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植物类黄酮的化学生态学意义

杨才琼[1,2],杨文钰[1,2*],刘　江[1,2,3*]

[1]农业部西南作物生理生态与耕作重点实验室;[2] 四川省作物带状复合种植工程技术研究中心;

[3]四川农业大学生态农业研究所,成都 611130

摘　要:类黄酮在植物中广泛分布,具有重要的化学生态学功能,包括微生物信息交流、病虫害防御、化感作用等。本文综述了近年来植物类黄酮与生物环境互作机理方面的研究进展,以期为类黄酮化学生态学功能的开发利用提供参考。

关键词:类黄酮;生物环境;植物防御;化感作用

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Advances on Chemical Ecology of Plant Flavonoids

YANG Cai-qiong[1,2],YANG Wen-yu[1,2*],LIU Jiang[1,2,3*]

[1]*Key Laboratory of Crop Ecophysiology and Farming System in Southwest,Ministry of Agriculture*;

[2]*Sichuan Engineering Research Center for Crop Strip Intercropping system*;[3]*Institute of Ecological Agriculture,Sichuan Agricultural University,Chengdu;611130,China*

Abstract: Flavonoids were a class of 2-phenylchromone compounds produced by plants. They have many biological activities and were widely distributed in plants. The diverse physiological and biochemical properties of flavonoids make them involved in many interactions between plants and environmental factors,including the exchange of information with microorganisms and protection against phytophagous insects and pathogenic bacteria. Flavonoids were also an important class of allelochemicals. Flavonoids interact with a variety of environmental factors,including biological and non-biological aspects;this article describes the interaction of flavonoids in plant and biological environment.

Key words:flavonoids;biological environment;plant defense;allelopathy

类黄酮是一类 2-苯基色原酮类化合物,拥有万余种结构变体,其合成起始于丙二酰辅酶 A 和 4-香豆酸辅酶 A(图 1),与木质素具有共同的合成前体,也有一些特殊的类黄酮的合成起始于辅酶 A,如肉桂酸和二羟基香豆酸。类黄酮按其骨架可分为查尔酮、黄烷酮、黄酮、黄酮醇、异黄酮、花青素和紫檀素等,而糖基化、丙二酰基化、羟基化、异戊烯基化、乙酰基化修饰以及聚合反应最终导致了该化合物家族的多样性,这些化学修饰对类黄酮的溶解性、移动性和降解性均有重要影响。类黄酮的结构和分子特性的多样性,使得它能与各类亚细胞中的靶标相互作用,从而影响植物、微生物和动物的生物学活性[1],是植物发挥化学生态学功能的重要载体之一。类黄酮影响植物多种生理功能,包括抑制生长素的运输[2],植物化学防御、化感作用和抗氧化[3]等,同时,它们也能影响花朵的着色以帮助植物吸引传粉者[4]。类黄酮在大多数植物组织中均有分布,包括叶片,种荚,籽粒以及根,其中根部组织是类黄酮释放到外界的主要方式之一[5,6],类黄酮可以在植物的根尖和根冠中积累,并通过根系分泌或者组织脱落的方式释放到外界环境中。植物根系分泌的类黄酮是植物与植物以及植物与微生物之间进行信号交流的媒介。大量的证据表明,类黄酮在豆科植物的进化过程中扮演着重要的角色,它们不仅参与豆科植物与微生物的共生[7],也影响根部结瘤的形成[8],并且通过在根部的内源性积累而影响植物根部的发育。类黄酮与多种环境因子均有互作,包括生物和非生物两个方面,本文主要介绍类黄酮在植物与生物环境之间的互作。

1　植物-动物信息交流

类黄酮几乎在植物的所有部位都有合成。它们

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*通信作者　E-mail:jiangliu@sicau.edu.cn,mssiyangwy@sicau.edu.cn

