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腐植酸的组成结构及其对作物根系调控的研究进展

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摘要:【目的】综述腐植酸的结构及其对作物根系调控方面的研究进展，为腐植酸的进一步资源化利用提供理论依据。【主要进展】1) 腐植酸结构复杂、功能多样，由 C、H、O、N 和 S 等元素构成。腐植酸是多价酚型芳香族化合物与氮化合物的缩聚物，其裂解产物主要有烷烃类、饱和醇类、非饱和线性醇类、吡啶类等，其形成机制主要基于氨基糖缩合理论、多酚理论和木质素理论。采用核磁共振、漫反射傅里叶变换红外光谱、表面加强拉曼光谱、X 射线吸收近边结构和 X 射线吸收光谱法表征可知，各类来源腐植酸中均含有芳香碳、羧基碳、羰基碳和羟基碳等结构。化学改性可以改变腐植酸的功能组成，而氧化是增加腐植酸含氧官能团数量的重要方式，它可以使腐植酸或者煤中的 H/C 值、O/C 值提高，腐植酸分子量向小分子量方向转移，增加羧酸、醇、胺、酯、醚等含氧基团数量。2) 腐植酸含有很多活性官能团，具有较高的物理、化学和生物活性。腐植酸活性功能团对养分的有效性有双向调控，可影响植物生长的原生代谢和次生代谢过程，其对植物生长的影响与其结构关系密切，它可促进作物养分吸收，提高土壤中养分含量，综合调控作物生长环境，改善作物体的养分吸收、同化和利用状况。3) 根系对腐植酸的响应是腐植酸促进植物生长的最初动力，它可通过影响根系形态、根系养分吸收、根系基因表达等来影响根系的生长发育，腐植酸对作物根系的作用效果受其来源、浓度、分子量、官能团、结构和成分的影响。【研究展望】今后应加强腐植酸结构特征研究，提高对腐植酸效果的机理认识。腐植酸对作物生长调控特别是对作物根系的调控机理的研究方式与实际有较大差距，因此，建立非破坏性手段还原腐植酸的结构特征，研究腐植酸对作物根系生长的作用机理，值得重视。

关键词: 腐植酸；结构；氧化；根系调控

Advances in humic acid structures and their regulatory role in maize roots

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Abstract:【**Objectives**】We summarized the humic acid structures and the current research effort on using humic acid to promote root growth and provided a theoretical basis for further humic acid utilization.【**Main advances**】1) Humic acid has a complex structure and diverse functions. It comprises C, H, O, N, and S elements. The acid is a polycondensate of polyvalent phenolic aromatic compounds and N compounds. Its pyrolysis products mainly include alkanes, saturated alcohols, unsaturated linear alcohols and pyridines, unsaturated linear alcohols and pyridines. The mechanism of humid acid formation is mainly based on amino sugar condensation theory, polyphenol theory, and lignin theory. Humic acid is characterized by nuclear magnetic resonance, diffuse reflectance Fourier transform infrared spectroscopy, surface-enhanced Raman spectroscopy, X-ray absorption near-edge structure, and X-ray absorption spectroscopy. Our review shows that humic acids from

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various sources contain aromatic carbon, carboxyl carbon, carbonyl carbon, hydroxyl carbon, and other structures. Chemical modification can change the functional composition of humic acids, and oxidation is an important process for increasing the number of oxygen-containing functional groups in humic acids. Oxidation can increase the H/C ratio and O/C ratio in humic acids or coal, reduce the molecular weight of humic acid, and increase the number of oxygen-containing groups such as carboxylic acid and alcohol amine, ester, ether, and so on. 2) Humic acid contains many active functional groups and has high physical, chemical, and biological activities. Its active functional group has two-way regulation on the availability of nutrients, affecting plant growth's primary and secondary metabolic processes. Its impact on plant growth is closely related to its structure. Humic acid can promote crop nutrient absorption and improve soil nutrient contents, comprehensively regulate the growth environment of crops, and improve the nutrient absorption, assimilation, and utilization of crops. 3) The response of roots to humic acid is the initial driving force for promoting plant growth. It can affect root growth and development by affecting root morphology, root nutrient absorption, and root gene expression. The effect of humic acid on crop roots is affected by its source, concentration, molecular weight, functional group, structure, and composition. 【**Recommendations and Prospects**】 It is very important to strengthen research on the structural characteristics of humic acid and improve the understanding underlying the mechanism of its effect. The research methods on how humic acid improves crop growth regulation, especially the mechanism of regulating crop roots, are far from reality. Therefore, establishing a non-destructive method to restore the structural characteristics of humic acid and studying its mechanism on the growth of crop roots are worthy of attention.

