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药用植物中黄酮的生物合成及提取工艺研究进展

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摘要:目的 通过对药用植物中黄酮类化合物的生物合成影响因素、提取工艺等相关文献的系统整理和比较,对影响药用植物中黄酮类化合物合成的非生物因素如干旱胁迫、盐胁迫和紫外(ultraviolet,UV)胁迫,以及非生物因素如线虫入侵、病原菌感染进行了系统论述。在应对干旱胁迫时,大量黄酮化合物如同复杂的缓冲溶液,通过生物合成和转化源源不断地从根部输出,为清除活性氧提供条件,精准而迅速地维持植物体内活性氧守衡,从而对变幻莫测的环境做出有效的应答;短期盐胁迫通过激活抗氧化酶活性来缓解细胞膜损伤;紫外辐射、光照强度通过促进黄酮化合物的合成来实现其抗逆性;而面对生物胁迫,黄酮作为植物特异性抗毒素,能对入侵生物产生杀伤作用,从而保护植物。此外,对药用植物中的黄酮类化合物的提取方法,包括超声辅助提取、微波辅助提取(microwave assisted extraction,MAE)、酶提取进行了总结归纳,对溶剂的分类及其对提取效率的影响进行了系统描述,以期为药用植物中黄酮类成分的广泛应用提供一定的参考。尽管胁迫对黄酮的合成具有一定的促进作用,但中药的应用讲究整体性,胁迫是否会破坏药用植物在治疗作用当中的完整性仍有待探究。

关键词:药物植物;黄酮;生物合成;提取
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Research Progress on Biosynthesis and Extraction Process of Flavonoids in Medicinal Plants

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Abstract:Through a systematic review and comparison of relevant literature on the biosynthesis factors and extraction processes of flavonoids in medicinal plants,this paper systematically discussed the abiotic factors that affect the synthesis of flavonoids in medicinal plants,such as drought stress,salt stress and ultraviolet(UV)stress,as well as abiotic factors such as nematode invasion and pathogen infection. When dealing with drought stress,a large amount of flavonoids act as complex buffer solutions,continuously exported from the roots through biosynthesis and transformation,providing conditions for clearing reactive oxygen species and accurately and rapidly maintaining the balance of reactive oxygen species in the plant body,thus effectively responding to the ever-changing environment. Short-term salt stress alleviates cell membrane damage by activating antioxidant enzyme activity. UV radiation and light intensity promote the synthesis of flavonoids to achieve their stress resistance. In the face of biological stress,flavonoids,as plant specific antitoxin,can have a killing effect on invading organisms,thereby protecting plants. In addition,the extraction methods of flavonoids from medicinal plants,including ultrasonic-assisted extraction,microwave assisted extraction and enzyme extraction,were summarized. A systematic description was provided on the classification of solvents and their impact on extraction efficiency in order to provide some reference for the widespread application of flavonoids in medicinal plants. Although the stress has a certain promoting effect on the synthesis of flavonoids,the application of traditional Chinese medicine emphasizes integrity,and whether stress will damage the integrity of medicinal plants in therapeutic effects still needs to be explored.

Keywords:medicinal plants;flavonoids;biosynthesis;extraction

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黄酮是一类由植物次生代谢产生的天然多酚化合物，广泛存在于植物中，在 4000 余种植物中均有分布。作为众多中药的有效成分，黄酮是抗氧化、自由基清除、抗菌等药理活性的物质基础。诸多研究表明，黄酮能产生与阿尔兹海默病、肿瘤细胞、帕金森以及动脉粥样硬化和心血管保护作用相关的各类有益生化以及抗氧化作用[1-4]，是医药、保健品、化妆品，甚至食品生产中不可或缺的一部分[5]。药用植物是天然黄酮的主要贡献者，黄酮可分为黄烷酮、黄烷醇、异黄酮、黄酮醇、花青素等[6]。迄今为止，被报道的黄酮已有 6000 多种[7]。黄酮成分主要存在于豆科、芸香科、蔷薇科、菊科等药用植物中；其中，芸香科富含黄烷酮类化合物，如柚皮素、橙皮素等，而相比于其他科属，豆科植物中的黄酮醇、异黄酮、黄烷酮等更为丰富，其丰富是多维度的，包括种类以及含量，故本文从黄酮的生物合成影响因素、提取工艺等方面进行了系统整理和比较，以期为药用植物中黄酮成分的深入发展提供一定的参考。

