·生态学专栏·
DOI:10.16605/j.cnki.1007-7847.2023.07.0173

# 向川安瘿蜂寄生白栎虫瘿和成瘿枝的代谢组比较

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**摘 要**: 虫瘿是植物受致瘿昆虫产卵和取食等刺激而异常生长形成的不正常组织。营养假说认为虫瘿组织营养物质的含量高于寄主植物的成瘿部位, 而次生代谢产物的含量低于寄主植物的成瘿部位。向川安瘿蜂(*Andricus mukaigawae*)属膜翅目(Hymenoptera)瘿蜂科(Cynipidae), 在白栎(*Quercus fabri*)枝条上形成虫瘿。本文基于非靶向代谢组, 使用高效液相色谱 - 质谱检测、鉴定和比较向川安瘿蜂幼虫期虫瘿与寄主植物成瘿枝的代谢物。研究结果表明, 向川安瘿蜂虫瘿和成瘿枝的代谢物组成存在差异; 虫瘿的脂肪含量均高于成瘿枝, 虫瘿的 4 种单宁和 4 种黄酮物质的含量均低于成瘿枝, 这支持营养假说; 虫瘿的氨基酸含量均低于成瘿枝, 部分酚类物质的含量高于成瘿枝, 这不支持营养假说。

**关键词**: 向川安瘿蜂; 虫瘿; 非靶向代谢组; 营养假说
**中图分类号**: Q948 **文献标志码**: A **文章编号**: 1007-7847(2024)01-0048-08

# Comparison of Metabolome of *Quercus fabri* Twigs and Associated Galls Induced by *Andricus mukaigawae*

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**Abstract:** Galls are the abnormal tissues formed by the abnormal growth of plants stimulated by the oviposition and feeding of gall insects. The nutritional hypothesis suggests that the content of nutrients in gall tissues is higher than that in the gall forming parts of the host plants, while the content of secondary metabolites is lower than that in the gall forming parts of host plants. *Andricus mukaigawae* belongs to the family Cynipidae of the order Hymenoptera. It forms galls on the branches of white oak (*Quercus fabri*). Herein, based on the non-targeted metabolome, metabolites in galls and host plants at the larval stage of *A. mukaigawae* were detected, identified and compared using high-performance liquid chromatography-mass spectrometry (HPLC-MS). The results showed that there were differences in metabolite composition between the galls and the galled branches. Lipid content of the galls was higher than that of the galled branches, and the contents of four kinds of tannins and four kinds of flavonoids of the galls were lower than those of the galled branches, which supported the nutrient hypothesis. However, the amino acid content of the galls was lower than that of the galled branches, and the content of some phenolics was higher than that of the galled branches, which did not support the nutrient hypothesis.

**Key words:** *Andricus mukaigawae*; gall; non-targeted metabolome; trophic hypothesis
(*Life Science Research*, 2024, 28(1): 048-055)

虫瘿是植物响应致瘿昆虫产卵和取食等刺激而异常生长形成的非正常组织[1]。致瘿昆虫的主要类群包括瘿蚊、瘿蜂、瘿蚜、叶蜂、木虱和蓟马等[2]。瘿蜂(膜翅目: 瘿蜂科)为致瘿昆虫第二大类群, 其

**收稿日期**: 2023-07-04; **修回日期**: 2023-09-20; **网络首发日期**: 2023-11-01
**基金项目**: 国家重点研发计划项目(2018YFE0127100)
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幼虫生活于虫瘿的虫室内, 以虫瘿为食, 而成虫一般不取食, 在合适时机于虫瘿咬破一个羽化口而逃离虫瘿[3–4]。向川安瘿蜂(*Andricus mukaigawae*)营一化性两性生殖, 于白栎(*Quercus fabri*)枝条上形成虫瘿, 其幼虫期为 7—10 月[5]。虫瘿为致瘿昆虫提供了躲避天敌的避难所、适宜生存的小环境和丰富的食物, 其化学物质的组成和寄主植物存在差异[6]。

