

基于转录组测序解析麦红吸浆虫对小麦 防御物质解毒代谢的分子机制



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摘要: 为筛选麦红吸浆虫 *Sitodiplosis mosellana* 参与解毒代谢小麦防御性次生物质的关键基因, 以分别取食阿魏酸等次生物质含量差异显著的高抗小麦品种晋麦47和高感小麦品种西农822的麦红吸浆虫幼虫为材料, 采用BGISEQ-500高通量测序平台对其进行转录组测序, 分析差异表达基因并对其进行GO分类和KEGG通路富集分析, 筛选在麦红吸浆虫解毒代谢中起关键作用的相关基因; 采用实时荧光定量PCR技术对部分差异表达基因的表达水平进行验证。结果显示: 取食两个小麦品种的麦红吸浆虫幼虫转录组共获得42 505条 unigene, 其中差异表达基因3 566个, 2 188个在取食抗虫小麦的麦红吸浆虫幼虫中显著上调, 大多数基因参与细胞进程和代谢进程, 具有结合、催化和转运蛋白酶的活性, 在有毒物质降解与代谢途径显著富集。在取食抗虫小麦的麦红吸浆虫幼虫中共筛选到26个显著上调的解毒酶基因, 其中6个谷胱甘肽-S-转移酶 (glutathione S-transferase, GST)、7个细胞色素P450酶系 (cytochrome P450, CYP450)、4个尿苷二磷酸糖基转移酶 (UDP-glycosyl transferase, UGT) 和9个ATP结合盒 (ATP-binding cassette, ABC) 转运蛋白基因。随机选取的13个差异表达解毒酶基因的实时荧光定量PCR结果的表达趋势与转录组测序结果基本一致。表明筛选获得的GST、CYP450、UGT和ABC转运蛋白基因可能在麦红吸浆虫对小麦防御性次生物质的解毒代谢和适应抗性寄主防御中起着重要作用。

关键词: 麦红吸浆虫; 植物次生物质; 转录组; 解毒代谢; 防御相关基因

Transcriptome analysis reveals the molecular mechanisms of detoxification metabolism of red wheat blossom midge *Sitodiplosis mosellana* in response to wheat defensive compounds

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Abstract: To identify key genes involved in the detoxification metabolism of wheat defensive secondary metabolites in red wheat blossom midge *Sitodiplosis mosellana*, larvae feeding on a highly resistant wheat cultivar Jinmai 47 and a highly susceptible wheat cultivar (Xinong 822), which differ significantly in the contents of defensive secondary compounds (e.g. ferulic acid), were subjected to comparative transcriptome sequencing using the BGISEQ 500 platform. Differentially expressed genes (DEGs) were identified and analyzed by Gene Ontology classification and Kyoto Encyclopedia of Genes and Genomes pathway enrichment to screen genes potentially involved in detoxification metabolism. In

addition, the expression levels of selected DEGs were validated by real-time quantitative PCR (RT-qPCR). A total of 42 505 unigenes were obtained from the combined transcriptomes, among which 3 566 genes were differentially expressed. Compared with larvae fed on the susceptible wheat cultivar, 2 188 DEGs were significantly upregulated in larvae fed on the resistant cultivar. Most of these genes were associated with cellular and metabolic processes and were enriched in functions related to binding, catalytic activity, and transport, with significant enrichment in pathways involved in the degradation and metabolism of toxic substances. A total of 26 detoxification enzyme genes were significantly upregulated in larvae fed on resistant wheat, including six glutathione *S*-transferases (GSTs), seven cytochrome P450 monooxygenases (CYP450s), four UDP-glycosyltransferases (UGTs) and nine ATP-binding cassette (ABC) transporter genes. RT-qPCR analysis of 13 randomly selected DEGs showed expression patterns largely consistent with the transcriptome sequencing results. These findings suggest that the identified GST, CYP450, UGT, and ABC transporter genes may play pivotal roles in the detoxification metabolism of wheat defensive secondary metabolites and in the adaptation of *S. mosellana* to resistant host plants.

Key words: *Sitodiplosis mosellana*; plant secondary metabolite; transcriptome; detoxification metabolism; defense-related gene

麦红吸浆虫 *Sitodiplosis mosellana* 是北半球小麦生产上最主要的害虫之一 (Shrestha & Reddy, 2019; Li et al., 2023), 成虫于小麦抽穗期盛发并产卵, 幼虫孵化后吸食正在灌浆的小麦籽粒汁液, 造成麦粒瘪瘦、空壳或霉烂, 严重时减产 30%~50%, 甚至颗粒无收 (Wang et al., 2022)。实践证明种植抗虫小麦是控制该害虫的最安全、经济和有效的措施, 然而目前生产上种植的大多数小麦品种不抗麦红吸浆虫 (武予清等, 2013; 郝亚楠等, 2014)。因此探究麦红吸浆虫克服抗性寄主防御的分子机制, 对于促进小麦与麦红吸浆虫互作关系的理解和加速抗虫小麦的培育具有重要意义。

酚类、生物碱等植物次生物质是植食性昆虫化学防御的基础, 在植物抗虫性中发挥着重要作用 (Su et al., 2018; Jahan et al., 2025)。在与植物互作过程中, 植食性昆虫也发展了一套包括细胞色素 P450 酶系 (cytochrome P450, CYP450) (Li et al., 2024)、谷胱甘肽 *S*-转移酶 (glutathione *S*-transferase, GST) (Yang et al., 2017; Chen et al., 2025)、羧酸酯酶 (carboxylesterase, CarE) (Johan et al., 2021)、尿苷二磷酸糖基转移酶 (UDP-glycosyl transferase, UGT) 和 ATP 结合盒 (ATP-binding cassette, ABC) 转运蛋白 (Zhang GJ et al., 2022) 在内的解毒酶系来克服植物次生物质的防御。植食性昆虫对植物次生物质的解毒分为 3 个阶段: 首先由 CYP450 和 CarE (I 相解毒酶) 对其进行初级氧化或水解, 将其转化为更易代谢的中间产物; 随后 GST

