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# 大气二氧化碳浓度升高下丛枝菌根真菌对植物生长发育影响的研究与展望

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## 摘 要

**从枝菌根(Arbuscular Mycorrhiza, AM)真菌，能够与80%以上的陆生高等植物根系形成有益共生体，调控退化生态系统的恢复与重建。文中综述国内外有关AM真菌与二氧化碳($CO_2$)之间相互作用的主要研究成果，AM真菌共生与$CO_2$之间的相互作用对植物吸收营养物质以及土壤环境的影响，揭示AM真菌调控植物生长与环境修复的微生物机制，并提出当前研究存在的问题及今后研究的建议，展望AM真菌在全球气候变化形式下的研究与应用，旨在为退化生态系统恢复重建提供一个新的理论视角，并为加快AM真菌这一高效生物技术的应用提供帮助。**

## 关键词

从枝菌根真菌，共生，植物生长，环境修复，生态系统恢复

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# Research and Prospect of Arbuscular Mycorrhizal Fungi on Plant Growth and Development under Elevated Atmospheric Carbon Dioxide Concentration

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## Abstract

**Arbuscular mycorrhiza (AM) fungi can form beneficial symbionts with more than 80% of the roots**

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**of terrestrial higher plants, regulating the restoration and reconstruction of degraded ecosystems. This paper reviews the main research achievements on the interaction between AM fungi and carbon dioxide at home and abroad, the effect of the interaction between AM fungi symbiosis and $CO_2$ on plant uptake of nutrients and soil environment, and reveals the microorganisms that AM fungi regulate plant growth and environmental remediation. Mechanism, and put forward the existing problems in current research and suggestions for future research, and prospect the research and application of AM fungi in the form of global climate change, aiming to provide a new theoretical perspective for the restoration and reconstruction of degraded ecosystems, and to accelerate the development of AM fungi. The application of high-efficiency biotechnology can help.**

## Keywords

**Arbuscular Mycorrhizal Fungi, Symbiosis, Plant Growth, Environmental Restoration, Ecosystem Restoration**

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## 1. 引言

截止到 2022 年 1 月，大气二氧化碳(A$CO_2$)已达到 417.99 ppm，预计到本世纪末，A$CO_2$将超过 550 ppm (https://www.CO$_2$.earth)。升高的 $CO_2$ (e$CO_2$)浓度直接影响植物光合作用。从枝菌根(Arbuscular Mycorrhizal, AM)真菌在自然界中分布广泛，可与植物根系共生形成共生体—菌根。在全球范围内，每年从植物到菌根共生体转移的碳水化合物和脂肪酸高达 50 亿吨[1]，是对土壤碳储量的重要投入。作为回报，AM 真菌的定植可以提高寄主植物的适应性，特别是向植物提供额外的磷(P) [2] [3]氮(N)和锌(Zn) [4]。菌根是由宿主植物根系和菌根真菌双方所构成的，菌根共生体对 $CO_2$ 浓度升高所作出的响应取决于双方各自的特点，所以对于不同的植物与菌根组合来说结果往往很不一致[5]。其中共生促进可能是由于 A$CO_2$ 浓度升高促进了植物的光合作用，因此宿主植物向地下部分转移的光合产物增加，从而刺激了菌根的活性。[6]

“碳肥效应”是导致 A$CO_2$ 升高下碳固定率增加的原因，尤其是在温带地区的 C3 物种中[7]，其中包括一些世界上最具经济和社会意义的植物。由于光合作用目前在 A$CO_2$ 下不受碳限制，因此在 e$CO_2$ 下生长的植物通常表现出减少的光呼吸损失和增加的净光合速率。A$CO_2$ 增加对作物-AM 真菌关联的影响程度尚不清楚。鉴于 A$CO_2$ 在调节光合速率[8]和随后的碳代谢中的关键作用，AM 真菌如何改善和驱动 A$CO_2$ 的变化对作物生长和营养的影响值得进一步研究。本文对国内外有关 A$CO_2$ 浓度升高影响植物-AM 真菌共生的研究报道进行简要概述。