营养假说认为, 虫瘿营养物质的含量高于寄主植物, 而次生代谢产物的含量低于寄主植物, 这为致瘿昆虫提供了丰富的食物[7]。研究表明, 瘿蜂[8–9]、瘿蚜[10–12]和瘿蚊[13–15]等虫瘿的游离氨基酸总量、总糖和总脂的含量高于寄主植物, 这支持营养假说。虫瘿表面积累大量的次生代谢物质, 主要类型包括酚类、萜类和生物碱等。例如, 五倍子积累大量鞣酸, 没食子积累大量没食子酸, 枸杞瘿螨虫瘿叶片积累大量黄酮化合物, 这些物质均具有显著的抑菌和抗虫作用, 在医药及化工产业使用广泛[16]。有研究表明, 瘿蜂[8]、瘿蚊[17]、瘿蚜[18]、叶蜂[19]和瘿姬小蜂[20]虫瘿的总酚含量高于寄主植物, 瘿蚜虫瘿的萜类物质[21]与木虱[22]、瘿蚊[23]和蓟马虫瘿[24]的生物碱含量高于寄主植物, 这并不支持营养假说。相关研究使用非靶向代谢组较系统地分析了瘿蚊[25–27]和瘿姬小蜂[28]的虫瘿与寄主植物的代谢物差异以验证营养假说。但目前尚无研究系统分析瘿蜂虫瘿和寄主植物的代谢物差异。

本文首次基于非靶向代谢组, 使用高效液相色谱–质谱检测和鉴定了向川安瘿蜂幼虫期虫瘿和寄主植物成瘿枝的代谢物, 比较了向川安瘿蜂虫瘿和成瘿枝代谢物的差异, 分析了差异代谢物富集的京都基因和基因组数据库(Kyoto Encyclopedia of Genes and Genomes, KEGG)通路, 同时讨论了向川安瘿蜂虫瘿和成瘿枝代谢物整体上存在差异的原因及部分差异代谢物对向川安瘿蜂幼虫潜在的影响。这一研究结果将为向川安瘿蜂虫瘿形成的分子机制提供参考, 并且为工业和食品中重要化合物的开发提供依据。

## 1　材料和方法

### 1.1　样本的采集

白栎上的向川安瘿蜂虫瘿和成瘿枝于 2021 年 9 月采集自湖南省邵阳市雀塘镇(111°34′48″E, 27°19′12″N)。成瘿枝指的是虫瘿着生的枝条。首先用超纯水冲洗样本表面, 然后以液氮速冻样本 30 min, 随后将其置于样本袋以干冰保存带回实验室, 并保存于–78 ℃的超低温冰箱。用尖头镊取出虫瘿内的向川安瘿蜂幼虫。虫瘿和枝条的样本量均为 8 个。

### 1.2　代谢物的提取和检测

样本放置于 Lab–1A–50 冻干机[博医康(北京)仪器有限公司]中真空冷冻干燥 72 h。干燥后, 每个样本取 50 mg 置于 2 mL 离心管中, 利用 Wonbio–96c 型冷冻组织研磨仪(上海万柏生物科技有限公司)研磨(–10 ℃, 30 Hz, 6 min)至粉末状。加入 400 μL 提取液, 使用 SBL–10TD 型超声提取仪(宁波新芝生物科技股份有限公司)在 5 ℃和 40 kHz 下提取代谢产物。提取液是体积比为 4∶1 的甲醇和水, 含 0.02 mg/mL 的内标(L–2–氯苯丙氨酸)。样本在–20 ℃静置 30 min 后, 以 13 000*g*、4 ℃离心 15 min, 吸取上清, 用 0.22 μm 微孔滤膜(Whatman, Maidstone, UK)过滤样品。每个样本的滤液均移取 10 μL 混合以制备质控样本。

滤液保存于进样瓶中, 用于后续的超高效液相色谱–串联质谱(ultra–high performance liquid chromatography–tandem mass spectrometry, UPLC–MS/MS)检测。检测过程中, 每 6 个样本插入 1 个质控样本, 以检测分析的稳定性。使用超高效液相色谱串联傅里叶变换质谱(UHPLC–Q Exactive, 赛默飞公司)检测代谢物。对于每个样本, 2 μL 滤液经 HSS T3 色谱柱(100 mm × 2.1 mm i.d., 1.8 μm; Waters, Milford, USA)分离后进入质谱检测。

