International Journal of Medicinal Mushrooms, 20(5):451–458 (2018)

Detection of Quantitative Trait Loci Underlying Yield-Related Traits in Shiitake Culinary-Medicinal Mushroom, *Lentinus edodes* (Agaricomycetes)

Wen-bing Gong,[1,2] Lei Li,[3] Yan Zhou,[1] Yin-bing Bian,[1] Hoi-shan Kwan,[3] Man-kit Cheung,[3] & Yang Xiao[1,*]

[1]Institute of Applied Mycology, Huazhong Agricultural University, Wuhan, People's Republic of China; [2]Institute of Bast Fiber Crops, Chinese Academy of Agricultural Sciences, Changsha, People's Republic of China; [3]School of Life Sciences, The Chinese University of Hong Kong, Shatin, Hong Kong SAR, People's Republic of China

*Address all correspondence to: Yang Xiao, Institute of Applied Mycology, Huazhong Agricultural University, No.1 Shizishan Street, Hongshan District, 430070 Wuhan, P. R. China; xiaoyang@mail.hzau.edu.cn or xyfungi@163.com

ABSTRACT: Increasing yield is a principal goal when breeding *Lentinus edodes*. The detection of quantitative trait loci (QTLs) underlying yield and its related traits, precocity and the number of fruiting bodies (NFs), is important in order to breed high-yield cultivars. Using composite interval mapping (CIM), we mapped a total of 25 QTLs responsible for precocity, NFs, and yield in 2 segregating populations of *L. edodes*. QTLs for the 3 traits were mapped on 5 different linkage groups, contributing 5.9% to 15.4% of the phenotypic variation. Colocated QTLs were also found underlying multiple traits, implying the presence of a genic pleiotropic effect or tightly linked genes. This is, to our knowledge, the first report of the genetic dissection of precocity, NFs, and yield using QTL mapping in *L. edodes*. Findings of this study will facilitate marker-assisted breeding of high-yield cultivars of *L. edodes*.

KEYWORDS: colocalization, medicinal mushrooms, *Lentinus edodes*, QTL mapping, yield-related traits

ABBREVIATIONS: CIM, composite interval mapping; **CI**, confidence interval; **LOD**, likelihood of odds; **MAS**, marker-assisted selection; **NF**, number of fruiting bodies; **QTL**, quantitative trait locus; **WF**, weight of a single fruiting body

I. INTRODUCTION

Shiitake culinary-medicinal mushroom, *Lentinus edodes* (Berk.) Singer (=*Lentinus edodes*, Marasmiaceae, Agaricomycetes), is one of the most widely cultivated edible mushroom species worldwide. *L. edodes* is important not only as an edible mushroom with a delicious taste but also as a traditional medicinal mushroom in Asia.[1] Many reports have highlighted the pharmacological effects of lentinan, isolated from the fruiting bodies of shitake mushrooms, on the human immune system.[2,3]

Despite its significant and rewarding properties, breeding elite cultivars of shiitake mushroom is a principal problem for the shiitake industry. High yield, good quality, resistance to diseases, and precocity are always the primary goals of breeding to genetically improve mushroom species, including *L. edodes*. Similar to *Agaricus bisporus*,[4] the yield of *L. edodes* comprises 2 interrelated components, the number of fruiting bodies (NF) and the weight of a single fruiting body (WF). On the basis of a global view of phenotypic trait variation, we investigated the relations between yield and yield-component traits of shiitake.[5] Yield and yield-component traits of shiitake were found to exhibit a triangular relation, and NF was more closely related to yield than to WF. Significant negative correlation was also observed between precocity and yield. Strains that fruit earlier tend to produce numerous but small fruiting bodies.[4,5]

Most of the important agronomic traits of shiitake are quantitative traits controlled by multiple genes or quantitative trait loci (QTLs), the genetic architectures of which are complicated and largely unknown.[5] Consequently, it is arduous to improve these traits genetically through the use of conventional breeding

1521-9437/18/$35.00

methods such as phenotype-based selection. QTL mapping, which couples molecular markers and phenotypes and provides an efficient tool to genetically determine quantitative traits.[4] It is also profitable to implement marker-assisted selection (MAS), which improves the accuracy and efficiency of selection in breeding schemes.[6]