和 UGT (II 相解毒酶) 催化 I 相产物与还原型谷胱甘肽或糖分子结合以增加水溶性; 最终 ABC 转运蛋白 (III 相解毒酶) 介导结合产物外排 (李欣莲等, 2022; Wang HD et al., 2024)。近些年, 关于昆虫解毒酶基因参与植物次生物质解毒代谢和寄主适应的研究愈来愈多。例如, 二化螟 *Chilo suppressalis* 在次要寄主茭白 *Zizania latifolia* 上能完成发育, 与取食主要寄主水稻相比, 取食该寄主后其体内 6 个 GST、16 个 P450、13 个 CarE、1 个 UGT 和 1 个 ABC 转运蛋白基因的表达式上调 (Zhong et al., 2017); 柠檬素和槲皮素处理可以诱导柑橘大实蝇 *Bactrocera minax* 体内 ABC 转运蛋白基因表达上调 (Zhang L et al., 2022); *BtGSTs5* 在烟粉虱 *Bemisia tabaci* 对十字花科植物主要次生物芥子油苷的代谢和防御适应中发挥着重要作用 (Halon et al., 2015)。目前国内外关于小麦与麦红吸浆虫的关系也有研究, 例如陈锐等 (2020) 发现灌浆期小麦籽粒中次生物质阿魏酸、单宁含量与小麦对吸浆虫抗性以及麦红吸浆虫幼虫体内 GST 和 CarE 活性显著正相关, 但是在解毒代谢植物次生物质及寄主适应中哪些解毒酶基因起关键作用尚不清楚。

为明确麦红吸浆虫体内在解毒代谢植物次生物质及寄主适应中起关键作用的解毒酶基因, 本文以取食次生物质含量高的抗虫小麦晋麦 47 和感虫小麦西农 822 的麦红吸浆虫幼虫为材料, 通过比较转录组测序分析取食这两个小麦品种的麦红吸浆虫幼虫基因差异表达情况, 挖掘在次生物质解毒代谢中起关键作用的 CYP450、GST、CarE、UGT 及 ABC 转运蛋

白基因,从转录组数据库中随机挑取13个差异表达的解毒酶基因,采用实时荧光定量PCR(real-time quantitative, RT-qPCR)技术对其进行验证,以期为进一步深入研究解毒酶基因在寄主植物适应中的作用及利用关键解毒酶基因沉默技术管理害虫提供参考。

1 材料与方法

1.1 材料

供试小麦品种:晋麦47和西农822种子由西北农林科技大学农学院提供;这两个小麦品种生育期相近,抽穗期(敏感期)与麦红吸浆虫羽化高峰期吻合,其分别对麦红吸浆虫表现高抗和高感,且晋麦47灌浆早期籽粒中阿魏酸、单宁等防御性次生物质含量显著高于西农822(郝亚楠等,2014;高贺等,2016;陈锐等,2020)。

供试昆虫:将两个供试小麦品种在播种适期分别播于陕西省周至县麦红吸浆虫严重发生的田块中,试验地不施用任何农药,小麦在田间自然感虫;待小麦灌浆初期,采集感虫麦穗,剥穗,采集分别取食两个小麦品种的麦红吸浆虫2龄幼虫,2龄幼虫根据虫体大小、颜色和Y型尖骨片有无判断(Gagné & Doane, 1999);将收集的幼虫每40头装于1个2 mL冻存管中,作为1个生物学重复,置于液氮中速冻,于-80 °C中保存备用,每个处理至少重复3次。

试剂和仪器:Trizol试剂、PrimeScript™ RT Reagent Kit with gDNA Eraser反转录试剂盒、SYBR Premix EX Taq™ II实时荧光定量试剂盒,宝生物工程(大连)有限公司。NanoDrop 2000微量分光光度计,赛默飞世尔科技有限公司;Agilent 2100生物分析仪,安捷伦科技有限公司;Gel Doc XR+凝胶成像分析系统、IQ5实时荧光定量PCR仪,美国Bio-Rad公司。

1.2 方法

1.2.1 麦红吸浆虫幼虫RNA的提取与测序

取试虫按照Trizol试剂说明书提取试虫总RNA,使用微量分光光度计、生物分析仪和1.5%琼脂糖凝胶检测其浓度和质量,取 $1.8 < OD_{260nm}/OD_{280nm} < 2.0$ 且RNA完整值 ≥ 7.0 的样品构建cDNA文库。利用BGISEQ-500测序平台对文库进行测序。文库构建和测序委托深圳华大基因科技有限公司进行。每个处理重复3次,每个重复40头试虫。

1.2.2 麦红吸浆虫转录组测序数据组装及功能注释

利用SOAPnuke软件对测序得到的原始数据进行过滤,去除接头序列、低质量和未配对数据,获得高质量的数据,并进行碱基质量分析。利用Trinity

2.15.1软件对clean read进行序列拼接与组装,采用Tgicl 2.1软件进行聚类去冗余后获得最终的unigene库。以 $E < 10^{-5}$ 为阈值,使用BLASTX软件将获得的unigene与NR、Pfam、KEGG、Swiss-Prot、KOG、GO和NT七大数据库进行比对得到功能注释。

