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丛枝菌根共生：一种减轻气候变化对植物影响的策略

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摘　要

大气二氧化碳(ACO$_2$)浓度升高(eCO$_2$)、全球气候变暖等问题可能会对植物产生严重影响，丛枝菌根真菌(AMF)可以与大多数植物形成共生关系，减轻生物和非生物胁迫对植物产生的影响，为保护作物产量提供了一个重要的补充措施。本文综述了植物-AMF共生对ACO$_2$浓度升高或气候变暖的响应，以及这些响应为未来气候变化情景下如何调节土壤和植物体有机碳(C)、氮(N)、磷(P)动态提供了深入的见解，揭示了AMF在植物应对非生物挑战方面的应用潜力。

关键词

二氧化碳，气候变暖，丛枝菌根真菌，共生，非生物胁迫

Arbuscular Mycorrhizal Symbiosis: A Strategy to Mitigate the Impact of Climate Change on Plants

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Abstract

Elevated atmospheric carbon dioxide (ACO$_2$) concentration (eCO$_2$), global warming and other

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issues may have a serious impact on plants. Arbuscular mycorrhizal fungi (AMF) can form a symbiotic relationship with most plants, reduce the impact of biological and abiotic stress on plants, and provide an important supplementary measure to protect crop yield. This paper summarizes the response of plant-AMF symbiosis to the increase of ACO_2 concentration or climate warming, and these responses provide in-depth insights on how to regulate the dynamics of organic carbon (C), nitrogen (N) and phosphorus (P) in soil and plant under the future climate change scenario, and reveal the application potential of AMF in plant response to abiotic challenges.

Keywords

Carbon Dioxide, Climate Warming, Arbuscular Mycorrhizal Fungi, Symbiosis, Abiotic Stress

1. 引言

自工业革命以来，全球地表温度已经上升 0.74℃，预计到 2100 年还将进一步上升 1.8℃，达到 3.6℃[1]。气候变暖可能会促进植物生长[2]，但同时也会增强土壤中 C 的微生物分解，从而将土壤 CO_2 排放到大气中[3] [4]，正向反馈到气候变暖中[5]。截止到 2022 年 12 月，大气二氧化碳(ACO_2)已达到 417.51 ppm，预计到本世纪末，ACO_2 将超过 550 ppm (https://www.co2.earth/)。二氧化碳(eCO_2)浓度升高直接影响植物的光合作用，从而增强固碳和干物质积累[6]。eCO_2 对植物干物质积累的促进不仅引起了碳(C)、氮(N)、磷(P)和钾(K)浓度的变化，并且还引起了从土壤到植物的养分循环[7]。但当 eCO_2 作用下的固 C 能力超过其在植物中产生新汇的能力时，植物的光合速率就会降低，以平衡源汇能力[8]。此外，植物的生产力需要更多的营养供应来匹配它们在 eCO_2 下增加的 C 同化[9] [10]。因此，土壤养分的有效性在决定植物对 eCO_2 的响应方面起着至关重要的作用[11]。在 eCO_2 条件下，植物生长总是低于预期值，这与 eCO_2 导致植物体缺 N 有关[12] [13]。Igarashi 等[14]证明，更高的 N 供应是克服 N 限制的必要条件，eCO_2 通过加速植物的生长速率而加强了 N 的限制，但可以通过满足 N 需求(与 N 素形态无关)，从而增加生物量。这预示着，未来在 eCO_2 背景下，更多的 N 素肥料将在农业生产中被投入使用，但过量的 N 会通过对土壤有机 C、N 组成与数量的影响而改变土壤的供 N 能力[15]，不利于可持续农业的发展，所以选择一些有利于植物吸收土壤 N 素的微生物群是一个很好的策略。

在全球气候变化背景下，植物－微生物互作是当前生物学和生态学研究热点[16]。丛枝菌根真菌(arbuscular mycorrhizal fungi, AMF)可以与 80%的陆生植物形成共生关系，使寄主植物能够获得更多的营养，主要是 N 和 P，以交换自身生长所需的 C [17]。一些研究表明，AMF 可以增强植物对干旱、高温、盐度和极端温度等非生物胁迫的抗性[18] [19] [20] [21]，说明 AMF 可能有助于上调寄主植物的耐受机制，同时也能阻止关键代谢途径的下调[22]。尽管 AMF 在促进气候胁迫下植物生长具有巨大潜力，但我们对 AMF 如何诱导耐受机制的调节以及触发的串扰知之甚少[23]。鉴于 CO_2 或温度在调节光合速率[24]和随后的 C 代谢中的关键作用，气候变暖或大气 CO_2 浓度增加对作物-AMF 关联的影响值得进一步研究。基于此，本研究通过查阅 1994~2022 年来国内外学者对 CO_2 浓度或温度升高对植物-AMF 的影响的相关研究，分析 CO_2 浓度或温度升高对 AMF 群落、寄主植物生长的影响。在此期间，总体发文量不多，直接相关论文 38 篇，其中以 CO_2 相关论文最多。

