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·专题论坛·

芳香植物精油的抗菌性及在动物生产中的应用

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摘要 芳香植物精油为具特征性气味的挥发性油状液体, 是从芳香植物中提取的一种重要次生代谢物质。芳香植物精油的抗菌活性由其化学成分和浓度决定, 其中酚类、含氧萜类和萜烯类在抗菌方面表现出较强的活性。芳香植物精油的抗菌机制主要涉及脂肪酸外膜的改变、细胞质膜的损坏、质子动力的消耗、代谢物及离子泄露。在畜牧业生产体系中, 抗生素的无序使用不仅可能引发“超级细菌”的产生, 其残留亦会造成畜产品不安全和环境污染。芳香植物精油作为一种天然植物抗菌剂, 毒性较低且无残留, 作为饲料添加剂可用于维持动物机体的健康, 有望成为重要的抗生素替代品。该文阐述了芳香植物精油的活性成分、抗菌作用机制及其在动物生产中的应用, 为抗菌机理研究和新技术开发利用提供了理论依据。

关键词 芳香植物精油, 化学成分, 抗菌活性, 抗生素替代品, 动物生产

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在畜牧业生产体系中, 抗生素的无序使用不仅可能引发“超级细菌”的产生, 其残留亦会造成畜产品安全和环境污染问题。抗生素的滥用导致人类细菌耐药性增加, 直接或间接地影响了人类健康。有研究显示, 抗生素耐药性每年可导致70多万人死亡(Li et al., 2018)。病原菌对抗生素产生耐药性的途径多种多样, 包括酶降解、主动外排和靶标改变等。根据2013年《中国畜禽养殖中抗生素使用情况调查报告》数据, 国内年产抗生素为2.1×10^5 t, 国内消费量为1.8×10^5 t, 其中用于动物产业的抗生素为9.7×10^4 t, 约占54%, 饲料企业所用抗生素价值高达30–35亿元。中国科学院广州地球化学研究所应光国课题组首次公布了我国抗生素的使用量以及排放量清单, 环境中常见的36种抗生素的排放量高达5.38×10^4 t, 抗生素的使用量与细菌耐药率存在正相关, 大型养殖场的动物粪便和饲料中均检出多种抗生素, 广东和广西等养猪、养鸡大省抗生素的污染较为严重(Zhang et al., 2015a)。抗生素的滥用制约着我国养殖业的健康发展, 抗菌药的耐药性目前已发展成为全球面临的挑战性问题, 仅通过研发新的抗生素难以应对愈演愈烈的耐药性。因此, 减少抗生素的使用是畜牧业健康发展的重要措施, 寻找具有抗菌作用的抗生素替代品是保持当前畜牧生产效率的有效途径。2018年世界动物卫生组织发布的《兽用抗菌药物使用情况年报》显示, 全球有86个国家和地区禁止将抗菌药作为促生长剂。2019年, 世界卫生组织已将抗微生物耐药性列为全球十大健康威胁之一。自2015年起, 我国农业部已先后禁止6种兽用抗菌药用于食品动物生产(于洋等, 2019)。

芳香植物精油是植物自身合成的天然抗菌剂, 抗菌活性由其化学成分和浓度决定。目前, 芳香植物的抗菌、抗氧化和抗炎等特性已在大量研究中得到证实(Rao et al., 2019)。鉴于芳香植物精油的抗菌性, 芳香植物在动物生产中的应用越来越广泛。中华人民共和国农业部1773号和2038号公告中规定117种药食同源天然植物可作为饲料原料使用, 其中包含多种芳香植物(如薄荷(*Mentha pulegium*)和迷迭香(*Rosmarinus officinalis*))。农业农村部第194号公告规定, 自2020年1月1日起, 停止生产和进口除中药外的所有

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促生长类药物饲料添加剂。这些政策的出台有力推动了天然植物饲料原料产品的开发和利用。本文以芳香植物资源为基础, 探讨了不同芳香植物精油及其单体成分的抗菌性, 解析了不同化学结构与抗菌效果之间的相关性, 为开发利用芳香植物精油作为饲料添加剂提供理论依据。

1 芳香植物与植物精油

芳香植物全世界有3 600多种, 在地中海沿岸的欧洲诸国以及中国、中亚、印度和南美等地分布广泛(Bakkali et al., 2008), 主要集中于唇形科、菊科、芸香科、樟科、伞形科、百合科、蔷薇科、十字花科、姜科和豆科等。目前, 很多国家和地区都开展了芳香植物的引种和栽培, 形成了各具特色的芳香产业。中国对芳香植物的利用也有悠久的历史, 早在5000多年前炎帝神农时代, 芳香植物便被用于除瘟驱疫及清净身心,《诗经》、《楚辞》以及《山海经》等先秦历史典籍里存在较多芳香植物的记录。现代社会, 芳香植物作为一类新兴的经济作物, 因富含药用成分, 常被用于食品工业、日化工业和医药等, 随着“芳香疗法”和“园艺疗法”的兴起, 芳香植物的应用越来越受到人们的青睐。

芳香植物精油主要通过水蒸馏法从花序、茎、叶片、根以及种子等不同植物组织中获得。植物精油大多存在于特定的分泌组织, 如腺毛细胞(牛至(*Origanum vulgare*))、油管(茴香(*Foeniculum vulgare*))、分泌腔(柑橘(*Citrus reticulata*))和油细胞(肉桂(*Cinnamomum cassia*))等。植物精油是天然混合物, 包含萜类、萜烯类、醇类、醛类、酮类、酯类和酚类等约20–60种化学成分, 这些化学成分所占比例大不相同, 多数以微量形式存在, 其中2–3种主要组分含量达20%–70%。例如, 牛至精油含24种化合物, 占精油总量的97.29%–98.63%, 其中香芹酚和百里香酚占精油总成分的74.59% (Kosakowska et al., 2019)。同种芳香植物因生长环境或采收时期不同, 所含精油的成分、性质和含量也不同(Bakkali et al., 2008)。此外, 植物的不同部位所含精油成分也存在差异, 牛至叶和花混合精油中香芹酚占30.73%、百里香酚占18.81%, 茎中香芹酚和百里香酚则分别占6.02%和3.46%, 根中二者分别占3.27%和1.08% (Han et al., 2017)。

2 芳香植物精油的抗菌活性比较

2.1 芳香植物精油的抗菌性

植物精油是重要的次生代谢产物, 主要是为其自身抵抗真菌、细菌和病毒的侵害以及防御昆虫和食草动物的咬食。据报道, 牛至、百里香(*Thymus vulgaris*)和肉桂等芳香植物精油具有广谱抗菌性, 精油含有的多种化学成分之间存在结构差异性, 这使其在抗菌功能方面具有多样性(表1)。抗菌评价系统中, 最低抑菌浓度(minimum inhibitory concentration, MIC) (即在体外培养细菌18–24小时后可抑制病原菌生长的最低药物浓度)是衡量抗菌差异最常用的指标, MIC越小表明药物的抗菌作用越强。

2.2 芳香植物精油的抗菌成分

植物精油独特的抗菌作用取决于其含有的化学成分, 植物精油的抗菌能力与其活性分子的官能团和结构排列有关, 其不同化学成分往往具有协同抗菌作用。在众多活性成分中, 酚类的抗菌性最强, 其次是醛类、醇类、酮类、酯类和烃类(Marinelli et al., 2018)。虽然精油成分的化学结构对其杀菌效果的影响还不完全清楚, 但大量研究表明化学结构的亲脂性以及羟基(-OH)、甲氧基(-OCH3)和烯烃键的存在对精油抗菌能力的发挥有重要作用, 这些官能团往往具有消耗质子动力、影响菌液pH值以及细菌氧化磷酸化等作用(Castillo-López et al., 2017; Zhang et al., 2020)。具有这些结构特征的化合物(如香芹酚、百里香酚、肉桂醛和丁子香酚)拥有显著的杀菌活性。牛至、百里香、肉桂和丁子香(*Syzygium aromaticum*)等芳香植物精油因此类化合物含量较高而具有较强的抑菌活性(Burt, 2004)。本文主要对植物精油中抗菌活性较好的酚类、含氧萜类和萜烯类进行抗菌活性的阐述(图1)。

酚类化合物: 酚类中的游离羟基以及离域电子对精油的抗菌活性至关重要, 香芹酚、百里香酚和丁子香酚均因酚羟基的存在而具有显著的杀菌作用(图1)。两种化学型牛至精油对6种革兰氏阴性和阳性细菌的抑制结果显示, 香芹酚型牛至精油(主成分为香芹酚, 约占75%)对6种菌株的抑制作用均高于另一种化学型牛至精油(主成分为松油烯-4-醇, 约占25%) (Aligiannis et al., 2001)。3种化学型牛至精油对金黄色葡

表1 常见芳香植物精油的主要成分和依据MIC指标的抗菌性评价

Table 1 Major components of essential oils (EOs) extracted from common aromatic plants and their antimicrobial activities based on MIC values