## 2. $CO_2$ 的升高对 AM 真菌侵染的影响

大量研究表明，e$CO_2$ 对大部分 C3 植物具有显著的积极作用，因为它刺激了光合 C 的同化，从而增加了光合产物向菌根共生植物的根的转移，支持其共生关系[9] [10] [11]。AM 的形成通常增加了在 e$CO_2$ [12] [13] [14]作用下寄主植物的叶片、茎和根生物量的产生。

Shi S 等[15]发现升高的 $CO_2$ 浓度显著增加了 *F. mosseae* 对蚕豆(Vicia faba)的菌根定植率。苑学霞等[16]采用水稻(*Oryza sativa* L.)、冬小麦(*Triticum aestivum* L.)轮作的耕作方式和 FACE (Free-air $CO_2$ enrichment)开放试验系统，结果表明在前 6 周时间内，侵染率逐渐增加，6 周时都达到 30%以上，从第 6 周到第 10

周菌根侵染率基本保持不变。但与对照组相比 $CO_2$ 浓度升高对 AM 真菌的侵染能力没有显著影响。苑学霞等[17]在另一项试验中利用试验室 $CO_2$ 培养箱模拟 $CO_2$ 浓度倍增环境，初步研究了 $CO_2$ 浓度倍增对 AM 真菌 *Glomus caledonium Nicoison* & *Gerdemann* 及其对绿豆(*Phaseolus radiatus L.*)接种效应的影响。结果表明，绿豆生长 14 d 时，$CO_2$ 浓度倍增对 AM 真菌及绿豆生长没有显著影响。绿豆生长 28 d 和 42 d 后，$CO_2$ 浓度倍增显著增加了 AM 真菌的侵染率和产菌丝量；O’Neill 等[18]试验结果表明 $CO_2$ 浓度升高使北美鹅掌楸(*Liriodendron tulipifera*)根部菌根总的侵染量随着时间稳定增加。姚凯骞[19]的研究发现通过 $CO_2$ 加富能够提高番茄根系菌根真菌的侵染率以及侵染密度。Roughier 和 Read [20]的研究发现在 $CO_2$ 浓度升高条件下，长叶车前(*Plantago lanceolata*)在试验的第 104 天与第 76 天相比菌根真菌侵染率提高 50%。汪杏芬等[21]使用开顶式 $CO_2$ 加倍装置对玉米(*Zea mays* L.)“农大 3138”、小麦(*Triticum aestiv um* L.)“青 323”、大豆(*Glycine max* L.)“科农 4 号”进行试验，实验结果表明玉米中侵染强度被显著促进，活力则无显著改变。在小麦中泡囊–丛枝菌根(VAM)侵染活力和强度均显著增加，这可能与 C3 植物总体而言对 $CO_2$ 浓度倍增更敏感有关。同为 C3 植物的大豆则表现出菌根侵染活力和强度对 $CO_2$ 浓度加倍的不敏感性。Staddon [22]研究了 $CO_2$ 浓度升高对长叶车前和白花三叶草菌根影响结果表明菌根真菌侵染率以及外生菌丝密度增加。

上述研究表明不同碳途径植物对 $ACO_2$ 浓度变化的响应不同。AM 真菌与大多数植物相互作用，比其他真菌的耐寒性更低；因此，$ACO_2$ 浓度升高导致的气候变化可能使真菌介导的增加营养物质转移到植物上，可以加强互惠关系。通过刺激光合作用，$CO_2$ 值的上升可以降低支持 AM 真菌的碳成本，这也可以加强互惠共生[23]。未来气候变化时，在 VAM 侵染的植物类型中，C3 非豆科植物的菌根因其侵染活力和强度均受促进，因此它们的幼苗获益程度最大，其次为 C4 植物，C3 植物中豆科植物又次之，而非菌根侵染植物仅能从根系表面积的增加得益，处于劣势，这将导致植物群落组成的改变，甚至可能影响群落中物种的多样性[24]。尽管单独因素的作用不太可能导致菌根共生分解[25]，需要更近一步研究关于多因素变化组合和其他人类群落相互作用对植物与 AM 真菌交互作用的影响，以预测菌根对于环境变化的适应性。

