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# 黄腐酸生理学功能及促进作物生长机理研究进展

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**摘要：**黄腐酸作为腐殖酸重要组成成分，对改良土壤、促进植物生长发育、提高植物抗逆性等具有重要作用。该文从黄腐酸促进种子萌发、增强根系生长发育、促进养分吸收进而提高作物产量、改良品质等方面阐述黄腐酸生理学功能，系统总结黄腐酸促进作物生长的可能机制，对黄腐酸研究的关键因子、与根土互作的内在联系和系统性做了展望。为进一步理解黄腐酸功能多样性提供理论依据，对农业生态可持续发展具有重要意义。

**关键词：**黄腐酸；生理作用；作物生长
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# Advances in Physiological Functions of Fulvic Acid and Its Mechanism of Promoting Crop Growth

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**Abstract:** Fulvic acid is a key component of humic acid, which plays an important role in enhancing soil property, improving plant growth, and promoting plant stress resistance. The physiological functions of fulvic acid were reviewed from the aspects of promoting seed germination, enhancing root growth, promoting nutrient absorption, and improving crop yield and quality, etc. The possible mechanism of fulvic acid promoting crop growth was systematically summarized, and the key factors of fulvic acid research and the internal relationship with systemization of root-soil was further looked forward. These would provide theoretical basis for further understanding of the functional diversity of fulvic acid, which is of great significance for ecological and sustainable agriculture development.

**Key words:** Fulvic acid; Physiological effects; Crop growt

黄腐酸又名富里酸，是腐殖酸类物质的重要组成成分，外观呈灰褐色，由碳、氧等元素组成[1]，具有较强的负载量和生理活性[2–3]，还具有阳离子交换能力、吸附分散能力及络合作用[4–5]。自然界中黄腐酸来源主要包括 2 大类，一类是生化黄腐酸，由秸秆、糠渣与生物灰等副产物通过生物发酵技术形成；二是矿源黄腐酸，由动植物的残体通过土壤微生物转化，经过工业提取而成[6]。2 种类型形成方式不同，但都具有相同的结构和类似功能。黄腐酸具有多种官能团结构特征[7]，可以促进土壤中较大粒子直径的团聚体、微团聚体的形成[8]，有效增加土壤孔隙度、调节土壤 pH 值，提高土壤结构特性[9]，改善土壤水分养分蓄积能力，增强土壤微生物活动[10–11]。因此，农业生产中将其作为生长素发挥激素作用来提高养分吸收，刺激植物生长。近年来，随着黄腐酸在农业中应用增多，黄腐酸的生理

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功能和作用效果受到越来越多的研究和关注。已有研究表明，黄腐酸生物学功能较为广泛，具体可归纳为促进种子萌发[12]、增强植物根系发育和增加分蘖[13]、提高叶绿素含量[14]、促进植物对营养元素的吸收[15]、减小气孔开度、降低蒸腾速率、提高光合作用速率[16]、增加作物产量和改善果实品质[17]。黄腐酸促进植物生长机理可分为调控土壤和植株 2 方面，具体包括：(1) 调节作物根系分泌物；(2) 增强光合作用，调节内源激素水平；(3) 调控基因表达等直接作用机理和改善根际环境方面的间接作用机理。本文基于前人研究，系统梳理黄腐酸生理学功能，分析和总结黄腐酸有效促进作物生长的机理，旨在为黄腐酸高效利用和开发提供理论依据和技术支撑。

# 1 黄腐酸生理学功能

## 1.1 促进种子萌发

大量研究表明，不同浓度黄腐酸对种子萌发有显著促进效果。分别将燕麦(*Avena sativa*)种子置于不同浓度黄腐酸稀释液中，燕麦种子活力提高，种子发芽率增加[18]。对藜麦(*Chenopodium quinoa*)采用不同浓度黄腐酸浸种并喷施后，藜麦发芽率、出苗率、幼叶可溶性蛋白含量(SP)、脯氨酸(Pro)和过氧化物酶(POD)活性提高，电导率和丙二醛(MDA)含量降低，藜麦幼苗的抗旱能力明显增强[19]。另外, 适宜浓度的黄腐酸可以缓解镉胁迫对种子萌发的影响。黄腐酸浓度为 100 mg/L 时，受镉胁迫的玉米(*Zea mays*)种子发芽率、发芽势和发芽指数分别为 95.24%、86.24%和 81.02%，与未受镉胁迫处理差异不显著[20]。这可能是因为镉胁迫破坏作物幼苗的抗氧化酶系统，引起植株体内产生活性氧、抑制植物光合作用，导致植株生长发育受到抑制[21]; 此外，施用适量黄腐酸可显著增加幼苗叶片中 SP、Pro 含量，超氧化物歧化酶(SOD)和过氧化氢酶(CAT)活性提升，显著降低 MDA 含量，缓解镉胁迫对植株抗氧化酶系统的破坏作用，提高光合色素(叶绿素 a、叶绿素 b 和类胡萝卜素)含量，增强植物光合作用，促进种子萌发和维持生长[22]。但是，黄腐酸用量并非越大越好，高浓度黄腐酸对种子萌发有抑制效果，研究表明，黄腐酸可促进小麦(*Triticum aestivum*)发芽的范围更大，但生化黄腐酸和矿源黄腐酸只在 20 和 40 mg/L 的低浓度可以促进小麦发芽，高浓度表现出抑制效果[23]。