色谱条件: 流动相 A 为 95%水+5%乙腈(含 0.1%甲酸), 流动相 B 为 47.5%乙腈+47.5%异丙醇+5%水(含 0.1%甲酸); 流速为 0.40 mL/min; 柱温为 40 ℃。分离梯度: 0~0.1 min, 流动相 B 从 0 线性升至 5%; 0.1~2.0 min, 流动相 B 从 5%线性升至 25%; 2.0~9.0 min, 流动相 B 从 25%线性升至 100%; 9.0~13.0 min, 流动相 B 维持 100%; 13.0~13.1 min, 流动相 B 从 100%线性降至 0; 13.1~16.0 min, 流动相 B 维持 0。质谱条件: 正负离子扫描模式采集样品质谱信号, 扫描范围为70~1 050 m/z; 采用离子喷雾电压, 正离子电压 3 500 V, 负离子电压 2 800 V; 离子源加热温度 400 ℃。$MS^1$ 和 $MS^2$ 的分辨率分别为 70 000 和 17 500。

代谢组的检测和鉴定由上海美吉生物医药科技有限公司完成。代谢物的原始数据已提交 MetaboLights 数据库, 编号为 MTBLS4633。

### 1.3 代谢物的鉴定和统计分析

使用软件Progenesis QI 1.0版(Waters, Milford, USA)对代谢物数据进行基线过滤、保留时间校正、峰识别和对齐, 得到含保留时间、质荷比和峰强度等的原始数据矩阵。将代谢物的一级、二级质谱信息与代谢数据库HMDB (Human Metabolome Database; https://hmdb.ca/, 2023-07-04)和Metlin (https://metlin.scripps.edu/, 2023-07-04)进行匹配, 并鉴定代谢物。在原始矩阵中, 移除在质控样本中峰强度的相对标准偏差(标准差/均值)>30%的代谢物, 然后对其余代谢物峰强度进行总和归一化和 $\log_{10}$ 对数化处理, 得到预处理的数据矩阵。基于预处理的数据矩阵, 使用R语言进行后续的统计分析。

本文统计了向川安瘿蜂虫瘿和成瘿枝各代谢物的峰强度的均值及差异倍数(fold change, FC)。差异倍数指的是向川安瘿蜂虫瘿和成瘿枝代谢物的峰强度均值的比值。使用Wilcoxon秩和检验分析向川安瘿蜂虫瘿和成瘿枝各代谢物的峰强度是否存在显著差异, 并通过fdrtool函数(fdrtool包)校正 $P$ 值。另外, 使用opls函数(ropls包)计算向川安瘿蜂虫瘿和成瘿枝各代谢物的相对变量权重值(variable important in projection, VIP), 并进行偏最小二乘判别分析(partial least squares discriminant analysis, PLS-DA)。PLS-DA分析中, 置换检验的次数为200, 参数 $R^2$ 和 $Q^2$ 分别表示拟合效果和预测能力, 用于评价PLS-DA分析的可靠性。$R^2X$ 和 $R^2Y$ 分别表示OPLS-DA所建模型能够解释X和Y矩阵信息的百分比。

根据以下标准筛选向川安瘿蜂虫瘿和成瘿枝的差异代谢物: VIP>1, $P<0.05$。将经HMDB和Metlin数据库鉴定的差异代谢物注释到KEGG数据库的代谢通路, 并使用enrichKEGG函数(clusterProfiler包)进行差异代谢物的KEGG代谢通路富集分析, 使用Benjamini法校正 $P$ 值。富集率指的是本研究在该代谢通路的差异代谢物数量与背景代谢集在该通路的全部代谢物数量的比值。

## 2 结果

### 2.1 向川安瘿蜂虫瘿和成瘿枝代谢物的分类

本研究共检出向川安瘿蜂虫瘿和成瘿枝代谢物16 435种, 其中, Metlin和HMDB数据库分别鉴定679和1 471种, 共1 854种。根据HMDB数据库的化合物分类标准, 向川安瘿蜂虫瘿与成瘿枝的脂质和类脂分子(lipids and lipid-like molecules)、苯丙类和聚酮类(phenylpropanoids and polyketides)以及含氧有机化合物(organic oxygen compounds)类代谢物数量较多, 分别为664、235和173种, 占HMDB数据库已鉴定代谢物总数的比例依次为45.14%、15.98%和11.76% (表1)。