为鉴定取食两个小麦品种的麦红吸浆虫转录组之间的差异表达基因,采用Bowtie2 2.5.3软件将6个样本测序得到的clean read与unigene库比对,应用RSEM 1.3.3软件计算各样本对应基因的FPKM (fragments per kilobase of transcript per million fragments mapped)值。应用DESeq2 1.46.0软件对基因表达量进行差异显著性分析,将FPKM值差异倍数(fold change, FC) ≥ 2 或 $FC \leq 0.5$ 且 $P \leq 0.001$ 的基因定义为差异表达基因,计算上调表达与下调表达的基因数量,并对其进行GO功能分类和KEGG通路富集分析。

1.2.3 麦红吸浆虫差异表达解毒酶基因的筛选鉴定

GST、CarE、CYP450、UGT和ABC转运蛋白在昆虫对植物次生物质解毒代谢和寄主适应中发挥着重要作用(Wang ZY et al., 2024; Feng et al., 2025)。因此,基于1.2.2中差异表达基因功能注释结果,本研究重点分析GST、CYP450、CarE、UGT和ABC转运蛋白相关基因的差异表达情况,并通过NCBI BLASTX比对明确基因家族。

1.2.4 差异表达解毒酶基因的RT-qPCR验证

取1.2.1取食两个小麦品种的麦红吸浆虫样品的总RNA,参照PrimeScript™ RT Reagent Kit with gDNA Eraser反转录试剂盒说明书合成cDNA,作为模板。从转录组数据库中随机挑取13个差异表达的解毒酶基因,其中4个GST基因(Unigene5995_All、CL89、Contig4_All、CL1917、Contig4_All和CL501、Contig5_All)、4个ABC转运蛋白基因(CL2975、Contig4_All、CL3984、Contig12_All、CL2725、Contig3_All和CL1344、Contig24_All)、2个CarE基因(CL473、Contig14_All和CL2556、Contig2_All)、2个CYP450基因(Unigene14034_All和Unigene13912_All)和1个UGT基因(CL2808、Contig1_All),通过Primer Premier 6.0软件设计其定量引物(表1)。以麦红吸浆虫GAPDH(GenBank登录号为KR733066)为内参基因,在实时荧光定量PCR仪上,按照SYBR Premix EX Taq™ II试剂盒说明书进行RT-qPCR分析。20 μL PCR反应体系:cDNA模板1.6 μL、10 μmol/L上下游引物各0.8 μL、SYBR Premix EX Taq™ II

10 μL , ddH₂O 补至 20 μL 。PCR 反应程序: 95 $^{\circ}\text{C}$ 预变性 30 s; 95 $^{\circ}\text{C}$ 变性 10 s, 60 $^{\circ}\text{C}$ 退火 30 s, 循环 40 次; 接着进行熔解曲线分析。采用 $2^{-\Delta\Delta\text{CT}}$ 法 (Livak &

Schmittgen, 2001) 计算 13 个解毒酶基因的相对表达量, 将其分别与转录组数据计算的 13 个解毒酶基因的 $\log_2\text{FC}$ 进行比较。

表 1 本研究所用的引物

Table 1 Primers used in this study

基因 ID Gene ID	基因类型 Gene type	上游引物序列(5'-3') Forward primer(5'-3')	下游引物序列(5'-3') Reverse primer(5'-3')
<i>Unigene14034_All</i>	CYP450	GTCATTGCCTCCGTTGC	GCCGCAAGAAGGACATCAG
<i>Unigene13912_All</i>	CYP450	ACGATCTGACCTATATTTGGG	CCATATACTCGGCTCACTGGT
<i>CL473.Contig11_All</i>	CarE	GCCACCAATCAACGATC	CATGACTGGCAGTTTTGTC
<i>CL2556.Contig2_All</i>	CarE	ATGGGAAGGTGAATTTTACGC	CTATCGAACGAATGTGGTGC
<i>Unigene5995_All</i>	GST	CGGCTTGGGATATTCTGGAACG	TTTAGGGTGTGGTGGTGGTCC
<i>CL89.Contig4_All</i>	GST	CTTGACTTGGACCTTGAATC	TAGCAAAGCCATCGGTATC
<i>CL1917.Contig4_All</i>	GST	AACGCGCTCAAGTGGATTCT	ACGATCCTCAGGCATTTCCGG
<i>CL501.Contig9_All</i>	GST	CGACGATGGATTGCTCTTTGG	TCTGGATTTGCTGGAGCTTTGG
<i>CL2808.Contig1_All</i>	UGT	TTGCTGAAGACGGTAATGAAGTGAC	TCCCAGGAATGCTCAAGAAACACT
<i>CL2975.Contig4_All</i>	ABC	GCTGGTGGCATTCACTTTGG	ACGTTTTGAATGACACGCCG
<i>CL3984.Contig12_All</i>	ABC	GCAAGTCTCAGTGGTGGTCA	TGCACTCAAAGGTCGTCAA
<i>CL2725.Contig3_All</i>	ABC	TACGGGGAAAATGTCGGTTCG	CGGTTCCACCAGCCACATAGT
<i>CL1344.Contig24_All</i>	ABC	TGTGCACCAACATCATTAC	GTGACCAAATCGAGCAATG
<i>GAPDH</i>	GADPH	CCATCAAAGCAAGCAAGA	CAGCACGGAGCACAAGAC

1.3 数据分析

应用 SPSS 22.0 软件对试验数据进行统计分析, 采用非配对 t 检验对每个基因表达水平进行差异显著性检验。

2 结果与分析

2.1 麦红吸浆虫幼虫转录组测序和组装结果

分别取食两个小麦品种的麦红吸浆虫幼虫 3 个样本的转录组测序原始数据已上传至国家生物信息中心 GSA 数据库 (登录号为 CRA027809)。原始数

据去除接头和低质量的序列后, 6 个样本的 clean read 数均超过 66.85 Mb, 有效数据 GC 含量均超过 38.00%, Q20 碱基比例均超过 98.00%, Q30 碱基比例不低于 91.00%; 利用 Trinity 和 Tgicl 软件对获得的高质量 read 进行序列组装和去冗余后共得到 42 505 条 unigene, unigene 的平均长度为 1 985 bp, N50 长度为 3 744 bp (表 2)。同时分别取食两个小麦品种的麦红吸浆虫幼虫的 3 个样本间重复性较好, 表明测序数据和组装结果可靠, 可用于进一步分析。