Key words: humic acid; structural; oxidation; root regulation

腐植酸是动植物遗骸经过微生物的分解和转化，以及地球化学、物理的一系列变化过程而形成积累起来的一类具有多种官能团的大分子有机弱酸混合物[1–2]。它能够调控肥料的释放和转化，改善肥料理化性状，刺激根系生长，提高根系对养分的吸收，进而提高作物产量和肥料利用率，减少施肥带来的环境压力。因此，腐植酸被用于制备绿色高效肥料新产品，以更好地调控根系的吸收功能，大幅度提高肥料利用率[3–5]。

腐植酸的生物活性与其结构息息相关，不同结构的腐植酸对植物生长的原生代谢和次生代谢过程调控效果不同。从堆肥材料中分离出的腐植酸富含羧基基团和疏水结构[6]，从蚯蚓粪中提取的腐殖质疏水性结构较为明显[7]，风化煤中提取的腐植酸能增加玉米根系碳水化合物、蛋白质、多肽和氨基酸类物质的含量，减少其在茎中的积累[8]。施用纯化的褐煤腐植酸可改变黄瓜主要生理根对缺铁响应的转录调控[9]，腐植酸与根细胞壁相互作用可以降低根际的导水率[10]。Piccolo 等[11]、Nardi 等[12–13]认为聚合程度低、分子量小的腐植酸可增加玉米根表面积，提高玉米根系 H^+-ATP酶和 H^+-PPase 酶的活力，而 Canellas 等[14]、Zandonadi 等[15]认为聚合程度高、分子量大的腐植酸有助于提高玉米根系 H^+-ATP 酶和 H^+-PPase 酶的活力。因此，需要进一步深入研究腐植酸的结构与其生物活性之间的关系。

1　腐植酸的组成与结构

1.1　腐植酸的组成

腐植酸因其来源、形成方式的不同，可以分为天然腐植酸和人工腐植酸。天然腐植酸包括土壤腐植酸、水体腐植酸、煤类腐植酸；人工腐植酸包括生物发酵腐植酸、化学合成腐植酸和氧化再生腐植酸。以来源方式又可分为原生腐植酸、再生腐植酸和合成腐植酸[16]。腐植酸主要由 C、H、O、N 和 S 等元素构成，C 和 O 两种元素的含量范围分别为 42%～67% 和 25%～45%，远高于 H、N 和 S。腐植酸还含有少量的 Ca、Mg、Fe 和 Si 等元素[17]，腐植酸的元素组成与其形成时的环境条件 (尤其是前体) 关系很大[18]。腐植酸的元素摩尔比可表征其芳香度和氧化程度，C/H 值越大，芳香度越高，不饱和度越高；O/C 值越大，氧化程度越高。泥炭腐植酸的氧化度不高，但是其缩合度却比猪粪腐植酸高得多。腐植酸是多价酚型芳香族化合物与氮化合物的缩聚物，由几百种有机化合物组成[19]，其裂解产物主要有烷烃类、饱和醇类、非饱和线性醇类和吡啶类等[20–21]，这些化合物来源于碳水化合物、脂类、蛋白质和木质素