2. eCO_2对土壤中 AMF 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 C 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 C 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[25] [26]。

eCO_2间接改变了土壤 AMF 群落，这种改变一般认为，eCO_2主要通过影响植物向菌根的 C 分配来间接影响 AMF 群落[27]。大部分研究认为，eCO_2会增加 AMF 的多样性，增强其活性。如 Sanders 等[28]以夏枯草(*Prunella vulgaris* L.)为研究对象，证明当 CO_2浓度升高时，AMF 外部菌丝长度是普通环境 CO_2浓度处理组的 5 倍，表明 CO_2浓度升高促进了 AMF 生物量向外部菌丝的分配。Wang 等[29]研究发现，当 CO_2浓度升高时，植物有机物含量和总 P 含量增加，并且 eCO_2显著提高根外菌根真菌菌丝体生物量，揭示 AMF 在森林生态系统的养分吸收和 C 循环中发挥着关键作用。Frew 等[30]研究发现，eCO_2会增强植物光合作用，从而增加植物的养分需求，进一步导致 AMF 的丰度和定殖量的普遍增加。但也有部分研究表明，eCO_2对 AMF 没有显著影响[31]。Zheng 等[32]在研究 eCO_2和其他因素之间相互作用如何影响 AMF 的过程中发现，eCO_2对 AMF 多样性和群落组成无显著影响，eCO_2对土壤总生物量、AMF 和腐生真菌的影响并不显著。Thirkell 等[33]通过采用稳定的放射性同位素示踪剂研究 AMF 介导的养分吸收，实验结果表明，在 CO_2升高的情况下，N 素吸收在品种间都有着显著的差异，但总体而言，真菌向植株转移的 N 含量都有着减少的趋势，而根系 P 浓度基本不受 CO_2浓度的影响。Garcia 等[34]研究了暖温带森林中 AMF 对空气 CO_2浓度响应，发现 AMF 对 CO_2浓度的增加没有显著的响应，CO_2浓度对 AMF 根系定殖的影响随时间而异。造成这种研究结论不同的原因很大可能是因为不同的寄主植物对 eCO_2的响应不同以及 AMF 和寄主植物之间的相互作用不同，并且 eCO_2对 AMF 的作用还受到土壤中的元素的有效性的影响[35]。AMF 在同一个属中不同种对 eCO_2的响应也不同，Klironomos 等[36]试验结果表明，三齿蒿(*Artemisia tridentata* Nutt.)接种根内球囊霉(*Glomus intraradices*)和幼套球囊霉(*Glomus etunicatum*) 16 周后，两种 AMF 的侵染率、外生菌丝的长度以及土壤中孢子数在 eCO_2条件下均有所增加，但接种 *G.intraradices* 处理组，三齿蒿各个指标的增加量均高于接种 *G. etunicatum* 处理组。但在 eCO_2条件下，土壤中 AMF 的多样性普遍低于未受干扰的土壤，其中以球囊霉科(Glomeraceae)为主(表 1)。

事实上，我们对 AMF 物种多样性的理解在很大程度上取决于方法学的发展和新技术的应用。AMF 的多样性差异受到土壤、寄主植物、环境条件和农业实践等多种因素的影响。当环境中 CO_2浓度升高，一些 AMF 物种表现出投机行为，原因可能是其主要将能量投入后代的生产中，并进化出在不利环境中有利的特性[39]。

3. eCO_2对 AMF 共生植物生长的影响

在 eCO_2 [40] [41] [42]作用下，C3 植物组织的营养浓度普遍降低。有学者对 7761 个观察结果进行 meta 分析，结果显示，平均 689 ppm eCO_2使植株 N、P、K 含量降低 7%~15%，其中 N 的下降幅度大于 P 和 K [40] [43]。而在 eCO_2条件下，接种 AMF，植物 N、P、K 含量得到改善，例如，接种 AMF 的刺槐(*Robinia pseudoacacia* L.) [44]在 710 ppm eCO_2条件下的植株总 P 仅降低了 22%，而无 AMF 定植植物，其总 P 含量则减少 50%。Baslam 等[45]研究结果显示，eCO_2会减少莴苣(*Lactuca sativa* Linn.)叶片中养分的积累，但接种 AMF 可以改善莴苣叶片中矿质养分(如 P、Cu、Fe 等)和抗氧化化合物(类胡萝卜素、酚类、花青素、抗坏血酸)的积累。Gavito 等[46]研究结果表明，eCO_2对豌豆(*Pisum sativunl*)菌根的形成和菌根吸收土壤 P 的功能均无显著影响。Chen 等[47]研究表明，在 730 ppm eCO_2下，接种 AMF 增强了长叶车前对 ^{15}N 的吸收，但对羊茅(*Festuca arundinacea*)无影响，这表明在 eCO_2条件下，AMF 对植物养分吸收的影响可能具有种特异性[48]。

Table 1. AMF species isolated from soil under elevated CO_2
表 1. CO_2升高条件下从土壤中分离出的 AMF 物种

应力类型 Stress type	属(种数) Genus (number of species)	主要物种 Major species	参考文献 References
CO_2	球囊霉目 Glomerales (5) 巨孢囊霉目 Gigasporales (4) 多孢囊霉目 Diversisporales (2) 原囊霉目 Archaeosporales (1) 类球囊霉目 Paraglomerales (1)	聚丛球囊霉 *Glomus aggregatum* 异形根孢囊霉 *Rhizophagus irregularis* 明球囊霉 *Glomus clarum*	[37]
	球囊霉目 Glomerales (13) 巨孢囊霉目 Gigasporales (6) 多孢囊霉目 Diversisporales (5) 类球囊霉目 Paraglomerales (1) 原囊霉目 Archeosporales (1)	聚丛球囊霉 *Glomus aggregatum* 异形根孢囊霉 *Rhizophagus irregularis* 微丛球囊霉 *Glomus microaggregatum*	[38]