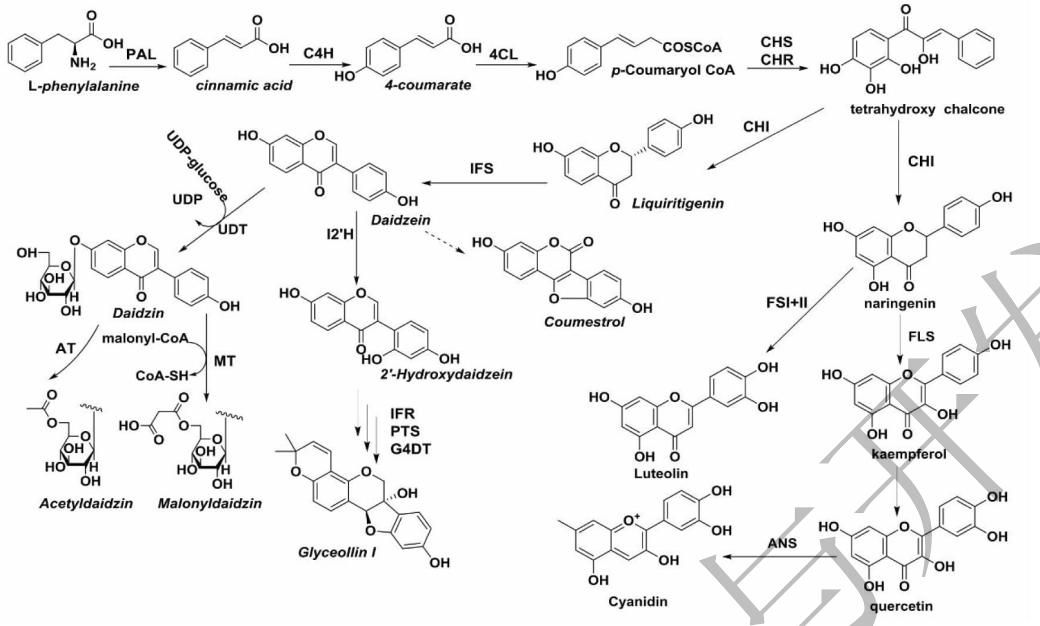

图 1　类黄酮的合成通路

Fig. 1　Synthesis pathway of flavonoids

为水果,花卉和种子提供颜色,香味和味道,使它们成为昆虫,鸟类或哺乳动物的引诱物,从而帮助植物进行花粉或种子的传播[9]。植物释放各种化学物质,以遏制和吸引昆虫,黄酮类化合物能够调节昆虫的产卵和摄食习性。如,柚皮素,橙皮素-7-*O*-芸香糖苷和槲皮素-3-*O*-芸香糖苷能刺激凤尾蝶(*Papilio machaon*)在柑橘类植物幼叶上产卵[10],黄柏苷能刺激绿带翠凤蝶(*Papilio maackii*)产卵,却对蓝凤蝶(*Papilio protenor*)产卵具有抑制作用[11];槲皮素-3-*O*-芸香糖苷对黑脉金斑蝶(*Danaus plexippus*)产卵也具有有抑制作用[12]。亚麻荠(*Camelina sativa L*)叶片中的槲皮素糖苷能够趋避十字花科植物的害虫跳甲[13]。此外,某些昆虫能够吸纳植物产生的类黄酮并储存在它们的角质层中用于防御天敌或者吸引同伴。而对于另一些昆虫而言,类黄酮则会降低其食物营养,甚至起到毒害作用[14]。

土壤线虫是植物根部的寄生动物,包括根结、囊肿和根损害线虫,它们构成一些主要的根病原体。这些病原线虫多数具有丰富的植物寄主源。线虫一般固定栖息在植物根部的某个部位,为取食而使植物细胞快速重复分裂从而形成囊肿[15]。已有研究表明,多种酚酸类化合物对线虫和植物之间的互作有明显的影响,尤其是黄酮醇类成分,如:山柰酚和槲皮素可以抑制根结线虫的运动性和趋化性[16]。结瘤线虫和囊肿线虫入侵植物根系能够在入侵部位诱导植物类黄酮合成通路的表达,有研究者猜想类黄酮可能在结瘤形成过程中参与了调节植物生长素的转运和积累[17]。但是类黄酮的这种调节作用在不同植物和线虫种类中存在差异,在缺乏类黄酮的条件下,线虫仍能在蒺藜苜蓿根部形成囊肿,尽管囊肿的大小以及细胞的分裂程度会受到影响[18]。而拟南芥和烟草在缺乏类黄酮的条件下,线虫的侵染和囊肿的形成不会受到明显的影响[19]。当然,并非所有的类黄酮都能够促进线虫在植物根部的寄生,某些异黄酮也能影响线虫的运动和孵化,具有驱避线虫的功能[20]。类黄酮虽然对寄主植物自身的生长影响不大,但是异黄酮释放到根际后能够在一定程度上改变线虫的运动性,甚至改变植物根系对线虫的吸引性。

