.