近年来，转基因 *Bt* 作物的推广应用为鳞翅目害虫的防治和缓解环境压力提供了有效途径。然而，有研究表明，eCO_2会导致 *Bt* 作物中 N 基化合物(即 *Bt* 毒素蛋白)显著降低[49] [50] [51]，从而对生态环境产生负面影响。在eCO_2作用下，茉莉酸(JA)、乙烯(ET)和水杨酸(SA)是植物对蚜虫的次级防御物质[52] [53]。Wang 等[54]研究表明，eCO_2环境下，接种 AMF 苏格兰斗管囊霉(*Funneliformis caledonium*)可提高 *Bt* 玉米产量，提高 *Bt* 玉米内源(JA、SA)和外源(*Bt* 毒素)二级防御物质的表达水平，最终提高 *Bt* 作物的抗虫能力，这将有助于确保 *Bt* 作物在气候变化下的可持续利用和安全性。Michael 等[55]通过向异形根孢囊霉(*Rhizophagus irregularis*)提供 ^{33}P，向小麦(*Triticum aestivum* L.)提供 $^{14}CO_2$，测试了增加 C 库强度(即食草性蚜虫)和增加 C 源强度(即升高 CO_2浓度)对菌根共生菌之间资源交换的研究，证明外部生物 C 汇可以限制植物 C 向 AMF 的分配，而不妨碍菌根的营养吸收。

总的来说，eCO_2条件下，接种 AMF 对植物生长有一定影响，植物和 AMF 之间的资源交换存在环境依赖性，eCO_2可能会增强或削弱植物对食草昆虫的防御，部分原因是 C 基和 N 基防御代谢物以及植物营养物质，特别是蛋白质含量的变化[56]。植物种类以及生活型的差异也会对 AMF 的生理活动产生影响。但是不同的生理活动会有不同的反应，存在着高度的变异性[57]。

4. 环境温度升高对 AMF 和寄主植物的影响

气候变化因子对菌根影响的研究主要集中在eCO_2的影响上，而温度的影响则被忽视[46]。温度是最重要的非生物胁迫之一，温度的轻微升高会对作物生长、籽粒灌浆和最终产量产生负面影响[58]。Jagdish 等[59]报道，短期或长期高温等热胁迫对植物的生长和产量有不利影响。AMF 通过提高寄主植物对营养物质的吸收[60]、提高 PSII 的光合速率和光化学性质[61] [62] [63] [64]、改善渗透调节[65]、抗氧化活性[66] [67]和繁殖能力[68]来缓解温度升高对寄主植物的影响。Mathur 等[69]研究结果显示，玉米植株的光合参数在环境温度升高后降低了，但接种 AMF 后恢复。Jumrani 等[70]报道，与不接种 AMF 植株相比，接种 AMF 的大豆在高温下表现出更好的生长、光合参数和种子产量，说明 AMF 可减轻温度升高对光合器官结构和功能的损伤。

环境温度升高也会直接影响 AMF [71]。Rillig 等[72]研究表明，随着环境温度的提高，土壤 AMF 菌

丝长度增加 40%以上，且 AMF 根系定植量有明显增加的趋势。次年，寄主植物根系重量没有显著变化，但 AMF 的根系定植率显著增加。并且在升温试验地块中，球囊霉素相关蛋白浓度(一种由 AMF 菌丝产生的糖蛋白，在土壤聚集中起重要作用)降低，五个直径等级的土壤团聚体水稳定性也显著降低，这些结果表明，生态系统变暖可能刺激 AMF 的 C 分配。Yang 等[73]发现，模拟增温对 AMF 的多样性无显著影响，但显著影响了 AMF 的群落组成，这与 Shi 等[74]研究结果相反，说明不同植物种类差异影响 AMF 对升温的响应。王谭国艳等[71]通过模拟增温试验证明，环境温度升高主要降低了植物根际 AMF 的孢子密度，还可能通过影响植物的群落组成间接影响 AMF 的孢子群落结构。石国玺等[75]证明，增温对 AMF 群落的影响和作用机制是依处理时间长短而异的。长期、短期增温分别降低了 45.7%和 80.0%的 AMF 物种丰富度，长期增温对 AMF 物种丰富度的负效应由根生物量降低所介导，而短期增温的负效应由土壤 N 限制所介导。此外，长期、短期增温不仅能改变 AMF 群落的物种组成和谱系组成，还导致驱动 AMF 群落构建的生态学过程从环境过滤向环境过滤和竞争排斥的中和作用转变。Qiu 等[76]研究发现，变暖诱导了 AMF 和寄主根之间的平衡，并刺激大豆农业生态系统中有机 C 的分解。此外，变暖改变了 AMF 的群落组成，有利于具有高营养吸收菌丝表面的 *Paralomus* 属，而不是易于保护土壤有机 C 的 *Glomus* 属。

在 AMF 在升温环境下生长的各种机制中，海藻糖的产生也应该被提到。海藻糖是 AMF 中一种常见的储备碳水化合物，但也是一种参与了防御反应分子。其通过稳定细胞结构来保护细胞，并使蛋白质在应激条件下维持其天然构象[77]。Ocón 等[78]研究了在升温环境下，*R. irregularis* 中海藻糖含量以及中性海藻糖酶和海藻糖-6-磷酸酶的转录调控及其活性，结果显示，长时间或密集地暴露于高温(37℃)，会引起 *R. irregularis* 中海藻糖含量增加，并且证明了海藻糖-6-磷酸(*GiTPS2*)转录本的瞬时上调与酶活性的适度增加相关。相比之下，中性海藻酶(*GiNTH1*) RNA 的积累没有变化，但在大多数情况下，温度升高促进了其活性。在应激停止后，海藻糖恢复到基础浓度，这表明中性海藻糖酶活性在热休克恢复中的作用。这些数据表明，海藻糖在 AMF 热休克恢复过程中发挥作用。