	物种	主要成分	作用菌种	MIC	参考文献
唇形科 (Lamiaceae)	牛至(*Origanum vulgare*)	香芹酚(64.86%)、对伞花烃(8.35%)和百里香酚(4.22%)	耐甲氧西林金黄色葡萄球菌	0.4 mg·mL^{-1}	Cui et al., 2019
	百里香(*Thymus vulgaris*)	百里香酚(51.34%)、对伞花烃(18.35%)和石竹烯(4.26%)	枯草芽孢杆菌、金黄色葡萄球菌、大肠杆菌和耻垢分枝杆菌	0.075–1.1 mg·mL^{-1}	Al Maqtari, 2011
	迷迭香(*Rosmarinus officinalis*)	1,8-桉树脑(26.54%)、α-蒎烯(20.14%)和樟脑(12.88%)	表皮葡萄球菌、金黄色葡萄球菌和枯草芽孢杆菌等	0.03%–1.0% (v/v)	Jiang et al., 2011
	唇萼薄荷(*Mentha pulegium*)	长叶薄荷酮(70.66%)和新薄荷醇(11.21%)	金黄色葡萄球菌、枯草芽孢杆菌和大肠杆菌等	1.25–10 μL·mL^{-1}	Abdelli et al., 2016
	土荆芥(*Chenopodium ambrosioides*)	α-萜品烯(40.73%)和对伞花烃(21.81%)	金黄色葡萄球菌	≥1.024 mg·mL^{-1}	de Morais Oliveira-Tintino et al., 2018
	薰衣草(*Lavandula* x *intermedia lavandin* 'Grosso')	芳樟醇(35.8%)、1,8-桉树脑(19.8%)和α-蒎烯(8.7%)	蜡状芽孢杆菌和大肠杆菌	0.94–1.87 (v/v%)	Garzoli et al., 2020
菊科 (Asteraceae)	蓍(*Achillea millefolium*)	大根香叶烯(1.1%–46.6%)、桧烯(4.0%–38.9%)和冰片(4.7%–24.9%)	金黄色葡萄球菌、表皮葡萄球菌、变形链球菌和肺炎克雷伯菌等	0.125–0.5 mg·mL^{-1}	Verma et al., 2017
	金盏花(*Calendula officinalis*)	α-杜松醇(20.6%)、香芹酮(17.9%)和荜澄茄烯(10.1%)	表皮葡萄球菌、金黄色葡萄球菌和大肠杆菌等	10–200 mg·mL^{-1}	Sahingil, 2019
伞形科 (Apiaceae)	茴香(*Foeniculum vulgare*)	茴香脑(50.4%)、甲基胡椒酚(22.4%)和柠檬烯(11.4%)	鼠伤寒沙门氏菌和大肠杆菌	0.0075–2.0 (v/v%)	Bisht, 2014
禾本科 (Poaceae)	亚香茅(*Cymbopogon nardus*)	香叶醇(33.88%)、香茅醛(27.55%)和香茅醇(14.40%)	金黄色葡萄球菌、表皮葡萄球菌和粪肠球菌	0.125–8 mg·mL^{-1}	Pontes et al., 2019
樟科 (Lauraceae)	肉桂(*Cinnamomum cassia*)	肉桂醛(85.06%)和甲氧基肉桂醛(8.79%)	金黄色葡萄球菌、大肠杆菌、产气肠杆菌、铜绿假单胞菌和霍乱弧菌等	0.075–0.6 mg·mL^{-1}	Ooi et al., 2006
	山苍子(*Litsea cubeba*)	β-柠檬醛(39.25%)、α-柠檬醛(30.9%)和柠檬烯(8.28%)	耐甲氧西林金黄色葡萄球菌	0.5 mg·mL^{-1}	Hu et al., 2019
	猴樟(*Cinnamomum bodinieri*)	芳樟醇(69.94%)和樟脑(10.90%)	大肠杆菌	200 μL·L^{-1}	Wu et al., 2019
桃金娘科 (Myrtaceae)	蓝桉(*Eucalyptus globulus*)	对伞花烃(12.58%–37.82%)、α-蒎烯(10.41%–13.39%)和1,8-桉树脑(7.71%–13.23%)	金黄色葡萄球菌、耐甲氧西林金黄色葡萄球菌和蜡状芽孢杆菌等	1–4 mg·mL^{-1}	Salem et al., 2018

MIC: 抑菌浓度评价 MIC: Minimum inhibitory concentration

萄球菌和大肠杆菌等6种致病菌的抑制结果显示，香芹酚含量占79%和60.8%的牛至精油抑制作用较强，而香芹酚占比较低的牛至精油(以石竹烯及其氧化物为主要成分，占49.4%)抗菌性较弱(Al Hafi et al., 2016)。香芹酚和百里香酚为同分异构体，二者因酚羟基位置不同而对不同细菌的抑制活性和作用效果有所差别，百里香酚对沙门氏菌的抑制作用高于香芹酚和丁子香酚(Burt, 2004; Miladi et al., 2017)。

含氧萜类化合物：以1,8-桉树脑为主要成分的白千层精油对大肠杆菌、鼠伤寒沙门氏菌和枯草芽孢杆菌具有较强的抑制活性，对表皮葡萄球菌、金黄色葡萄球菌和变形链球菌具有中等抑制活性(Padalia et al., 2015)。萜品烯-4-醇相较于α-甜没药醇、α-萜品烯、桉树脑以及橙花叔醇对弯曲杆菌的抑制作用更强(Kurekci et al., 2013)。萜品醇对金黄色葡萄球菌具极强的杀菌活性，香茅醇和香叶醇对大肠杆菌的抑制作用显著(Guimaraes et al., 2019)。肉桂醛对沙门氏菌的抑制作用最强，其次是百里香酚、丁子香酚和香芹酚(Chen et al., 2019)。通过成分标准品以及14种柑橘精油抑菌实验表明，芳樟醇对大肠杆菌和金黄色葡萄球菌等的抑制活性最强，显著高于柠檬烯、月桂烯、α-蒎烯和β-蒎烯(Guo et al., 2018)。

萜烯类化合物：以石竹烯为主要成分的大麻(*Cannabis sativa*)精油对金黄色葡萄球菌和枯草芽孢

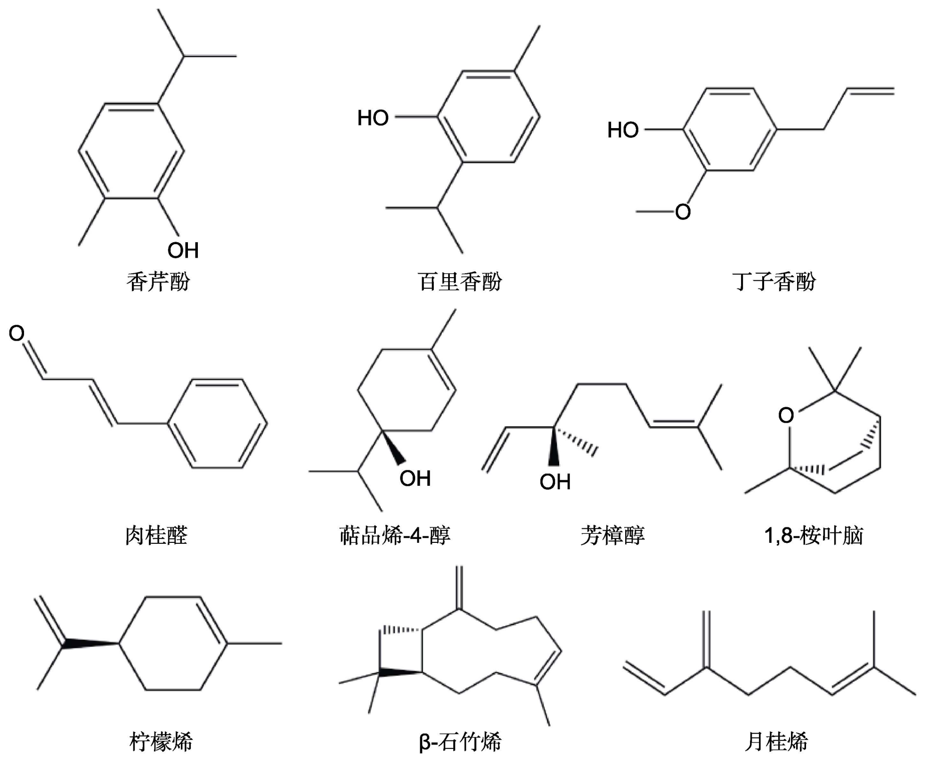

图1　植物精油中主要抗菌成分(酚类、含氧萜类和萜烯类)的化学结构

Figure 1　Chemical structures of major antimicrobial constituents (Phenols, oxygenous terpenoids, and terpenes) in plant essential oils