### 2.2 向川安瘿蜂虫瘿和成瘿枝代谢物组成的整体比较

PLS-DA分析表明, 向川安瘿蜂虫瘿和成瘿枝代谢物在整体上明显不同, 其中第一和第二主

**表1 HMDB数据库所鉴定代谢物的分类、数量和相对丰度**

**Table 1 The classification, number and relative abundance of total and differential metabolites identified by HMDB**

| Metabolite classification | Number (relative abundance)$^A$ | Number (relative abundance)$^B$ |
|---|---|---|
| Lipids and lipid-like molecules | 664 (45.14%) | 171 (40.43%) |
| Phenylpropanoids and polyketides | 235 (15.98%) | 86 (20.33%) |
| Organic oxygen compounds | 173 (11.76%) | 45 (10.64%) |
| Organoheterocyclic compounds | 162 (11.01%) | 45 (10.64%) |
| Benzenoids | 98 (6.66%) | 35 (8.27%) |
| Organic acids and derivatives | 96 (6.53%) | 31 (7.33%) |
| Nucleosides, nucleotides and analogues | 16 (1.09%) | 5 (1.18%) |
| Lignans and neolignans | 12 (0.82%) | 3 (0.71%) |
| Organic nitrogen compounds | 8 (0.54%) | 1 (0.24%) |
| Alkaloids and derivatives | 4 (0.27%) | 1 (0.24%) |
| Hydrocarbons | 2 (0.14%) | 0 |
| Organosulfur compounds | 1 (0.07%) | 0 |
| Total | 1 471 (100.00%) | 423 (100.00%) |

注: $^A$ 为人类代谢组数据库(HMDB)鉴定的总代谢物的数量和相对丰度; $^B$ 为人类代谢组数据库(HMDB)鉴定的差异代谢物的数量和相对丰度。

Notes: $^A$ refers to the number and relative abundance of total metabolites identified by HMDB. $^B$ refers to the number and relative abundance of differential metabolites identified by HMDB.

成分分别能解释变异的 71.90%和 9.17% ($R^2X$=0.81, $R^2Y$=0.99, $Q^2$=0.97) (图 1)。

### 2.3　向川安瘿蜂虫瘿和成瘿枝的差异代谢物及其富集的 KEGG 代谢通路

向川安瘿蜂虫瘿和成瘿枝的差异代谢物共检出 6 647 种。其中, Metlin 和 HMDB 数据库分别鉴定差异代谢物 239 和 423 种, 共 508 种。根据 HMDB 数据库的化合物分类标准, 在向川安瘿蜂虫瘿和成瘿枝的差异代谢物中, 脂质和类脂分子、苯丙类和聚酮类以及含氧有机化合物类代谢物数量较多, 分别为 171、86 和 45 种, 其相对丰度分别为 40.43%、20.33%和 10.64% (表 1)。向川安瘿蜂虫瘿的 isomarasmone、benzenepropanedioate 和反式玉米素核糖苷(*trans*-zeatin riboside)的相对含量较成瘿枝的高且差异倍数较大(图 1), 其差异倍数的对数值分别为 3.473 087、1.900 577 和 1.858 436。

在 Metlin 和 HMDB 数据库鉴定的差异代谢物中, 共 125 种存在于 KEGG 数据库的 45 条代谢通路。KEGG 代谢通路的富集分析表明, 向川安瘿蜂虫瘿和成瘿枝的差异代谢物在黄酮合成(flavonoid biosynthesis)、类黄酮合成(isoflavonoid biosynthesis)和色氨酸代谢(tryptophan metabolism)通路的富集率较高, 分别为 0.150、0.140 和 0.108 (图 2)。黄酮合成、类黄酮合成和色氨酸代谢分别具差异代谢物 9、7 和 9 个。在黄酮合成和类黄酮合成通路中, 柚皮素(naringenin)、香橙素(dihydrokaempferol)、三羟基异黄酮(genistein)、刺芒柄花素(formononetin)、美迪紫檀素(medicarpin)、黄豆黄素(glycitein)在向川安瘿蜂虫瘿中的相对含量高于成瘿枝(图 2)。另外, 色氨酸代谢通路的 L-犬尿氨酸(L-kynurenine)、氨基粘康酸半醛(aminomuconic acid semialdehyde)、黄尿酸(xanthurenic acid)、methyl-