The dissection of complex agronomic traits of edible mushrooms through QTL mapping is a more recent development than its use in animal or plant species.[4,7] A few QTLs of agronomic traits (such as traits related to yield and quality) have been documented in several edible mushrooms, including *A. bisporus*,[4,8–10] *Pleurotus ostreatus*,[11–13] and *P. eryngii*.[7] QTLs have been reported for growth of *L. edodes* mycelia.[14,15] We recently recovered QTL hotspots underlying 7 morphological traits related to characteristics of fruiting bodies, including WF and traits related to the pileus and stipe.[16]

However, little is known about the genetic architecture of precocity, NF, and yield of shiitake. Genetic effects of individual loci controlling these yield-related traits remain indeterminate. Also, the genetic mechanism for phenotypic correlations of agronomic traits is bewildering. In this study, we used QTL mapping to define the genomic regions underlying shiitake precocity, NF, and yield.

II. MATERIALS AND METHODS

A. Mushroom Strains and Mapping Populations

All the tested *L. edodes* strains and mapping populations were generated and used previously.[15,16] Briefly, 2 monokaryon parents (L205-6 and W1-26) were generated from single-spore cultures of the cultivated strains L205 and WX1. Then, 146 single-spore isolates of the L205-6 × W1-26 hybrid were selected as the monokaryon population for genotyping and for constructing a genetic linkage map. For phenotyping of agronomic traits, 2 dikaryon populations (LQ-15 and LQ-64) were produced by pairing the 146 single-spore isolates with the monokaryon strains 741-15 and 741-64, respectively. All the *L. edodes* strains were preserved at the Institute of Applied Mycology, Huazhong Agricultural University, Wuhan, China.

B. Phenotype Determination and QTL Mapping

Two independent fruiting trials of the dikaryons LQ-15 and LQ-64 were conducted previously at Huazhong Agricultural University.[5] Precocity represents the time interval (days) from inoculation to the first picking of fruiting bodies. Yield (grams per bag) represents the total weight of fruiting bodies per bag during the entire harvest. As a key component of yield, NF denotes the total mean number of fruiting bodies per bag. Based on a genetic linkage map comprising 572 markers,[16] QTLs were analyzed using composite interval mapping (CIM) with Windows QTL Cartographer version 2.5.[17] The threshold for declaring significant QTLs was set to $P = 0.05$ by applying 1000 genome-wide permutation tests. Confidence intervals (CIs) were supported by likelihood of odds (LOD)-1. Detailed descriptions of the QTL analysis, including parameter settings, nomenclature, and the visualization of QTLs on the genetic map, were provided previously.[16] For different traits, mapped QTLs with overlapping CIs were considered to be colocated when the genetic positions of the LOD score peak of QTLs were in overlapping regions.

III. RESULTS

Phenotypes for the precocity, NF, and yield in LQ-15 and LQ-64 were evaluated previously.[5] All 3 traits followed a continuous distribution. For precocity, NF, and yield, CIM detected a total of 25 QTLs on 5 linkage groups (MLG2, MLG4, MLG6, MLG7, and MLG12) (Table 1, Fig. 1). Individual QTLs explained

TABLE 1: QTLs for Precocity, the Number of Fruit-Bodies, and Yield Detected in LQ-15 and LQ-64

