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专论与综述

低温刺激对食用菌子实体形成的研究进展

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摘　要：探究低温刺激子实体形成过程的组学数据能为食用菌的工厂化低碳高效栽培及广温型品种的选育提供参考。本文首先通过主成分分析对食用菌低温刺激子实体形成的类型进行低温型(11−19 ℃)和冷压型的划分(≤10 ℃)。在此基础上，综述了食用菌两种类型的低温刺激子实体形成过程的研究进展。食用菌低温刺激子实体形成过程中都涉及信号转导、胁迫响应、基础代谢、细胞分化、细胞结构变化等代谢过程。随着低温型到冷压型的刺激温度下降，糖代谢可能转向脂代谢为子实体形成提供能量。

关键词：食用菌；低温刺激；子实体形成；功能基因组学；功能基因

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Advances in low temperature stimulation for the fruiting body formation of edible fungi

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Abstract: Exploring the process of low temperature stimulating fruiting body formation (LSFF) can provide a reference for the industrialized low-carbon efficient cultivation of edible fungi and the breeding of varieties with wide temperature ranges. This study first performed principal component analysis to classify LSFF of edible fungi into the low-temperature type (11−19 °C) and the cold stress type (≤10 °C). On this basis, the research progress in the two types of LSFF in edible fungi was reviewed. The LSFF in edible fungi involves the metabolic processes such as signal transduction, stress response, basic metabolism, cell differentiation, and cell structure changes. With the decrease in the stimulation temperature from the low-temperature type to cold stress type, the sugar metabolism may shift to lipid metabolism to provide energy for fruiting body formation.

Keywords: edible fungi; low temperature stimulation; fruiting body formation; functional genomics; functional gene

我国的食用菌资源丰富，将近千种，约一百多种食用菌被广泛栽培食用，市面常见的食用菌约 20 种[1]。香菇(*Lentinus edodes*)、金针菇(*Flammulina velutipes*)、黑木耳(*Auricularia auricula*)、杏鲍菇(*Pleurotus eryngii*)等品种年产量可达 $2\times10^6-1\times10^7$ t[2]。食用菌从孢子萌发为营养菌丝到成熟的子实体再产生孢子，这一生长周期受多种环境因子的影响，诸如温度、湿度、光照、空气和酸碱度等。环境因子的变化可以直接影响子实体的形成。例如：高温会使香菇菌丝抗逆性减弱，超过阈值后造成菌丝死亡[3]；强光照射抑制菌丝生长，适当强度的光照对子实体分化有利[4]；空气中氧气浓度高有助于菌丝生长及其子实体分化，高浓度二氧化碳则对食用菌生长有抑制作用[5]；多数食用菌的最适生长 pH 值为 5.0−8.0，在 pH 8.0 以上的碱性环境会停止生长[6]。工厂化栽培是食用菌生产发展的重要方向，而工厂化栽培重要的特点就是需要环境因子模块化，选择最适宜的环境因子，对工厂化低碳高效栽培具有重要的理论和实践价值。

温度作为影响子实体发育的关键因子[7]，影响菌丝的生长速度和子实体的质量[8]。这与食用菌的生命活动依赖于一系列功能蛋白有关，而蛋白活性与温度的变化密切相关[6]。如草菇(*Volvariella volvacea*)纤维二糖水解酶 Vvcbh1-1

在 4 ℃时活性升高引发草菇菌丝的低温自溶[9]；张介弛等[10]发现黑木耳在 20 ℃发菌时菌丝生长较好，耳质好、产量高，相较 25 ℃发菌产量提高 37.9%；田景花等[11]发现杏鲍菇子实体对温度较敏感，错过原基形成温度(15 ℃)将不再出菇。食用菌子实体分化需要较低的温度，最佳分化温度往往低于菌丝生长温度[12]，食用菌原基形成和子实体分化需要低温诱导或者温差的刺激[13]。

低温诱导是促进许多食用菌子实体结实的主要手段[14]。Weiser 等[15]首先提出了植物抗寒过程中需要特异基因的激活和新蛋白诱导合成的观点，低温刺激食用菌结实的分子机理核心也可以认为是这一概念的延伸，即冷诱导基因的表达与调控。