上述研究表明，评价 AMF 在缓解植物高温胁迫中作用的研究往往是基于其对菌根化植物生理性状的影响[79]。同时，土壤微生物群落也是决定植物生产性能的一个重要因素，并可能为 AMF 介导的胁迫缓解提供重要的见解[80]。但目前对 AMF 如何响应气候变暖还没有一致的结论，这有待后续更深入的研究。

5. 总结与展望

随着气候变化加剧，需要更加关注土壤健康和重要的微生物群，尤其是 AMF。AMF 作为一种促进植物健康生长的生物肥料，可以减轻许多预期的与气候变化相关的非生物和生物胁迫。AMF 通过消耗植物根系中富含 C 的分泌物，帮助植物在 eCO_2 条件下维持源－汇平衡。由于群落由数千种根际物种组成，因植物种类和土壤类型而异，所以有必要确定对植物最有利的物种和菌株，从而更好地了解植物和土壤微生物之间的相互作用，以最有效地缓解气候变化对土壤和植物造成的影响，但在 eCO_2 或环境变暖条件下，AMF 与植物之间的信号转导机制仍有待研究。建议可以优先考虑以下几个方面：1) 建立分室培养系统，利用 ^{15}N、^{33}P、^{14}C 等同位素标记元素探究环境变化对 AMF 根外菌丝转运土壤中不同常量营养素的影响[55] [81] [82]，目前国内外菌根真菌学者对同位素示踪技术在菌根代谢方面有较多应用。2) 研究思路方面可以设计 eCO_2 和环境温度双因素试验，eCO_2 和增温交互作用对 AMF 和菌根化植物的影响。需要注意的是，生物因素，如真菌和植物的种类，以及非生物因素，CO_2 浓度以及温度设置。3) 研究策略上要注重动态分析。不同时间处理和分析的样本，得到的 AMF 对于环境变化的响应可能不一致。4) 加强对 AMF 生态功能的研究。eCO_2 和升温是全球性问题，AMF-植物共生体之间的 C-养分交换的互惠性是高度依赖于环境的，因此，分离筛选可能适应 CO_2 或温度胁迫的 AMF 可能是一种潜在的生物技术工具，接种植物，以成功恢复退化的生态系统。

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参考文献

[1] Stocker, T.F., Qin, D., Plattner, G.K., *et al*. (2013) Climate Change 2013: The Physical Science Basis.

[2] Reich, P.B., Sendal, K.M. and Stefanski, A. (2018) Effects of Climate Warming on Photosynthesis in Boreal Tree Species Depend on Soil Moisture. *Nature*, **562**, 263-267. https://doi.org/10.1038/s41586-018-0582-4

[3] Crowther, T.W., Todd-Brown, K.E.O. and Rowe, C.W. (2016) Quantifying Global Soil Carbon Losses in Response to Warming. *Nature*, **540**, 104-108.

[4] Pries, C.E.H., Castanha, C., Porras, R., *et al*. (2017) The Whole-Soil Carbon Flux in Response to Warming. *Science*, **1319**, 1420-1423. https://doi.org/10.1126/science.aal1319

[5] Van Gestel, N., Shi, Z., Van Groenigen, K.J., *et al*. (2018) Predicting Soil Carbon Loss with Warming. *Nature*, **554**, E4-E5. https://doi.org/10.1038/nature25745

[6] Wang, S.H., Zhang, Y.G., Ju, W.M., *et al*. (2020) Recent Global Decline of CO_2 Fertilization Effects on Vegetation Photosynthesis. *Science*, **370**, 1295-1300.

[7] Aljazairi, S., Arias, C. and Nogues, S. (2014) Carbon and Nitrogen Allocation and Partitioning in Traditional and Modern Wheat Genotypes under Preindustrial and Future CO_2 Conditions. *Plant Biology*, **17**, 647-659. https://doi.org/10.1111/plb.12280

[8] Parvin, S., Uddin, S., Tausz-Posch, S., *et al*. (2020) Carbon Sink Strength of Nodules but Not Other Organs Modulates Photosynthesis of Faba Bean (*Vicia faba*) Grown under Elevated [CO_2] and Different Water Supply. *New Phytologist*, **227**, 132-145. https://doi.org/10.1111/nph.16520

[9] Jakobsen, I., Smith, S.E., Smith, F.A., *et al*. (2016) Plant Growth Responses to Elevated Atmospheric CO_2 Are Increased by Phosphorus Sufficiency but Not by Arbuscular Mycorrhizas. *Journal of Experimental Botany*, **67**, 6173-6186. https://doi.org/10.1093/jxb/erw383

[10] Dabu, X., Li, S. and Cai, Z. (2019) The Effect of Potassium on Photosynthetic Acclimation in Cucumber during CO_2 Enrichment. *Photosynthetica*, **57**, 640-645. https://doi.org/10.32615/ps.2019.073

[11] Shi, S., Luo, X., Dong, X., *et al*. (2021) Arbuscular Mycorrhization Enhances Nitrogen, Phosphorus and Potassium Accumulation in *Vicia faba* by Modulating Soil Nutrient Balance under Elevated CO_2. *Fungi* (*Basel*), **7**, Article 361. https://doi.org/10.3390/jof7050361