## 1.2 促进根系生长

外源添加黄腐酸有助于增强根系生长，提高代谢途径，促进作物生长，缓解逆境胁迫。研究表明，与空白对照相比，添加不同程度黄腐酸后，小麦总根长、根系表面积、体积，根尖数和主根长均增加，黄腐酸促进了小麦主根的生长，显著提高了小麦根系氮吸收效率[24]。另有研究表明，高浓度的硝酸盐胁迫下，白菜含水量降低，光合色素降低，植株的氮代谢途径减缓，白菜(*Brassia chinensis*)生长受到抑制[25]；外源添加黄腐酸明显促进白菜根系伸长，提高植株对硝态氮的吸收，增强循环过程中氮代谢酶活性，加快植株铵态氮的同化，促进白菜植株生长[26]。

施用适当浓度的黄腐酸有助于促进水稻根系的生长和发育，根系长度、数量和干物质量增加, 根系吸收营养能力增强[27]。党祝庆等[28]研究表明，外源添加黄腐酸钾显著提高了根系平均直径，与单施化肥和空白处理相比，添加黄腐酸钾的根系活力显著提高，且根系 SOD、POD、CAT 酶活性显著高于其他处理。说明黄腐酸钾与化肥配施可显著刺激作物根系旺盛生长，提高根系活力，延缓根系衰老, 促进作物地上部的生长发育。黄腐酸能促进根部生长的主要原因，是它的分子量低，更容易被植物吸收和利用，刺激作物根部生长和发育[29]。研究表明, 黄腐酸通过激活根部的生长激素和一氧化氮调节的信号通路，刺激整个根系的生长，促进根和根毛的增殖[30]，增强根际养分吸收能力，促进植物生长。

## 1.3 促进作物养分吸收

黄腐酸通过促进根系的伸长生长和加粗生长, 增加侧根数量，提高根际养分的吸收能力。研究表明，化肥与黄腐酸配施能够显著降低土壤中的钠离子和氯离子含量，提高作物养分吸收效率和增加作物偏生产力[31]。黄腐酸钾与化肥混合施用，能够提高化肥的利用效率[32]，黄腐酸钾能够直接促进植物对钾、钙、镁、硅肥的吸收，提高土壤中的有效养分含量，从而达到改善植物生长的目的[33]。此外, 黄腐酸可以增加磷钾肥肥效，保护水溶性磷肥，促进作物对磷的吸收，同时具有溶蚀作用，能够促进土壤中钾的释放，提高土壤速效钾含量[34]。研究表明，施用黄腐酸可显著提高土壤中硝铵态氮含量、速效磷和速效钾含量[35]。李军等[36]研究表明，合理施用黄腐酸，玉米的产量增加 10.2%~12.6%，氮肥利用率提高 8.0%~10.5%，大量施用黄腐酸可以提高土

壤中的氮养分含量，但会降低产量。

黄腐酸类肥料可显著提高农田土壤的土壤肥力，其机制是黄腐酸可显著增加土壤中有益微生物数量和土壤磷酸酶(AP)、脲酶(URE)、CAT 和蔗糖酶(SC)活性[37]，土壤有益微生物群落结构的改变和土壤酶活性提升是促进作物养分吸收的重要基础，表现为增施黄腐酸可显著提高土壤有机质和速效养分含量[12]，研究表明，当黄腐酸与控释尿素配合施用时不仅可以促进作物对氮素的吸收，还可以提高作物生长关键期对磷元素的需求，显著提高元素的利用效率[38–39]。