1 影响植物中黄酮合成的因素

黄酮广泛存在于植物界，植物的次生代谢是产生该类物质的主要途径。不同种属植物其代谢物质积累量必定有所差异，此类化合物的动态变化不仅受植物激素的调控，还受各类环境因子的影响（如插页XXXⅢ图 1 所示）：包括非生物胁迫，如重金属胁迫、干旱胁迫、紫外线（ultraviolet，UV）、盐胁迫；植物寄生线虫、真菌和细菌等生物胁迫[8-12]，亦会促使其代谢产物有所偏差，这些差异代谢物是植物进化出的生物机械，以抵御外界瞬息万变的条件。

1.1 非生物胁迫

1.1.1 干旱胁迫 由于全球气候变化，干旱的发生愈发频繁，波及范围更为广泛，植物生长发育受制于干旱胁迫的情况愈发突出。干旱作为影响植物生长、发育、代谢物积累的关键因素，植物为应对其影响，形成了活性氧清除的两大自我防御策略——酶类抗氧化剂、非酶类抗氧化剂，二者相互协调，共同抵抗水分缺失造成的活性氧过量[13]。黄酮类化合物作为非酶类抗氧化剂的重要组成部分，在遭遇干旱胁迫后，总黄酮含量有所上升：铁皮石斛在经轻度干旱处理后，其黄酮类代谢产物含量在重度干旱胁迫下达到顶峰，且对石斛自身生长并未造成影响，石斛对干旱逆境具有较好的耐受力，采收前可进行适度的干旱胁迫，有助于提高石斛品质[14]；干旱胁迫下柴胡的次生代谢产物更易向地下部分迁移，以此来应对水分缺失带来的不利影响，当水分缺失持续加剧，柴胡生长受阻，活性物质积累最终也会减少，复水后，产物积累又将步入正轨[15-16]；渐进性干旱胁迫会显著影响黄芩苷生物合成上游关键酶的表达模式，适当的干旱处理导致基因表达增加，过度表达又将减少[16]；黄芩素、白杨素、圣草酚等生理活性较强的多羟基游离黄酮累积量的升高，使得黄芩能更有力地应对水分缺失困境，尤其是黄芩素、黄芩苷被称为黄芩的根特异性黄酮[17-19]：大量该类化合物如同复杂的缓冲溶液，通过生物合成和转化源源不断地从根部输出，为清除活性氧提供条件，精准而迅速地维持植物体内活性氧守衡，从而对变幻莫测的环境做出有效的应答[18,20]。

1.1.2 盐胁迫 土壤盐度是关乎作物萌发、生长以及作物产量的关键因素，盐胁迫下的植物会发生一系列的生理变化，如短期盐处理一定程度上能激活过氧化物酶、超氧化物歧化酶、过氧化氢酶等抗氧化酶活性[21]；植物自身生长也会受到抑制，在盐浓度过高的情况下，绝大部分植物甚至无法完成萌发，但盐碱地也并非是不毛之地：在耐盐植物面前，低浓度盐胁迫或许是其代谢物积累的温床，盐浓度过高，作物生命力减弱，其活性物质也不会无休止地增长[22]。相比于干旱，盐胁迫对植物细胞膜的破坏是杀伤性的，盐胁迫会造成植物细胞膜脂的过氧化，造成不可逆的膜损伤，细胞膜的完整性无法维持，从而引起植物抗逆性减弱[23]。盐胁迫下的水飞蓟次生代谢产物合成增加，叶片中总黄酮积累量与胁迫时间呈正相关，在前期的短暂下降过后，通过改变酶活性或者分解渗透调节物质来实现对自身的保护，从而积累代谢物[24]；外源硅能提高不同时期盐胁迫下的甘草茎、叶当中的总黄酮含量，为甘草非药用部位的开发利用提供了可能[25]；适当的盐胁迫能促进黄芩黄酮类化合物的积累，但促进作用十分有限[26-27]。