表 2 麦红吸浆虫幼虫转录组数据统计分析和 unigene 组装结果

Table 2 Statistical summary of transcriptome sequencing data and unigene assembly for *Sitodiplosis mosellana* larvae

处理 Treatment	样本 Sample	Clean reads/ Mb	GC/%	Q20/%	Q30/%	unigene 数量 No. of unigenes	unigene 平均长度 Mean unigene length/bp	N50 长度 N50 length/bp
取食晋麦 47 的幼虫 Larvae feeding on Jinmai 47	1	66.85	38.49	98.13	91.83	31 805	1 449	2 771
	2	71.72	38.46	98.09	91.70	33 618	1 448	2 885
	3	69.72	38.44	98.11	91.79	32 265	1 478	2 883
取食西农 822 的幼虫 Larvae feeding on Xinong 822	1	69.68	38.52	98.14	91.92	30 556	1 451	2 728
	2	69.71	38.48	98.03	91.57	31 588	1 517	2 855
	3	67.52	38.58	98.14	91.87	30 458	1 501	2 851
合计 Total		-	-	-	-	42 505	1 985	3 744

Q20: 质量值 ≥ 20 的碱基所占比例; Q30: 质量值 ≥ 30 的碱基所占比例; N50: 不小于总长 50% 的拼接转录本长度。Q20: Proportion of bases with a quality score ≥ 20 ; Q30: proportion of bases with a quality score ≥ 30 ; N50: the length at which the cumulative length of assembled unigenes reaches at least 50% of the total assembly length.

2.2 麦红吸浆虫幼虫差异表达基因功能注释

与取食感虫小麦的麦红吸浆虫幼虫相比, 取食抗虫小麦的麦红吸浆虫幼虫中共检测到 3 566 个差

异表达基因, 其中 2 188 个基因上调表达, 1 378 个基因下调表达 (图 1)。与七大数据库进行比对, 在 3 566 个差异表达基因中 3 102 个被注释, 占比为

86.99%，其中注释到NR数据库的基因数量最多，为2 893个，占比为占81.13%，Pfam、KEGG、Swiss-Prot、KOG、GO和NT数据库注释到的基因数量分别为2 691、2 505、2 487、2 418、1 381和1 273个。

2.3 麦红吸浆虫幼虫差异表达基因GO功能注释

在生物进程类别中，取食抗虫小麦后上调和下调表达的基因富集数量较多的分别为细胞进程、代谢进程、生物调节、生物过程调控和刺激响应；在细胞组分类别中，取食抗虫小麦后上调和下调基因富集数量较多的分别为细胞、细胞组分、膜、膜组分和细胞器；在分子功能类别中，取食抗虫小麦后上调和下调基因富集数量较多的分别为结合活性、催化活性、结构分子活性、转运活性和转运调节活性(图2)。在以上功能条目中，取食抗虫小麦后上调表达的基因数量均超过下调表达基因数量，其中细胞进程、代谢进程、细胞、细胞组分、结合活性和催化活性条目

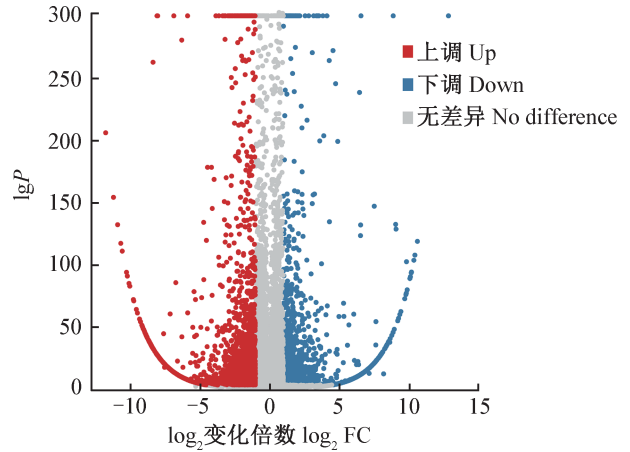


图1 取食抗感小麦的麦红吸浆虫幼虫差异表达基因数量
Fig. 1 Number of differentially expressed genes in *Sitodiplosis mosellana* larvae feeding on resistant and susceptible wheat