2　植物化感作用

植物与植物之间既存在正向互作也存在负向互作,这可能与类黄酮的种类和浓度有关[21]。负面影响主要是基于抑制其他植物幼苗的萌发和生长,通常情况下,黄酮类化合物通过根部分泌到土壤中,抑制种子萌发,但是也可以在叶子甚至花粉中存在,它们掉落到周围土壤后抑制其它植物的萌发[10]。例如,5,7,4′-三羟基-3′,5′-二甲氧基黄酮是水稻中重要的化感物质之一,它能有效抑制稗草(*Echinochloa crusgalli* L.)等杂草种子的萌发[22]。多年生豆科饲

草植物苜蓿(*Medicago sativa* L.)和三叶草(*Trifolium pratense* L)能很好的抑制其它杂草的生长,但随着种植时间的延长,均易发生自毒作用[23],导致其植株数量和产量显著降低。瑞香狼毒(*Stellera chamaejasme L.*)是我国西北草原上一种毒性侵略杂草,可以通过化感作用抑制周围植物的生长,其根系分泌的 neochamaejasmin B,mesoneochamaejasmin A,chamaejasmenin C,genkwanol A,daphnodorin B 和 dihydrodaphnodorin B 等类黄酮化感物质对拟南芥幼苗有明显的抑制作用[24]。Mandal 等人发现,在种子和幼苗形成过程中,许多豆科植物根系均能释放黄酮类酚类物质[1],这些小分子成分在刺激豆科植物根系结瘤的同时也能抑制土壤中其它生物的生长[26]。

类黄酮化感作用的强弱,与其在土壤中的半衰期有关。Kong 等研究发现,糖苷易分解,在土壤中很难长时间存在,而苷元拥有更长的半衰期,并且在土壤表面的流动性低;因此,类黄酮苷元在土壤中发挥的化感作用比糖苷更强[27]。Puia 等研究发现,白三叶草根部土壤中占优势的类黄酮苷元主要为芒柄花素、苜蓿紫檀素以及山柰酚,其中山柰酚在土壤中的存在时间最长,而其它组分均被快速分解,这说明,山柰酚可能是白三叶草主要的类黄酮化感物质[28]。类黄酮参与植物化感作用已被人们广泛接受,但其化感作用机制尚未完全阐明。化感物质潜在的作用机理包括:细胞生长抑制,ATP 产生障碍及生长素抑制等[29]。也有报道显示,黄烷醇能通过引发活性氧波动,从而激活 Ca^{2+} 信号级联和根系死亡[10]。

3 植物-微生物共生

黄酮类化合物可以作为物种间共生关系的特定传播者,特别是共生细菌。土壤低氮浓度能够诱导黄酮类物质的积累,类黄酮则作为固氮细菌的引诱剂促使固氮细菌将低浓度的氮转移到植物细胞,而固氮细菌反过来利用植物产生的光合产物。豆科植物类黄酮具有调控共生根瘤菌结瘤功能,其通过调控细菌 *nod* 基因表达,从而触发固氮根瘤菌的趋化性[26]。如:木犀草素是一种存在于苜蓿种子分泌物中的黄酮,在苜蓿根瘤菌(*Rhizobium meliloti*)中诱导结瘤基因(*nod*)表达,并作为细菌的生物化学特异性化学引诱剂。苜蓿根瘤菌 RCR2011 对 4′,7-二羟基黄酮,4′,7-二羟基黄烷酮和 4,4′-二羟基-2-甲氧基查耳酮都具有非常类似的趋化反应[30]。研究表明,类黄酮既能正向诱导 *nod* 基因,也能负向抑制 *nod* 基因的表达,并控制根瘤的形成,影响固氮作用。如:大豆苷元和染料木素能诱导慢生根瘤菌(*Bradyrhizobium japonicum*)*nod* 基因的表达,却抑制中华根瘤菌(*Sinorhizobium meliloti*)*nod* 基因的表达;柚皮素能刺激结瘤蛋白在豌豆根瘤菌(*Rhizobium leguminosarum*)中的形成,而槲皮素则抑制其形成[10,30]。