[12] Kimball, B.A., Mauney, J.R. and Nakayama, F.S. (1993) Effects of Increasing Atmospheric CO_2 on Vegetation. *Vegetation*, **104**, 65-75. https://doi.org/10.1007/BF00048145

[13] Ainsworth, E.A. and Long, S.P. (2005) What Have We Learned from 15 Years of Free-Air CO_2 Enrichment (FACE)? A Meta-Analytic Review of the Responses of Photosynthesis, Canopy Properties and Plant Production to Rising CO_2. *New Phytologist*, **165**, 351-371. https://doi.org/10.1111/j.1469-8137.2004.01224.x

[14] Igarashi, M., Yi, Y. and Yano, K. (2021) Revisiting Why Plants Become N Deficient under Elevated CO_2: Importance to Meet N Demand Regardless of the Fed-Form. *Frontiers in Plant Science*, **12**, Article 726186. https://doi.org/10.3389/fpls.2021.726186

[15] 刘金山，戴健，刘洋，等. 过量施氮对旱地土壤碳、氮及供氮能力的影响[J]. 植物营养与肥料学报，2015，21(1): 112-120.

[16] 王亚杰，段廷玉. AM 真菌对植物挥发性物质影响的研究现状与展望[J]. 草地学报, 2020, 28(5): 1185-1195.

[17] Smith, S.E. and Read, D.J. (2010) Mycorrhizal Symbiosis. Academic Press, Cambridge.

[18] Birgander, J., Rousk, J. and Olsson, P.A. (2017) Warmer Winters Increase the Rhizosphere Carbon Flow to Mycorrhizal Fungi More than to Other Microorganisms in a Temperate Grassland. *Global Change Biology*, **23**, 5372-5382. https://doi.org/10.1111/gcb.13803

[19] Rillig, M.C., Wright, S.F., Shaw, M.R., *et al*. (2002) Artificial Climate Warming Positively Affects Arbuscular Mycorrhizae but Decreases Soil Aggregate Water Stability in an Annual Grassland. *Oikos*, **97**, 52-58. https://doi.org/10.1034/j.1600-0706.2002.970105.x

[20] Oliveira, T.C., Cabral, J.S.R., Santana, L.R., *et al*. (2022) The Arbuscular Mycorrhizal Fungus *Rhizophagus clarus* Im-

proves Physiological Tolerance to Drought Stress in Soybean Plants. *Scientific Reports*, **12**, Article No. 9044. https://doi.org/10.1038/s41598-022-13059-7

[21] Qin, W., Yan, H., Zou, B., *et al*. (2021) Arbuscular Mycorrhizal Fungi Alleviate Salinity Stress in Peanut: Evidence from Pot-Grown and Field Experiments. *Food and Energy Security*, **10**, e314. https://doi.org/10.1002/fes3.314

[22] Nanjareddy, K., Arthikala, M.K., Gómez, B.M., *et al*. (2017) Differentially Expressed Genes in Mycorrhized and Nodulated Roots of Common Bean Are Associated with Defense, Cell Wall Architecture, N Metabolism, and P Metabolism. *PLOS ONE*, **12**, e0182328. https://doi.org/10.1371/journal.pone.0182328

[23] Xiao, X., Chen, J., Liao, X., *et al*. (2022) Different Arbuscular Mycorrhizal Fungi Established by Two Inoculation Methods Improve Growth and Drought Resistance of *Cinnamomum migao* Seedlings Differently. *Biology*, **11**, Article 220. https://doi.org/10.3390/biology11020220

[24] Kooi, C.J., Reich, M., Löw, M., *et al*. (2016) Growth and Yield Stimulation under Elevated CO_2 and Drought: A Meta-Analysis on Crops. *Environmental and Experimental Botany*, **122**, 150-157. https://doi.org/10.1016/j.envexpbot.2015.10.004

[25] Wicklow, D.T. and Carroll, G.C. (1981) The Fungal Community: Its Organization and Role in the Ecosystem. Marcel Dekker, New York.

[26] Allison, S., Hanson, C. and Treseder, K. (2007) Nitrogen Fertilization Reduces Diversity and Alters Community Structure of Active Fungi in Boreal Ecosystems. *Soil Biology and Biochemistry*, **39**, 1878-1887. https://doi.org/10.1016/j.soilbio.2007.02.001

[27] 宋鸽，王全成，郑勇，等. 丛枝菌根真菌对大气 CO_2 浓度升高和增温响应研究进展[J]. 应用生态学报，2022, 33(6): 1709-1718.

[28] Sanders, I., *et al*. (1998) Increased Allocation to External Hyphae of Arbuscular Mycorrhizal Fungi under CO_2 Enrichment. *Oecologia*, **117**, 496-503. https://doi.org/10.1007/s004420050685

[29] Wang, C., Zong, S. and Li, M.H. (2019) The Contrasting Responses of Mycorrhizal Fungal Mycelium Associated with Woody Plants to Multiple Environmental Factors. *Forests*, **10**, 973-973. https://doi.org/10.3390/f10110973

[30] Frew, A. and Price, J.N. (2019) Mycorrhizal-Mediated Plant-Herbivore Interactions in a High CO_2 World. *Functional Ecology*, **33**, 1376-1385. https://doi.org/10.1111/1365-2435.13347