Locus, by Trait	Linkage Group	Position of LOD Score Peak (cM)	Marker Nearest LOD Score Peak	LOD	Additive Effect of QTLs[a]	R^2 (%)	Confidence Interval (cM)[b]	Monokaryon Strains	
								741-15	741-64
Precocity									
fp-IV-1	MLG4	66.9	MAT-A	5.3	9.74	13.1	62.3–78.9		Y
fp-IV-2	MLG4	89.5	ghf30-2-160	3.1	−8.39	8.1	88.2–91.2	Y	
fp-IV-3	MLG4	95.7	S548-ID1	3.4	−9.65	10.7	94.5–97.6	Y	
fp-IV-4	MLG4	106.6	icb-2-210	3.0	−9.96	11.0	105.9–108.8	Y	
fp-VII-1	MLG7	80.2	ME3-EM5-980	6.0	−10.19	15.1	79.6–81.8		Y
fp-VII-2	MLG7	92.2	zin2-4-360	3.6	8.48	10.3	90.7–92.4		Y
fp-XII-1	MLG12	12.2	exg2-3-550	3.6	7.74	8.6	7.7–14.1		Y
NF									
nf-II-1	MLG2	54.8	icb-2-260	3.6	2.57	9.6	54.1–55.5	Y	
nf-II-2	MLG2	58.7	ME4-EM3-500	3.5	2.88	9.3	58.3–59.8	Y	
nf-II-3	MLG2	64.0	man1-4-350	5.6	2.43	12.9	63.5–64.3		Y
nf-II-4	MLG2	72.5	tel-2-480	4.6	2.51	13.9	70.5–74.8		Y
nf-IV-1	MLG4	95.7	S548-ID1	3.5	−2.05	9.1	95.1–97.8		Y
nf-VI-1	MLG6	12.9	S560-ID1	6.6	2.72	15.4	12.4–13.9		Y
nf-VI-2	MLG6	19.3	tyr-3-380	3.9	2.14	9.6	18.6–20.6		Y
nf-VI-3	MLG6	73.6	gpd-4-350	3.6	1.74	9.2	72.4–77.2	Y	
nf-VII-1	MLG7	68.0	mip-2-170	5.5	−2.44	12.7	67.7–70.5		Y
nf-VII-2	MLG7	73.4	rab-4-295	5.7	−2.62	14.3	72.6–73.9		Y
nf-VII-3	MLG7	81.2	ME3-EM5-980	5.1	2.61	15.2	79.6–83.2		Y
Yield									
y-II-1[c]	MLG2	64.0	man1-4-350	2.0	8.40	5.9	63.2–64.4		Y
y-IV-1	MLG4	31.8	ME7-EM8-960	3.5	18.35	9.5	31.7–32.9	Y	
y-IV-2	MLG 4	40.2	ME6-EM3-80	5.2	22.32	13.7	39.5–41.1	Y	
y-IV-3	MLG 4	47.7	S150-ID1	3.9	20.53	12.0	47.2–47.9	Y	
y-VI-1	MLG 6	73.6	gpd-4-350	3.9	19.46	10.0	73–76.2	Y	
y-VII-1	MLG 7	59.6	S655-ID1	3.0	−16.60	7.4	58–62.3	Y	
y-VII-2	MLG 7	81.2	ME3-EM5-980	3.8	13.00	14.0	79.9–84.2		Y

LOD, likelihood of odds; NF, number of fruiting bodies; QTL, quantitative trait locus; Y, the QTL was mapped in LQ-15 or LQ-64.

[a]Minus signs (−) indicate that the favorable allele of the QTL came from W1-26, while the favorable allele of the remaining QTL came from L205-6.

[b]Confidence intervals are supported by LOD-1.

[c]A weak QTL was detected by an LOD threshold of 2.0. Other QTLs were detected by an LOD threshold based on 1000 permutations.

5.9% to 15.4% of phenotypic variation. In LQ-15, 11 QTLs were identified, including 3 for precocity, 3 for NF, and 5 for yield. In LQ-64, CIM mapped 14 QTLs, including 4 for precocity, 8 for NF, and 2 for yield.

For precocity, 7 QTLs were mapped among the 2 populations, contributing 8.1% to 15.1% of the phenotypic variation. In LQ-15, QTLs *fp-IV-2*, *fp-IV-3*, and *fp-IV-4* were mapped on MLG4. All these QTLs showed negative additive effects with favorable alleles from W1-26. Of these QTLs, *fp-IV-3* linked with S548-ID1. In LQ-64, 4 QTLs for precocity (*fp-IV-1*, *fp-VII-1*, *fp-VII-2*, and *fp-XII-1*) were mapped on 3 linkage groups (MLG4, MLG7, and MLG12). The QTL *fp-IV-1* showed a positive effect, whereas

FIG. 1.