等。腐植酸的主要成分是芳香酸和甲基化酚，芳香衍生物主要是苯二羧酸二甲基酯，是由木质素的侧链经微生物氧化降解生成，甲基化酚主要来源于木质素[22–24]。腐植酸形成机制基于 3 个主要理论[17]，分别为氨基糖缩合理论、多酚理论和木质素理论 (图 1)。在腐植酸形成过程中，植物残体经过微生物的分解可以产生糖类、氨基化合物、多酚、木质素降解物等，这些物质通过物理和化学键相互结合形成腐殖物质，因此，腐植酸裂解产物中才会有较多的含氮化合物 (主要是杂环和脂环化合物)、脂肪族化合物 (主要是烃类、一元羧酸和二元羧酸的甲基化酯)、木质素产物 (主要是甲基化酚)、碳水化合物 (糖类) 和芳香族化合物 (腐植酸的基本组成构架，由羧基、羟基等连接在苯环上形成) 等[20]。此外，腐植酸的热解曲线也显示出腐植酸的物质组成。当高温处理时，腐植酸产生因多糖降解、酸基脱羧和脂肪醇脱水，氮化合物和长链碳氢化合物的分解，芳香族结构的燃烧和 C—C 键解离的放热峰[25]。

1.2 腐植酸的结构

腐植酸的结构复杂、组成多样，是不均一且多分散混合物，因此，无法准确表征其结构，只能采用化学分析、光谱分析和物理学分析等来描述其主要结构特征[21]。研究腐植酸结构的方法有破坏性和非破坏性两类。破坏性方法主要有化学滴定法、紫外-可见光谱法、热解、降解和快速原子轰击质谱、凝胶渗透色谱法、尺寸排阻色谱法、X 射线散射法、超速离心法、气相渗透压法、冰点降低法和质谱法[21]。化学滴定法可用于测定腐植酸的含氧官能团和絮凝限度，紫外–可见光谱法可用于测定腐植酸的 E4/E6 值，热解、降解和快速原子轰击质谱可用于测定腐植酸的物质组成，热解过程中可加入四甲基氢氧化铵以增加对腐植酸极性基团的保护[18]，凝胶渗透色谱法、尺寸排阻色谱法、X 射线散射法、超速离心法、气相渗透压法、冰点降低法和质谱法用于测定腐植酸的相对分子质量，而凝胶渗透色谱法和尺寸排阻色谱法用于测定腐植酸的表观相对分子质量。非破坏性方法主要有核磁共振、漫反射傅里叶变换红外光谱、表面加强拉曼光谱、X 射线吸收近边结构和 X 射线吸收光谱，通过这些方法可以分析腐植酸的碳构架和氢构架 (图 2)。

腐植酸官能团含量是其结构特征的重要体现。腐植酸的羧基/醇羟基值 (A/B) 反映腐殖物质氧化度和芳香度的高低，A/B 越低，氧化度越低，芳香度越高[18]。一般来讲，随着腐殖化进程的推进，羧基、甲氧基和羰基含量下降，酚羟基含量增加[26]。E4/E6 值越大，芳构化程度越低，相对分子质量越小。腐植酸结构受其来源和形成前体的影响较大。采用核磁共振、漫反射傅里叶变换红外光谱、表面加强拉曼光谱、X 射线吸收近边结构和 X 射线吸收光谱法研究发现，各类来源腐植酸中均含有芳香碳、羧基碳、羰基碳和羟基碳等结构，但其吸收强度不同[27–33]。与土壤和水体中的腐植酸相比，煤炭腐植酸