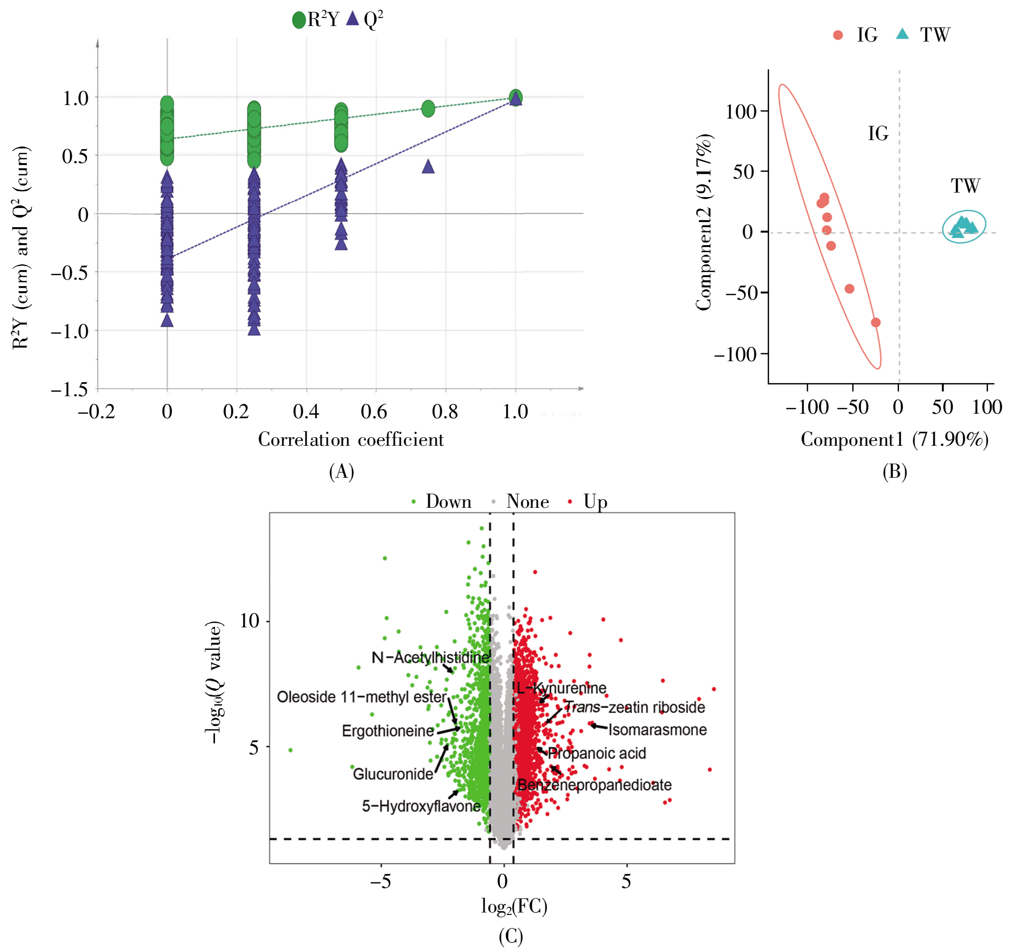


**图 1　向川安瘿蜂虫瘿和成瘿枝的 OPLS-DA 置换检验图、得分图和火山图**

(A) 向川安瘿蜂虫瘿和成瘿枝的 OPLS-DA 模型验证图; (B) 向川安瘿蜂虫瘿(IG)和成瘿枝(TW)的 OPLS-DA 图; (C) 向川安瘿蜂虫瘿和成瘿枝代谢物的火山图。

**Fig.1　Volcano and OPLS-DA plot of metabolites in host twigs and insect galls of *A. mukaigawae***

(A) OPLS-DA model verification diagram of host twigs and insect galls of *A. mukaigawae*; (B) OPLS-DA map of host twigs (TW) and insect galls (IG) of *A. mukaigawae*; (C) Volcanic maps of the metabolites in host twigs and insect galls of *A. mukaigawae*.