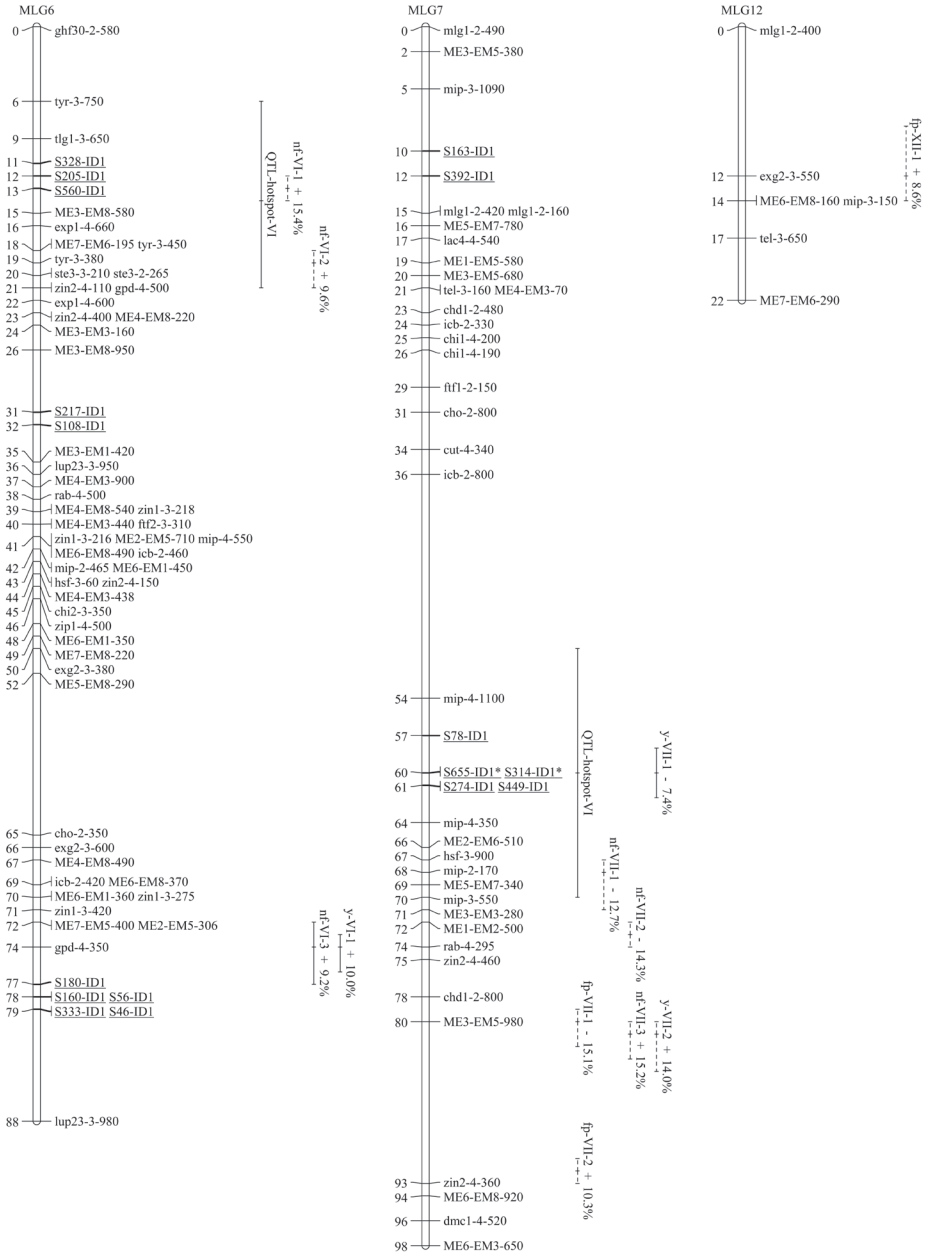

FIG. 1: Locations of QTL for precocity, the number of fruiting bodies, and yield detected in LQ-15 and LQ-64. Only linkage groups harboring QTLs are presented. QTLs are shown on the right side of the linkage groups. The plus (+) or minus (−) symbol following each QTL indicates the additive effect of QTLs: a minus sign indicates that the favorable allele of the QTL came from the parental strain W1-26, whereas a plus sign means that the favorable allele of the QTL came from the parental strain L205-6. R^2 values represent the percentage of explained phenotypic variation, and the length of each QTL bar represents the LOD-1 confidence interval. The position of the LOD peak is presented by a short line in the QTL bar. Solid lines represent QTLs mapped in LQ-15, and dashed lines indicate QTLs mapped in LQ-64. QTL hotspots represent regions controlling the shape of fruiting bodies.[16] QTLs for precocity, the number of fruiting bodies, and yield are showed in green, blue, and red, respectively. LOD, likelihood of odds; QTL, quantitative trait loci.

the remaining QTLs showed negative effects. The mating-type locus (*MAT-A*) was included in the CI of *fp-IV-1*.