### 1.4 提高产量

黄腐酸能够提高作物产量，已在国内外大量研究中得到证实。研究表明，施用矿源黄腐酸钾对西红柿(*Lycopersicon esculentum*)有明显增产效果，增产率达到 6.56%~8.68%，差异达到极显著水平[40]。含黄腐酸肥料能够促进花生(*Arachis hypogaea*)的生长，随着黄腐酸肥用量的增加，花生的产量显著提高[41]。经黄腐酸处理的芸豆(*Phaseolus vulgaris*)叶面积、植株干重及产量均高于对照，与对照相比，增产高达 49.99%[42]。不同用量黄腐酸处理葡萄(*Vitis vinifera*)的单株产量都显著提高，其中 33 g/ind.处理单株产量最高，达到 10.57 kg，比对照增产 39.08%，其次是 11 g/ind.处理，比对照增产 33.81%[43]。

除了直接施用黄腐酸能够增产外，含有黄腐酸的缓释肥料同样具有增产效果。研究表明，施用黄腐酸缓释肥小麦增产潜力均高于施用尿素，表明黄腐酸缓释肥在生产上对小麦具有较高的增产潜力[44]。此外，含黄腐酸固废肥施加到白菜，促进了白菜植株的生长发育，提高了植株鲜重，与对照相比，含黄腐酸固废肥促进作物增产 16.2%[45]。磷酸二胺配施黄腐酸也提高了土壤中速效养分含量，增加了土壤养分供应强度，使小麦产量和经济效益明显增加[46]。

### 1.5 改善品质

大量研究表明，外源施用黄腐酸肥料，不但能够提高作物产量，而且可有效改善果实品质。与对照相比，单施化肥及其与黄腐酸钾配施，单果重显著增加，且果实可溶性固形物、维生素含量、糖酸比和硬度明显提高[47]。且有研究表明，黄腐酸对作物品质的影响，不受添加方式的影响。叶面喷施黄腐酸抗蒸腾剂可改善瑞士灵葡萄中的总酚和黄酮含量，降低葡萄和葡萄酒中花色苷的积累，改善葡萄和葡萄酒的品质[48]。选取 4 种不同类型的黄腐酸施用于骏枣(*Ziziphus jujuba*)，结果表明不同类型黄腐酸均可以提高骏枣维生素 C、可溶性糖含量(SS)、糖酸比和 SP 含量[49]；另有试验表明，干旱胁迫下，黄腐酸可显著提高黄瓜(*Cucumis sativus*)水分利用效率，促进黄瓜营养物质的积累，增加果实中维生素、游离氨基酸(FAC)、SS 和 SP 含量，降低单宁(HT)含量，明显改善黄瓜品质[50]。黄腐酸肥料对土壤具有改良作用，通过离子交换、螯合、络合和吸附等形式，活化土壤养分，提高土壤酶活性，促进维生素含量和糖酸比的提高，这也可能是黄腐酸肥料改善作物品质的显著原因[51]。

## 2 黄腐酸促进作物生长机理

### 2.1 直接作用机理

#### 2.1.1 调节作物根系分泌物

研究表明，定量对比不同采收期内白菜，施用腐植酸类物质(腐植酸钠与黄腐酸)后白菜根系分泌物中黄酮含量增加。与空白组相比，施用黄腐酸和腐植酸钠后，对白菜根系中的维采宁-2、异荭草苷、圣草次苷、牡荆素、芦丁、水仙苷、橙皮苷和地奥司明共 8 种黄酮类成分含量有不同程度的提升作用[27]。其中，浇灌黄腐酸的提升效果优于腐植酸钠效果[27]。藻类植物中添加黄腐酸可以促进根系分泌物的产生，从而保护细胞膜防止进一步裂解，在酸性及中性条件下，铜绿微囊藻的藻毒素合成受到抑制作用，黄腐酸作为有益物质在一定程度上抑制藻毒素的释放[52]。

植物在胁迫条件下，根系分泌物会受到明显影响，而根际分泌物的累积和变化，会形成自毒物质，影响作物生长发育(图 1)，严重时产生病害。一方面，黄腐酸可以减少病害发生，如施用黄腐酸复合肥的植株叶片平均发病率降低了 50%，明显减少了香草酸和对羟基苯甲酸等酚酸类化感自毒物质积累[53–54]；另一方面，黄腐酸调控的根系分泌物积累和光合能力提升在作物抵抗胁迫过程中形成了相辅相成的良性循环效应[55]。Poetsch 等[56]研究表明，黄腐酸能提高根系草酸、柠檬酸、苹果酸、酒石酸和琥珀酸等有机酸积累，降低根系中乳酸和乙酸含量，促进根系分泌酸类相关基因的表达，这种生理效应将有利于活化土壤中磷元素，促进植物对磷的吸收；降低植株叶片中花青素积累，减少自毒效应，促进植株生长发育。