杆菌的抑制作用较显著, 且与抗生素环丙沙星存在协同作用(Nafis et al., 2019)。柠檬烯对金黄色葡萄球菌有显著的抑制活性, 与抗生素诺氟沙星对金黄色葡萄球菌和铜绿假单胞菌分别存在协同和拮抗作用(de Araújo et al., 2020)。月桂烯对金黄色葡萄球菌、大肠杆菌和肠炎沙门氏菌具有显著的抑制作用(Wang et al., 2019a)。

2.3　芳香植物精油的抗菌机理

植物精油的普遍疏水性促进其与细菌脂质双分子层互作, 精油化合物在双分子层中大量积累最终导致细胞破裂。大约90%–95%革兰氏阳性细菌的细胞壁由肽聚糖组成, 该特征可使疏水性化合物较易穿透细菌细胞。与革兰氏阳性细菌相比, 革兰氏阴性细菌由细胞外膜、肽聚糖和细胞内膜组成, 厚厚的外膜降低了渗透性, 并且具有亲水性脂多糖结构, 因此革兰氏阴性细菌对疏水性精油的抵抗力更强(Burt, 2004)。芳香植物精油通过不同的作用途径对致病菌活性产生抑制作用, 主要包括以下4个方面(图2A)。

(1) 脂肪酸外膜的改变: 亲脂性化合物与磷脂膜成分互作导致膜结构发生巨大变化, 物理结构扭曲引起膜的膨胀和不稳定, 增加膜的流动性和渗透性(Marinelli et al., 2018)。精油中酚类化合物的抗菌性主要通过酚羟基起作用, 它们极易进入由脂肪酸链组成的细胞外膜, 造成细胞膜膨胀以及流动性增强(Marinelli et al., 2018; Salehi et al., 2018)。碱性磷酸酶(alkaline phosphatase, AKP)存在于脂肪酸外膜和细胞质膜之间, 其活性可以反映细胞的完整性。研究发现牛至精油处理后的菌体AKP酶活性显著升高, 表明脂肪酸外膜的完整性受到破坏(陈梦玲等, 2020)。Helander等(1998)研究了同分异构体香芹酚和百里香酚以及肉桂醛对大肠杆菌和鼠伤寒沙门氏菌的抑制机理, 阐明香芹酚和百里香酚以类似的方式分解脂肪酸外膜, 并推测肉桂醛渗透进入脂肪酸外膜进而影响细胞的内部活动。月桂烯通过渗入脂肪酸外膜导致脂质缩合并使稳定性降低, 膜的破坏进一步导致细菌死亡(Połeć et al., 2020)。

(2) 细胞质膜的破坏: 芳香植物精油可以抑制并

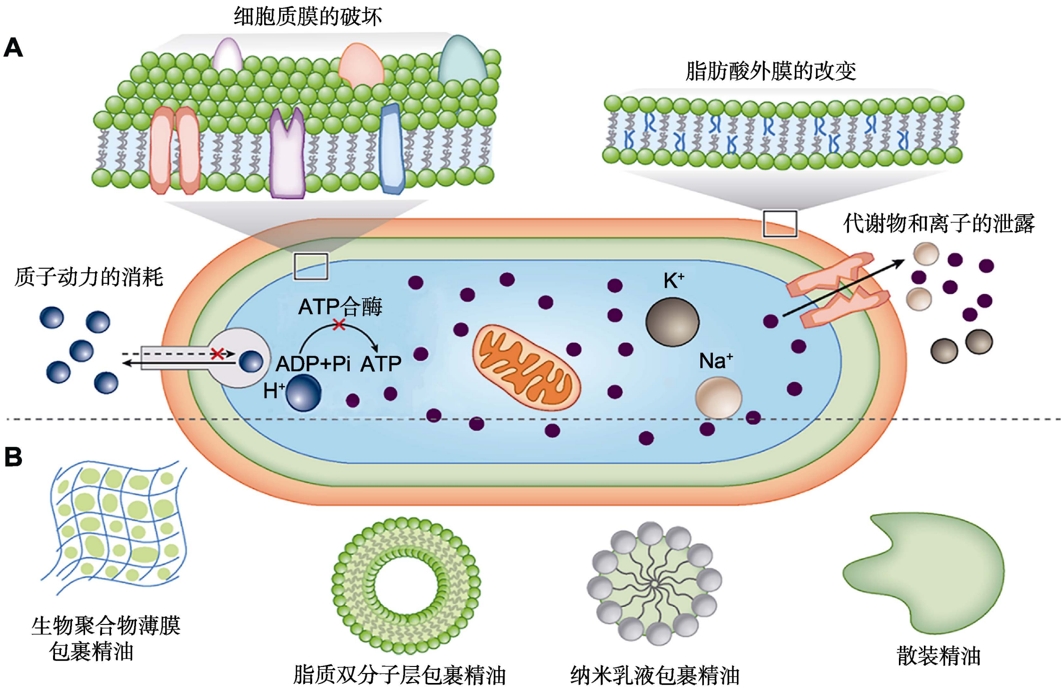

图2 精油的作用机制和包埋方式(改自Rao et al., 2019)
(A) 散装精油和不同的包埋方式; **(B)** 精油的作用机制和作用靶点。

Figure 2 Mechanisms of action and delivery systems of essential oils (EOs) (modified by Rao et al., 2019)
(A) Bulk essential oils (EOs) and different types of EO encapsulation; **(B)** Proposed mechanisms of action and target sites of EOs.

破坏细胞质膜，百里香精油对金黄色葡萄球菌的生物膜形成具有明显的抑制作用(Sharifi et al., 2018)。用百里香精油处理蜡状芽孢杆菌后，细胞膜电位明显下降，表明细胞膜去极化，细胞的代谢活动受到影响(Kang et al., 2018)。精油单体成分香芹酚、肉桂醛、丁子香酚以及芳樟醇均会破坏已经形成的细胞质膜(Zhang et al., 2020)。肉桂醛可以抑制耐甲氧西林金黄色葡萄球菌生物膜的形成以及膜合成基因*sarA*的表达(Jia et al., 2011)。用肉桂醛处理耐甲氧西林金黄色葡萄球菌后，层黏连蛋白结合蛋白(laminin binding protein, LBP)、弹性蛋白结合蛋白(elastin binding protein, EBP)以及纤维蛋白原结合蛋白(fibrinogen binding protein, FIB)等细胞膜相关编码基因表达下调，细胞膜代谢活动显著降低(Kot et al., 2020)。

(3) 质子动力的消耗: 膜结构破坏后容易引起质子动力的消耗，进而影响线粒体呼吸、电子转移链、底物氧化以及主动转运。质子动力通过ATP合酶可转化为ATP，用于多种细胞功能，而质子动力消耗后会抑制ATP的合成(Bajpai et al., 2013)。香芹酚以羟基作为跨膜离子交换剂，消耗质子动力，引起细菌细胞中阳离子的扰动，从而增加细胞膜的渗透性，最终导致细胞内容物流失(Saad et al., 2013)。Cao等(2020)研究表明，柠檬醛和香芹酚可引起阪崎肠杆菌质子动力的消耗，降低细胞内pH，影响三羧酸循环，同时激发细菌自卫反应，噬菌体休克蛋白(phage shock protein, PSP)操纵子以及*pspA*、*pspB*、*pspC*和*pspD*基因表达上调，以维持质子动力、减少细胞能量消耗和修复细胞膜。

(4) 代谢物和离子的泄露: 芳香植物精油引起的细菌细胞膜破坏会导致细胞内容物流失，从而加剧细菌的死亡。用牛至精油处理耐甲氧西林金黄色葡萄球菌后溶液的电导率增高，表明Na^+和K^+等泄露，而K^+在维持酶的活化和胞内pH方面有一定作用(Cui et al., 2019)。用百里香精油处理蜡状芽孢杆菌后，胞外蛋白质和ATP含量明显增多，表明细胞膜破裂引起内容物流失(Kang et al., 2018)。用野胡麻(*Dodartia orientalis*)精油处理大肠杆菌、金黄色葡萄球菌和肠炎链球菌12小时，在260 nm下吸收值逐渐增强，表

明胞内核酸泄漏(Wang et al., 2017)。

此外, 精油中的成分也会影响细胞正常活动所必需的酶和蛋白等的合成。例如, 酚类化合物的羟基会抑制细菌ATP酶, 从而影响ATP的合成(Swamy et al., 2016)。香芹酚诱导大肠杆菌O157:H7产生大量的热激蛋白60 (heat shock protein 60, HSP60), 抑制鞭毛蛋白的合成, 导致细菌无法运动(Burt et al., 2007)。丁子香酚抑制蜡状芽孢杆菌中淀粉酶和蛋白酶的合成(Burt, 2004)以及细菌组氨酸脱羧酶活性(Swamy et al., 2016)。