For NF, we identified 3 QTLs in LQ-15 and 8 QTLs in LQ-64, which contributed 9.1% to 15.4% of the phenotypic variation. Four QTLs (*nf-II-1* and *nf-II-2* identified in LQ-15, and *nf-II-3* and *nf-II-4* detected in LQ-64) clustered on MLG2 and showed positive effects with favorable alleles from L205-6. On MLG4, QTL *nf-IV-1*, detected in LQ-64, linked with S548-ID1. On MLG6, 3 QTLs (*nf-VI-1* and *nf-VI-2* mapped in LQ-64, and *nf-VI-3* mapped in LQ-15) showed positive effects with favorable alleles from L205-6. Furthermore, *nf-VII-1*, *nf-VII-2*, and *nf-VII-3* identified in LQ-64 formed a cluster on MLG7.

For yield, 7 QTLs were detected across the 2 populations. In LQ-15, 3 QTLs (*y-IV-1*, *y-IV-2*, and *y-IV-3*) clustered on MLG4, explaining 9.6% to 13.7% of the phenotypic variation. Furthermore, 2 QTLs (*y-VI-1* linked with gpd-4-350 on MLG6 and *y-VII-1* linked with S655-ID1 on MLG7) were also mapped in LQ-15. In another population, LQ-64, a weak QTL (*y-II-1*) for yield, with an LOD score of 2.0, was mapped and found to be colocated with *nf-II-3* on MLG2. Another QTL (*y-VII-2*) was located on MLG7 and contributed to 14.0% of the phenotypic variation. Apart from *y-VII-1*, all the other QTLs detected in the 2 populations showed positive effects, and L205-6 contributed the favorable alleles.

In this study, QTLs for the 3 traits were not randomly distributed throughout the genome. Most of them were mapped on MLG2, MLG4, MLG6, and MLG7. Furthermore, several QTLs for different traits were found to be colocated on pleiotropic regions (Fig. 1). Across the 2 segregating populations, 3 NF-QTLs (*nf-II-3*, *nf-VI-3*, and *nf-VII-3*) were colocated with 3 yield-related QTLs (*y-II-1*, *y-VI-1*, and *y-VII-2*), respectively. All these QTLs showed positive effects, with L205-6 contributing the favorable alleles. On MLG7, QTL *fp-VII-1* for precocity was found to be colocated with *nf-VII-3* and *y-VII-2*. Also, *fp-IV-3* and *nf-IV-1* were colocated on MLG4.

IV. DISCUSSION

Given the great significance of breeding high-yield cultivars in the shiitake industry, this study was designed to demarcate genomic regions harboring QTLs responsible for yield and yield-related traits in *L. edodes*. A total of 25 QTLs for precocity, NF, and yield were mapped across 2 populations. Phenotypic variation explained by these QTLs was small, ranging from 5.9% to 15.4%. This could be explained by the complex polygenic nature of these traits. Our result showed that these 3 traits may mainly be governed by QTLs with small effects, indicating that pyramiding these minor QTLs to genetically improve shiitake yield would be challenging.

The breeding of high-yield cultivars is a crucial target in genetic breeding of *L. edodes*. WF and NF are 2 mutual restriction components of shiitake yield.[5] Improving NF would increase the yield, but the mushrooms would be smaller. The breeding of elite cultivars needs to balance NF and WF. A previous study detected QTLs underlying WF and traits related to the pileus and stipe.[16] More than 85% of QTLs controlling the shape of fruiting bodies were mapped in 6 genomic regions, defined as QTL hotspots. Most of the WF-related QTLs were within these hotspot regions, whereas the majority of QTLs for NF and yield resided outside the hotspot regions (Fig. 1). Furthermore, W1-26 contributed the majority of favorable alleles for WF-related QTLs, whereas most of the favorable alleles for NF- and yield-related QTLs came from L205-6. These results suggest the feasibility of simultaneous genetic improvement of the 2 yield-component traits. Dissecting genetic effects of individual loci by QTL mapping would be useful to stack the favorable alleles of the 2 yield-component traits.

