



# Phenotypic evaluation and analysis of important agronomic traits in the hybrid and natural populations of *Lentinula edodes*



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## ABSTRACT

Several important agronomic traits of shiitake strains in two hybrid populations and a natural population were evaluated through three independent fruiting trials. The correlations among the agronomic traits of shiitake were also analyzed using multivariate statistical methods. Results showed that wild shiitake strains in the natural population had a wider range of phenotypic variation than those in the two hybrid populations. Interestingly, several strains with superior phenotypes related to precocity and increasing number of fruiting bodies were found in the natural population. Then, factor analysis indicated that the three major factors (single fruiting body, yield and precocity) accounted for over 80% of the total variance. To further examine relative contributions of yield-component traits (the number of fruiting bodies and the weight of single fruiting body) to yield through path analysis, our results demonstrated that the number of fruiting bodies was the key component influencing yield. This is the first report on the phenotypic analysis of yield and other agronomic traits using multiple populations in shiitake. Our study not only advances the knowledge of correlations between agronomic traits, especially between yield and yield-component traits, but also provides useful information for utilizing valuable natural resources to develop high-yield shiitake cultivars in future.

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## 1. Introduction

*Lentinula edodes* (also called Xianggu or shiitake), a nutrition-rich edible mushroom, has been cultivated for centuries in China (Chakravarty, 2011). This mushroom has been widely consumed as one of the most delicious culinary delicacies in the Orient and recently adopted in the West (Turfo et al., 2008). Besides the delicious taste, *L. edodes* has attracted tremendous interests for its pharmacological effects. Lentinan, a polysaccharide isolated from the fruiting bodies of *L. edodes*, is well known for the anticancer and antiviral activities (Zhang et al., 2011). Moreover, *L. edodes* has been widely applied in dye decolorization and bioconversion of lignocellulosic wastes (Boer et al., 2004; Philippoussis et al., 2007).

Increasing yield is a principal pending problem in *L. edodes* industry, as it is limited both by improvements of cultivation techniques and high-yield commercial cultivars. Numerous medium

formulas were designed to optimize the production practices of *L. edodes* (Royse and Sanchez, 2007; Özçelik and Pekşen, 2007; Shen et al., 2008), whereas the studies on genetic improvement of yield were still rare. Like *Agaricus bisporus* (Foulongne-Oriol et al., 2012), the yield of *L. edodes* is a complex trait, which could be divided into two interrelated components, the number of fruiting bodies (NF) and the weight of single fruiting body (WF). Moreover, there are also intricate relationships between yield and many other agronomic traits, such as traits on the basidiocarp (Lin, 1995; Lin et al., 2004, 2006). Uncovering the relationships between different traits will contribute to clarify and determine the desirable criteria for selecting superior individuals, and be of great practical importance in breeding programs (Al-Tabbal and Al-Fraihat, 2012).

Most of the important agronomic traits are quantitative traits controlled by polygenic system, their genetic architectures are not yet clear. Quantitative trait loci (QTLs) mapping is powerful for genetic dissection of complex quantitative traits (Li et al., 2010). Like other edible mushrooms (Foulongne-Oriol, 2012), current linkage map of *L. edodes* is based on the haploid progenies. Paradoxically, the phenotypic evaluation of many traits such as NF, WF and yield were performed at the dikaryotic stage. Thus, the creation of dikaryons by crossing the haploid progenies with the

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other compatible testers is important for phenotype identification. Evaluation and analysis of quantitative traits in these segregation populations provide the prerequisites for QTL mapping and the subsequent genetic improvement in *L. edodes*.

Owing to the wide range of genetic variability, natural germplasm resources are extensively used as valuable resources of favorable genes for traits of interest in crop genetic improvement (Xiao et al., 1996; Fernie et al., 2006). In edible mushrooms like *A. bisporus*, the wild strains have also been found to be the valuable resources for several important agronomic traits, including yield and disease resistance (Sonnenberg et al., 2005; Largeau et al., 2005; Foulongne-Oriol et al., 2012). However, there are few reports on the utilization of natural germplasm in breeding programs of *L. edodes*. The cultivars of Chinese shiitake are very homogeneous genetically and the shiitake industry still depends on an extremely small gene pool (Chiu et al., 1996). The wild shiitake strains show more genetic variability than the cultivated ones (Chiu et al., 1996). As the origin and the major producer, China harbors abundant natural germplasm resources of *L. edodes* (Chiu et al., 2000). To date, most of the studies have focused on estimating the genetic diversity of *L. edodes* natural germplasm in China (Dai and Lin, 2001; Sun and Lin, 2003; Xu et al., 2005; Xiao et al., 2010). Although analyzing the phenotypic variation in shiitake natural germplasm is of great practical significance for breeding programs, there has no studies on phenotypic evaluation of wild shiitake strains been reported.

This study aimed to (1) investigate the phenotypic variation of agronomic traits in two hybrid populations and a natural population of *L. edodes*, and (2) reveal the relationships among important traits of *L. edodes* by multivariate statistical analyses. Also, the potential values of some strains with favorable traits for *L. edodes* breeding were also discussed.