中上调基因的数量均超过300个，分别为316、309、306、380和346个(图2)。

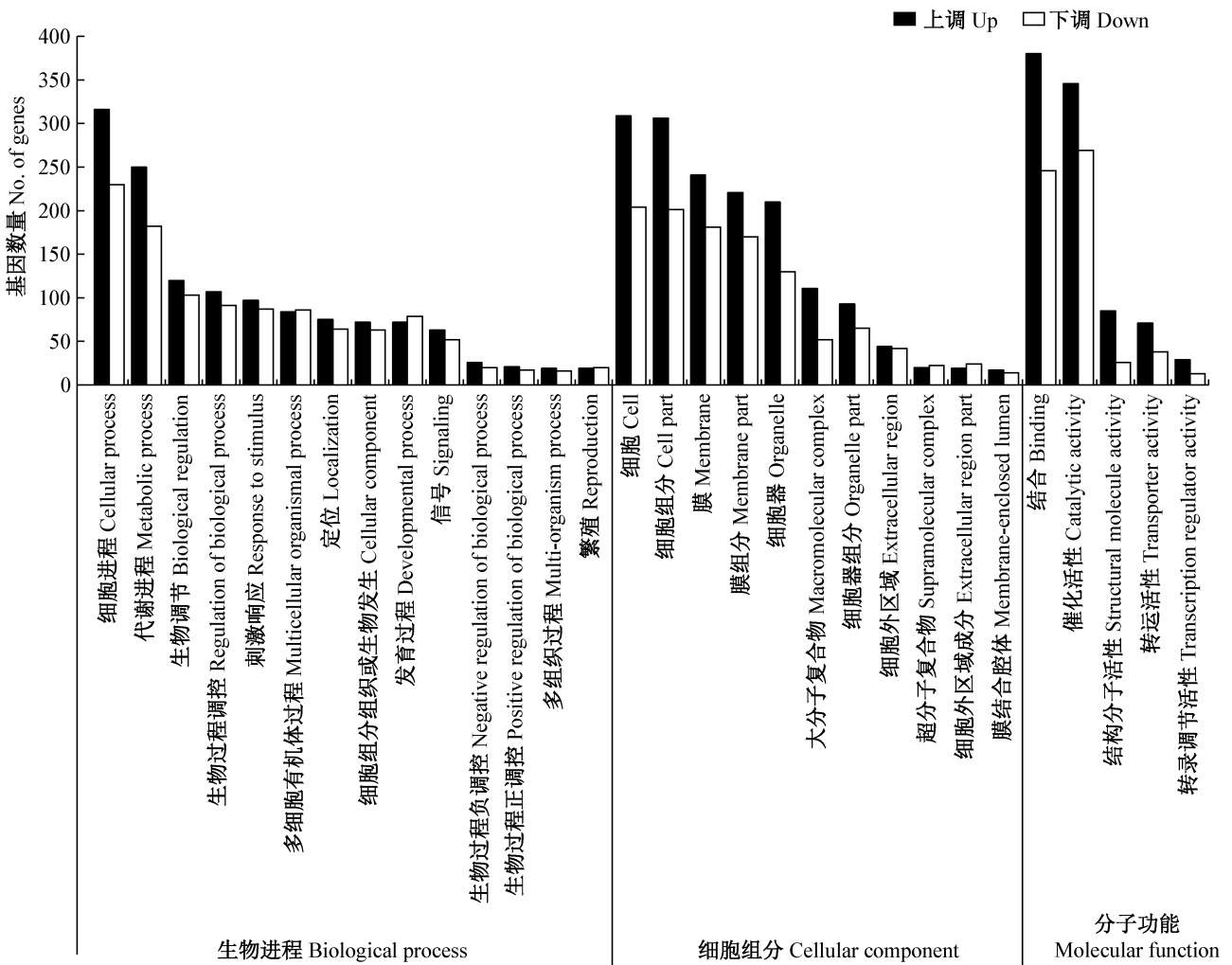


图2 取食抗感小麦的麦红吸浆虫幼虫差异表达基因GO功能注释

Fig. 2 GO functional annotation of differentially expressed genes in *Sitodiplosis mosellana* larvae feeding on resistant and susceptible wheat

麦红吸浆虫幼虫中显著下调,且均属于保幼激素酯酶(juvenile hormone esterase, JHE)(表3)。

表3 取食抗感小麦的麦红吸浆虫幼虫转录组间差异表达的解毒酶基因

Table 3 Differentially expressed detoxification enzymes genes between transcriptomes of *Sitodiplosis mosellana* larvae feeding on resistant and susceptible wheat