2.1.2 增强光合作用，调节内源激素水平

黄腐酸可以提高多种酶活性和叶绿素含量，提高新陈代谢能力，加强光合作用，增加干物质的积累，提高作物抗逆性。研究表明，与对照相比，干旱胁迫下燕麦叶片光合色素含量、净光合速率、蒸腾速率、气孔导度均显著降低，添加黄腐酸后，叶片叶绿素 a、类胡萝卜素显著提高，电子传递效率、光化学效率和最大光化学效率显著增加[57]。黄腐酸显著提高了干旱胁迫下燕麦幼苗的光合作用及其抗氧化能力，缓解干旱对燕麦幼苗的伤害，进而促进燕麦植株的生长[58]。

另有研究表明，叶面喷施黄腐酸可以缓解由于外界硝酸盐胁迫对小白菜(*Brassica campestris* ssp. *Chinensis*)带来的伤害[59]，同时黄腐酸处理还提高了小白菜叶部的光合色素含量以及谷氨酸代谢途径的多种酶活，大大激活了植物的氮代谢功能[60]，促进蛋白质的合成，通过激活苯丙烷类代谢途径提升作物的抗性[61]。事实上，黄腐酸处理对小白菜光合作用的增强主要是可以降低小白菜体内的 MDA 含量，提升 SOD、CAT 和 POD 活性，同时可以使得活性氧代谢基因 Cu/Zn-SOD、POD、CAT 和 APX 的相对表达水平显著提升[62]。另外，干旱胁迫下，施用黄腐酸后，可以增加黄瓜幼苗的叶绿素含量和光合作用能力，增加净光合速率和实际光化学效率，维持叶绿体结构，提高单位面积吸收捕获光能以及光电子传递的量子总量，并增强相关酶活性和内源激素水平[63]。

2.1.3 诱导基因表达

有研究表明，黄腐酸促进了作物根系转录基因变化[64]，上调了氮代谢、营养转运体和水解酶等生物学过程的相关基因[64]，例如，通过对黄腐酸处理的小麦花期旗叶碳氮代谢相关酶活性及基因表达分析表明，与对照相比，小麦花期旗叶中磷酸烯醇式丙酮酸羧化酶等相关酶的活性显著提高，碳代谢、氮代谢、糖代谢和氨基酸代谢过程增强，对应基因 *TraesCS6B*、*TraesCS3D* 等的代谢通路明显上调[65]。这些基因的显著上调影响了激素信号转导、糖代谢、氨基酸代谢过程的改变[66]，黄腐酸正是通过影响糖代谢、碳氮代谢相关的初级代谢基因的表达[67]，诱导的小麦叶片特异上调表达的基因富集到激素传导途径[68]，参与对含氮化合物的响应、对酸性化学物质的响应、脱落酸反应、光合作用等代谢途径[69]，提高碳氮代谢过程[70]，进而影响小麦的营养物质的积累和生理生长。

还有研究表明，黄腐酸上调了脂质合成相关基因的表达[57]，通过上调相关基因，改善抗坏血酸、谷胱甘肽和黄酮类化合物的代谢，进而改善干旱胁迫带来的负面影响[26]。干旱胁迫导致活性氧的快速积累，在植物组织中，在细胞水平上引起多种负面效应[71]，施加黄腐酸后，植物体内抗坏血酸含量增加，参与抗坏血酸生物合成和循环途径的相关酶活增强，*GPI* 和 *PMI* 基因表达上调，因干旱胁迫导致的负面效应也因抗坏血酸的作用而减弱。

黄腐酸还可借助调节相关物质合成来影响植物的生长，施用黄腐酸可提高植株生长参数，增加含量光合色素、类胡萝卜素、总酚浓度[72]，通过调节 *SDKH*、*PAL*、*MKK* 等基因表达，增强抗坏血酸代谢、类黄酮生物合成，提高植物干旱胁迫下茶叶的抗氧化能力[72]。黄腐酸也可在对抗非生物胁迫的斗争中发挥生物兴奋剂的潜在作用。施用黄腐酸减轻了玉米的水分胁迫损害，通过维持叶绿素含量和气体交换提高吲哚乙酸等含量，调节气孔运动和相关基因表达，保障植株正常生长[52–53]。在逆境胁迫下，黄腐酸通过独立于脱落酸[73]的信号机制对水稻(*Oryza sativa*)产生保护作用，施用黄腐酸可显著上调 *PAL*、*4CL*、*CHS*、*F3'H*、*FLS* 基因表达[74]。