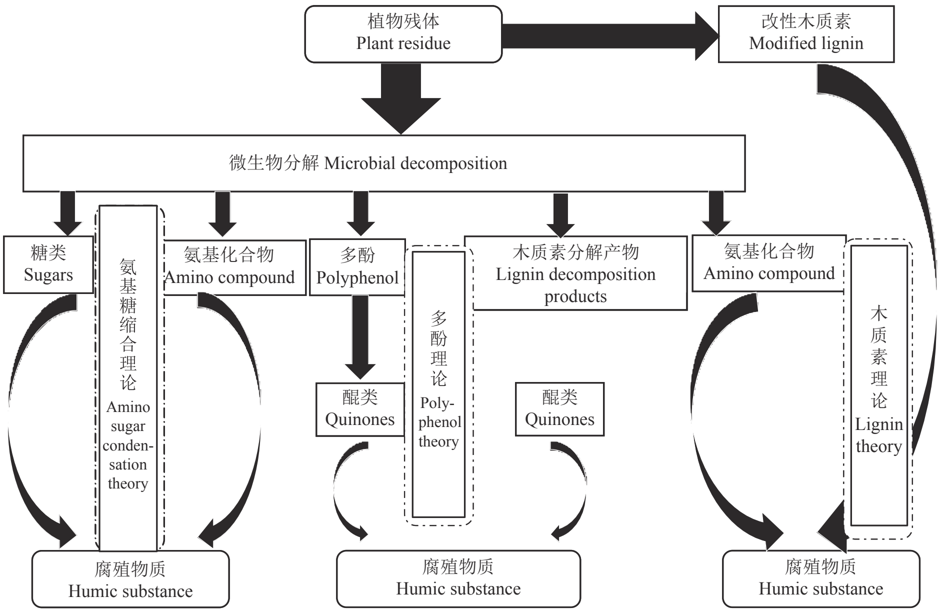

图 1 腐殖物质形成机制[17]

Fig. 1 Mechanisms for the formation of humic substances

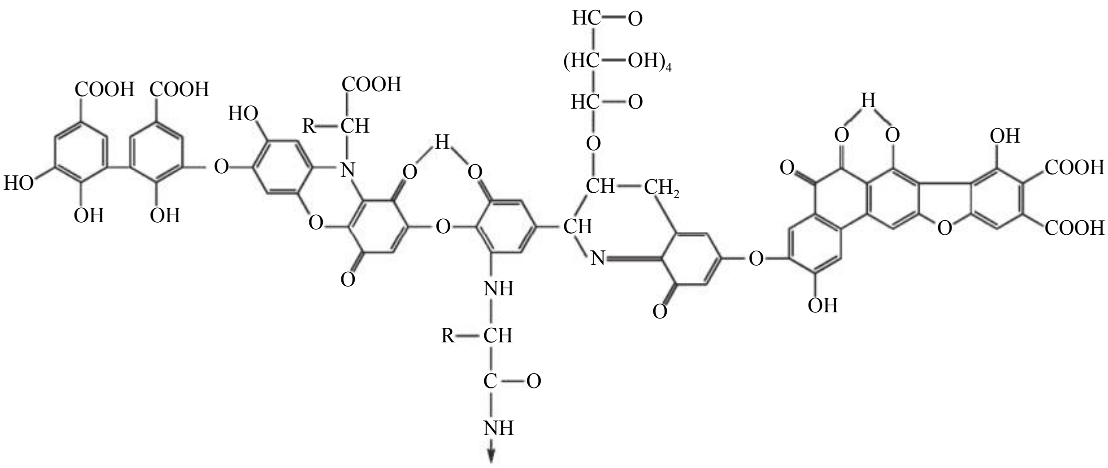

图 2　Stevenson 腐植酸模型

Fig. 2　Humic acid model by Stevenson

的结构更复杂，含更多缩合芳香结构[21]。褐煤腐植酸的骨架是由 2～5 个环缩合而成的稠环芳核，通过烷烃桥键、醚键、羰基等随机链接组成，分子间还通过金属离子桥和氢键等缔合成超分子结构[21]。目前，腐植酸的典型结构是 Stevenson 的腐植酸模型[17]。

1.3　化学改性对腐植酸组成和结构的影响

化学改性可以改变腐植酸的功能组成，常用的化学改性方法有氧化、磺化、胺化、微波活化等，经过磺化、胺化、共聚等化学改性后的腐植酸较改性前的降滤失性能有较大改善[34]，而氧化是增加腐植酸含氧官能团数量的重要方式。目前常用的腐植酸氧化方法有过氧化氢氧化法[35–36]、碱性 CuO-NaOH 氧化法[37–38]、碱性高锰酸钾氧化法[39–41]、硝酸氧化法[42]和次氯酸钠氧化法等。高锰酸钾氧化可以增加腐植酸中烷基碳和芳香碳的含量，降低芳香度[38–41]。过氧化氢氧化可以增加腐植酸中羰基、羧基和氧烷基的含量，减少芳香碳、氧芳香碳和烷基的含量[43]。过氧化氢法氧化煤腐植酸的机理：首先，煤中的弱—C—O—键断裂，产生 CO_2 和大量水溶性有机化合物，同时在化合物的稠合芳环周围形成许多羧基；然后，具有羧基的芳族环逐渐分解以产生小分子酸，一些芳环也会氧化生成小分子酸；随着氧化的进行，氧化煤残渣中脂肪族化合物和羧基增加[35–36]。通过碱性高锰酸钾氧化甲基化腐殖物质鉴定的主要产物为苯羧酸、酚酸和脂肪族二羧酸，苯羧酸包括一系列 2-、3-和 4-苯羧酸，这主要是由脂族侧链的氧化形成的[39–41]，高锰酸钾酸性氧化和高锰酸钾碱性氧化均可以增加腐植酸的 H/C 值[7]。腐植酸经硝酸氧化后可以获得各种脂肪族二羧酸、苯羧酸、羟基苯甲酸和硝基化合物等[42]。