分类 Classification	家簇 Clade	转录组 ID Transcriptome ID	log ₂ FC	基因注释信息 Gene annotation	序列相似度 Sequence similarity/%	
细胞色素 P450 CYP450	CYP3	<i>Unigene14034_All</i>	9.093	甘蓝瘦蚊 <i>Contarinia nasturtii</i> probable CYP450 6d5 (XP_031634047.1)	71.54	
		<i>CL3109.Contig3_All</i>	3.152	甘蓝瘦蚊 <i>C. nasturtii</i> probable CYP450 6d5 (XP_031625354.1)	68.50	
		<i>CL1371.Contig1</i>	-1.187	甘蓝瘦蚊 <i>C. nasturtii</i> probable CYP450 9f2 (XP_031624496.1)	76.55	
	CYP4	<i>CL1569.Contig7</i>	-1.364	甘蓝瘦蚊 <i>C. nasturtii</i> probable CYP450 28d1 (XP_031636400.1)	76.27	
		<i>CL3817.Contig2_All</i>	1.029	甘蓝瘦蚊 <i>C. nasturtii</i> CYP450 4C1-like (XP_031639341.1)	86.90	
		<i>CL481.Contig1_All</i>	1.778	甘蓝瘦蚊 <i>C. nasturtii</i> CYP450 4V2-like (XP_031635316.1)	64.27	
		<i>Unigene13912_All</i>	1.813	甘蓝瘦蚊 <i>C. nasturtii</i> CYP450 4V2-like (XP_031635316.1)	79.64	
		<i>Unigene5814_All</i>	-1.893	甘蓝瘦蚊 <i>Bradysia coprophila</i> CYP450 4c3 (XP_037051038.1)	66.36	
		Mito	<i>CL1608.Contig10_All</i>	7.076	甘蓝瘦蚊 <i>C. nasturtii</i> CYP450 12A2-like (XP_031617812.1)	71.88
			<i>CL1095.Contig5_All</i>	-1.825	甘蓝瘦蚊 <i>C. nasturtii</i> CYP450 315a1, mitochondrial (XP_031629833.1)	70.33
羧酸酯酶 CarE	JHE	<i>Unigene14050_All</i>	-1.098	咸水按蚊 <i>Anopheles aquasalis</i> JHE (XP_050088425.1)	50.00	
		<i>CL2556.Contig2_All</i>	-1.051	伪蕈蚊 <i>Pseudolycoriella hygida</i> JHE, partial (KAJ6636804.1)	64.59	
		<i>Unigene740_All</i>	-1.009	印度谷螟 <i>Plodia interpunctella</i> JHE (XP_053602680.1)	32.35	
		<i>CL473.Contig14_All</i>	-2.927	库斯塔尼按蚊 <i>Anopheles coustani</i> JHE-like (XP_058121864.1)	50.52	
谷胱甘肽-S- 转移酶 GST	GSTe	<i>Unigene14206_All</i>	2.640	甘蓝瘦蚊 <i>C. nasturtii</i> GST E10 (NP_611324.1)	62.56	
		<i>Unigene5995_All</i>	1.758	黑腹果蝇 <i>Drosophila melanogaster</i> GSTE12 (NP_001246500.1)	58.45	
		<i>CL89.Contig4_All</i>	1.083	甘蓝瘦蚊 <i>C. nasturtii</i> GSTe15 (QZZ63300.1)	68.42	
	GSTd	<i>CL501.Contig5_All</i>	7.709	甘蓝瘦蚊 <i>C. nasturtii</i> GSTe13 (XP_031625775.1)	93.17	
		<i>Unigene927_All</i>	2.297	毁侧沟茧蜂 <i>Microplitis demolitor</i> GST D1 (XP_008554402.1)	67.44	
		<i>CL1917.Contig4_All</i>	1.937	黑森瘦蚊 <i>Mayetiola destructor</i> delta GST (ABG56084.1)	83.00	
		<i>CL2145.Contig1_All</i>	-1.038	银足白蛉 <i>Phlebotomus argentipes</i> GST delta class (AVD30033.3)	53.70	
尿苷二磷酸 糖基转移酶 UGT	UGT1	<i>CL820.Contig4_All</i>	1.034	甘蓝瘦蚊 <i>C. nasturtii</i> UGT 1-3-like (XP_031639028.1)	68.02	
	UGT2	<i>Unigene13674_All</i>	1.020	甘蓝瘦蚊 <i>C. nasturtii</i> UGT 2B7-like (XP_031638675.1)	65.57	
		<i>Unigene13401_All</i>	1.229	甘蓝瘦蚊 <i>C. nasturtii</i> UGT 2B1-like (XP_031639549.1)	49.81	
	UGT3	<i>CL2808.Contig1_All</i>	1.175	甘蓝瘦蚊 <i>C. nasturtii</i> UGT 3A2-like (XP_031634156.1)	76.63	
ABC 转运蛋白 ABC transporter	ABCA	<i>CL943.Contig3_All</i>	2.228	甘蓝瘦蚊 <i>C. nasturtii</i> ABCA3 (XP_031626961.1)	81.86	
		<i>CL2975.Contig4_All</i>	1.517	甘蓝瘦蚊 <i>C. nasturtii</i> ABCA12 (XP_031627903.1)	78.89	
		<i>Unigene13493_All</i>	1.068	甘蓝瘦蚊 <i>C. nasturtii</i> ABCA3 like (XP_031638209.1)	57.66	
	ABCC	<i>Unigene18134_All</i>	7.824	伪蕈蚊 <i>P. hygida</i> ABCC4 (KAJ6642099.1)	63.68	
		<i>Unigene2148_All</i>	1.643	伪蕈蚊 <i>P. hygida</i> ABCC4 (KAJ6642099.1)	56.75	
		<i>CL3984.Contig12_All</i>	1.498	伪蕈蚊 <i>P. hygida</i> ABCC4 (KAJ6642099.1)	55.20	
		<i>CL1670.Contig1_All</i>	-2.075	伪蕈蚊 <i>P. hygida</i> ABCC4 (KAJ6642099.1)	59.08	
		<i>CL458.Contig7_All</i>	-1.186	伪蕈蚊 <i>P. hygida</i> ABCC4 (KAJ6642099.1)	49.88	
		<i>Unigene16570_All</i>	-1.783	伪蕈蚊 <i>P. hygida</i> ABCC4 (KAJ6642099.1)	55.35	
		ABCD	<i>CL2227.Contig2_All</i>	-1.298	甘蓝瘦蚊 <i>C. nasturtii</i> ABCD (XP_031628539.1)	91.91
	ABCF	<i>CL1344.Contig24_All</i>	1.713	甘蓝瘦蚊 <i>C. nasturtii</i> ABCF2 (XP_031626578.1)	93.97	
	ABCG	<i>CL4159.Contig1_All</i>	1.175	甘蓝瘦蚊 <i>C. nasturtii</i> ABCG20 (XP_031631158.1)	91.23	
		<i>CL2725.Contig3_All</i>	1.113	甘蓝瘦蚊 <i>C. nasturtii</i> ABCG4 (XP_031638739.1)	85.52	
<i>CL367.Contig17_All</i>		-1.172	甘蓝瘦蚊 <i>C. nasturtii</i> ABCG23 (XP_031629128.1)	85.24		
	<i>CL1631.Contig2_All</i>	-2.357	甘蓝瘦蚊 <i>C. nasturtii</i> ABCG4 (XP_031623092.1)	87.10		

基因注释信息: 对应 ORF 序列经 BLASTX 比对后, 同源序列中亚家族信息明确的最佳项。Gene annotation: The best BLASTX hit with clearly defined subfamily information among homologous sequences from other species based on the ORF sequence.