**2.2 间接作用机理**

通过改善根际土壤环境，促进作物生长。黄腐酸对根际土壤环境的改善包括土壤理化性质的改善、土壤微生物的调节和土壤酶活性的提升。

研究表明，增施黄腐酸可显著增加土壤中较大颗粒的土壤团粒数量，增加土壤团粒结构的稳定性，显著改善土壤的物理性质[75]。同时，黄腐酸盐的缓冲能力强，能够在土壤中产生离子交换作用，从而提高酸性土壤的 pH，降低碱性土壤的 pH[76]。因此，黄腐酸常被加工成改善土壤理化性质的改良剂。谷端银等[77]的研究表明，在黄瓜栽培过程中喷施黄腐酸液，可显著降低其含盐量和 pH 值。而在设施番茄种植过程中增施黄腐酸钾肥料，可显著降低土壤的容重，且随着黄腐酸钾用量的增多其作用效果显著增加[41]。

研究表明，与常规施肥相比，施用黄腐酸使根际土壤 pH 和 EC 值、$K^+$和 $Na^+$含量降低，进而影响了土壤微生物多样性[78]。盐碱胁迫下土壤微生物优势菌门主要为变形菌门、酸杆菌门、放线菌门和芽单胞菌门，添加有机高分子复配材料和以黄腐酸为

主的复合材料型改良剂的处理后，土壤中放线菌门和厚壁菌门的相对丰度增加。碱胁迫下施用含黄腐酸的 2 种改良剂后，变形菌门、酸杆菌门和疣微菌门的相对丰度增加[79]。这一方面是由于盐化和碱化胁迫土壤中，添加黄腐酸具有减碱作用和脱盐效果，另一方面，土壤中微生物种类和数量丰富，优势菌群占比较高，并且在添加改良剂后盐化土壤的耐受性比碱化土壤的更高；有机高分子复配材料和以黄腐酸为主的复合材料的应用可以通过改变土壤结构和微环境进一步影响菌群多样性[80]。

另有研究表明，施用矿源黄腐酸钾肥料后，西红柿根际土壤 URE 活性增加了 4.21%~10.53%，土壤转化酶活性增加 2.67%~7.25%，AP 活性增加 2.76%~11.52%，并且各种酶活性随着矿源黄腐酸钾施用量的增加而有所提高[81]。不同浓度黄腐酸对小麦根际土壤中 URE、AP、CAT 和 SC 的活性均有明显促进作用，对 CAT 活性促进效果最明显[82]。土壤酶系统是土壤生理活性中的最强部分，土壤酶活性变化与土壤养分吸收利用和植株生长存在紧密关系[83]。黄腐酸通过增强土壤酶活性，改善根际土壤环境，促进植株对土壤养分的吸收和利用。

## 3 展望

黄腐酸通过刺激种子萌发、促进根系生长、提高养分吸收利用等方式直接刺激植物生长，提高作物产量，改善作物品质[45–46]。其根本原因是通过调控根系分泌物，调节内源激素水平[70]，调控基因表达[84]等方式增强作物抗逆性和有效影响根际土壤微生物群落结构和有效酶活性，改善根际环境，促进植物生长发育。黄腐酸对作物生长的影响受黄腐酸种类、浓度、作物生长周期[9–10]等多因素的影响，因而，黄腐酸对作物生长影响的关键因子的研究显得十分重要。目前，人们对黄腐酸促进植物生长方面的研究有了长足进步[11–15]，研究内容和方法逐渐深入，但现有研究仍有一些局限，主要包括：(1) 黄腐酸发挥作用受到诸多因子的影响，在黄腐酸促进植物生长过程中，关键因子如何发挥作用和影响黄腐酸功能，需要进一步分析和探索。深入研究影响黄腐酸促进植物生长的关键因子，有助于为黄腐酸作用于农业生产提供依据。(2) 黄腐酸是近年研究的热点，但是，大部分研究局限于黄腐酸对植物生长有利和促进的方面[85–86]，有研究表明，过量添加黄腐酸会对植物生长有反作用[23]，那么抑制作物生长的黄腐酸含量和浓度的临界值是多少，其作用机理还有待研究。(3) 黄腐酸对土壤中微生物群落结构的影响研究多停留在对微生物数量的研究层面[87]，对功能性微生物的影响研究有待进一步探索，而黄腐酸与功能微生物的内在联系与研究有助于进一步探索黄腐酸如何促进土壤养分活化与吸收，为黄腐酸的有效利用提供一定的理论依据。(4) 黄腐酸的研究多是对植物直接影响[88]，如何从根-土互作方面，系统揭示黄腐酸促进植物生长和对土壤改良三者之间的内在联系，对黄腐酸的进一步开发和利用具有重要意义。

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