目前，转录组学、蛋白质组学、代谢组学等功能基因组学能系统地研究冷诱导基因的表达与调控[16]。例如，蛋白质组学技术可以研究蛋白质的组成、表达、结构、功能和相互作用，揭示特定生命过程的内在机制，在更深层次上探索生命活动的规律[17]。考虑到低温刺激子实体结实的温度区间范围差异幅度较大(大约 20 ℃)，我们首先在已有食用菌温型分类的基础上，对食用菌低温刺激温型进行了进一步的划分。鉴于组学技术已经在食用菌子实体形成的研究中大量应用[18]，重点对不同低温型的组学研究进行了总结。围绕低温刺激子实体形成的相关通路和基因的功能进行了讨论，以期为食用菌工厂化低碳高效栽培及广温性品种选育提供理论参考。

1 食用菌温型划分

温度是食用菌生长的重要环境因素，在其菌丝生长、子实体形成等阶段都有相应的最适温度。一些食用菌能在环境温度不变即恒温条件下完成子实体的分化，称为恒温结实。一些食用菌需要温差刺激才能分化出子实体，称为变温结实，如香菇、金针菇等[6]。

根据原基分化所需的温度不同可将食用菌分为低温型、中温型和高温型[19]。庞杰等[14]根据菌丝和子实体生长的温度需求详细分析了 29 种食用菌，将其细分为四大类：第一类为低温结实型食用菌，子实体分化温度范围 13.8−19.4 ℃，低于菌丝生长温度范围(21.1−24.4 ℃)；第二类为中温型食用菌，菌丝和子实体发育所需温度相近(17.9−27 ℃)；第三类为高温结实型，菌丝生长温度(24−29 ℃)低于子实体的分化温度(27.6−31.7 ℃)；第四类为高温型，菌丝和子实体发育所需温度均较高(27−37 ℃)。本文为探究低温刺激对子实体形成的影响，将子实体形成温度低于 20 ℃的低温结实型进一步分为 2 个类型(图 1，表 1)：(1) 低温型(11−19 ℃)，包括香菇、真姬菇(*Hyjpsizygus marmoreus*)、双孢蘑菇(*Agaricus bisporus*)和秀珍菇(*Pleurotus geesteranus*)等。(2) 冷压型(≤10 ℃)，包括金针菇、白灵菇(*Pleurotus nebrodensis*)和滑菇(*Pholiota nameko*)等。

2 低温刺激对低温型食用菌子实体形成的影响

食用菌在长期的进化中产生许多适应温度逆境的能力。基因组、转录组等组学分析技术的发展拓宽了人们对食用菌子实体形成的认知，成为研究细胞功能和表型的热点[29]。当外界温度下降时，一系列特异基因的表达集中于能量代谢、氧化还原酶活性和靶蛋白降解等过程[30]。诱导蛋白在抵御低温渗透、稳定酶的结构、胞外酶代谢中发挥作用，协调细胞内各项代谢水平从而使细胞适应新的环境[31]。