3 芳香植物精油在动物生产中的应用

随着养殖业集约化和规模化发展, 动物因细菌感染而死亡给我国养殖业造成很大的经济损失, 抗生素虽能抑制畜禽某些疾病的发生, 但其带来的负面影响亦不容忽视。基于植物精油的抗菌性, 将其加入动物饲料中可有效替代抗生素以减弱病菌的致病性, 改善反刍动物瘤胃发酵。以香芹酚为主要成分的植物精油可抑制猪体内的大肠杆菌及家禽产气荚膜梭菌, 改善坏死性肠炎, 促进猪、鸡和鹌鹑等禽畜的肠道健康, 净化养殖环境, 增强动物的免疫力, 促进动物生长, 为人类提供无污染和无残留的动物性食品。植物精油是多种化合物的混合物, 每种化学成分的生物活性和作用机理都有其自身特性, 致使植物精油在动物实验中的效果各不相同(表2)。

3.1 提高动物的消化吸收能力

动物肠道内菌群平衡是影响消化吸收能力的重要因素, 植物精油可选择性地影响肠道微生物群落, 而肠道菌群平衡有助于提高动物的消化吸收能力(周洋等, 2018)。高酚含量的饲料添加剂组分之间存在协同作用, 可促进动物生长并影响肠道菌群, 进而影响动物的生长代谢(Giannenas et al., 2019)。例如, 反刍动物中的纤维素分解细菌可将纤维素消化成能发酵的葡萄糖, 进而用于微生物发酵及提供动物使用的底物(否则纤维素不会被宿主利用)。因此, 植物精油可通

表2 芳香植物精油在动物生产中的应用评价

Table 2 Evaluation of the effects of essential oils extracted from common aromatic plants on animal production

动物	植物材料	效果	参考文献
羊	牛至(*Origanum vulgare* ssp. *hirtum*)	抑制产甲烷菌, 改善瘤胃发酵	Paraskevakis, 2018
	迷迭香(*Rosmarinus officinalis*)	影响生物氢化细菌, 促进瘤胃发酵	Kholif et al., 2017
牛	百里香(*Thymus vulgaris*)和锡兰肉桂(*Cinnamomum zeylanicum*)	产甲烷菌的相对丰度降低, 琥珀酸纤维杆菌和白色瘤胃球菌的数量下降, 植物精油添加剂可作为瘤胃发酵调节剂	Khorrami et al., 2015
	百里香	对引起牛乳腺炎的金黄色葡萄球菌和乳房链球菌等有抑制作用	Mullen et al., 2014
	精油混合物	抑制牛呼吸系统疾病相关的细菌病原体	Amat et al., 2017
猪	精油混合物	直肠大肠杆菌和总厌氧菌数量降低, 免疫球蛋白增多	Zeng et al., 2015
	精油混合物	乳酸杆菌增多, 粪便中大肠杆菌数量减少	Li et al., 2012
	精油混合物	乳酸杆菌增多	Zhang et al., 2015b
	精油混合物	粪便中乳酸菌增多, 大肠杆菌数量减少	Zhang et al., 2016
鸡	牛至(*O. vulgare*)	盲肠大肠杆菌减少, 乳酸菌无影响	Roofchaee et al., 2011
	精油混合物	乳酸菌等肠道菌群发生变化	Liu et al., 2017
	精油混合物	抑制沙门氏菌繁殖, 减少交叉感染	Alali et al., 2013
	精油混合物	抑制产气荚膜梭状芽孢杆菌, 治疗坏死性肠炎	Jerzsele et al., 2012
	精油混合物	蛋白酶与精油具有协同作用, 回肠中乳杆菌密度增加而大肠杆菌减少	Park and Kim, 2018
鹌鹑	西亚百里香(*T. spicata*)	改善肠道微生物组成, 有利于其健康生长	Aksu et al., 2014
	迷迭香	大肠杆菌和沙门氏菌等肠道致病菌减少	Mahgoub et al., 2019
鱼	盆牛至(*O. onites*)	促进生长, 有效避免加氏乳球菌感染	Diler et al., 2017
	冬牛至(*O. heracleoticum*)	促进生长, 对嗜水气单胞菌感染的抵抗力增强	Zheng et al., 2009
	甜橙(*Citrus sinensis*)	抑制链球菌感染, 具有免疫调节作用	Acar et al., 2015

过定向选择有助于动物代谢的特定菌群，增强饲料转化，促进动物生长(Kim et al., 2012)。低蛋白饲料中添加牛至精油可调节肠道细菌，从而改善动物的生长性能和营养消化率(Cheng et al., 2018)。

3.2 改善动物消化道菌群的分布

饲料中添加牛至和大蒜(*Allium sativum*)精油可以减少肉鸡肠道梭状芽孢杆菌和链球菌的数量(Kırkpınar, 2011)。百里香、牛至以及肉桂等混合精油可降低瘤胃微生物的数量，同时使甲烷产量以及乙酸盐与丙酸盐的比率降低，进而调节瘤胃发酵(Lin et al., 2012)。香芹酚、肉桂醛以及辣椒油树脂的混合物可以增加早期断奶仔猪盲肠的乳杆菌数量，提高空肠中乳酸杆菌与肠杆菌的比例(Manzanilla et al., 2006)。百里香酚和肉桂醛可以提高鸡肠道乳酸杆菌的数量，降低大肠杆菌的数量(Jamroz et al., 2006)。总之，芳香植物精油的添加可以提高肠道中益生菌与有害菌的比例。有害细菌的减少可有效避免动物被屠宰时的胴体污染，且植物精油活性成分在代谢组织中的积累可以抑制腐败或致病细菌的生长，从而延长肉类产品的货架期。

3.3 缓解动物病害

奶牛犊易因病原菌引起的腹泻而死亡，植物混合精油的添加可以抑制肠道病原菌(乳酸菌、纤维素和淀粉分解菌等则不受影响)，缓解腹泻(Santos et al., 2015)。以柠檬烯为主要成分的柑橘精油对引起小猪腹泻的大肠杆菌有显著抑制作用，而对肠道益生菌(乳酸杆菌)的抑制作用很小。同时，细菌群落与体内氧化应激也存在相关性，乳酸杆菌与氧化应激呈负相关，而大肠杆菌与氧化应激呈强正相关，精油的添加可降低体内的氧化应激反应(Ambrosio et al., 2019)。以肉桂醛为主要成分的肉桂精油对引起牛乳腺炎的金黄色葡萄球菌和大肠杆菌等致病菌有高效抑制作用(Zhu et al., 2016)。百里香和迷迭香精油可抑制鱼病原链球菌毒力基因*SagA*的表达，减少溶血素产生，从而缓解由链球菌引起的鱼类相关疾病(Soltani et al., 2014)。

3.4 增强动物的免疫力

肠道微生物群与黏膜免疫系统存在密切联系，植物精油与微生物互作可改变肠道中淋巴细胞的分布及肠道免疫系统的发育和功能，提高动物自身的免疫能力(Zhai et al., 2018)。百里香酚、香芹酚以及牛至精油作为鱼饲料添加剂，可使食用8周后的鱼的嗜水气单胞菌感染率降低，免疫系统相关酶(如溶菌酶、超氧化物歧化酶和过氧化氢酶)的活性升高(Zheng et al., 2009)。以百里香酚和肉桂醛为主要成分的混合精油可减少断奶仔猪肠道大肠杆菌的数量，降低腹泻发生率，同时增加淋巴细胞转化和白细胞吞噬率及提高血液中免疫球蛋白IgA和IgM的水平，增强其免疫力(Li et al., 2012)。

4 植物精油功能研究的新技术

4.1 植物精油组配的抗菌性应用

植物精油的抗菌活性不是一种特定作用模式的结果，而是多种活性成分对细菌细胞不同细胞器各种靶标的协同作用。牛至与百里香混合精油比各自单方精油对蜡状芽孢杆菌、大肠杆菌、单核细胞增生李斯特菌和铜绿假单胞菌的抑制作用更强(Gutierrez et al., 2008)。肉桂和丁香(*Syzygium aromaticum*)精油配合使用对大肠杆菌的生长具有拮抗作用，但二者协同抑制单核细胞增生李斯特菌、蜡状芽孢杆菌和小肠结肠炎耶尔森氏菌的生长(Goñi et al., 2009)。肉桂醛与百里香酚(或香芹酚)合用对鼠伤寒沙门氏菌具有协同抑制作用(Zhou et al., 2007)。百里香酚、丁子香酚和香芹酚的结构相似，三者低浓度组合具有协同抗菌作用(Bassolé and Juliani, 2012)。除百里香酚和香芹酚外，ρ-伞花烃作为香芹酚合成前体，是牛至精油的另一主要成分，其抗菌作用较弱，但可促使细菌细胞膜膨胀从而协助香芹酚透过细胞质膜，这表明精油不同成分之间存在协同抑菌作用(Bouhaddouda et al., 2016)。此外，植物精油与抗生素结合使用对致病菌的生长也往往具有协同抑制作用。土荆芥(*Chenopodium ambrosioides*)精油与抗生素诺氟沙星组合对金黄色葡萄球菌有协同抑制作用(de Morais Oliveira-Tintino et al., 2018)。椒样薄荷(*Mentra piperita*)精油与头孢他啶配合使用可协同抑制绿脓杆菌的生长(李慧等, 2011)。牛至、百里香精油与氟喹诺酮类抗生素组合可抑制耐氟喹诺酮肺炎链球菌的生长(Ghafari et al., 2018)。