类黄酮对根瘤的调节作用与结瘤蛋白(NodD)的结合密切有关。根瘤菌存在许多参与植物信号识别的基因和蛋白质,如 NodD、NodA、NodB 和 NodC[31]。激活 NodD 蛋白使类黄酮与 *nod* 基因启动子区域中强烈保守的 nod-box 序列结合并诱导其转录,使得结瘤因子在固氮菌中合成并释放,从而激活寄主植物多个代谢过程,致使植物为固氮菌提供共生环境。释放的结瘤因子被植物细胞膜表面的 Nod 受体识别[32],该受体由具有两个或三个赖氨酸序列(LysM)和胞内激酶结构域(LysMRLK)的细胞外结构域组成[33]。Nod 因子结合受体蛋白后,受体蛋白启动信号激酶级联反应,DMI1,DMI2,NFP 和 NSP 蛋白均参与其中[34]。Nod 因子响应初期,植物细胞内钙水平和根毛细胞骨架会发生变化,导致根细胞分裂,根瘤形成[35]。此外,根瘤形成初期,豆科植物诱导异黄酮合成相关的基因表达,如大豆根瘤菌诱导苯丙氨酸裂解酶(PAL)和查尔酮合酶(CHS)基因;某些 Nod 因子还能上调表达异黄酮合酶(IFS)基因[2]。有人提出,黄酮类化合物随后干扰生长素的运输,从而促进细胞分裂[37](见图 2)。

类黄酮对菌根的形成也有非常重要的作用,主要是影响植物与定殖在根部皮质组织中的土壤真菌之间的共生作用。虽然黄酮类化合物在这种共生关系中的作用还没有得到充分的认识,但它们对菌根具有调控作用。研究表明,黄酮类物质可以促进丛枝菌根真菌孢子的萌发以及菌丝的分支和菌根的定植[37]。蒺藜苜蓿根部的代谢物分布揭示了黄酮类化合物在不同阶段的重要积累[38]。刺芒柄花素能刺激菌根菌在大豆根系表面定植,尤其在缺磷条件,更能刺激其定植活力[7]。此外,菌根真菌的刺激也会诱导类黄酮的表达。如,对洋葱(*Allium cepa* L.)进行菌根菌接种可以作为生物胁迫,并导致黄酮醇

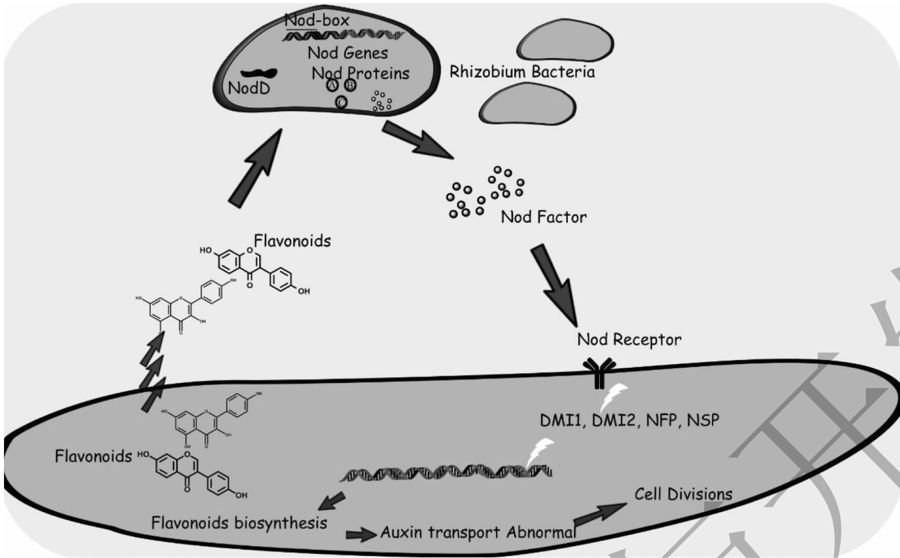

图 2 类黄酮在豆科植物与根瘤菌互作中的作用

Fig. 2 The role of flavonoids in the interactions between nitrogen-fixing bacteria and

和相关基因的表达增加[39]。

4 类黄酮与植物抗病性

类黄酮在植物对病原菌的防御中发挥着重要的作用。这种防御作用可能是非特异性的,部分由其抗氧化性质决定。目前,已报道的类黄酮参与植物防御的方式有以下几种:1)植物在受到病原真菌袭击时,类黄酮被运送到植物的受感染部位,并积累在坏死或邻近细胞的细胞壁中,引起局部过敏反应和细胞程序性死亡[40];2)通过调节生长素(IAA)活性来促进植物结构和组织的收紧,从而导致组织分化,促进愈伤组织和侵填体形成,并且封闭维管系统以防止病原体感染[10];3)类黄酮也可以直接参与抑制病原体的酶,尤其是那些消化植物细胞壁的酶;4)直接抑制真菌孢子发育和菌丝伸长的作用[41]。此外,类黄酮抗菌活性机制是基于其对微生物粘附能力和细胞包膜转运蛋白的灭活能力的基础上。脂溶性黄酮类化合物也可能破坏微生物膜,改变其流动性并可能干扰呼吸链[42]。