[31] Clark, N.M., Rillig, M.C. and Nowak, R.S. (2009) Arbuscular Mycorrhizal Fungal Abundance in the Mojave Desert: Seasonal Dynamics and Impacts of Elevated CO_2. *Journal of Arid Environments*, **73**, 834-843. https://doi.org/10.1016/j.jaridenv.2009.03.004

[32] Zheng, J., Cui, M., Wang, C., *et al*. (2022) Elevated CO_2, Warming, N Addition, and Increased Precipitation Affect Different Aspects of the Arbuscular Mycorrhizal Fungal Community. *Science of the Total Environment*, **806**, Article ID: 150522. https://doi.org/10.1016/j.scitotenv.2021.150522

[33] Thirkell, T.J., Pastok, D. and Field, K.J. (2020) Carbon for Nutrient Exchange between Arbuscular Mycorrhizal Fungi and Wheat Varies According to Cultivar and Changes in Atmospheric Carbon Dioxide Concentration. *Global Change Biology*, **26**, 1725-1738. https://doi.org/10.1111/gcb.14851

[34] Garcia, M.O., Ovasapyan, T., Greas, M., *et al*. (2008) Mycorrhizal Dynamics under Elevated CO_2 and Nitrogen Fertilization in a Warm Temperate Forest. *Plant & Soil*, **303**, 301-310. https://doi.org/10.1007/s11104-007-9509-9

[35] Reid, J.P., Adair, E.C., Hobbie, S.E., *et al*. (2012) Biodiversity, Nitrogen Deposition, and CO_2 Affect Grassland Soil Carbon Cycling but Not Storage. *Ecosystems*, **15**, 580-590. https://doi.org/10.1007/s10021-012-9532-4

[36] Klironomos, J.N., Ursic, M. and Rillig, M. (1998) Interspecific Differences in the Response of Arbuscular Mycorrhizal Fungi to *Artemisia tridentata* Grown under Elevated Atmospheric CO_2. *New Phytologist*, **138**, 599-605. https://doi.org/10.1046/j.1469-8137.1998.00141.x

[37] Wolf, J., Johnson, N.C., Rowland, D.L., *et al*. (2001) Elevated CO_2 and Plant Species Richness Impact Arbuscular Mycorrhizal Fungal Spore Communities. *New Phytologist*, **157**, 579-588. https://doi.org/10.1046/j.1469-8137.2003.00696.x

[38] Antoninka, A., Reich, P.B. and Johnson, N.C. (2011) Seven Years of Carbon Dioxide Enrichment, Nitrogen Fertilization and Plant Diversity Influence Arbuscular Mycorrhizal Fungi in a Grassland Ecosystem. *New Phytologist*, **192**, 200-214. https://doi.org/10.1111/j.1469-8137.2011.03776.x

[39] Sy’korová, Z., Ineichen, K., Wiemken, A., *et al*. (2007) The Cultivation Bias: Different Communities of Arbuscular Mycorrhizal Fungi Detected in Roots from the Field, from Bait Plants Transplanted to the Field, and from a Greenhouse Trap Experiment. *Mycorrhiza*, **18**, 1-14. https://doi.org/10.1007/s00572-007-0147-0

[40] Du, C., Wang, X., Zhang, M., *et al*. (2019) Effects of Elevated CO_2 on Plant C-N-P Stoichiometry in Terrestrial Ecosystems: A Meta-Analysis. *Science of the Total Environment*, **650**, 697-708. https://doi.org/10.1016/j.scitotenv.2018.09.051

[41] Treseder, K.K. (2004) A Meta-Analysis of Mycorrhizal Responses to Nitrogen, Phosphorus, and Atmospheric CO_2 in Field Studies. *New Phytologist*, **164**, 347-355. https://doi.org/10.1111/j.1469-8137.2004.01159.x

[42] Butterly, C.R., Armstrong, R., Chen, D., *et al*. (2015) Carbon and Nitrogen Partitioning of Wheat and Field Pea Grown with Two Nitrogen Levels under Elevated CO_2. *Plant and Soil*, **391**, 367-382. https://doi.org/10.1007/s11104-015-2441-5

[43] Loladze, I. (2014) Hidden Shift of the Ionome of Plants Exposed to Elevated CO_2 Depletes Minerals at the Base of Human Nutrition. *eLife*, **3**, e02245. https://doi.org/10.7554/eLife.02245

[44] Olesniewicz, K.S. and Thomas, R.B. (1999) Effects of Mycorrhizal Colonization on Biomass Production and Nitrogen Fixation of Black Locust (*Robinia pseudoacacia*) Seedlings Grown under Elevated Atmospheric Carbon Dioxide. *New Phytologist*, **142**, 133-140. https://doi.org/10.1046/j.1469-8137.1999.00372.x

[45] Baslam, M., Garmendia, I. and Goicoechea, N. (2012) Elevated CO_2 May Impair the Beneficial Effect of Arbuscular Mycorrhizal Fungi on the Mineral and Phytochemical Quality of Lettuce. *Annals of Applied Biology*, **161**, 180-191. https://doi.org/10.1111/j.1744-7348.2012.00563.x

[46] Gavito, M.E., Schweiger, P. and Jakobsen, I. (2002) P Uptake by Arbuscular Mycorrhizal Hyphae: Effect of Soil Temperature and Atmospheric CO_2 Enrichment. *Global Change Biology*, **9**, 106-116. https://doi.org/10.1046/j.1365-2486.2003.00560.x

[47] Chen, X., Tu, C., Burton, M.G., *et al*. (2007) Plant Nitrogen Acquisition and Interactions under Elevated Carbon Dioxide: Impact of Endophytes and Mycorrhizae. *Global Change Biology*, **13**, 1238-1249. https://doi.org/10.1111/j.1365-2486.2007.01347.x

[48] 孙颖盈，王欣雨，祝晨琳. 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[J]. 植物学研究, 2022, 11(3): 299-305.