## 2. Materials and methods

### 2.1. Fungal strains and populations

All the tested strains were preserved in the Institute of Applied Mycology, Huazhong Agricultural University (HZAU). The two hybrid populations used in this study were constructed as described previously (Gong et al., 2014). Briefly, the dikaryon L6-26 was generated from the mating between two compatible monokaryons L205-6 (mating type:  $A_1B_1$ ) and W1-26 ( $A_2B_2$ ). The 146 single spore isolates (SSIs) were generated from a mature fruit body of L6-26. As tester monokaryons, 741-15 ( $A_3B_3$ ) and 741-64 ( $A_4B_4$ ), were derived from mycelia of a wild dikaryotic strain LeQC741S (CCTCC AF 2013009) by protoplast regeneration as described by Kawasumi et al. (1987). Four days-old mycelia were used in preparation of protoplasts. Optical microscope was used to check their monokaryotic nature by the absence of clamp connections. The mating types of 741-15 and 741-64 were verified by mating compatibility tests as described previously (Kwan and Xu, 2002). The two hybrid populations, each consisting of 146 strains (genotypes), were generated by mating (1) the 146 SSIs with 741-15 (will be called population LQ-15 herein) and (2) the 146 SSIs with 741-64 (will be called population LQ-64 herein). The natural population consisted of 93 wild shiitake strains, which were originated from 14 Chinese provinces (belong to eight different floristic regions) covering a wide range of geographical and ecological conditions (Xiao et al., 2010). The 93 wild strains in the natural population were either collected from natural reserves and remote mountainous areas that are far from cultivation sites or donated by professional research institutes. Two commercial shiitake cultivars (HuaXiang-8 and L607) were used as controls for comparisons of the agronomic traits of the tested strains in the experiments.

**Table 1**

Agronomic traits measured in the cultivation experiments.

Trait (units)	Description
Precocity (d)	Time interval (in days) from incubation to harvest of the first fruiting body
Pileus diameter (mm) <sup>a</sup>	Average diameter of pileus, determined as the mean of two perpendicular diameters
Pileus thickness (mm) <sup>a</sup>	Average thickness of pileus
Pileus weight (g) <sup>a</sup>	Average weight of pileus
Stipe length (mm) <sup>a</sup>	Average length of stipe
Stipe diameter (mm) <sup>a</sup>	Average diameter of stipe
Stipe weight (g) <sup>a</sup>	Average weight of stipe
Weight of single fruiting body (g/per)	Ratio of the yield to number of fruiting bodies harvested during whole harvest time
Number of fruiting bodies (per/bag)	Average number of total fruiting bodies per bag during the whole harvest time
Yield (g/bag)	Total weight of fruiting bodies per bag during the whole harvest time

Note: <sup>a</sup>Calculated by using data for selected fruiting bodies of each genotype. Pileus weight and stipe weight were not investigated in the natural population.

### 2.2. Experimental design and phenotypic evaluation

Three independent fruiting trials (F-15, F-64 and F-NP) were conducted from September 2012 to May 2013 in HZAU (Hubei, China, 114.35° E, 30.48° N). The mentioned 146, 146 and 93 genotypes in LQ-15, LQ-64 and the natural population, were respectively arranged in F-15, F-64 and F-NP for phenotypic evaluation. These shiitake strains were grown in plastic culture bags (15 cm in fold diameter, 30 cm in length) containing 1 kg (wet wt.) sterilized mixed sawdust medium (79% hardwood sawdust, 20% wheat bran, and 1% gypsum). The dry weight of the mixed substrates was about 400 g in each culture bag. The moisture content of the mix was adjusted to about 60% (Shen et al., 2008). The weight proportion of inoculated spawn to sawdust medium was approximately 8% (w/w). 12 culture bags were prepared for each genotype, and then incubated at 24 °C in the dark after inoculation. After the completion of spawn running and formation of brown film, these bags were transferred into three independent mushroom houses (one mushroom house for one population). In this study, shiitake were cultivated in the simple mushroom houses without automatic temperature control device, and the temperatures in those mushroom houses were changed along with the changing environmental conditions. The management of the mushroom houses was followed as description of Wang et al. (2010). In each mushroom house, tested strains with two commercial cultivars were allocated according to a randomized-block design. In the mushroom houses for LQ-15 and LQ-64, two blocks were designed, six bags of each genotype were included in each replication. Three blocks were designed in the mushroom house for the natural population, each replication consisted of four bags of each genotype. The target agronomic traits measured in the experiments are listed in Table 1. Two traits, pileus weight and stipe weight, were not investigated in the natural population.

### 2.3. Statistical analysis

The phenotypic data of agronomic traits were analyzed independently in each shiitake population by the following statistical procedures using the packages of Statistical Package for the Social Sciences (SPSS, version 17 for Windows, SPSS Inc., Chicago, IL, USA). For each trait in the three populations, analysis of variance (ANOVA) was performed to assess the effects of genotypes on phenotypes according to the model:  $Y = \mu + G + \varepsilon$ , where  $G$  is the genotypic effect. The degree of phenotypic variability for each trait was estimated using the coefficient of variation (CV). The paired sample t-tests

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