4.2 植物精油包被技术的抗菌性应用

植物精油易挥发，有效成分不稳定，这些缺点限制了其应用，而精油包被技术的发展可解决此类问题。包被是将一种或几种材料的混合物嵌入(或表面上覆盖)另一种或几种材料混合物的技术。香芹酚包被后可实现在消化道内定点释放，更好地发挥其抗菌作用，拓展了其应用范围(张永刚，2012)。精油常见包埋方式包括通过纳米乳液、脂质双分子层和生物聚合物薄膜等手段(图2B)。纳米乳液比其它类型的包埋方式物理稳定性更好，与散装精油相比抗菌活性更强(Rao et al., 2019)。百里香精油与壳聚糖复合形成纳米颗粒后抗菌能力显著升高(Sotelo-Boyás et al., 2017)。牛至精油在β-环糊精中包封成纳米微胶囊后具有长达11天的连续缓释过程，极大地拓宽了其应用领域(Kotronia et al., 2017)。牛至精油与生物银纳米粒子结合，对金黄色葡萄球菌的抑制作用存在协同增效功能(Scandorieiro et al., 2016)。丁香精油经海藻酸钠和乳化剂包封后，对金黄色葡萄球菌及鼠伤寒沙门氏菌的抑制活性显著增强(Radünz et al., 2019)。脂质体是自发形成的表面活性剂传递系统，能够在水溶液中将植物精油包封于脂质双分子层的非极性区域(Rao et al., 2019)。牛至精油中分离出的香芹酚和百里香酚经脂质体包封后，对金黄色葡萄球菌和铜绿假单胞菌等的抑制作用显著增强(Liolios et al., 2009)。脂质体包裹的茶树(*Camellia sinensis*)精油和银离子对铜绿假单胞菌、金黄色葡萄球菌及白色念珠菌具有显著抑制作用(Low et al., 2013)。此外，有研究表明精油成分香芹酚、百里香酚、丁子香酚和肉桂醛在饲喂动物2小时后，会被它们的胃和近端小肠几乎完全吸收(Manzanilla et al., 2006)，而精油微胶囊化可有效避免其被前肠完全吸收，使得精油可在后肠行使抗菌功能并改变微生物群落的生态系统。植物精油微胶囊化后可实现在动物肠道中定点释放，进而在消化道不同部位发挥作用(de Lange et al., 2010)。

4.3 植物精油功能的组学研究应用

快速发展的“组学”技术推进了精油的抗菌机制研究。利用转录组学、蛋白质组学、代谢组学和宏基因组等手段，可揭示植物精油作用于细菌后基因、蛋白、代谢物水平以及细菌群落的改变，并可确定其潜在的细胞靶标，以筛选有效植物精油。微生物通过小信号分子进行胞间通信和信息共享(包括抗生素抗性以及生物膜形成)的能力被称为群体感应(quorum sensing, QS)。Wang等(2019b)通过转录组分析发现，用丁子香酚处理耐药肺炎克雷伯菌后群体感应信号分子*AI-2*相关基因的表达下调，进而抑制细菌的生长繁殖。Liu等(2019)通过转录组和蛋白质组联合分析揭示了肉桂醛可通过调节沙门氏菌*SIPA*和*SIPB*基因的转录表达，抑制毒力蛋白SPI-1产生，从而保护被沙门氏菌感染的宿主细胞。此外, Li等(2018)通过对猪肠道微生物组和代谢组联合分析，发现饲料中添加精油后，猪肠道内芽孢杆菌和乳杆菌等有益菌数量明显增加，结肠中的微生物代谢谱发生变化，氨基酸、脂质和蛋白质代谢加快(Li et al., 2018)。Reyer等(2017)对空肠和肝组织进行转录组分析，发现精油会引起肉鸡的碳水化合物和脂肪酸代谢增强，进而改善肉鸡的生产性能。Lei等(2019)对山羊瘤胃进行了宏基因组学分析，发现精油-钴配合物可影响瘤胃微生物群落的分布，提高饲料转化率和减少氨气排放。

5 小结

在减抗和替抗政策下，畜牧业开始向“绿色养殖”发展，寻找抗生素替代品是目前畜牧业发展的当务之急。芳香植物精油因其独特的抗菌性能，作为饲料添加剂的发展前景广阔，但同时也存在一些问题。(1) 植物精油种类多样、成分复杂、易挥发且易氧化；并且植物精油的化学成分、含量和活性会因物种、组织部位、地理位置、土壤条件、收获季节、气候条件和害虫等因素发生较大的变化(潘岩等，2012; Asensio et al., 2015; Gerami et al., 2016)。例如，冬季二次采收的迷迭香精油对大肠杆菌和金黄色葡萄球菌等的抑制作用更强(石雷等, 2015)。(2) 芳香植物精油添加剂进入动物体后需要经过胃肠道的消化吸收，胃肠道通过具有许多神经和受体的化学感应系统感知化学物质和微生物，而复杂的肠道生态系统导致芳香植物精油的抗菌机制目前并不十分清楚。(3) 缺乏芳香植物精油应用的新技术研发。例如，不同植物精油的组配和包埋技术对抗菌功能效果的提升有重要作用，组学技术对功能机制研究有很强的推动作用。基于上述问题，提出以下3方面建议：(1) 在国家芳香植物种质资源库建设的基础上，进一步完善芳香植物精油成分

数据库，为杀菌剂的选择提供基础性数据；(2) 针对动物生产中的主要病害进行更广范的芳香植物精油抗菌性评价，运用多组学技术深入解析芳香植物精油的抗菌机制；(3) 加强芳香植物精油应用技术的开发利用，包括精油组配技术、包埋技术和安全性评价技术等，以解决动物生产中替代抗生素问题，促进畜牧业的可持续发展。

参考文献

陈梦玲，蓝蔚青，李函笑，任智楚，芦子萱，谢晶 (2020). 牛至精油对腐生葡萄球菌抑制作用机制. 食品科学 **41**, 46–51.

李慧，白红彤，王晓，姜闯道，张金政，石雷 (2011). 椒样薄荷、薄荷和苏格兰留兰香精油与抗生素的协同抑菌功能. 植物学报 **46**, 37–43.

潘岩，白红彤，李慧，姜闯道，石雷 (2012). 栽培地区、采收季节和株龄对迷迭香精油成分和抑菌活性的影响. 植物学报 **47**, 625–636.

石雷，潘岩，李慧，白红彤 (2015). 一种采收迷迭香的方法和制备具有抑菌活性提取物的方法. 中国专利，CN2012101-58838.4. 2015-07-01.

于洋，方亮星，周宇峰，孙坚，廖晓萍，刘雅红 (2019). 畜牧业发展中抗菌药应用的“利”与“刃”. 中国科学院院刊 **34**, 152–162.

张永刚 (2012). 植物源抗菌剂香芹酚定点释放包被技术的开发. 博士论文. 长沙: 中国科学院亚热带农业生态研究所. pp. 1–194.

周洋，彭艳，周小秋 (2018). 植物精油对动物生长和免疫力的影响及其作用机制. 动物营养学报 **30**, 37–43.

Abdelli M, Moghrani H, Aboun A, Maachi R (2016). Algerian *Mentha pulegium* L. leaves essential oil: chemical composition, antimicrobial, insecticidal and antioxidant activities. *Ind Crops Prod* **94**, 197–205.

Acar Ü, Kesbic OS, Yılmaz S, Gültepe N, Türker A (2015). Evaluation of the effects of essential oil extracted from sweet orange peel (*Citrus sinensis*) on growth rate of tilapia (*Oreochromis mossambicus*) and possible disease resistance against *Streptococcus iniae*. *Aquaculture* **437**, 282–286.

Aksu T, Aksu MI, Önel SE, Yakan A, Kaya DA, Baylan M (2014). Effect of thyme oil (*Thymbra spicata* l. var. *spicata*) on meat quality in Japanese quails. *Europ Poult Sci* **78**, 10.1399/eps.2013.6.

Al Hafi M, El Beyrouthy M, Ouaini N, Stien D, Rutledge D, Chaillou S (2016). Chemical composition and antimicrobial activity of *Origanum libanoticum*, *Origanum ehrenbergii*, and *Origanum syriacum* growing wild in Lebanon. *Chem Biodivers* **13**, 555–560.

Al Maqtari MAA, Alghalibi SM, Alhamzy EH (2011). Chemical composition and antimicrobial activity of essential oil of *Thymus vulgaris* from Yemen. *Turk J Biochem* **36**, 342–349.

Alali WQ, Hofacre CL, Mathis GF, Faltys G (2013). Effect of essential oil compound on shedding and colonization of *Salmonella enterica serovar* Heidelberg in broilers. *Poult Sci* **92**, 836–841.

Aligiannis N, Kalpoutzakis E, Mitaku S, Chinou IB (2001). Composition and antimicrobial activity of the essential oils of two *Origanum* species. *J Agric Food Chem* **49**, 4168–4170.