[49] Chen, F.J., Wu, G., Ge, F., *et al*. (2005) Effects of Elevated CO_2 and Transgenic *Bt* Cotton on Plant Chemistry, Performance, and Feeding of an Insect Herbivore, the Cotton Bollworm. *Entomologia Experimentalis et Applicata*, **115**, 341-350. https://doi.org/10.1111/j.1570-7458.2005.00258.x

[50] Wu, G., Chen, F.J., Ge, F., *et al*. (2011) Impacts of Elevated CO_2 on Expression of Plant Defensive Compounds in *Bt*-Transgenic Cotton in Response to Infestation by Cotton Bollworm. *Agricultural and Forest Entomology*, **13**, 77-82. https://doi.org/10.1111/j.1461-9563.2010.00508.x

[51] Liu, Y.M., Dang, Z.H., Parajulee, M.N., *et al*. (2019) Interactive Effects of [CO_2] and Temperature on Plant Chemistry of Transgenic *Bt* Rice and Population Dynamics of a Non-Target Planthopper, *Nilaparvata lugens* (Stål) under Different Levels of Soil Nitrogen. *Toxins*, **11**, Article 261. https://doi.org/10.3390/toxins11050261

[52] Sun, Y.C., Guo, H.J., Zhu-Salzman, K., *et al*. (2013) Elevated CO_2 Increases the Abundance of the Peach Aphid on Arabidopsis by Reducing Jasmonic Acid Defenses. *Plant Science*, **210**, 128-140. https://doi.org/10.1016/j.plantsci.2013.05.014

[53] Guo, H.J., Sun, Y.C., Li, Y.F., *et al*. (2014) Elevated CO_2 Alters the Feeding Behaviour of the Pea Aphid by Modifying the Physical and Chemical Resistance of *Medicago truncatula*. *Plant, Cell & Environment*, **37**, 2158-2168. https://doi.org/10.1111/pce.12306

[54] Wang, L., Wang, X., Gao, F., *et al*. (2021) AMF Inoculation Can Enhance Yield of Transgenic *Bt* Maize and Its Control Efficiency against *Mythimna separata* Especially under Elevated CO_2. *Frontiers in Plant Science*, **12**, Article 655060. https://doi.org/10.3389/fpls.2021.655060

[55] Charters, M.D., Sait, S.M. and Field, K.J. (2020) Aphid Herbivory Drives Asymmetry in Carbon for Nutrient Exchange between Plants and an Arbuscular Mycorrhizal Fungus. *Current Biology*, **30**, 1801-1808.E5. https://doi.org/10.1016/j.cub.2020.02.087

[56] Kretzschmar, F.D.S., Aidar, M.P.M., Salgado, I., *et al*. (2009) Elevated CO_2 Atmosphere Enhances Production of Defense-Related Flavonoids in Soybean Elicited by No and a Fungal Elicitor. *Environmental and Experimental Botany*, **65**, 319-329. https://doi.org/10.1016/j.envexpbot.2008.10.001

[57] Luo, Y. (2003) Response of Soil Microorganism to Elevated Atmospheric CO_2 Concentration. *Journal of Ecology and Environment*, **12**, 357-360.

[58] Hasanuzzaman, M., Nahar, K., Alam, M.M., *et al*. (2013) Physiological, Biochemical and Molecular Mechanisms of Heat Stress Tolerance in Plants. *International Journal of Molecular Sciences*, **14**, 9643-9684. https://doi.org/10.3390/ijms14059643

[59] Jagadish, S.V.K., Way, D.A. and Sharkey, T.D. (2021) Plant Heat Stress: Concepts Directing Future Research. *Plant, Cell & Environment*, **44**, 1992-2005. https://doi.org/10.1111/pce.14050

[60] Barzana, G., Aroca, R., Bienert, G.P., *et al*. (2014) New Insights into the Regulation of Aquaporins by the Arbuscular Mycorrhizal Symbiosis in Maize Plants under Drought Stress and Possible Implications for Plant Performance.

Plant—Microbe Interaction, **27**, 349-363. https://doi.org/10.1094/MPMI-09-13-0268-R

[61] Ruíz-Sánchez, M., Aroca, R., Munoz, *et al*. (2010) The Arbuscular Mycorrhizal Symbiosis Enhances the Photosynthetic Efficiency and the Antioxidative Response of Rice Plants Subjected to Drought Stress. *Plant Physiology*, **167**, 862-869. https://doi.org/10.1016/j.jplph.2010.01.018

[62] Zhu, X.C., Song, F.B. and Xu, H.W. (2010) Arbuscular Mycorrhizae Improves Low Temperature Stress in Maize via Alterations in Host Water Status and Photosynthesis. *Plant and Soil*, **331**, 129-137. https://doi.org/10.1007/s11104-009-0239-z

[63] Zhu, X.C., Song, F.B., Liu, S.Q., *et al*. (2012) Arbuscular Mycorrhizae Improves Photosynthesis and Water Status of *Zea mays* L. under Drought Stress. *Plant*, *Soil and Environment*, **58**, 186-191. https://doi.org/10.17221/23/2011-PSE