## 3. $eCO_2$ 与 AM 真菌共同作用对土壤的影响

### 3.1. 对土壤养分的影响

Shi S 等[26]研究显示 $eCO_2$ 显著增加了蚕豆土壤中的有机碳，降低了土壤中硝态氮( $NO_3^-$-N)含量。而且无论是否有 AM 真菌定植，对土壤中有效氮(AN)、有效磷(PN)和有效钾(KN)均无影响。$eCO_2$ 条件下的接种 AM 真菌的土壤中氨态氮( $NH_4^+$-N)含量比普通环境 $CO_2$ 条件下提高 19.7%，而 $eCO_2$ 条件下不接种 AM 真菌的土壤中 $NH_4^+$-N 含量则比普通环境 $CO_2$ 下高 15.6%。由此可以见 AM 真菌在 $eCO_2$ 和普通环境 $CO_2$ 条件下均显著提高了土壤有机碳、AN、$NO_3^-$-N、PN 和 KN 含量。此外，$CO_2$ × AM 真菌的显著相互作用仅表现在 $NH_4^+$-N 中。事实上，考虑到相应的 $CO_2$ 随植物光合用的波动，夜间株高处的环境 $CO_2$ 浓度在通常高于白天[27]，其在另一项试验中表明[28] AM 真菌的定殖增加了土壤 N、P 和 K 的有效性，特别是在 $eCO_2$ 的白天，植物–土壤对 $eCO_2$ 的交互反馈可能决定了土壤 N、P 和 K 的增加或减少，以及微生物群落的组成和活动。

一般来说，C 直接或间接地通过植物的根和/或菌根流入土壤。在 $eCO_2$ 的作用下，有更多的 C 可用于菌根的生长和发育，因此这些额外的 C 刺激了 AM 真菌的关联[29]。反过来，AM 真菌加速了 $eCO_2$ 作用下土壤有机质分解为 N 和 P [30]。其中在 500~610 ppm $eCO_2$ 下易于转化酶和脲酶活性，表明有机 C-N 化合物的分解、N 和其他营养物质的释放，导致微生物的普遍激活[31]。土壤酶活性的相对增加也可能归

因于在 $eCO_2$ 条件下产生的较高的生物量产量，因此对 N、P、K 的需求更大[32]。事实上，本研究中，日间 $CO_2$ 下可用 N、P、K 的显著下降支持了这一观点。一项分析显示，$eCO_2$ 诱导的营养限制可能会增加土壤酶活性[33]。然而，在 $eCO_2$ 条件下，AM 真菌小麦幼苗的土壤 AN、AP 和 AK 水平显著高于非 AM 真菌小麦幼苗，这表明 AM 真菌的存在可以在 $eCO_2$ 条件下提供更好的土壤肥力。

## 3.2. 对土壤中 AM 真菌群落的影响

随着 $ACO_2$ 浓度的增加，土壤中真菌群落的组成和功能可能会发生变化。真菌作为分解者和植物共生体，可以调节生态系统碳循环的速率。真菌群落组成对这一速率特别重要，因为复杂土壤碳的分解需要比任何单一真菌物种所能提供的更多的酶多样性[34] [35]。

AM 真菌的丰度可能会随着 $ACO_2$ 值的增加而增加。当植物固定并将更多的碳分配给根系时，它们可能需要更多的土壤氮和磷来支持不断增长的增长。因为菌根真菌对获取土壤氮和磷很重要，这两种营养物质经常限制陆地净初级生产力(NPP)——$CO_2$ 时，植物可能更多倾向菌根组合。

在同一个属中不同种对 $ACO_2$ 浓度升高的响应也不同。Klironomos 等[36]对 *A. tridentate* 接种根内球囊霉(*Glomus intraradices*)和幼套球囊霉(*Glomus etunicatum*) 16 周时间后测定各种指标，试验结果表明，两种菌根真菌的侵染率、外生菌丝的长度以及土壤中孢子数在 $CO_2$ 浓度升高时都有所增加，但是各个指标的增加量根内球囊霉都比幼套球囊霉大。Wolf 等[37]研究了 560 $\mu mol \cdot mol^{-1}$ 和 368 $\mu mol \cdot mol^{-1}$ $CO_2$ 浓度下不同栽培环境中不同丛枝菌根真菌的响应，试验发现，在单一栽培条件下，用于试验的 11 种丛枝菌根真菌中只有明球囊霉(*Glomus clarum*)在高浓度 $CO_2$ 中显著增加，而在多种作物栽培条件下，影响不显著。而氮水平对丛枝菌根真菌的孢子和种类没有影响，$CO_2$ 和 N 交互作用对丛枝菌根的区系也没有影响。