Amat S, Baines D, Alexander TW (2017). Antimicrobial activities of commercial essential oils against the bovine respiratory pathogen *Mannheimia haemolytica* and analysis of their chemical composition and cytotoxicity on bovine turbinate cells. *J Anim Sci* **95**, 122–123.

Ambrosio CMS, Ikeda NY, Miano AC, Saldaña E, Moreno AM, Stashenko E, Contreras-Castillo CJ, Da Gloria EM (2019). Unraveling the selective antibacterial activity and chemical composition of citrus essential oils. *Sci Rep* **9**, 17719.

Asensio CM, Grosso NR, Juliani HR (2015). Quality characters, chemical composition and biological activities of oregano (*Origanum* spp.) essential oils from central and Southern Argentina. *Ind Crops Prod* **63**, 203–213.

Bajpai VK, Sharma A, Baek KH (2013). Antibacterial mode of action of *Cudrania tricuspidata* fruit essential oil, affecting membrane permeability and surface characterristics of food-borne pathogens. *Food Control* **32**, 582–590.

Bakkali F, Averbeck S, Averbeck D, Idaomar M (2008). Biological effects of essential oils. *Food Chem Toxicol* **46**, 446–475.

Bassolé IHN, Juliani HR (2012). Essential oils in combination and their antimicrobial properties. *Molecules* **17**, 3989–4006.

Bisht DS, Menon KRK, Singhal MK (2014). Comparative antimicrobial activity of essential oils of *Cuminum cyminum* L. and *Foeniculum vulgare* Mill. seeds against *Salmonella typhimurium* and *Escherichia coli*. *J Essent Oil Bear Plants* **17**, 617–622.

Bouhaddouda N, Aouadi S, Labiod R (2016). Evaluation of chemical composition and biological activities of essential oil and methanolic extract of *Origanum vulgare* L. ssp. *glandulosum* (Desf.) Ietswaart from Algeria. *Int J Pharmacogn Phytochem Res* **8**, 104–112.

Burt S (2004). Essential oils: their antibacterial properties and potential applications in foods. *Int J Food Microbiol* **94**, 223–253.

Burt SA, van der Zee R, Koets AP, de Graaff AM, van Knapen F, Gaastra W, Haagsman HP, Veldhuizen EJA (2007). Carvacrol induces heat shock protein 60 and inhibits synthesis of flagellin in *Escherichia coli* O157:H7. *Appl Environ Microbiol* **73**, 4484–4490.

Cao YF, Zhou AL, Zhou DG, Xiao XL, Yu YG, Li XF (2020). *Cronobacter sakazakii* CICC 21544 responds to the combination of carvacrol and citral by regulating proton motive force. *LWT-Food Sci Technol* **122**, 109040.

Castillo-López RI, Gutiérrez-Grijalva EP, Leyva-López N, López-Martínez LX, Heredia JB (2017). Natural alternatives to growth-promoting antibiotics (GPA) in animal production. *J Anim Plant Sci* **27**, 349–359.

Chen CH, Yin HB, Upadhayay A, Brown S, Venkitanarayanan K (2019). Efficacy of plant-derived antimicrobials for controlling *Salmonella* Schwarzengrund on dry pet food. *Int J Food Microbiol* **296**, 1–7.

Cheng CS, Xia M, Zhang XM, Wang C, Jiang SW, Peng J (2018). Supplementing oregano essential oil in a reduced-protein diet improves growth performance and nutrient digestibility by modulating intestinal bacteria, intestinal morphology, and antioxidative capacity of growing-finishing pigs. *Animals* **8**, 159.

Cui HY, Zhang CH, Li CZ, Lin L (2019). Antibacterial mechanism of oregano essential oil. *Ind Crops Prod* **139**, 111498.

de Araújo ACJ, Freitas PR, Barbosa CRD, Muniz DF, Rocha JE, da Silva ACA, Oliveira-Tintino ADD, Jaime RF, da Silva LE, Confortin C, do Amaral W, Deschamps C, Barbosa JM, de Lima NTR, Tintino SR, Coutinho HDM (2020). GC-MS-FID characterization and antibacterial activity of the *Mikania cordifolia* essential oil and limonene against MDR strains. *Food Chem Toxicol* **136**, 111023.

de Lange CFM, Pluske J, Gong J, Nyachoti CM (2010). Strategic use of feed ingredients and feed additives to stimulate gut health and development in young pigs. *Livest Sci* **134**, 124–134.

de Morais Oliveira-Tintino CD, Tintino SR, Limaverde PW, Figueredo FG, Campina FF, da Cunha FAB, da Costa RHS, Pereira PS, Lima LF, de Matos YMLS, Coutinho HDM, Siqueira-Júnior JP, Balbino VQ, da Silva TG (2018). Inhibition of the essential oil from *Chenopodium ambrosioides* L. and α-terpinene on the NorA efflux-pump of *Staphylococcus aureus. Food Chem* **262**, 72–77.

Diler O, Gormez O, Diler I, Metin S (2017). Effect of oregano (*Origanum onites* L.) essential oil on growth, lysozyme and antioxidant activity and resistance against *Lactococcus garvieae* in rainbow trout, *Oncorhynchus mykiss* (Walbaum). *Aquacult Nutr* **23**, 844–851.

Garzoli S, Petralito S, Ovidi E, Turchetti G, Laghezza Masci V, Tiezzi A, Trilli J, Cesa S, Casadei MA, Giacomello P, Paolicelli P (2020). *Lavandula* x *intermedia* essential oil and hydrolate: evaluation of chemical composition and antibacterial activity before and after formulation in nanoemulsion. *Ind Crops Prod* **145**, 112068.

Gerami F, Moghaddam PR, Ghorbani R, Hassani A (2016). Effects of irrigation intervals and organic manure on morphological traits, essential oil content and yield of oregano (*Origanum vulgare* L.). *An Acad Bras Ciênc* **88**, 2375–2385.

Ghafari O, Sharifi A, Ahmadi A, Fasaei BN (2018). Antibacterial and anti-PmrA activity of plant essential oils against fluoroquinolone-resistant *Streptococcus pneumoniae* clinical isolates. *Lett Appl Microbiol* **67**, 564–569.

Giannenas I, Bonos E, Filliousis G, Stylianaki I, Kumar P, Lazari D, Christaki E, Florou-Paneri P (2019). Effect of a polyherbal or an arsenic-containing feed additive on growth performance of broiler chickens, intestinal microbiota, intestinal morphology, and lipid oxidation of breast and thigh meat. *J Appl Poult Res* **28**, 164–175.

Goñi P, López P, Sánchez C, Gómez-Lus R, Becerril R, Nerín C (2009). Antimicrobial activity in the vapour phase of a combination of cinnamon and clove essential oils. *Food Chem* **116**, 982–989.

Guimarães AC, Meireles LM, Lemos MF, Guimaraes MCC, Endringer DC, Fronza M, Scherer R (2019). Antibacterial activity of terpenes and terpenoids present in essential oils. *Molecules* **24**, 2471.

Guo JJ, Gao ZP, Xia JL, Ritenour MA, Li GY, Shan Y (2018). Comparative analysis of chemical composition, antimicrobial and antioxidant activity of citrus essential oils from the main cultivated varieties in China. *LWT-Food Sci Technol* **97**, 825–839.

Gutierrez J, Barry-Ryan C, Bourke R (2008). The antimicrobial efficacy of plant essential oil combinations and interactions with food ingredients. *Int J Food Microbiol* **124**, 91–97.

Han F, Ma GQ, Yang M, Yan L, Xiong W, Shu JC, Zhao ZD, Xu HL (2017). Chemical composition and antioxidant activities of essential oils from different parts of the oregano. *J Zhejiang Univ Sci B* **18**, 79–84.

Helander IM, Alakomi HL, Latva-Kala K, Mattila-Sandholm T, Pol I, Smid EJ, Gorris LGM, von Wright A (1998). Characterization of the action of selected essential oil components on gram-negative bacteria. *J Agric Food Chem* **46**, 3590–3595.

Hu W, Li CZ, Dai JM, Cui HY, Lin L (2019). Antibacterial activity and mechanism of *Litsea cubeba* essential oil against methicillin-resistant *Staphylococcus aureus (MRSA)*. *Ind Crops Prod* **130**, 34–41.

Jamroz D, Wertelecki T, Houszka M, Kamel C (2006). Influence of diet type on the inclusion of plant origin active substances on morphological and histochemical characteristics of the stomach and jejunum walls in chicken. *J Anim Physiol Anim Nutr* **90**, 255–268.

Jerzsele A, Szeker K, Csizinszky R, Gere E, Jakab C, Mallo JJ, Galfi P (2012). Efficacy of protected sodium butyrate, a protected blend of essential oils, their combination, and *Bacillus amyloliquefaciens* spore suspension against artificially induced necrotic enteritis in broilers. *Poult Sci* **91**, 837–843.