indolepyruvate、formamino–benzoylacetate 和吲哚–3–乙醛(indole–3–acetaldehyde)在向川安瘿蜂虫瘿中的相对含量亦高于成瘿枝(图 2)。

### 2.4 向川安瘿蜂虫瘿和成瘿枝的主要差异营养物质与次生代谢产物

向川安瘿蜂虫瘿和成瘿枝的主要差异营养物质与次生代谢产物共 26 种(表 2)。其中, 虫瘿的 *N*–乙酰–L–组氨酸(*N*–acetylhistidine)和色氨酰赖氨酸(tryptophyl–lysine)含量均低于成瘿枝; 虫瘿的 4 种单宁和 4 种黄酮物质的含量均低于成瘿枝, 而部分酚类物质的含量高于成瘿枝(表 2)。

## 3 讨论

### 3.1 向川安瘿蜂虫瘿和成瘿枝代谢物组成的整体差异

向川安瘿蜂虫瘿和成瘿枝的代谢物组成在整体上存在差异, 这同瘿蚊[25–27]和瘿姬小蜂[28]虫瘿与寄主植物代谢物组成的研究一致。我们认为, 向川安瘿蜂虫瘿和成瘿枝代谢物组成的整体差异可能与瘿蜂虫瘿和寄主植物基因表达的差异及虫瘿部分营养物质的来源有关。虫瘿的部分营养物质来源于寄主植物。研究表明, 还原性糖、总可溶性糖和淀粉等营养物质可从寄主植物未成瘿部位转移到小麦瘿蚊虫瘿内[29]; 瘿绵蚜虫瘿的营养物质源于未成瘿叶片[30]。我们推测白栎其他部位的光合作用产物可能通过维管组织运输到向川安瘿蜂虫瘿。

虫瘿和寄主植物基因表达的差异可能影响相应代谢物的组成。近期, 转录组的研究表明约 20%基因的表达在瘿蜂虫瘿和寄主植物间存在差异[31]。瘿蜂虫瘿的苯丙氨酸解氨酶基因的表达高于寄主植物[32–33], 苯丙氨酸解氨酶基因的表达影响酚类物质的合成, 而瘿蜂虫瘿多酚[8]的相对含量亦高于寄主植物。另外, 在瘿蜂虫瘿中, 共 16 个与氨基酸合成相关的基因高表达于寄主植物[31], 而瘿蜂虫瘿的游离氨基酸含量亦高于寄主植物[9]。因此, 我们认为, 向川安瘿蜂虫瘿大量基因的表达可能和成瘿枝存在差异, 从而影响许多代谢物的组成和含量, 进而影响代谢物的整体差异。