2.1 低温型食用菌的信号感知与转导

G 蛋白偶联受体(G protein-coupled receptor, GPCR)在 cAMP 信号通路中起着关键作用。碳

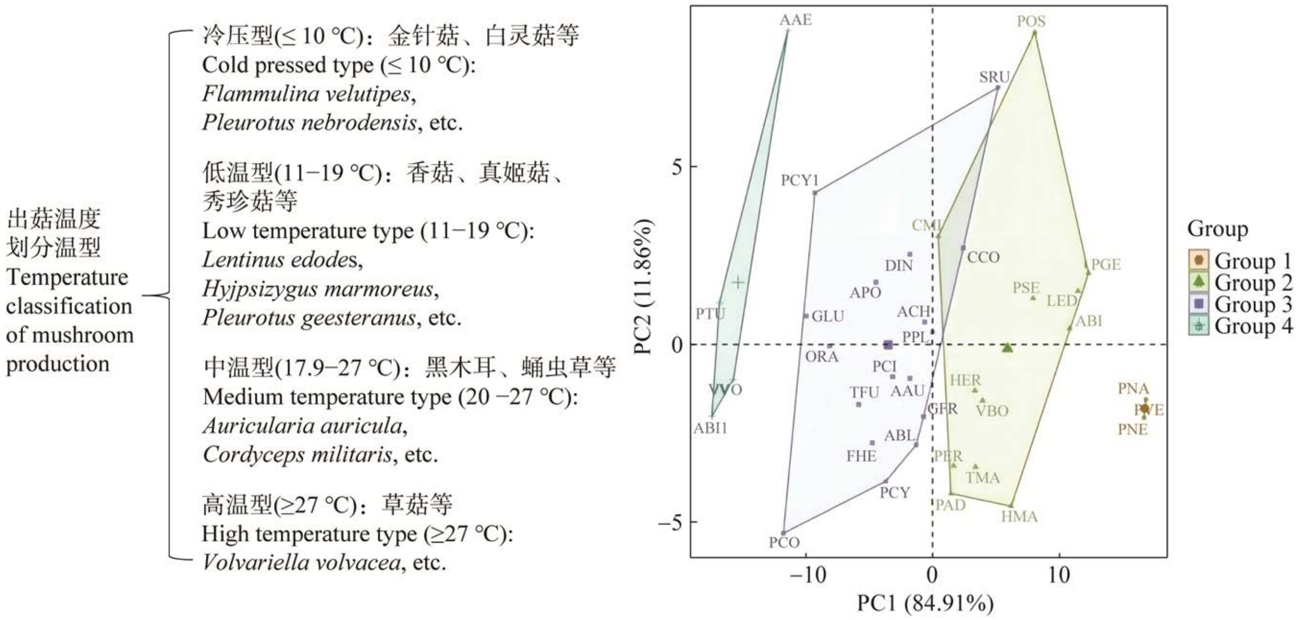

图 1　食用菌子实体分化温度的主成分分析　以子实体分化的最适温度区间的均值作为划分标准：低于 11 ℃为冷压型(group 1)，11−19 ℃为低温型(group 2)，17.9−27 ℃为中温型(group 3)，高于 27 ℃的作为高温型(group 4)；FVE 为 *Flammulina velutipes* 的第一个单词的第一位和后一个单词的前两位的缩写，以此类推；子实体分化温度数据引用庞杰等报道的数据[14]

Figure 1　Principal component analysis of fruiting body differentiation temperature. The average value of the optimal temperature range for the differentiation of the fruiting body is taken as the division standard, the temperature below 11 ℃ is cold pressing type (group 1), 11−19 ℃ is low temperature type (group 2), 17.9−27 ℃ is medium temperature type (group 3), and the temperature above 27 ℃ is high temperature type (group 4); FVE is the abbreviation of the first digit of the first word and the first two digits of the last word of *Flammulina velutipes*, and so on; The fruiting body differentiation temperature data refer to the date reported by Pang[14].

源会被 G 蛋白偶联受体 1 (G protein-coupled receptor 1, GPR1)感知，激活 G 蛋白 α 亚单位 2 (G protein alpha subunit 2, GPA2)，GPA2 激活腺苷酸环化酶(adenylyl cyclase, AC)提高胞内 cAMP 浓度[32]，过表达 G 蛋白 α 亚基基因 *GANI* 也能提高内源 cAMP 水平，产生的 cAMP 经过 G 蛋白介导的信号转导诱导结实[33-34]。灰盖鬼伞(*Coprinopsis cinerea*)在菌丝扭结时加入 AC 抑制剂后无法形成原基，外源添加 cAMP 能诱导子实体的形成[35]；杏鲍菇(12 ℃刺激)原基形成差异基因富集于 cAMP 信号转导、碳水化合物代谢和细胞壁降解[36]；高水平的 cAMP 能提高淀粉酶和漆酶活性[34]，表明子实体形成需要大量能量，cAMP/PKA 信号转导途径是子实体形成的关键。

2.2　低温型食用菌子实体发育的调控基因表达

锌指蛋白、DNA 结合蛋白均可作为转录因子调控子实体的发育[37-38]。C2H2 (Cys_2His_2)型锌指蛋白在双孢蘑菇子实体整个发育阶段明显上调[39]，可能参与菌丝聚集到原基的转换[40]。C2H2 型锌指蛋白在干旱、低温等胁迫下有增强作物低温耐受力的作用[41]，能调控大部分胁迫基因的表达[42]，在丝状真菌中广泛参与碳代谢调控，参与纤维素降解相关酶的表达[43]，因此 C2H2 型锌指蛋白上调表明双孢蘑菇子实体形成期间对碳源的需求增加。DNA 结合蛋白基因