1.1.3 紫外胁迫 近年来由于环境恶化，平流层臭氧消耗加剧，紫外线辐射的流入将会加剧。已有研究表明：长期处于高强度 UV 辐射下的植物可迅速产生过量的活性氧，对生物分子（核酸、蛋白质、生物膜）等造成氧化损伤[28-29]。由于不同黄酮的 UV 吸收能力不等，当植物遭受 UV 和强光时，出于屏障保护，在植物表皮及叶肉细胞会产生黄酮的积累[9,30]，值得一提的是，黄酮的吸光特性不仅与其亚类密切相关，还取决于骨架上取代基类型[31]，故植物能合成不同的生物保护黄酮[29]，UV 胁迫对黄酮生物合成的诱导作用表明 UV 照射可能是提高中药营养物质和药用价值的有效策略[32-33]：UV 辐射通过诱导黄酮生物合成途径基因的表达，提高青蒿黄酮的积累[34]；UV 辐射对葫芦巴幼苗的生长有正向促进作用，暴露在 UV 下的葫芦巴会产生花青素等黄酮，黄酮的增加是生物活性化合物增加的有力证据[35]；黄芪生长过程中对 UV 有捕捉，UV 辐射能显著诱导黄酮在黄芪体内的蓄积：黄芪的各器官表现出对 UV 高强度的响应，根、茎、叶异黄酮积累明显[36]。桑叶中含有大量的糖基黄酮，糖基赋予黄酮结构复杂性以及功能多样性[37]：糖基黄酮是桑树抗 DNA 损伤、活性氧积累、脂质过氧化、膜损伤和光合色素降解等的物质基础[38]；高海拔地区的银杏黄酮是低海拔地区的 1.59 倍，在生长受限的情况之下，黄酮的积累增多。辐射、光照强度对其合成有明显的促进作用[39]。

1.2 生物胁迫

生物胁迫是对植物生长发育不利的各种生物因素的总称，生物胁迫贯穿在植物生长的始终。超敏反应是植物抗病的主要机制：诱导裂解酶、产生植物抗毒素和增强细胞壁功能[17,40]。植物抗毒素是植物为响应害虫和病原体而释放以抵御疾病和致病剂的化学物质，黄酮是植物防御系统探索最多的次生代谢产物[41-42]。当植物因感染病原体和害虫而遭受胁迫时，黄酮在内的各种防御性次生代谢物合成将增加[9,42]。黄酮通过参与植物激素调节的传导、影响蛋白激酶活性引起植物的系统性防御[43]，合成的增加或因病原体、细菌、真菌和线虫感染，或由摄食昆虫诱导所致[44-45]：黄芪被镰刀菌侵染后，黄酮

合成显著上调[46]，银杏遇真菌侵染后，患上叶斑病的同时，病叶的黄酮含量有所升高[47]。

1.2.1 线虫入侵 植物寄生线虫在作物上的感染仍旧是生产上较为棘手的问题。许多生物防治剂的低效性与长期以来对土壤微生物菌群的忽略有关：微生物群与土壤中的线虫天然相关，在一定程度上保护了线虫免受微生物拮抗剂的侵害[48]。然而，植物根系分泌物是植物超敏反应的重要环节，决定了寄主－微生物的相互交流，黄酮是根系分泌的微生物拮抗剂，是抵御病原体或寄生虫的第一道防线，也可引发线虫的抗性[19]：芽孢杆菌能产生杀线虫和杀真菌作用，是潜在的生物防治菌株，但其抗线虫机制不是直接的，而是植物介导的[19,49]。根系分泌物不能主导线虫的入侵。线虫为了到达根部，需要穿过根部一到几毫米厚的土壤空间，称为根际，是植物根系与土壤之间相互作用的主要区域[50－53]。山柰酚、杨梅素、槲皮素和芦丁会对线虫幼虫产生致命伤害。万寿菊、金桔、黄芪、拟南芥等均能产生黄酮作为抵抗线虫的屏障[52,54－55]。黄酮作为植物特异性抗毒素，能对各生命阶段的线虫产生致命威胁，线虫的入侵一定程度促进了其合成。