2　腐植酸对植物生长的调控

2.1　腐植酸对植物生长的影响

腐植酸可促进植物生长，增加植物地上部和根系的干物质重[44–47]。Rose 等[48]采用 Meta 分析方法研究了腐殖质对植物生长的影响，结果发现，施用腐植酸后，植物地上部生物量和根干重均显著增加，但其增加幅度因腐植酸的来源、浓度、植物生长环境、植物类型和腐植酸的施用方式而异。来自于堆肥的腐植酸促进地上部生长的效果最好，来自于土壤的腐植酸次之，来自于泥炭的腐植酸表现最差。当植物受到盐度、重金属毒性、养分缺乏等胁迫时，高腐植酸施用量可更有效地结合过量的阳离子来减轻重金属或盐度胁迫。植物类型不同腐植酸的效果不同，腐植酸对单子叶植物的促生效果最好，对双子叶植物次之，对木本植物则有抑制作用。对植物地下部而言，来源于家畜粪便堆肥的腐植酸表现最好，而来源于土壤的腐植酸表现有所下降。对不同的植物栽培方式而言，腐植酸对土培植物的表现最好，对水培的植物表现最差，对植物类型而言，腐植酸对双子叶植物的根生长影响最显著，对木本植物的根没有抑制作用，但表现不如对草本植物的效果[49–50]。

腐植酸对植物生长的影响与其结构特性关系密切。Muscolo 等[50]综述了腐殖物质与植物生长发育之间的关系，结果发现，蚯蚓粪中存在植物生长调节物质，可促进植物生长，从蚯蚓粪中提取的低分子量级分含有特定的生物活性物质，更能促进拟南芥

和玉米幼苗根系的生长[51]。还有研究表明，低分子量腐植酸中含有较高含量的羧基和芳香族碳，因此具有较高的生物活性[52]。对于从风化煤中提取的腐植酸，其分子构象能促进黄瓜茎枝生长，提高 H^+-ATP 酶活性和硝酸盐浓度[53]，因此，继续深入研究腐植酸的结构对植物生长调控的影响意义重大。

腐植酸含有很多活性官能团，具有较高的物理、化学和生物活性[54–63]。小分子腐植酸被植物体吸收利用后，以类激素的方式调节植物体内的新陈代谢过程。Nardi 等[13]研究发现，小分子量腐植酸中较高含量的羧基碳和类赤霉素活性使其能增加玉米对硝酸盐的吸收。

2.2 腐植酸活性功能团对养分的有效性有双向调控

腐植酸中的羧基、羰基和酚羟基等官能团，具有较强的离子交换和吸附能力，施入土壤后，既可以固持土壤和肥料中过多的养分，又可以在其含量低时释放出来，因而可提高植物体对大、中、微量元素的利用效率[54]。将腐植酸直接添加在尿素中，腐植酸的各活性含氧官能团均能与尿素发生化学反应，并形成稳定性较高的化学键[55]，进而调节氮素的稳定释放，提高作物对氮素的吸收[58,64–65]。而且腐植酸与化学氮肥可发生反应形成腐植酸铵，从而减少氮素挥发和淋失[66]，在土壤中还可以通过配位作用、离子交换吸附作用、竞争吸附位点作用和增加磷酸盐的移动等方式来减少土壤对有效磷的固定。腐植酸的酸性功能团可吸附和贮存钾离子，防止土壤钾素的流失，同时减少黏土矿物对钾的固定。腐植酸化学螯合微肥可以增加作物对微量元素的吸收利用[3–5]。因此，腐植酸在调节植物养分吸收、增加土壤养分有效性和提高肥料利用率方面作用显著。