Andrew C. Procter [38]研究了德克萨斯州草原上的真菌群落对工业前到未来(250~500 ppm) $CO_2$ 梯度的响应，并研究了土壤特性如何影响真菌群落和对 $CO_2$ 的分解反应。对 AM 真菌数据集中的所有序列与 NCBI 数据库的 *Glomus* 属进行匹配。与真菌总 OTUs (operational taxonomic units)丰富度相似，AM 真菌 OTUs 丰富度不因土壤类型而不同。此外，AM 真菌的 OTUs 丰富度不受 $CO_2$ 处理影响。

## 4. $eCO_2$ 对 AM 真菌共生植物生长的影响

在 $eCO_2$ [39] [40] [41]作用下，C3 植物组织的营养浓度普遍降低。对 7761 个观察结果进行的 meta 分析显示，平均 689 ppm $eCO_2$ 使植株 N、P、K 浓度降低 7%~15%，其中氮的下降幅度大于 P 和 K [39] [42]。而在 $eCO_2$ 条件下，较低的植物 N、P、K 可以通过 AM 真菌共生而得到改善。例如，与无 AM 真菌定植植物减少 50%相比，56 日龄 AM-刺槐(*Robinia pseudoacacia L.*) [43]在 710 ppm $eCO_2$ 条件下的植株总磷仅降低了 22%。在 700 ppm $eCO_2$ 下，AM 真菌对莴苣(*Lactuca sativa Linn.*)的 K 浓度的正影响大于 $ACO_2$ [44]下。Chen 等[45]研究表明，在 730 ppm $eCO_2$ 下，接种 AM 真菌增强了长叶车前(*Plantago lanceolata* L.)对 $^{15}N$ 和总氮的吸收，而不是羊茅(*Festuca arundinacea*)的吸收，这表明在 $eCO_2$ 条件下，AM 真菌对植物氮吸收的影响具有种特异性。蚕豆(*Vacia faba* L.)与固氮菌结合，通过共生的氮固定在一定程度上减轻了氮缺乏[46]。在 550~750 ppm 下，莴苣(*Lactuca sativa Linn.*) [44]、水稻(*Oryza sativa L.*)、野稗(*Echinochloa crusgalli*) 57 的 P 和 K 浓度升高，而黄花蒿(*Artemisia annua Linn.*) [47]、番茄[48]和硬质小麦[49]中 P 和 K 浓度降低，牛至[50]和绿豆[51]变化不显著。此外，在 $eCO_2$ 条件下，气孔导度的降低和蒸腾速率可能会限制土壤中养分的质量流动，从而降低植株对 N、P、K、Ca、Mg 和 S [52] [53] [54]的吸收。

总的来说，AM 真菌与 $CO_2$ 协同植物生长有一定影响，进一步的 $eCO_2$ 研究应采用两种或两种以上的菌根真菌物种，无论是个体或多个物种，也与其他真菌或细菌物种结合，以测试它们的交互作用在其他全球环境变化情景下，如气候变暖或温度上升、干旱等，植物的生长和产量生产，以及田间土壤养分的有效性。

## 5. 展望

在 ACO$_2$ 上升的情况下，eCO$_2$ 的研究应使用多种 AM 真菌物种以及其他有益的真菌或细菌物种，以测试它们在其他全球变化事件(包括变暖和干旱)下对田间植物性能和土壤养分可用性的交互影响。菌根研究人员面临着在小规模过程中设计实验的困境，这些小规模过程有助于解决大规模问题，如全球变暖问题。此外植物菌根的形成和菌根真菌群落物种组成的改变还可能影响土壤 C 存储从而影响陆地土壤－植被系统在全球 CO$_2$ 变化下的反馈效应。

AM 真菌可能不是灵丹妙药，即农业强化的“可持续救世主”[55]，但 AM 真菌确实有潜力协助植物的营养同化。因此，AM 真菌可以在减少氮和磷基肥料的施用方面发挥重要作用，作为可持续土壤的更广泛战略的一部分。更好地了解环境－植物－微生物相互作用的机制对于未来的保护和维持农业集约化仍然很重要。

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