1.2.2 病原菌感染 病原菌感染也是威胁植物生长的因素，植物抗毒素的产生是防御病原菌感染的有效机制[56]。具有抗菌活性的代谢物被认为是抗病性的分子标志物，芸香科、豆科、茄科等药用植物能产生黄酮植物抗毒素[57]。果胶菌的侵染会诱导茶树中儿茶素、儿茶酚的合成及分泌，抑制真菌菌丝体生长[58－59]；黄酮醇也在一定程度上抵御了外来菌株的侵染[60－61]：槲皮素、花青素能抑制孢子菌分生孢子萌发和菌丝生长[62]。牡荆素能改变金黄色葡萄球菌表面疏水性以阻止其生物膜的形成[63]；黄酮亚类白杨素、黄酮醇亚类槲皮素和芦丁能够在低剂量下促进不规则根瘤孢子萌发和根系定植[64－65]，菌丝的形成会改变苯丙烷类、黄酮和异黄酮相关基因的表达，从而修饰黄酮[66]，糖基化、甲基化能增强黄酮抗菌功能，糖基化赋予了黄酮结构多样性以及功能复杂性[37]，部分黄酮未经糖基化，其抗菌活性降低甚至缺失。丛枝菌与葡萄的共生不仅增加了葡萄对水分胁迫、土壤盐度、重金属毒性等的耐受性，也增强了植株抵御胁迫的能力[67－68]；具体防御机制是：激活植株局部甚至全身防御过程，抑制部分微生态组成的活动[69－70]。当微生态失衡，根际黄酮含量会有所升高，以保证植物生命力。鉴于菌类与药用植物的微妙关系，药用植物通过菌类发酵后，次生代谢产物发生变化，不失为前体药物发现以及新药研发的新契机。

2 提取

中药有效成分的提取是药物疗效的基础，也是药物基础研究和实现商业价值的第一步。选取合适的提取方法对中药活性物质的研究具有重要意义。理想的提取方法应该具有无损、经济、省时、高效的特点。溶剂是影响活性物质溶出的先决条件，利用现代技术与传统提取方法相结合：超声辅助提取[71]、微波辅助提取[72]、酶辅助提取[73]等实现了对中药活性成分更有效地提取。

2.1 传统提取方法

我国对中药有效成分的提取历史悠久："伊尹制汤液"的传说反映了中华民族祖先们的提取意识，东晋时期，葛洪便用"青蒿一握，二升渍，绞取汁"的方法得到了治疗疟疾的有效成分，中药汤剂是临床治疗中比较常用的一种剂型；在民间用药中，以浸渍法所制得的药酒仍用作跌打损伤等，随着对用药方便、起效迅速药物的迫切需求，传统提取方法得到了改良，煎煮溶剂不再是单一的水，容器也不仅限于药罐。

2.2 超声波辅助提取

超声波辅助提取主要利用超声振荡所产生的强烈空化、高剪切、破碎、搅拌等多重效应加速黄酮进入溶剂，兼具绿色、经济、简便的优势[74－75]。其空化作用是在溶剂传播时产生的，是该方法的核心优势。该效应在溶剂中形成空化气泡，气泡在经历多个压缩和膨胀循环后，会发生内爆，从而产生强烈的湍流、碎裂和侵蚀细胞壁，促进物质间的传递和溶质扩散[76]。与传统方法相比，该方法所需溶剂量更少，能量输入低、所需温度低，生物活性物质损失低[77]，当各条件均实现量化后，响应曲面等优化方法的加入，使得提取更加科学。见插页XXXⅢ图2。

2.2.1 溶剂 溶剂是活性成分溶出的必要推动力，是影响黄酮提取率的第一要素[78]，溶剂类型影响超声的空化效应，对空化阈值影响尤为明显。液体间的内聚力是空化效应发生的最大阻碍，任何增大溶剂分子间作用力的行为都会导致空化阈值的升高，从而降低提取率。在"相似相溶"的大前提之下，低黏度、低表面张力的溶剂更为理想。黄酮的理想溶剂一般可分为三类：有机溶液、离子液体、深度共熔溶剂。

超声提取的常用溶剂有甲/乙醇溶液、丙酮水溶液等，黄酮结构中－OH的多寡直接影响其极性，该类溶剂与水相溶，混合后极性在一定范围内是可控的：乙醇浓度逐渐升高后，白刺叶中总黄酮含量和抗氧化活性显著增强，浓度升高至70%时，提取率下降[79]。过量的乙醇浓度引起了醇溶性杂质的饱和[80]，抑制了黄酮的溶出；55%的丙酮/水溶液是山楂黄酮的良好溶剂；对金丝桃苷、异槲皮素等有较好的提取率[81]。