表 1　低温结实型食用菌类型划分

Table 1　Classification of low temperature fruiting edible fungi

食用菌种类 Edible fungi species	菌丝生长适宜温度 Suitable temperature for mycelium growth (℃)	子实体分化适宜温度 Suitable temperature for fruiting body differentiation (℃)	参考文献 References
滑菇 *Pholiota nameko***	20−25	5−15	[14]
白灵菇 *Pleurotus nebrodensis***	22−25	−2−5	[20]
金针菇 *Flammulina velutipes***	22−24	6−14	[14]
双孢蘑菇 *Agaricus bisporus**	22−25	13−16	[14]
香菇 *Lentinus edodes**	23−25	12−17	[14]
姬菇 *Pleurotus cornucopiae**	20−25	12−15	[21]
大球盖菇 *Stropharia rugoso-annulata**	24−28	15−19	[14]
羊肚菌 *Morchella esculenta**	20−24	15−18	[22]
杏鲍菇 *Pleurotus eryngii**	20−22	14−15	[23]
秀珍菇 *Pleurotus geesteranus**	20−24	15−18	[24]
榛蘑 *Armillariella mellea**	23−25	14−20	[25]
元蘑 *Hohenbuehehelia serotina**	22	14	[26]
真姬菇 *Hyjpsizygus marmoreus**	20−25	12−16	[27]
大肥蘑菇 *Agaricus bitorquis**	18−22	15−18	[28]

*：低温型；**：冷压型

*: Low temperature type; **: Cold pressed type.

Le.cdc5 在香菇原基和幼子实体中高表达，延伸因子基因 *pri10022* 在香菇原基和成熟子实体中显著表达[44]，香菇冷刺激后基因表达和蛋白翻译高度活跃。新研究发现一个香菇 DNA 结合蛋白基因 *Le-Dd10*，敲除后不形成子实体[45]，Le-Dd10 蛋白有 56、27 和 14 kDa 三个分子量，在子实体形成较快的香菇品种中 14 kDa 蛋白表达较强；56−14 kDa 的变化可能对刺激子实体形成极其重要，然而 56、27 和 14 kDa 蛋白在原基和子实体之间的关系尚不清楚[45]。large fruiting body cap 1 (*LFC1*)基因编码的转录因子 LFC1 负调节金针菇(15 ℃刺激)子实体形成，敲除该基因促进子实体发育，出菇时间缩短 2 d，LFC1 同源物广泛存在于食用菌中，可用于蘑菇育种[46]。

泛素化修饰在细胞生长中有重大作用。通过泛素激活酶 E1、泛素结合酶 E2、泛素连接酶 E3 共同作用使蛋白质降解，参与信号转导、DNA 修复、异常蛋白代谢和应激反应等[47-48]。担子菌泛素蛋白复合物随着发育进程而变化[49]，鸡腿菇(*Coprinus comatus*)原基形成过程中，泛素与泛素蛋白结合物同时增加，在子实体发育成熟过程中菌柄下部比上部高[50]，真姬菇原基和幼子实体中也存在类似现象[51]。降解异常蛋白维持细胞稳态，得到的短肽和氨基酸可作为原料用于抵抗胁迫，这可能有利于原基形成。F-box 蛋白参与真核生物蛋白泛素化等多种生物学过程[52]，F-box 编码基因也被发现在金针菇、蜜环菌(*Armillaria mellea*)、裂褶菌(*Schizophyllum commune* Fr.)子实体阶段特异性表达[53]，表明 F-box 基因在伞菌子实体发育中具有重要作用。

真核翻译起始因子 2 (eukaryotic initiation factor 2, eIF2)几乎是所有 mRNA 翻译起始必需的，general control non-derepressible 2 (GCN2)是一种广泛分布在真核生物且参与氨基酸缺

乏、冷刺激等各种胁迫响应的蛋白激酶，通过磷酸化 eIF2 的 α 亚基抑制 eIF2-GDP 向 eIF2-GTP 转化，阻止翻译起始。然而在真姬菇 15 ℃刺激出菇时，GCN2 介导的翻译通路促进蛋白合成[54]。GCN2 介导的 eIF2α 磷酸化的应激反应机制在所有真核生物中并不相同。

2.3 低温型食用菌子实体中功能基因表达

细胞色素 P450 属于氧化酶系统，在真菌中参与解毒反应、次生代谢和生长发育调节[55]。已发现一个细胞色素 P450 基因在双孢蘑菇子实体中特异表达[56]。灰盖鬼伞 P450 编码基因突变能导致菌柄变短[57]，P450 基因在子实体形成中可能是保守的。双孢蘑菇子实体形成中(15 ℃低温刺激)的差异基因主要参与氨基酸代谢。大量氨基酸合成酶基因高表达，积累具有生理活性的氨基酸如精氨酸、脯氨酸、酪氨酸等[39]。氨基酸可作为合成其他物质的前体，如精氨酸可分解为鸟氨酸和尿素[58]。鸟氨酸可合成多胺提供氮源。脯氨酸在植物和食用菌非生物胁迫下维持代谢，也能作为分子伴侣清除活性氧，在低温胁迫下调节渗透压维持细胞稳态[59]。