黄酮类成分的抗菌能力与其结构密切相关,未被取代的类黄酮通常具有更高的抑菌活性,羟基化和甲基化会降低类黄酮抗菌活性,但甲基化类黄酮抑菌活性强于羟基化的类黄酮[43]。异黄酮、黄烷酮、黄酮醇均被报道具有抑菌活性。大豆异黄酮对黄曲霉具有抑制作用,其中染料木类黄酮的抑菌效果最佳。此外,异黄酮对炭疽病菌(*Colletotrichum truncatum*),菜豆壳球孢菌(*Macrophomina phaseolina*)、马铃薯坏疽病菌(*Phoma exigua*)、疫霉病菌(*Phytophthora sojae*)、立枯丝核菌(*Rhizoctonia solani*)、尖孢镰刀菌(*Fusarium oxysporum*)和大豆菌核菌(*Sclerotinia sclerotiorum*)等病原菌也有抑制作用[44]。Sakuranetin 是水稻中一类黄烷酮类植保素,对水稻稻瘟病菌和立枯丝核菌有强烈的抑制作用,其中以苷元和甲基化的 sakuranetin 的活性较高[43]。苜蓿属植物如紫花苜蓿和蒺藜苜蓿,在受到真菌或者细菌病原体侵染时会产生紫苜蓿素、维斯体素、维斯体酮等抗毒素,以抵御病原菌的侵染[45]。鹰嘴豆产生美迪紫檀素和高丽槐素,而豌豆素是豌豆中主要的植物抗毒素[46]。大豆抗毒素为紫檀素派生物,其受到病原菌如疫霉菌和球壳孢菌的特异性诱导[47]。大豆抗毒素对病原菌尤其是真菌性病原菌有强烈的抑制作用,如 *GmIFR* 过表达的大豆品种能够诱导更多的大豆抗毒素以应对大疫霉病菌的侵染[48]。目前已经报道的大豆抗毒素共 7 种,包括大豆抗毒素 I、II、III、IV、V、VI 以及呋喃型大豆抗毒素。抗毒素发挥作用的机制可能是引起植物过敏反应(HR)从而介导细胞的程序化凋亡[49,50]。有趣的是,某些紫檀素类抗毒素不会在植物根部积累而是通过根系分泌到土壤中发挥作用[16],这也表明,此类抗毒素可在病原菌接触根系之前便分泌到土壤中,从而抑制病原菌对根系的侵害。其他已报道的典型类黄酮抗菌活性研究结果如表 1 所示。

表 1　类黄酮响应病原刺激的实例

Table 1　Examples of flavonoids induced in crop plants in response to pathogens

植物名称 Plants	抗菌化合物 Antimicrobial compound	病原菌 Pathogen	参考文献 Ref.
菜豆 *Phaseolus vulgaris*	染料木素、大豆苷元、2-羟染料木素、拟雌内酯、异黄烷、Phaseollidin、Phaseollin、Kievitone、Dalbergioidin、Phaseollin	菜豆炭疽病菌 *Colletotrichum lindemuthianum*	51
蒺藜苜蓿 *Medicago truncatula*	美迪紫檀素、异黄酮	苜蓿茎点霉菌 *Phoma medicaginis*、白粉病菌 *Erysiphe pisi*	52
大豆 *Glycine max*	大豆苷元、染料木素、大豆抗毒素、拟雌内酯、芹菜素	疫霉病菌 *Phytophthora sojae*、菜豆壳球孢菌 *Macrophomina phaseolina*	53
拟南芥 *Arabidopsis thaliana*	槲皮素、芸香苷、漆黄素	丁香假单胞菌 *Pseudomonas syringae*、粗糙链孢菌 *Neurospora crassa*	54
葡萄 *Vitis vinifera*	槲皮素-3-O-葡萄糖苷	霜霉病菌 *Plasmopara viticola*	55
水稻 *Oryza sativa*	柚皮素、山柰酚、槲皮素、Sakuranetin	黄杆单胞菌 *Xanthomonasoryza*、米曲霉 *oryzae pv. oryzae*、稻瘟病菌 *Pyricularia oryzae*	56
芜菁 *Brassica rapa*	山柰酚糖苷	野油菜黄单胞菌 *Xanthomonas campestris*	57
紫花苜 *Medicago sativa*	美迪紫檀素、Sativan	刺盘孢菌 *Colletotrichum trifolii*	58
狭叶羽扇豆 *Lupinus angustifolius*	羽扇豆异黄酮、Wighteone	刺盘孢菌 *Colletotrichum trifolii*	59
菜豌豆 *Pisum sativum*	豌豆素、高丽槐素	颈腐病菌 *Nectria haematococca*	60