离子液体(ionic liquids，ILs)是一种液态的、熔点低于100 ℃的化学品，由不对称大尺寸阳离子与具有弱配位性质的有机或无机阴离子组成，也称为室温熔盐[82]。良好的溶解性，高黏度，出色的热稳定使其成为优良的溶剂选择[83]，其最大优势在于可设计性：ILs可以通过酸碱中和反应或季铵化反应一步合成，操作简单、成本低、无副产物、制备方便[84]。离子液体在分析化学领域的应用主要涉及以下几个方面：微波辅助萃取、超声波辅助提取的溶剂[85－86]；液－液萃取[87]、液相微萃取、固相微萃取的萃取剂[88－89]。ILs作为提取溶剂时，其独特的化学官能团能有效促进目标分析物和溶剂之间的相互作用，是黄酮类化合物的新型绿色提取溶剂。黄酮的溶出主要由阴离子控制的，相同的阳离子构成，阴离子的改变对黄酮提取率的影响更显著[90]：阴离子不仅改善了溶质－溶剂的相互作用，还能极大地破坏植物组织结构，且ILs水溶液能避免植物木质纤维的溶解而被广泛利用[91]。咪唑、噁唑等阳离子由于其芳香族结构也起着重要作用[92]，除了ILs组成外，浓度、液固比对提取率也有所影响：液固比太小，黄酮提取不完全；相反，液固比过大会导致溶液黏度增大，提取专属性降低，不利于ILs的提取转

移过程和回收。

此外,深度共熔溶剂(deep eutectic solvents,DESs)的属性与 ILs 的相似[93],相比于 ILs 以阴离子和阳离子相互作用而促进溶出,DESs 则是通常提供氢键受体(hydrogen - bond acceptor,HBA)和供体(hydrogen - bond donor,HBD)网络,促进目标分析物的溶解[94]。DESs 及其天然等价物(氨基酸、胆碱、糖)深度共熔溶剂,由于其优越的理化性质(高溶解度,低挥发性,化学和热稳定性等)以及可设计性,已成为传统有机溶剂及 ILs 的潜在替代品[95]。氢键和范德华相互作用使得 DESs 混合物的熔点低于单一组分[96]。DESs 通常是特异性溶剂,有多种配置可能性可以定制其物理和化学属性以适应不同的应用[97-98]。胺、羧酸、醇、多元醇通常组成 HBD,而 HBA 一般由季铵盐组成[99]。通常仅改变溶剂组成的一种或两种成分,就可产生大量化学性质各异的共熔混合物,超声强机械效应对植物结构的破坏使其更有利于将黄酮溶解到 DESs 中[100]。如氯化胆碱(ChCl)因其成本低、生物降解性强,与 HBD(如羧酸、尿素等)反应生成安全的 DESs,而成为应用最广泛的 HBA[101-102]。有文献报道,以氯化胆碱与乳酸、甘油、尿素组成的 DESs 对墨西哥牛至中的多酚物质进行提取,DESs 提取的总黄酮远高于甲醇的[103]。

2.2.2 *超声参数* 提取参数的优化对提高黄酮的提取率至关重要:提取时间、功率、温度等都被广泛研究。

最佳提取时间对样品类型和目标化合物的影响是深远的[104],ŞAHIN S 等[105]对超声提取多酚化合物的量与时间的关系建立函数,该过程主要分为两个阶段:前 10 ~ 20 min 内将药用植物细胞内的可溶性成分转移至表面,该阶段可提取 90% 的黄酮;第二阶段是通过扩散现象将目标物质从表面转移到溶剂中的过程,因黄酮种类及药用植物不同,超声时间从 20 ~ 100 min 不等。但超声时间过长,内能效应与机械效应会转化为一定的热能,热效应会破坏黄酮的化学结构,提取率会相应降低[31,106-107]。