疏水蛋白可以在潮湿环境中促进表面菌丝聚集[60]，当疏水蛋白分泌至细胞壁中时，菌丝越过水汽进入空气中形成气生菌丝，更多的气生菌丝有助于原基形成[61]。对外阻止膜对水的吸收，防止子实体被水浸泡[62]。香菇中疏水蛋白基因 *SC1*、*SC3* 在子实体形成时高表达[63]。水通路蛋白负责水和溶质运输，在金针菇菌柄中特异表达，可能加强水分和营养物质运输，促进菌柄和孢子发育。疏水蛋白和水通路蛋白特异表达时间可能与金针菇菌柄生长有关。水运输也是腐生真菌发育中的一个重要过程[64]，在白灵菇等多种食用菌子实体发育中受调控[53]。

漆酶是一类多酚氧化酶，在木质素降解、子实体发育中起重要作用[65]。漆酶基因在真姬菇发育过程中的原基期后表达逐渐上升，子实体形成后表达下降[66]；金针菇 15 ℃刺激出菇时胞外漆酶活性较高[65]，也能进一步证明漆酶与食用菌子实体形成密切相关。

碳水化合物活性酶(carbohydrate-active enzymes, CAZymes)调控基因在真菌中参与细胞壁构建，细胞壁自溶和重建是担子菌类食用菌子实体发育的基本过程[67]。丝状真菌细胞壁主要由几丁质和 β-1,3-葡聚糖组成[68]，细胞壁合成、裂解，多糖组分的变化在担子菌子实体菌柄发育中必不可少[69-70]。几丁质酶、甘露糖苷酶基因在香菇和金针菇子实体发育中上调表达[67,71]，赋予菌丝相互黏附扭结的可塑性[53]。有学者认为真菌细胞在增大过程中要依靠水解酶类的降解，使细胞壁松弛解除束缚满足生长需求[67]。灰盖鬼伞(高温型)子实体成熟过程中几丁质酶 ChiB1 表达量明显增加[72]。正常褐变的香菇糖苷水解酶基因在子实体形成时高表达[63]，表明细胞壁降解重塑可能是伞菌子实体发育的重要过程。真菌中还存在一类扩张蛋白，通过无水解过程破坏葡聚糖链或几丁质链之间的非共价键，促进细胞壁聚合物滑移，疏松重塑细胞壁结构[73]。扩张蛋白基因 *Fvexpl1* 在金针菇(15 ℃刺激)菌柄快速伸长中起作用，可作为提高金针菇产量的候选基因[74]。

3 低温刺激对冷压型食用菌子实体发育的影响

冷压型食用菌往往需要 10 ℃以下的低温刺激才可以出菇。Sakamoto 等[75]将金针菇置于 8 ℃下 14 d 后形成子实体，认为温度是诱导金针菇子实体的关键因素[76]。−1–2 ℃冷压刺激可以促进白灵菇子实体形成，刺激的时间越长，菇蕾形成时间越短[20]。下面列举冷压型食用

菌的子实体形成的研究，重点对金针菇在低温和冷压两种刺激下的应答机理进行比较总结。

3.1 冷压型食用菌信号感知与转导

细胞膜流动性的改变是食用菌感知冷刺激的首要变化，膜脂物理变化可直接调节膜上感应蛋白活性，以此传递低温信号到下级通路[77]。杏鲍菇−3 ℃刺激后磷脂酶和脂肪酸去饱和酶基因表达上调[78]，改变细胞膜组成以适应温度变化[79]。真菌中麦角甾醇参与膜功能域的形成、膜流动性和胞内转运，以及影响膜蛋白的定位等[80]。金针菇和肺形侧耳(*Pleurotus pulmonarius*) X57 菌株子实体形成时麦角甾醇合成通路活力上调[81-82]，推测麦角甾醇合成通路与原基形成有关。脂膜中磷脂酰肌醇 4,5-二磷酸[PI(4,5)P_2]含量随温度降低而降低，被磷脂酶水解产生第二信使 IP3，在内质网与配体门钙通道结合，开启钙通道，使胞内 Ca^{2+}浓度升高，激活各种钙依赖性蛋白[83]。金针菇菌丝和原基中钙依赖性蛋白激酶表达明显不同也证实了 Ca^{2+}作为第二信使参与冷信号转导[84-85]。Ca^{2+}信号和渗透调节基因在白灵菇 4 ℃刺激 3 d 后表达降低[86]，这与冷胁迫能诱导 Ca^{2+}浓度瞬时升高的结论[87]相一致。拟南芥(*Arabidopsis thaliana*)冷刺激时 OST1/SNRK2.6 激酶与渗透转运蛋白 ATANN1 相互作用磷酸化增强 Ca^{2+}转运活性[87]，Ca^{2+}信号与活性氧、MAPKS 信号通路交互作用提高细胞抗冻性[88]，真菌中可能也存在类似信号转导模式。