Jia P, Xue YJ, Duan XJ, Shao SH (2011). Effect of cinnamaldehyde on biofilm formation and sarA expression by methicillin-resistant *Staphylococcus aureus*. *Lett Appl Microbiol* **53**, 409–416.

Jiang Y, Wu N, Fu YJ, Wang W, Luo M, Zhao CJ, Zu YG, Liu XL (2011). Chemical composition and antimicrobial activity of the essential oil of rosemary. *Environ Toxicol Pharmacol* **32**, 63–68.

Kang JM, Liu L, Wu XX, Sun YY, Liu ZF (2018). Effect of thyme essential oil against *Bacillus cereus* planktonic growth and biofilm formation. *Appl Microbiol Biotechnol* **102**, 10209–10218.

Kholif AE, Matloup OH, Morsy TA, Abdo MM, Abu Elella AA, Anele UY, Swanson KC (2017). Rosemary and lemongrass herbs as phytogenic feed additives to improve efficient feed utilization, manipulate rumen fermentation and elevate milk production of Damascus goats. *Livest Sci* **204**, 39–46.

Khorrami B, Vakili AR, Mesgaran MD, Klevenhusen F (2015). Thyme and cinnamon essential oils: potential alternatives for monensin as a rumen modifier in beef production systems. *Anim Feed Sci Technol* **200**, 8–16.

Kim HB, Borewicz K, White BA, Singer RS, Sreevatsan S, Tu ZJ, Isaacson RE (2012). Microbial shifts in the swine distal gut in response to the treatment with antimicrobial growth promoter, tylosin. *Proc Natl Acad Sci USA* **109**, 15485–15490.

Kırkpınar F, Ünlü HB, Özdemir G (2011). Effects of oregano and garlic essential oils on performance, carcase, organ and blood characteristics and intestinal microflora of broilers. *Livest Sci* **137**, 219–225.

Kosakowska O, Węglarz Z, Bączek K (2019). Yield and quality of 'Greek oregano' (*Origanum vulgare* L. subsp. *hirtum*) herb from organic production system in temperate climate. *Ind Crops Prod* **141**, 111782.

Kot B, Sytykiewicz H, Sprawka I, Witeska M (2020). Effect of trans-cinnamaldehyde on methicillin-resistant *Staphylococcus aureus* biofilm formation: metabolic activity assessment and analysis of the biofilm-associated genes expression. *Int J Mol Sci* **21**, 102.

Kotronia M, Kavetsou E, Loupassaki S, Kikionis S, Vouyiouka S, Detsi A (2017). Encapsulation of oregano (*Origanum onites* L.) essential oil in β-cyclodextrin (β-CD): synthesis and characterization of the inclusion complexes. *Bioengineering* **4**, 74.

Kurekci C, Padmanabha J, Bishop-Hurley SL, Hassan E, Al Jassim RAM, McSweeney CS (2013). Antimicrobial activity of essential oils and five terpenoid compounds against *Campylobacter jejuni* in pure and mixed culture experiments. *Int J Food Microbiol* **166**, 450–457.

Lei ZM, Zhang K, Li C, Jiao T, Wu JP, Wei YB, Tian KC, Li C, Tang DF, Davis DI, Casper DP, Jiang H, Wang XL, Wang JF (2019). Ruminal metagenomic analyses of goat data reveals potential functional microbiota by supplementation with essential oil-cobalt complexes. *BMC Microbiol* **19**, 30.

Li SY, Ru YJ, Liu M, Xu B, Péron A, Shi XG (2012). The effect of essential oils on performance, immunity and gut microbial population in weaner pigs. *Livest Sci* **145**, 119–123.

Li Y, Fu XF, Ma X, Geng SJ, Jiang XM, Huang QC, Hu CH, Han XY (2018). Intestinal microbiome-metabolome responses to essential oils in piglets. *Front Microbiol* **9**, 1988.

Lin B, Lu Y, Wang JH, Liang Q, Liu JX (2012). The effects of combined essential oils along with fumarate on rumen fermentation and methane production *in vitro*. *J Anim Feed Sci* **21**, 198–210.

Liolios CC, Gortzi O, Lalas S, Tsaknis J, Chinou I (2009). Liposomal incorporation of carvacrol and thymol isolated from the essential oil of *Origanum dictamnus* L. and *in vitro* antimicrobial activity. *Food Chem* **112**, 77–83.

Liu Y, Yang X, Xin HL, Chen S, Yang CB, Duan YL, Yang XJ (2017). Effects of a protected inclusion of organic acids and essential oils as antibiotic growth promoter alternative on growth performance, intestinal morphology and gut microflora in broilers. *Anim Sci J* **88**, 1414–1424.

Liu Y, Zhang Y, Zhou YL, Wang TT, Deng XM, Chu X, Zhou TZ (2019). Cinnamaldehyde inhibits type three secretion system in *Salmonella* enterica serovar Typhimurium by affecting the expression of key effector proteins. *Vet Microbiol* **239**, 108463.

Low WL, Martin C, Hill DJ, Kenward MA (2013). Antimicrobial efficacy of liposome-encapsulated silver ions and tea tree oil against *Pseudomonas aeruginosa, Staphylococcus aureus* and *Candida albicans*. *Lett Appl Microbiol* **57**, 33–39.

Mahgoub SAM, El-Hack MEA, Saadeldin IM, Hussein MA, Swelum AA, Alagawany M (2019). Impact of *Rosmarinus officinalis* cold-pressed oil on health, growth performance, intestinal bacterial populations, and immunocompetence of Japanese quail. *Poult Sci* **98**, 2139–2149.

Manzanilla EG, Nofrarías M, Anguita M, Castillo M, Perez JF, Martín-Orúe SM, Kamel C, Gasa J (2006). Effects of butyrate, avilamycin, and a plant extract combination on the intestinal equilibrium of early-weaned pigs. *J Anim Sci* **84**, 2743–2751.

Marinelli L, Di Stefano A, Cacciatore I (2018). Carvacrol and its derivatives as antibacterial agents. *Phytochem Rev* **17**, 903–921.

Miladi H, Zmantar T, Kouidhi B, Chaabouni Y, Mahdouani K, Bakhrouf A, Chaieb K (2017). Use of carvacrol, thymol, and eugenol for biofilm eradication and resistance modifying susceptibility of *Salmonella enterica* serovar *Typhimurium* strains to nalidixic acid. *Microb Pathog* **104**, 56–63.

Mullen KAE, Lee AR, Lyman RL, Mason SE, Washburn SP, Anderson KL (2014). An *in vitro* assessment of the antibacterial activity of plant-derived oils. *J Dairy Sci* **97**, 5587–5591.

Nafis A, Kasrati A, Jamali CA, Mezrioui N, Setzer W, Abbad A, Hassani L (2019). Antioxidant activity and evidence for synergism of *Cannabis sativa* (L.) essential oil with antimicrobial standards. *Ind Crops Prod* **137**, 396–400.

Ooi LSM, Li YL, Kam SL, Wang H, Wong EYL, Ooi VEC (2006). Antimicrobial activities of cinnamon oil and cinnamaldehyde from the Chinese medicinal herb *Cinnamomum cassia* Blume. *Am J Chin Med* **34**, 511–522.

Padalia RC, Verma RS, Chauhan A, Goswami P, Verma SK, Darokar MP (2015). Chemical composition of *Melaleuca linarrifolia* Sm. from India: a potential source of 1,8-cineole. *Ind Crops Prod* **63**, 264–268.

Paraskevakis N (2018). Effects of dietary Greek oregano (*Origanum vulgare* ssp. *hirtum*) supplementation on rumen fermentation, enzyme profile and microbial communities in goats. *J Anim Physiol Anim Nutr* **102**, 701–705.

Park JH, Kim IH (2018). Effects of a protease and essential oils on growth performance, blood cell profiles, nutrient retention, ileal microbiota, excreta gas emission, and breast meat quality in broiler chicks. *Poult Sci* **97**, 2854–2860.

Połeć K, Broniatowski M, Wydro P, Hąc-Wydro K (2020). The impact of β-myrcene—the main component of the hop essential oil on the lipid films. *J Mol Liq* **308**, 113028.

Pontes EKU, Melo HM, Nogueira JWA, Firmino NCS, de Carvalho MG, Catunda FEA, Cavalcante TTA (2019). Antibiofilm activity of the essential oil of citronella (*Cymbopogon nardus*) and its major component, geraniol, on the bacterial biofilms of *Staphylococcus aureus*. *Food Sci Biotechnol* **28**, 633–639.

Radünz M, da Trindade MLM, Camargo TM, Radunz AL, Borges CD, Gandra EA, Helbig E (2019). Antimicrobial and antioxidant activity of unencapsulated and encapsulated clove (*Syzygium aromaticum* L.) essential oil. *Food Chem* **276**, 180–186.

Rao JJ, Chen BC, McClements DJ (2019). Improving the efficacy of essential oils as antimicrobials in foods: mechanisms of action. *Annu Rev Food Sci Technol* **10**, 365–387.