2.6 差异表达解毒酶基因的 RT-qPCR 验证

RT-qPCR 结果显示, *CL1917.Contig4_All* 和 *CL501.Contig5_All* 下调, 其他 11 个解毒酶基因均上

调, 与转录组测序结果的表达模式一致(图 4), 且大部分基因的 RT-qPCR 结果与 RNA-seq 结果差异不显著, 表明转录组数据可靠。

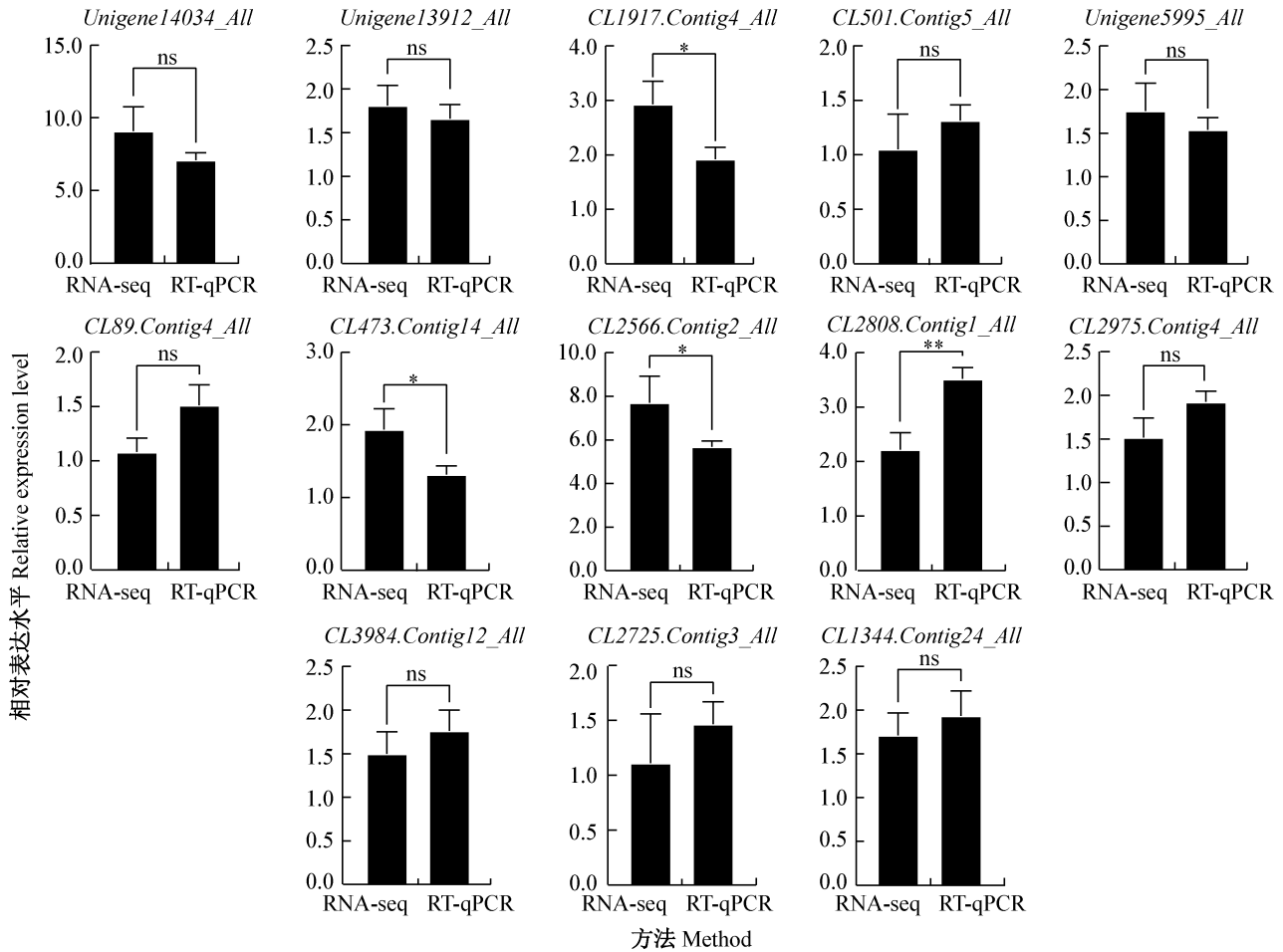


图 4 取食抗感小麦的麦红吸浆虫幼虫转录组间差异表达解毒酶基因的 RT-qPCR 验证

Fig. 4 RT-qPCR validation of differentially expressed detoxification enzyme genes between transcriptomes of *Sitodiplosis mosellana* larvae feeding on resistant and susceptible wheat

图中数据为平均数±标准误。*, ** 分别表示转录组测序结果和 RT-qPCR 结果经非配对 *t* 检验法检验差异显著 ($P < 0.05$ or $P < 0.01$)。ns 表示无显著差异。Data are presented as mean±SE. *, ** indicates significant differences between RNA-seq and RT-qPCR results according to an unpaired *t* test at $P < 0.05$ and $P < 0.01$, respectively. ns indicates no significant difference.

3 讨论

目前昆虫-植物互作关系的大多研究主要集中在作物抗虫方面(Li et al., 2016; Tu et al., 2018; Wang et al., 2022), 而关于昆虫克服抗性寄主防御的分子机制研究较少。近年来, 随着高通量测序技术的发展, 其凭借产出数据量大、成本低和速度快等优势, 在新基因发掘和功能基因鉴定上应用越来越广泛(吴顺骄等, 2023)。为探讨麦红吸浆虫适应抗性小麦防御的分子机制, 本研究利用 BGISEQ-500 高通量测序平台对取食抗感小麦的麦红吸浆虫幼虫进行了转录组测序和分析, 发现了 3 566 个差异表达