HOG-MAPK 传递低温等多种胁迫信号并促进甘油、阿拉伯糖醇、海藻糖合成。在高渗应激环境下控制信号传导和基因表达[89]，在酿酒酵母(*Saccharomyces cerevisiae*)、蓝藻(*Cyanobacteria*)、金针菇子实体发育中也被证实能响应低温胁迫[85]。低温胁迫响应通过 SLN1 支路实现[90-91]，外界低温刺激使得 SLN1 支路磷酸化被抑制，去磷酸化的 SSK1 结合 SSK2 和 SSK22，从而激活 PBS2 和 HOG1，激活的 HOG1 进入细胞核发挥功能[92-93]，开启转录调控。肺形侧耳 4 ℃低温处理后 HOG 通路中大部分基因都持续显著上调[94]。金针菇 10 ℃、白灵菇 4 ℃刺激 3 d 后膜系统、HOG1 型 MAPK 通路相关基因上调表达明显[51,85,95]。在拟南芥等模式生物中的 HOG 同源途径都能响应低温胁迫[96]。这表明 HOG-MAPK 通路对低温胁迫响应具有重要研究意义。

G 蛋白偶联受体(GPCRs)是最大的跨膜受体家族，介导运输功能蛋白到细胞内特定位置，调节膜运输以及连接到脂膜受体对不同信号分子做出反应[32,97]，参与真菌抵抗胁迫[98]。Yamada 等[99]将金针菇菌丝置于 8 ℃诱导子实体形成，发现 58i cDNA 编码的氨基酸序列与 G 蛋白 α 亚基类似，Northern blotting 结果表明不同种类的 G 蛋白在子实体形成时起作用。信息素受体基因 *PRLG*s 属于 GPCRs 家族，对外界刺激产生反应，在金针菇子实体期高表达[100]。GPCRs 家族在刺激机制中起着重要作用，深入研究 PRLGS 的多种功能将更有利于阐明食用菌子实体发育机理。

3.2 冷压型食用菌子实体发育的调控基因表达

转录因子基因 *PDD1* 的过表达能促进金针菇子实体形成，产量提高 33%，缩短出菇时间 4 d[101]。余颖豪等[13]利用转录组测序技术分析了金针菇菌丝和原基冷压(10 ℃)刺激后的 7 935 个差异表达基因，差异基因功能注释显示糖酵解过程中异构酶、磷酸化酶基因表达下调，柠檬酸合酶和脂代谢相关基因表达上调，提示冷压作用下主要由三羧酸循环(tricarboxylic acid cycle, TCA cycle)和脂质代谢产能；几丁质合酶基因表达下调而 β-葡聚糖合成相关基因表达上调，细胞壁成分发生变化，可能与原基形成相关。与

此对比，15 ℃刺激下金针菇原基中糖酵解相关酶基因表达较高，在原基形成时参与能量代谢[102]。金针菇在长期 12 ℃冷胁迫后葡萄糖-6-磷酸异构酶、β-葡萄糖苷酶、海藻糖酶活性显著提高，海藻糖酶能催化海藻糖转化为葡萄糖[103]。以上研究提示，冷压作用下金针菇启动脂代谢的供应能量的方式，而低温刺激则采用糖代谢的供应能量的方式。这与食用菌糖代谢相关酶受到冷压胁迫调控的报道[104]相吻合。