提取温度的提高总是伴随着提取率的提高。这种现象可能与化学键断裂,增加了黄酮的溶解度,以及加速扩散和传质有关[108]。超声的各工作参数是影响超声辅助提取率的关键因素,其中超声功率对黄酮提取率的影响是巨大的:在一定范围内,超声功率的提高有助于破碎细胞,黄酮更易被传递到溶出介质中[109-110],黄酮具有较好的稳定性,当功率持续升高,提取率未出现急剧下降[111],高强度超声波导致糖苷键的断裂,从而产生分子尺寸较短的果胶分子,进而导致分子和构象参数发生巨大的变化而对提取率产生影响[112]。

2.2.3 *微波辅助提取*(microwave assisted extraction,MAE) MAE 因在减少溶剂使用和降低能耗方面而备受关注,甚至已被开发为某些生物活性物质,尤其是柠檬烯的首选提取方法[113]。该提取方法消耗时间更少,降低了能量损耗,提高了提取效率,是理想的绿色提取方法[114]。MAE 是在封闭系统中进行加热,利用磁场、电场和微波加热直接影响极性材料,通过偶极旋转和离子传导机制转化为热,随着压力和温度的升高,植物细胞内部产生压力,导致细胞壁破裂并促进黄酮的释放[115-116],宏观上表现为溶质分子从样品基质向溶剂扩散释放[117],其能量传递极具针对性和选择性,几乎没有能量损失[118]。MAE 通过改善扩散常数来实现提取率的提高:首先,加速处于表面的活性成分向溶剂扩散;其次,促进细胞内部有效成分跨膜运输向溶剂扩散[119]。如中药黄芩含有大量黄酮,包括黄芩素、汉黄芩素等[120],MAE 的提取物拥有更大的抗氧化以及抗炎活性,总多酚含量以及单个黄酮含量均为最高值[121]。

2.3 *酶提取*

酶提取的机制主要涉及使用细胞壁降解酶来削弱甚至破坏含黄酮植物细胞壁的屏障作用,从而使细胞内黄酮更易进入溶剂,从而实现高效率的提取(如插页ⅩⅩⅩⅢ图 3)。酶辅助提取基于酶固有的催化能力、高度专属性,以及催化条件易实现等优势[122]。从植物中酶法提取黄酮是传统溶剂萃取的潜在替代方案。基于细胞壁结构,以及黄酮以糖苷的形式通过 - OH 或通过 - C - C - 键(C - 糖苷)与糖残基结合的事实[123-124],黄酮提取通常使用纤维素酶、果胶酶、各类糖苷酶以及复杂的混合酶[125]。果胶酶是木犀草素和芹菜素提取的特异性酶,对该类物质进行专属提取[126]。

此外,超声辅助酶提取是集超声的空化作用以及各类细胞壁降解酶的作用于一体的绿色、高效提取方法。酶是提取、修饰或合成天然来源的复杂生物活性化合物的理想催化剂[127],酶处理会破坏植物细胞壁,空化作用能增大第二阶段的扩散常数,从而加速黄酮的溶出,是一种黄酮提取的理想处理方法。

3 展望

尽管各类胁迫对植物生长造成不良影响,但植物在抵抗逆境中代谢产物的变化也给予中药研究众多思考:植物体为适应环境因素变化而形成的生物合成壁垒是其抗逆性的物质基础,它们是植物抵御不利外部环境的基本保护物质。次生代谢对于应对环境变化和维持植物稳态至关重要。与初级代谢相比,更易受到环境因素的影响[16]。环境因素调节能提高包括黄酮在内生物自身免疫组分的合成与积累,绝大部分中药野生品质量优于栽培品的奥秘或许也基于此;然而中药体系本就是一个复杂的整体,对于单体化合物的获取而言,多多益善是在用药需求上的期许,中药的应用往往是讲究整体性的,即使是单味药,其入血成分也并非是单一的;然而当某一单体含量出现变化时,中药药效体系是否发生变化,仍有待探究。

在黄酮提取过程中,超声辅助提取作为最常用的方法,其提取溶剂的发展是影响提取率的关键,从水、有机溶剂到离子液体、深度共熔溶剂的发展是从低效率向高效率、从污染到绿色的转变,在提高效率的基础上,减少生产过程中对环境的破坏,超声波对细胞壁的破坏是溶质能透过细胞膜,在溶剂出现的重要因素;此外,微波辅助提取,以及酶辅助提取为黄酮的提取提供了更多绿色高效的选择,尤其是蜗牛酶的出现为广谱黄酮提取率的提高以及提取范围的拓展作出了巨大贡献,加快了对黄酮更深层认识的脚步。