Because the development of strains that produce fruit early could greatly reduce the cost of commercial cultivation of *L. edodes*, improving precocity is also one of the main goals in the genetic improvement of shiitake.[5] Here we mapped a total of 7 QTLs for precocity. Six of them (except *fp-IV-2*) were also

detected by inclusive CIM (data not shown), indicating the reliability of these QTLs. The peak LOD score of *fp-IV-3* was 0.5 cM from S548-ID1, which was included in a cytochrome P450 gene.[16] Also, S548-ID1 was found to be linked with *nf-IV-1*. These results demonstrated the potential of S548-ID1 in marker-assisted selection. It is worth emphasizing that the entire harvest period for shiitake lasts several months.[18] Therefore, the genetic architecture of other traits related to maturity, such as duration of the harvest and peak fruiting period, should also be dissected.

Previous research has shown phenotypic correlations among precocity, NF, and yield.[5] In this study, QTLs for phenotype-correlated traits were found to be colocated on the same linkage groups. Although reports of QTL mapping for edible mushrooms are limited, colocalized QTLs have been frequently detected for related traits. In *P. ostreatus*, a region containing colocated QTLs involved in the genetic control of yield-related traits was found in linkage group VII.[12] In *A. bisporus*, QTLs for yield (kilograms per square meter) and its 2 elementary components, number (NF per square meter) and weight (grams per mushroom) were found to be colocated in 4 genomic regions on LGII, LGIII, LGIV, and LGX.[4] Similar results of QTL colocalization for the characteristic traits of fruiting bodies were also observed in *L. edodes*.[16] The detection of QTL colocalization suggests that either a single pleiotropic QTL controlling multiple traits or a few tightly linked QTLs for different traits are present in the same region.

Significantly correlated traits were found to share a higher number of common QTLs than traits without significant genetic correlations.[19] The more tightly 2 traits were correlated, the more QTLs they had in common.[20] In *L. edodes*, NF was more closely related to yield than WF (both are interrelated components of yield).[4] Based on the result of QTL mapping, 3 NF-related QTLs were colocalized with yield-related QTLs, whereas only 1 WF-related QTL was colocated with yield-related QTLs (data not shown). These results demonstrate that the close association between NF and yield may be attributed to the fact that NF and yield share more colocalized QTLs than do WF and yield.

In breeding schemes, colocated regions underlying multiple desirable traits could serve as useful targets in MAS. Taking as an example the colocated regions affecting NF and yield, because the desirable alleles of these QTLs were contributed by L205-6, MAS of these regions could simultaneously improve NF and yield. These molecular markers in the QTL colocated regions also have potential in marker-assisted introgression of favorable alleles. As mentioned for *L. edodes*,[5] some wild strains have desirable performance for NF. The introgression of favorable alleles from wild germplasms into elite cultivars could be a promising strategy to genetically improve shiitake NF and yield.

V. CONCLUSIONS

We determined here—to our knowledge for the first time—the genetic architecture of the precocity, NF, and yield of *L. edodes* using QTL analysis. A total of 25 QTLs were detected on 5 linkage groups, contributing 5.9% to 15.4% of the phenotypic variation. Mapped QTLs for precocity, NF, and yield explained only small amounts of phenotypic variation, suggesting that genetic improvement of these traits will be challenging in *L. edodes*. The detection of colocated QTLs for correlated traits suggests the presence of a pleiotropic locus or tightly linked loci. The findings presented here extend knowledge of the genetic basis of phenotypic correlation and are expected to facilitate the implementation of marker-based breeding strategies in *L. edodes*.

ACKNOWLEDGMENTS

This work was supported by the National Natural Science Foundation of China (Grant Nos. 31372117 and 31000929), the industry (Agriculture) Science and Technology Plans of Hubei Province (Grant No.

2012DBA19001), and Fundamental Research Funds for the Central Universities of China (Grant No. 2012ZYTS041).

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