Reyer H, Zentek J, Männer K, Youssef IMI, Aumiller T, Weghuber J, Wimmers K, Mueller AS (2017). Possible molecular mechanisms by which an essential oil blend from star anise, rosemary, thyme, and oregano and saponins increase the performance and ileal protein digestibility of growing broilers. *J Agric Food Chem* **65**, 6821–6830.

Roofchaee A, Irani M, Ebrahimzadeh MA, Akbari MR (2011). Effect of dietary oregano (*Origanum vulgare* L.) essential oil on growth performance, cecal microflora and serum antioxidant activity of broiler chickens. *Afr J Biotechnol* **10**, 6177–6183.

Saad NY, Muller CD, Lobstein A (2013). Major bioactivities and mechanism of action of essential oils and their components. *Flavour Fragr J* **28**, 269–279.

Sahingil D (2019). GC/MS-olfactometric characterization of the volatile compounds, determination antimicrobial and antioxidant activity of essential oil from flowers of calendula (*Calendula officinalis* L.). *J Essent Oil Bear Plant* **22**, 1571–1580.

Salehi B, Mishra AP, Shukla I, Sharifi-Rad M, del Mar Contreras M, Segura-Carretero A, Fathi H, Nasrabadi NN, Kobarfard F, Sharifi-Rad J (2018). Thymol, thyme, and other plant sources: health and potential uses. *Phytother Res* **32**, 1688–1706.

Salem N, Kefi S, Tabben O, Ayed A, Jallouli S, Feres N, Hammami M, Khammassi S, Hrigua I, Nefisi S, Sghaier A, Limam F, Elkahoui S (2018). Variation in chemical composition of *Eucalyptus globulus* essential oil under phenological stages and evidence synergism with antimicrobial standards. *Ind Crops Prod* **124**, 115–125.

Santos FHR, De Paula MR, Lezier D, Silva JT, Santos G, Bittar CMM (2015). Essential oils for dairy calves: effects on performance, scours, rumen fermentation and intestinal fauna. *Animal* **9**, 958–965.

Scandorieiro S, de Camargo LC, Lancheros CAC, Yamada-Ogatta SF, Nakamura CV, de Oliveira AG, Andrade CGTJ, Duran N, Nakazato G, Kobayashi RKT (2016). Synergistic and additive effect of oregano essential oil and biological silver nanoparticles against multidrug-resistant bacterial strains. *Front Microbiol* **7**, 760.

Sharifi A, Mohammadzadeh A, Zahraei Salehi T, Mahmoodi P (2018). Antibacterial, antibiofilm and antiquorum sensing effects of *Thymus daenensis* and *Satureja hortensis* essential oils against *Staphylococcus aureus* isolates. *J Appl Microbiol* **124**, 379–388.

Soltani M, Ghodratnama M, Ebrahimzadeh-Mosavi HA, Nikbakht-Brujeni G, Mohamadian S, Ghasemian M (2014). Shirazi thyme (*Zataria multiflora* Boiss) and rosemary (*Rosmarinus officinalis*) essential oils repress expression of sagA, a streptolysin S-related gene in *Streptococcus iniae*. *Aquaculture* **430**, 248–252.

Sotelo-Boyás M, Correa-Pacheco Z, Bautista-Baños S, Gómezy YGY (2017). Release study and inhibitory activity of thyme essential oil-loaded chitosan nanoparticles and nanocapsules against foodborne bacteria. *Int J Biol Macromol* **103**, 409–414.

Swamy MK, Akhtar MS, Sinniah UR (2016). Antimicrobial properties of plant essential oils against human pathogens and their mode of action: an updated review. *Evid Based Complement Alternat Med* **2016**, 3012462.

Verma RS, Joshi N, Padalia RC, Goswami P, Singh VR, Chauhan A, Verma SK, Iqbal H, Verma RK, Chanda D, Sundaresan V, Darokar MP (2017). Chemical composition and allelopathic, antibacterial, antifungal and *in vitro* acetylcholinesterase inhibitory activities of yarrow (*Achillea millefolium* L.) native to India. *Ind Crops Prod* **104**, 144–155.

Wang CY, Chen YW, Hou CY (2019a). Antioxidant and antibacterial activity of seven predominant terpenoids. *Int J Food Prop* **22**, 230–238.

Wang F, Wei FY, Song CX, Jiang B, Tian SY, Yi JW, Yu CL, Song ZB, Sun LG, Bao YL, Wu Y, Huang YX, Li YX (2017). *Dodartia orientalis* L. essential oil exerts antibacterial activity by mechanisms of disrupting cell structure and resisting biofilm. *Ind Crops Prod* **109**, 358–366.

Wang YM, Dong WL, Odah KA, Kong LC, Ma HX (2019b). Transcriptome analysis reveals AI-2 relevant genes of multi-drug resistant *Klebsiella pneumoniae* in response to eugenol at Sub-MIC. *Front Microbiol* **10**, 1159.

Wu KG, Lin YH, Chai XH, Duan XJ, Zhao XX, Chun C (2019). Mechanisms of vapor-phase antibacterial action of essential oil from *Cinnamomum camphora* var. *linaloofera* Fujita against *Escherichia coli*. *Food Sci Nutr* **7**, 2546–2555.

Zeng ZK, Xu X, Zhang Q, Li P, Zhao PF, Li QY, Liu JD, Piao XS (2015). Effects of essential oil supplementation of a low-energy diet on performance, intestinal morphology and microflora, immune properties and antioxidant activities in weaned pigs. *Anim Sci J* **86**, 279–285.

Zhai HX, Liu H, Wang SK, Wu JL, Kluenter AM (2018). Potential of essential oils for poultry and pigs. *Anim Nutr* **4**, 179–186.

Zhang D, Gan RY, Zhang JR, Farha AK, Li HB, Zhu F, Wang XH, Corke H (2020). Antivirulence properties and related mechanisms of spice essential oils: a comprehensive review. *Compr Rev Food Sci Food Saf* **19**, 1018–1055.

Zhang QQ, Ying GG, Pan CG, Liu YS, Zhao JL (2015a). Comprehensive evaluation of antibiotics emission and fate in the river Basins of China: source analysis, multimedia modeling, and linkage to bacterial resistance. *Environ Sci Technol* **49**, 6772–6782.

Zhang T, Zhou YF, Zou Y, Hu XM, Zheng LF, Wei HK,

Giannenas I, Jin LZ, Peng J, Jiang SW (2015b). Effects of dietary oregano essential oil supplementation on the stress response, antioxidative capacity, and *HSPs* mRNA expression of transported pigs. *Livest Sci* **180**, 143–149.

Zhang ZF, Rolando AV, Kim IH (2016). Effects of benzoic acid, essential oils and *Enterococcus faecium* SF68 on growth performance, nutrient digestibility, blood profiles, faecal microbiota and faecal noxious gas emission in weanling pigs. *J Appl Anim Res* **44**, 173–179.

Zheng ZL, Tan JYW, Liu HY, Zhou XH, Xiang X, Wang KY (2009). Evaluation of oregano essential oil (*Origanum heracleoticum* L.) on growth, antioxidant effect and resistance against *Aeromonas hydrophila* in channel catfish (*Ictalurus punctatus*). *Aquaculture* **292**, 214–218.

Zhou F, Ji BP, Zhang H, Jiang H, Yang ZW, Li JJ, Li JH, Yan WJ (2007). The antibacterial effect of cinnamaldehyde, thymol, carvacrol and their combinations against the foodborne pathogen *Salmonella typhimurium*. *J Food Saf* **27**, 124–133.

Zhu HM, Du M, Fox L, Zhu MJ (2016). Bactericidal effects of *Cinnamon cassia* oil against bovine mastitis bacterial pathogens. *Food Control* **66**, 291–299.

Antimicrobial Activity of Aromatic Plant Essential Oils and Their Application in Animal Production

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Abstract Essential oils (EOs), volatile oily liquid extracted from aromatic plants, are vital secondary metabolites with the characteristic odor. The antimicrobial activities are determined by chemical compositions and concentrations of EOs. Of these, phenols, oxygenous terpenoids and terpenes possess significant antimicrobial activities. The antimicrobial mechanisms of EOs mainly involve in the alteration of fatty acids outer membrane, damaging of cytoplasmic membrane, depletion of proton-motive force and leakage of metabolites and ions. In the production systems of animal husbandry, misuse of antibiotics leads to the generation of "super bacteria", and antibiotic residues cause the problems of animal by-products unsafety and environmental pollution. Aromatic EOs serve as natural antimicrobial agents with advantages of low toxicity and no residues, thus EOs can be used as feed additives to replace the antibiotics for animal health. This review article describes the active compounds and antimicrobial mechanisms of aromatic EOs as well as their applications in animal production, and emphasizes the application of new technologies in the research of antimicrobial mechanisms. This article will provide the theoretical basis for the application of aromatic EOs in the animal production.

Key words aromatic plant essential oil, chemical composition, antimicrobial activity, antibiotic alternatives, animal production

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