5　黄酮类化合物的应用前景

化学农药为提高农业生产效率做出了重要的贡献,随着使用量的逐年增加,化学农药对环境的潜在危害也日益凸显,人们越来越倾向于使用更安全的植物源农药。类黄酮已被证明对草地夜蛾(*Spodoptera frugiperda*)、果蝇(*Drosophila melanogaster*)和菜粉蝶(*Pieris rapae*)等昆虫有明显毒杀性,是植物源农药的理想候选者之一。根据类黄酮的抑菌特性,研究者通过基因工程结合传统的杂交育种方式改良亚麻类黄酮含量,从而获得了对镰刀菌有抗性的亚麻植株[61]。类黄酮具有影响线虫的运动和孵化作用,具有驱避线虫的功能[62],如黄酮醇柚皮素、芦丁和山奈酚能趋避线虫[63],若将其开发为拌种剂,对作物线虫的防止有重要的作用。而针对对线虫具有吸引性的类黄酮,可以设计线虫的"陷阱植物",并将这些植物与寄主作物间作,将有望减轻线虫对作物的伤害。5,7,4′-三羟基-3′,5′-二甲氧基类黄酮对稗草(*Echinochloa crus-galli*),莎草属(*Cyperus difformis*)和香附属植物(*Cyperus iria*)的杂草具有抑制活性[22]。瑞香狼毒(*Stellera chamaejasme* L.)分泌的类黄酮也对杂草表现出毒性作用[24];这些植物根系分泌的类黄酮为可以开发为植物源除草剂,也可以通过与其它作物间作来进行杂草防治。例如,豆科山蚂蝗属钩骨分泌的Isoschaftoside、Uncinanone A 和 Uncinanone B 可以抑制寄生性杂草独脚金的萌发和附着。山蚂蝗属植物分泌的某些类黄酮能诱导独脚金自杀性萌发[64],通过山蚂蝗属植物和其他作物间作或可实现对独脚金的廉价防控。此外,美的紫檀素、高丽槐素、大豆抗毒素等植物抗毒素可用于防治疫霉病菌、茎点霉菌、白粉菌和刺盘孢菌引起的真菌病害。白羽扇豆释放到根际的染料木黄酮和羟基异黄酮及其相应的糖苷化产物,可通过溶解铁结合磷和限制柠檬酸盐的微生物矿化,在其有效磷的捕获策略中发挥重要作用[65]。因此,在土壤贫瘠的地方,通过间作或套作白羽扇豆,将有望提高土壤中磷

的有效性。此外,类黄酮在花卉中得到广泛应用,基于代谢工程技术调控园艺植物类黄酮代谢途径的遗传修饰,可使矮牵牛、非洲菊、玫瑰、康乃馨、桔梗和特雷亚藜等产生新花色[66]。黄酮类化合物不仅对植物病原体有抑制作用,对危害人类的病原体也有重要的抑制作用。异刺桐素 A 和 2′-羟基赤藓素 A 对金黄色葡萄球菌、屎肠球菌、绿浓杆菌、肺炎双球菌、大肠杆菌等细菌具有较强的抑制活性[67]。山奈酚对革兰氏阳性/阴性菌以及真菌假丝酵母(*C. glabrata*)均具有抑制活性[68],类黄酮的此类特性可用于植物源抑菌剂和药用抗生素开发。

6 结论

类黄酮在昆虫信号交流、草食动物化学防御以及微生物-植物相互作用等诸多生态学过程中都起着重要的化学调控作用,但这种化学调控机理尚不完全清楚。类黄酮与生物环境的相互关系中涉及复杂的网络互作,其中,生物环境胁迫引发类黄酮的生物合成,而合成类黄酮的种类和数量因刺激因子与信号途径的作用方式和程度而异;在此过程中,植物如何接受环境信号,信号在植物体内如何转导,最后进入细胞核,从而激活类黄酮合成基因,其上下游通路间的相互关系如何等问题,均有待深入研究。

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