### 3.2 玉米素核糖苷和色氨酸代谢通路的吲哚–3–乙醛

在虫瘿的生长期, 虫瘿的快速发育与高含量

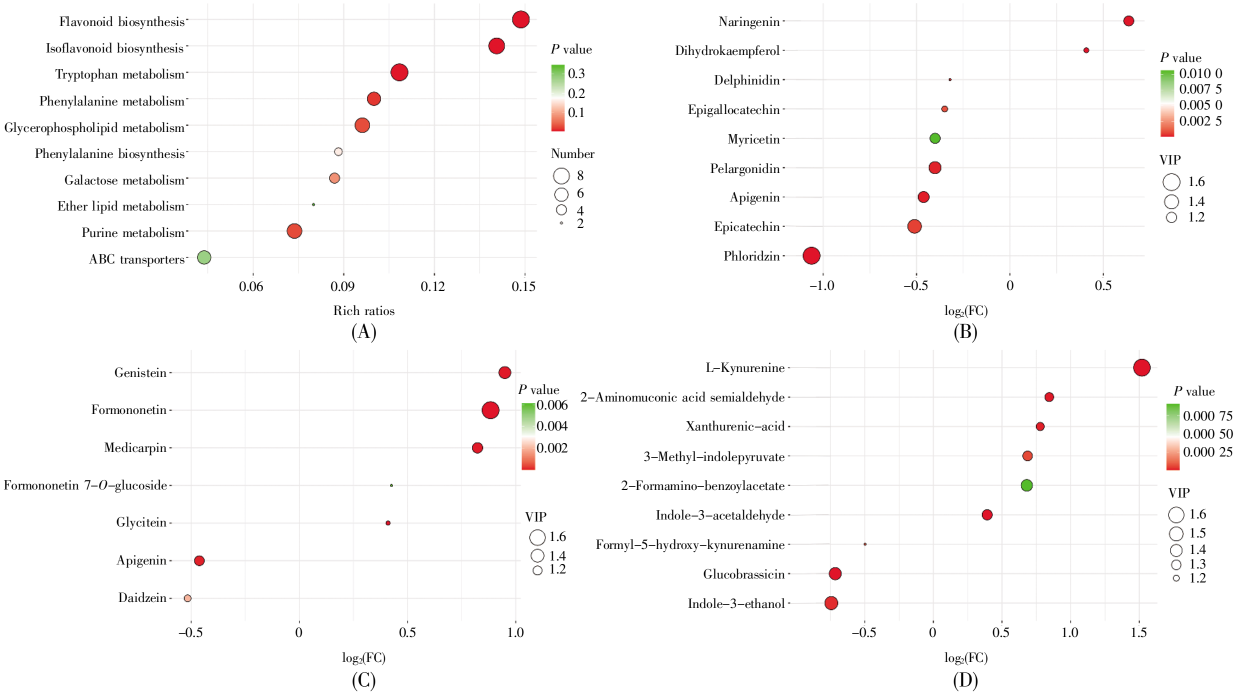


**图 2 向川安瘿蜂虫瘿和成瘿枝差异代谢物富集的 KEGG 代谢通路**

(A) 向川安瘿蜂虫瘿和成瘿枝差异代谢物富集的 KEGG 代谢通路(前 10 条); (B) 黄酮合成通路的差异代谢物; (C) 类黄酮合成通路的差异代谢物; (D) 色氨酸代谢通路的差异代谢物。

**Fig.2 KEGG metabolic pathways of differential metabolites in host twigs and insect galls of *A. mukaigawae***

(A) KEGG metabolic pathways with differentially enriched metabolites in host twigs and insect galls of *A. mukaigawae* (top 10); (B) Differential metabolites of flavonoid biosynthesis pathway; (C) Differential metabolites of isoflavonoid biosynthesis pathway; (D) Differential metabolites of tryptophan metabolism pathway.

表 2　向川安瘿蜂虫瘿和成瘿枝的主要差异营养物质与次生代谢产物

Table 2　Main differential nutrients and secondary metabolites of *A. mukaigawae* galls and gall-forming twigs

| Compound name | Category | Comparison of content* |
|---|---|---|
| **Amino acid and peptides** | | |
| *N*-Acetylhistidine | Amino acid analogues | Decrease |
| Tryptophyl-lysine | Peptide analogues | Decrease |
| **Lipids and lipid molecules** | | |
| Glucosylsphingosine | Glyceryl phosphatide | Increase |
| Mupirocin | Lipid acid | Increase |
| **Terpene** | | |
| Soyasapogenol B 3-*O*-b-D-glucuronide | Monoterpene | Decrease |
| Hydroxytanshinone | Diterpene | Increase |
| Mabioside D | Triterpene | Decrease |
| Notoginsenoside T2 | Triterpene | Increase |
| Glycinoeclepin B | Sesquiterpenes | Increase |
| Momordicoside L | Steroid | Increase |
| Corchoroside A | Steroid | Decrease |
| **Phenols** | | |
| Phloridzin | Flavonoid | Decrease |
| 5-Hydroxyflavone | Flavonoid | Decrease |
| 2′-Hydroxyisoorientin | Flavonoid | Decrease |
| Eriodictyol 7-(6-galloylglucoside) | Flavonoid | Decrease |
| Ptelatoside B | Phenolic glycosides | Decrease |
| Aloesol 7-glucoside | Phenolic glycosides | Decrease |
| Divanillyltetrahydrofuran ferulate | Furan | Increase |
| Isomarasmone | Furan | Increase |
| Biflorin | Naphthoquinones | Increase |
| 4-Hydroxy-benzenepropanedioate | Phenol ester | Increase |
| **Tetracarboxylic acid and its derivatives** | | |
| Sandoricin | Tetracarboxylic acid and its derivatives | Decrease |
| **Tannin** | | |
| Gallic acid 3-*O*-(6-galloylglucoside) | Hydrolyzable tannins | Decrease |
| Sanguiin H4 | Hydrolyzable tannins | Decrease |
| Vescalagin | Hydrolyzable tannins | Decrease |
| Acutissimin A | Complex tannins | Decrease |