2.3 腐植酸对植物原生代谢和次生代谢的影响

腐植酸可以影响植物的原生代谢和次生代谢过程。植物的原生代谢是指植物生存、生长和繁殖所必需的基本生物化学过程[52,60]。腐植酸可通过不同的方式来影响糖酵解和三羧酸循环中诸如磷酸葡萄糖异构酶、磷酸果糖激酶、苹果酸脱氢酶和葡萄糖激酶等酶的活性，其影响方式主要取决于腐植酸的分子量大小、分子特性和浓度[50]。腐殖物质的低分子量级分因具有较多的官能团，尤其是含有较多的羧基和酚基，其在改善植物新陈代谢中发挥重要作用。具有最少刚性分子构象的最小分子量级分，木质素部分含量最低，其他非木质素芳香族化合物含量最大，且具有最强的生物效应[67]。Zandonadi 等[15]从不同土壤物质中分离腐植酸，发现缩合的腐植酸化学结构因呈现出类生长素活性而更有利于刺激玉米根系生长、侧根和液泡膜 H^+-ATP 酶的增殖。

植物的次生代谢可定义为不直接参与植物生长发育的一系列有机化合物的代谢过程，其主要功能是保护植物抵御食草动物和病原体对植物的伤害。次生代谢的物质主要有萜烯类化合物、酚类化合物和含氮化合物三类[52,68]。喷施含腐植酸水溶肥、黄腐酸钾和黄腐酸精华液的叶面肥均可以提高柠檬次生代谢产物挥发油、总黄酮和总酚的含量，可以不同程度地改善柠檬的品质、口感及功能活性[69]。魏世平等[70]研究发现，腐植酸钾–苯并噻二唑能增加过氧化物酶、多酚氧化酶、苯丙氨酸解氨酶的活性和酚的含量，从而增加防御能力，而苯丙氨酸解氨酶是一种苯丙类化合物的关键酶，会导致水杨酸、植物抗毒素和类木质素聚合物等植物次生代谢物的产生。

3 腐植酸对作物根系生长的调控

根系作为腐植酸作用于植物体最先接触的器官，其对腐植酸的响应是促进植物生长的最初动力[71–73]。腐植酸可通过影响根系形态、根系养分吸收、根系基因表达等来影响根系的生长发育。腐植酸对作物根系形态的影响是其对根系生长影响的直观反应。前人研究了从不同来源获得的腐植酸影响根系增长、形态和根构型的能力。腐植酸对根系形态的影响大体分为两部分：1) 对单个根形态的影响。腐植酸可通过增加细胞数量，改变细胞大小和细胞类型，增加侧根和吸收型毛孔的数量等来促进根系生长[15, 74–76]。有研究认为，腐植酸刺激植物生长的机制之一是通过诱导质膜 H^+-ATP 酶的增加，使原生质体酸化，从而使细胞壁松动，促进细胞伸长。2) 对整株根形态的影响。腐植酸可以通过增加主次生根密度和分支数，改变根粗等来改善根构型[77–79]，继而从改善整株根的形态上来影响根系生长。腐植酸可以提高根系 H^+-ATP 酶的活性，增加离子跨膜运输动力的电化学质子梯度，促进离子和养分的吸收。Chen等[80]揭示了腐殖质对根系生长发育和微量元素摄取的刺激作用。特别是 Varanini 等[81]的研究表明，在加入腐植酸的盐水培养基中，番茄对矿物质营养摄取量显著增加，这可能是由于根细胞膜的渗透性增加所致。腐植酸对根系生长及其对养分吸收的促进作用与其对作物根系基因表达的影响密切相关[82–85]。腐植酸具有类似生长素和赤霉素的生理功能，这两类激素是控制根系发生和植物生长的正向调控因子[86–82]，GRAS1