3.3 冷压型食用菌子实体中的功能基因表达

冷压型刺激温度较低，细胞膜首先对低温做出反应，感受到冷信号后金针菇转变供能模式，可能由糖代谢转向脂代谢，秀珍菇也调节了营养物供应。前述冷压型食用菌冷压后差异基因富集于碳水化合物代谢过程、能量代谢、翻译调节、氧化还原酶活性和细胞壁重塑等，保护细胞免受损伤的同时准备形成子实体，这些研究都表明 10 ℃以下低温对于冷压型食用菌的子实体形成是必需的。

阿魏菇(*Pleurotus ferulae*)在 10 ℃冷压处理后漆酶活力明显提高，漆酶酶谱也发生变化，出现一条 33 kDa 的新酶带[105]。秀珍菇成熟菌丝胞外羧甲基纤维素酶、滤纸纤维素酶、半纤维素酶和淀粉酶活性与对照相比都随温度下降而增强，胞外漆酶活性则随温度下降而降低[106]。此结果表明冷压处理后秀珍菇酶谱和酶的活性都发生了变化，从利用木质素转为利用纤维素的酶谱转变。β-1,6-葡聚糖合成酶在细胞壁交联中具有重要作用，过表达 β-1,6-葡聚糖合成酶基因 *FFGS6* 能增加金针菇菌丝细胞宽度，提高搔菌后机械损伤恢复能力，但原基和子实体形成(8 ℃刺激)受到抑制，β-1,6-葡聚糖合成酶基因在大型真菌子实体发育和逆境反应中的作用尚不清楚[107]。

在金针菇原基阶段疏水蛋白基因显著上调[64]，并且基因有阶段表达的特性[68]。Northern blotting 结果显示金针菇疏水蛋白基因 *Fv-hyd1* 在菌丝中未表达，在原基和子实体(8 ℃刺激)中表达较高[108]。沉默疏水蛋白基因 *Hyd9* 能导致金针菇(10 ℃刺激)原基和子实体减少，高表达能增加气生菌丝有助于原基形成，这表明 *Hdy9* 在金针菇菌丝扭结时具有重要作用[61]。疏水蛋白在菌丝聚集时上调表达[109]，对疏水蛋白家族基因进行验证将有助于更深入地理解疏水蛋白的功能以及原基形成的机制。

本研究总结了子实体形成过程中差异基因的主要功能和富集通路，以及两种低温刺激类型的不同之处(图 2)。该模型突出 GPCRs、HOG-MAPK、cAMP/PKA 等信号转导在子实体形成过程中的调控作用，还提示了随着温度的下降功能模式从糖代谢到脂代谢的转换。

4 讨论与结论

工厂化栽培低温结实菌类能源消耗巨大，从分子层面研究不同类型的食用菌低温应答机理有助于培育广温型食用菌，对食用菌低碳高效栽培具有重大意义。温度是影响食用菌子实体分化发育的关键因素，大部分食用菌菌丝营养生长阶段的最适温度相近，而子实体生殖生长阶段的温度则有较大差距。因此，本文将低温结实类型进一步分为低温型(11−19 ℃)和冷压型(≤10 ℃)，结合子实体发育保守基因综述了它们受低温胁迫后的应答机制。

信号转导在两种温型的食用菌中暂未发现差异，G 蛋白、Ca^{2+}、cAMP/PKA、HOG-MAPK 等信号途径均有积极调控作用。冷压型食用菌会降低膜的流动性从而限制细胞生长。真菌通过增加膜脂中不饱和脂肪链的比例来保持低温下的膜流动性[110]，温度下降时细胞周期蛋白依赖性激酶连接了不同脂质合成途径，平衡各种