注: * 表示与成瘿枝相比, 向川安瘿蜂虫瘿中化合物含量的变化。

Note: * indicates the changes of compound contents in *A. mukaigawae*'s galls compared with the gall-forming branches.

的生长素和细胞分裂素相关。有研究报道, 向川安瘿蜂[34]、瘿蚊[35]、瘿蚜[36]、实蝇[37]、木虱[38]、叶蝉[39]、叶蜂[40]和麦蛾[41]等虫瘿的生长素和细胞分裂素含量高于寄主植物。在本研究中, 色氨酸代谢通路的吲哚-3-乙醛是植物生长素吲哚乙酸的前体, 而玉米素核糖苷是细胞分裂素玉米素的衍生物[42-43]。由于吲哚-3-乙醛可通过吲哚乙醛氧化酶转化为吲哚乙酸, 而玉米素核糖苷亦能转化为玉米素。我们认为, 向川安瘿蜂虫瘿高含量的吲哚-3-乙醛和玉米素核糖苷可能转化为高含量的吲哚乙酸和玉米素, 导致虫瘿快速发育。

### 3.3　向川安瘿蜂虫瘿和成瘿枝的部分营养物质与次生代谢产物的差异

虫瘿为许多致瘿昆虫提供了食物来源, 其糖、脂及氨基酸等营养物质的组成和含量均与寄主植物不同。我们的研究表明, 向川安瘿蜂虫瘿的脂类含量高于寄主植物。前期的相关研究已证实, 叶蜂[8]、瘿蚜[13]和瘿蚊[44]等虫瘿的总脂含量高于寄主植物。我们的研究和前人的研究一致, 支持营养假说。因此我们认为, 向川安瘿蜂虫瘿的营养物质含量高于成瘿枝, 可为向川安瘿蜂幼虫的生长发育提供丰富的营养。

单宁和黄酮为植物次生代谢产物[32], 参与植物对植食性昆虫的防御, 在植物-昆虫互作中具有重要作用[45-46]。单宁和黄酮均能抑制植食性昆虫的消化酶、乙酰胆碱酯酶和谷胱甘肽转移酶的活性, 影响植食性昆虫的生长, 甚至导致植食性昆虫的死亡[47-48]。另外, 单宁的功能性高分子材料具有独特的性质, 能够在溶液中有效地浓缩、分离, 具有去除蛋白质、生物碱和重金属盐等作用, 因而在生化、食品、医药和化工等行业有着广泛的应用前景[49]。我们的研究表明, 向川安瘿蜂虫瘿的单宁和

黄酮物质的含量低于成瘿枝。而前人的研究也表明, 叶蜂[19]、瘿蜂[50]和栗瘿蜂[51]虫瘿组织的单宁含量低于寄主植物, 这与我们的研究结果一致, 说明虫瘿中较低含量的单宁和黄酮有利于向川安瘿蜂幼虫的生长及发育。

总的来讲, 本文首次使用非靶向代谢组检测和鉴定了向川安瘿蜂幼虫期虫瘿与寄主植物成瘿枝的化学物质, 比较分析了向川安瘿蜂虫瘿和成瘿枝代谢物的差异。结果显示: 虫瘿的总脂含量均高于成瘿枝, 单宁和黄酮的含量均低于成瘿枝, 支持营养假说; 而虫瘿的氨基酸含量均低于成瘿枝, 部分酚类物质的含量高于成瘿枝, 不支持营养假说。这表明致瘿昆虫和寄主植物之间存在复杂的相互作用, 并不是差异代谢物的含量单一地上调或者下调。

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