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药用植物中黄酮的生物合成及提取工艺研究进展

（正文见 117－124 页）

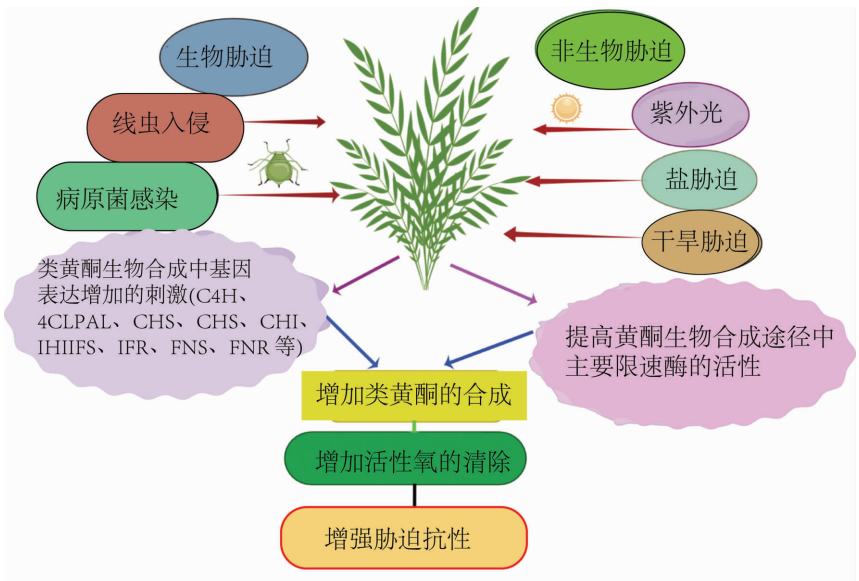


图 1　植物黄酮对环境变量的应答机制

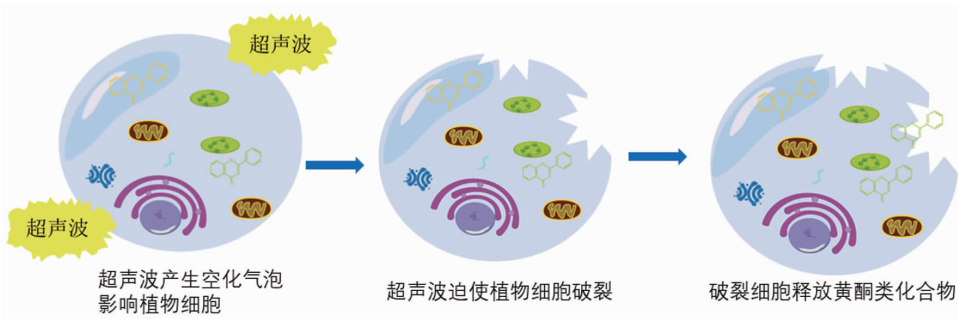


图 2　超声对黄酮提取的影响

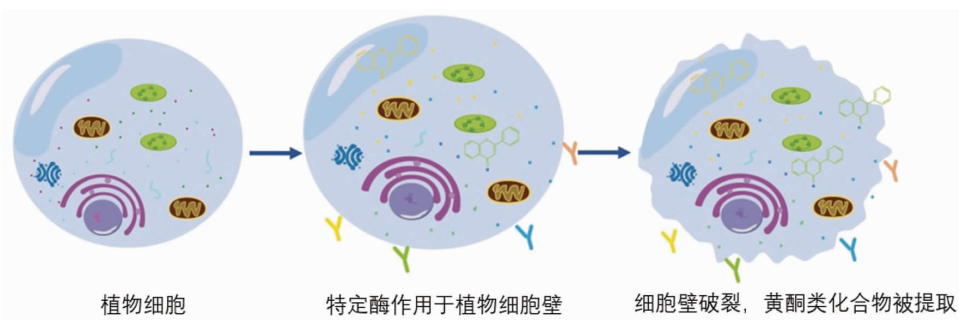


图 3　酶对细胞壁的溶解作用