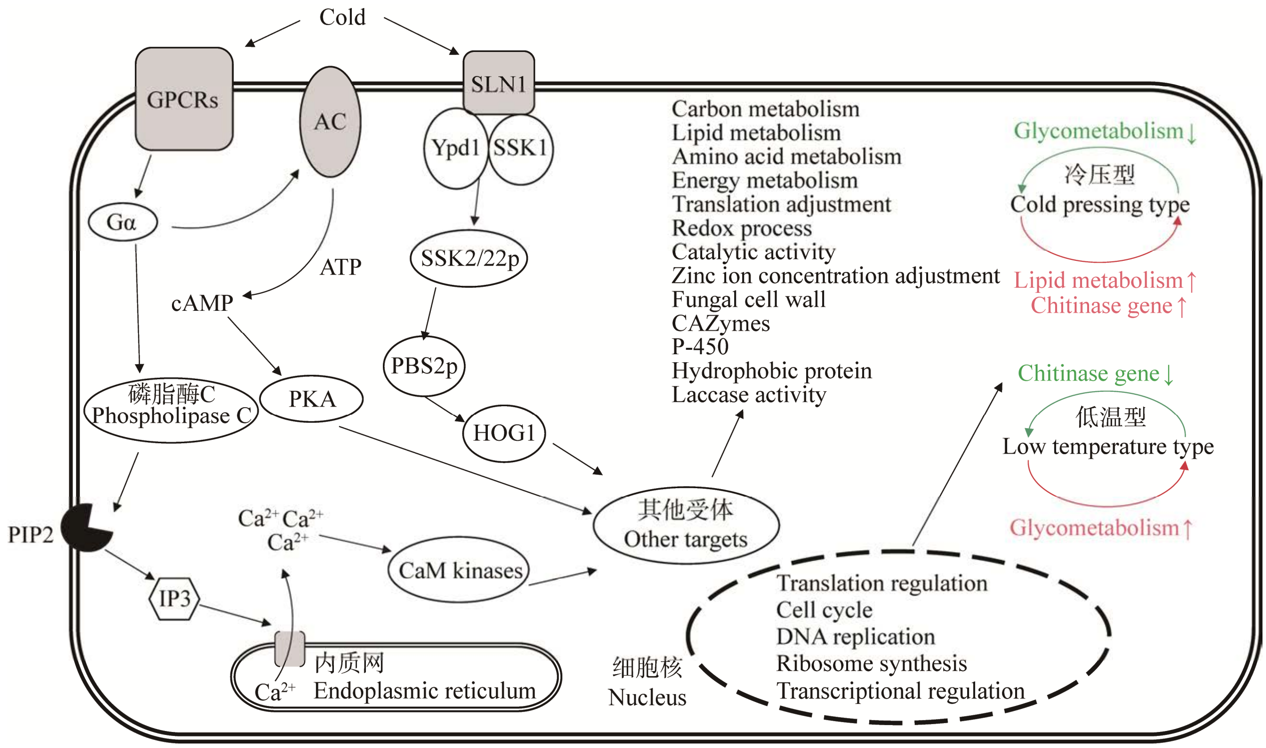

图 2　子实体形成过程中差异基因的主要功能和富集通路

Figure 2　Main functions and enrichment pathways of differential genes during fruiting body formation.

脂质丰度，是维持脂质稳定的核心调节因子[83]，这暗示了冷压刺激更多地影响了细胞膜的脂质结构，但细胞如何感知膜流动性改变，以及不同脂质丰度还需进一步研究[77]。

子实体发育调节中不同温型刺激下的金针菇能量利用存在明显的差异。金针菇 10 ℃冷压刺激时大部分糖酵解相关基因和几丁质酶基因下调，供能方式转向脂代谢；而在 15 ℃低温刺激下，糖酵解相关酶基因上调参与能量代谢[13,102]，这种由于冷压刺激带来的糖代谢转向脂代谢表达的模式是否是食用菌一般的调控模式，以及其在子实体形成中的作用仍需进一步探究。漆酶在两种温型食用菌子实体发育时均有重要作用(如金针菇、真姬菇、阿魏菇等)[111]，而秀珍菇漆酶活性随温度下降，各种纤维素酶活性增强，低温和冷压刺激下秀珍菇发生了酶谱转变，摄取的营养物变化与其子实体形成的关系有待进一步探究。

有研究显示锌离子浓度和酵母胁迫耐性有关，胞内有机锌可促进酵母菌体生长[112]，外源添加锌离子有利于细胞能量代谢和膜稳定，提高抗应激能力[113-114]。低温型香菇和冷压型金针菇 *pria* 基因在原基和幼子实体中高表达，此基因可显著降低锌离子积累，参与调控子实体发育[115]，而在其他中高温型食用菌如蜜环菌、虎皮香菇(*Lentinus tigrinus*)、灰盖鬼伞、裂褶菌中表达较低[64]。这表明 *pria* 基因调节锌离子浓度与不同温型的食用菌子实体形成变化趋势关联性不大，这种调节模式机理在子实体早期发育中仍然未知。

生物体是一个基因、蛋白、信号传递的综合体，由一条调控途径可以发掘出更多的调控网

络。探究食用菌在冷刺激后的胁迫响应有助于更好地理解食用菌子实体形成的分子机制。未来可根据多组学数据对冷胁迫相关基因进行功能验证，进而进行培育广温型食用菌的遗传工程改造，助力于食用菌高效栽培和低碳经济的发展。

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