是响应生长素[88]和赤霉素[89]的关键转录因子，它参与了这两类激素诱导的细胞分裂和膨大进程，具有促进生长和根系发生的作用，而一些低分子量的腐植酸 (黄腐酸) 能促进 GRAS1 的表达，这可能与黄腐酸中含有生长素或赤霉素类似物有关[89]。黄腐酸还可以刺激植物根系分泌质膜 H^+-ATP 酶，这种作用归因于电位的耗散和膜通透性的增加[90]，或通过某种翻译机制进行酶调节[13,77]。

有研究表明，低分子量的腐植酸具有更好的改善根构造、促进根系生长发育的功能，并可以通过生长素信号传导影响根系的生理代谢[12]。Canellas 等[79]研究表明，从蚯蚓粪中提取的腐植酸的上层结构中的异质和移动分子更有利于增加拟南芥和玉米的侧根数和根毛密度。Dobbss 等[7]、Canellas 等[91]研究发现，从蚯蚓粪中提取的腐植酸的疏水性指数与玉米、拟南芥和土豆中的侧根数量呈正相关。根系的伸长区和分生区包括小而密的分生组织细胞，这些细胞具有连续的代谢活性，易受侧根形成的影响。相关研究还观察到腐植酸处理对侧根出现部位的过度诱导，证明了腐植酸对侧根的出现有显著影响，这是因为腐植酸中含有类生长素的外源物质，从而促进侧根发生，改善根系形态。生长素是在植物中发现的第一种激素，是构成植物体最重要的形态发生化合物之一，生长素信号触发周期细胞群重新进入细胞周期并建立侧根有丝分裂位点[92]。生长素的感知和信号通路也是完成生长素生物学功能的必要条件[93]。而侧根的生长发育除了受内源生长素的影响，还受外源类生长素类物质的影响。此外，Loffredo 等[94]的研究结果表明，疏水性更强、缩合程度更高、富含更多 C、H、N 和酚类的腐植酸促进胡椒草根系生长的效果更好。

从蚯蚓粪中提取的腐植酸能够增加玉米、拟南芥和土豆的侧根数，提高 H^+-ATP 酶的活性，其效果与腐植酸的疏水性指数呈正相关[78,92]。从城市废弃物中提取的腐植酸能够促进玉米侧根的生长，并提高玉米根系 H^+-ATP 酶的活性，该作用效果主要归因于腐植酸含有较多的羧基并具有较强的疏水特性[6]。从土壤、蚯蚓粪和污泥中提取的腐植酸能够增加玉米有丝分裂位点、根鲜重、侧根数、根表面积和主根长，提高玉米 H^+-ATP 酶的活性，并且聚合程度低、分子量小的腐植酸具有更好的效果[11,13–14,52]。也有研究表明，从土壤中提取的腐植酸能够增加玉米侧根数，提高玉米根系 H^+-ATP 酶的活性，并且聚合程度高、分子量大的腐植酸的作用效果更好[14–15]。从土壤中提取的腐植酸在高浓度下，能够更好地促进燕麦对 K^+ 和 SO_4^{2-} 的吸收[95]。从泥炭、褐煤中提取的腐植酸自组装超分子结构中的生物活性分子能够促进小麦和玉米根系的生长发育[96–97]。因此，腐植酸的结构对其功能影响较大，但是其具体作用机制未有定论、仍待研究，在后期研究中，需根据不同的作物需求进行选择。

4 展望

腐植酸的结构特征研究是研究其对作物生长发育尤其是根系生长发育调控机制的重要基础。虽然在腐植酸结构的表征技术、调控作物生长发育的机理研究等方面取得了重要进展，但以下几个方面仍值得进一步探讨。目前常用的腐植酸结构的研究方法存在不同程度地改变腐植酸功能团类型和数量的问题，需加强核磁、远红外等非破坏性方法来校正已有方法所得的结果，对腐植酸做更为精准的表征。加强腐植酸次生产品对作物生长发育调控的机理研究，为特定生长环境和植物类型制备专用的腐植酸提供理论依据和技术支持。腐植酸具有一定的类激素活性，其作用机理到底是腐植酸本身含有的激素还是对植物体的刺激作用诱导产生的植物激素，又或者是腐植酸介导了植物体内的信号传导过程，从而改变了植物生长微环境的激素水平仍不确定，值得进一步研究。

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