基因, 其中编码结合活性和催化活性、参与细胞进程和代谢进程及运输和分解代谢、异生物质降解和代谢途径的基因富集数量较多, 且大多在取食抗虫小麦品种的麦红吸浆虫幼虫中上调表达。类似结果也在取食抗感大豆的大豆蚜 *Aphis glycines* (Bansal et al., 2014)、取食抗感甜菜的甜菜直斑蝇 *Tetanops myopaeformis* (Li & Smigocki, 2018) 和取食抗感作物的麦长管蚜 *Sitobion avenae* (Huang et al., 2019) 中发现, 表明取食抗虫作物可激活昆虫解毒/水解酶系及转运蛋白相关基因的表达, 从而提高酶活性, 进而克服寄主的抗性。

CYP450 是昆虫重要的 I 相解毒酶, 其可细分为

CYP2、CYP3、CYP4 和线粒体 CYP 四个亚家族 (Wang ZY et al., 2024)。取食抗性寄主冷蒿 *Artemisia frigida* 后亚洲小车蝗 *Oedaleus asiaticus* 体内 CYP450 基因表达量显著上调 (Huang et al., 2017); 防风宽蛾 *Depressaria pastinacella* 和棉蚜 *Aphis gossypii* 体内 CYP3 基因能分别代谢寄主内啉喃香豆素和棉酚 (Calla et al., 2020; Gao et al., 2022); 赤拟谷盗 *Tribolium castaneum* 体内 3 个 CYP4 基因在对其寄主中丁香酚的适应中发挥着关键作用 (Zhang YL et al., 2022)。本研究发现取食抗虫小麦后麦红吸浆虫幼虫体内 2 个 CYP3 和 3 个 CYP4 基因表达显著上调, 表明这些基因在其适应抗性小麦防御中发挥着重要作用。CarE 不仅能代谢含有酯键和酰胺键的有毒化合物, 也具备调控昆虫生长、代谢内源激素等功能 (Johan et al., 2021)。本研究筛选到的 4 个差异表达 CarE 基因均为 JHE, 且在取食抗虫小麦后其表达下调, 推测低水平的 JHE 可能在延长幼虫发育和取食及间接提高寄主适应中发挥着重要作用。

GST 是昆虫 II 相解毒酶的重要组分, 胞质型 GST 分为 6 个亚家族, 其中 delta 和 epsilon 亚家族不仅为昆虫特有 (Xia et al., 2022), 而且在昆虫对植物次生物质代谢和寄主适应中发挥着重要作用。例如, 黑森瘿蚊 *Mayetiola destructor* 能在黄酮类次生物质含量较高的抗虫小麦 *Iris* 上完成发育, 这与取食后其体内 *MdGST-1* 基因 (delta 亚家族) 的上调表达有关 (Mittapalli et al., 2007); 斜纹夜蛾 *Spodoptera littoralis* 体内 *GSTe1* 基因对硫代葡萄糖苷有强的代谢能力 (Zou et al., 2016); 舞毒蛾 *Lymantria dispar* 体内 *GSTe4* 基因对水杨苷和芦丁有强的代谢能力 (Ma et al., 2021); 褐飞虱 *Nilaparvata lugens* 体内 *NIGSTe1*、*NIGSTd2* 和 *NIGST1-1* 基因对水稻次生代谢物芦竹碱的代谢中起主导作用, 转入 *dsNIGST1-1* 后水稻植株对褐飞虱抗性增强 (Yang et al., 2021a, b)。UGT 通过将中间体与糖分子结合来增加其水溶性, 进而促进其外排。例如, 草地贪夜蛾 *S. frugiperda* 体内 *SfUGT33F32* 基因能与玉米丁布结合并解毒 (Wang HD et al., 2024); 棉铃虫 *Helicoverpa armigera* 体内糖基转移酶 UGT41B3 和 UGT40D1 能将棉酚糖基化, 促进其外排 (Krempl et al., 2016)。本研究发现取食阿魏酸和单宁等次生物质含量高的抗虫小麦后麦红吸浆虫幼虫体内 6 个 GST 基因 (3 个 delta 和 3 个 epsilon) 和 4 个 UGT 基因 (1 个 UGT1、2 个 UGT2 和 1 个 UGT3) 差异表达, 表明这些基因可能在麦红吸浆虫对抗虫物质代谢和寄主适应中起关

键作用。

ABC 转运蛋白是广泛存在于各种生物体内的一类重要跨膜蛋白, 其利用 ATP 水解产生的能量将胞内外源物质运出或隔离, 从而发挥解毒作用 (Strauss et al., 2013; Wu et al., 2019)。ABC 转运蛋白基因表达量的增加, 不仅与害虫抗药性 (Rösner & Merzendorfer, 2021; Guan et al., 2022) 有关, 也与昆虫对植物次生物质的耐受性和适应性密切相关。例如, 蓼蓍肖叶甲 *Chrysochus auratus* 体内 *CaABCB1-3* 基因上调表达后, 其对宿主有毒化合物-强心甙的耐受性提高 (Kowalski et al., 2020); 麦长管蚜 *Sitobion avenae* 对大麦的适应性与取食后其体内 *SaABCA5*、*SaABCB7*、*SaABCG1* 和 *SaABCG4* 基因的上调表达有关 (Huang et al., 2019)。本研究显示取食抗虫小麦后麦红吸浆虫幼虫体内 3 个 *ABCA*、3 个 *ABCC*、1 个 *ABCF* 和 2 个 *ABCG* 表达水平显著增加, 表明其可能在对寄主植物关键防御物质解毒过程中发挥重要作用。

综上所述, 本研究利用比较转录组技术分析了取食抗感小麦的麦红吸浆虫幼虫体内差异表达基因, 筛选出了取食抗虫小麦后显著上调表达的解毒酶基因。后续将通过原核表达、代谢分析、植物介导的 RNA 干扰等技术对这些解毒酶基因的功能进行解析, 为将来利用解毒酶基因沉默技术管理害虫的寄主适应性及提高作物抗性打下坚实的基础。

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