[64] Habibzadeh, Y., Pirzad, A., Zardashti, M.R., *et al*. (2013) Effects of Arbuscular Mycorrhizal Fungi on Seed and Protein Yield under Water Deficit Stress in Mung Bean. *Agronomy Journal*, **105**, 79-84. https://doi.org/10.2134/agronj2012.0069

[65] Porcel, R. and Ruiz-Lozano, J.M. (2004) Arbuscular Mycorrhizal Influence on Leaf Water Potential, Solute Accumulation, and Oxidative Stress in Soybean Plants Subjected to Drought Stress. *Journal of Experimental Botany*, **55**, 1743-1750. https://doi.org/10.1093/jxb/erh188

[66] Zhu, X.C., Song, F.B. and Xu, H.W. (2009) Influence of Arbuscular Mycorrhiza on Lipid Peroxidation and Antioxidant Enzyme Activity of Maize Plants under Temperature Stress. *Mycorrhiza*, **20**, 325-332. https://doi.org/10.1007/s00572-009-0285-7

[67] Wu, Q.S., Zou, Y.N., Liu, W., *et al*. (2010) Alleviation of Salt Stress in Citrus Seedlings Inoculated with Mycorrhiza: Changes in Leaf Antioxidant Defense Systems. *Plant*, *Soil and Environment*, **56**, 470-475. https://doi.org/10.17221/54/2010-PSE

[68] Lu, X. and Koide, R.T. (1994) The Effects of Mycorrhizal Infection on Components of Plant Growth and Reproduction. *New Phytologist*, **128**, 211-218. https://doi.org/10.1111/j.1469-8137.1994.tb04004.x

[69] Mathur, S., Agnihotri, R., Sharma, M.P., *et al*. (2021) Effect of High-Temperature Stress on Plant Physiological Traits and Mycorrhizal Symbiosis in Maize Plants. *Fungi* (*Basel*), **7**, 867. https://doi.org/10.3390/jof7100867

[70] Jumrani, K., Bhatia, V.S., Kataria, S., *et al*. (2022) Inoculation with Arbuscular Mycorrhizal Fungi Alleviates the Adverse Effects of High Temperature in Soybean. *Plants* (*Basel*), **11**, Article 2210. https://doi.org/10.3390/plants11172210

[71] 王谭国艳, 马志远, 李沛洋, 等. 短期增温对青藏高原高寒草甸不同植物根际丛枝菌根真菌的影响[J]. 草地学报, 2021, 29(9): 1959-1966.

[72] Rillig, M.C., Leifheit, E. and Lehmann, J. (2021) Microplastic Effects on Carbon Cycling Processes in Soils. *PLOS Biology*, **19**, e3001130. https://doi.org/10.1371/journal.pbio.3001130

[73] Yang, W., Yong, Z., Chen, G., *et al*. (2013) The Arbuscular Mycorrhizal Fungal Community Response to Warming and Grazing Differs between Soil and Roots on the Qinghai-Tibetan Plateau. *PLOS ONE*, **8**, e76447. https://doi.org/10.1371/journal.pone.0076447

[74] Shi, G., Yao, B., Liu, Y., *et al*. (2017) The Phylogenetic Structure of AMF Communities Shifts in Response to Gradient Warming with and without Winter Grazing on the Qinghai-Tibet Plateau. *Applied Soil Ecology*, **121**, 31-40. https://doi.org/10.1016/j.apsoil.2017.09.010

[75] 石国玺, 王芳萍, 马丽, 等. 长期、短期增温对高寒草甸 AM 真菌群落结构的影响[J]. 草地学报, 2021, 29(z1): 179-189.

[76] Qiu, Y., Guo, L., Xu, X., *et al*. (2021) Warming and Elevated Ozone Induce Tradeoffs between Fine Roots and Mycorrhizal Fungi and Stimulate Organic Carbon Decomposition. *Science Advances*, **7**, eabe9256. https://doi.org/10.1126/sciadv.abe9256

[77] Eroglu, A., Russo, M.J., Bieganski, R., *et al*. (2000) Intracellular Trehalose Improves the Survival of Cryopreserved Mammalian Cells. *Nature Biotechnology*, **18**, 163-167. https://doi.org/10.1038/72608

[78] Ocón, A., Hampp, R. and Requena, N. (2007) Trehalose Turnover during Abiotic Stress in Arbuscular Mycorrhizal Fungi. *New Phytologist*, **174**, 879-891. https://doi.org/10.1111/j.1469-8137.2007.02048.x

[79] Lennon, J.T. and Jones, S.E. (2011) Microbial Seed Banks: The Ecological and Evolutionary Implications of Dormancy. *Nature Reviews Microbiology*, **9**, 119-130. https://doi.org/10.1038/nrmicro2504

[80] Rui, J.L., Wang, S., An, J., *et al*. (2015) Responses of Bacterial Communities to Simulated Climate Changes in Alpine Meadow Soil of the Qinghai-Tibet Plateau. *Applied and Environmental Microbiology*, **81**, 6070-6077. https://doi.org/10.1128/AEM.00557-15

[81] 金海如, 丁国丽, 蒋湘艳, 孙颖盈. 一种生物组织硝态氮素中 ^{15}N 丰度的测定方法[P]. 中国专利, CN202210631176.1. 2022-09-06.

[82] Field, K.J., Cameron, D.D., Leake, J.R., *et al*. (2012) Contrasting Arbuscular Mycorrhizal Responses of Vascular and Non-Vascular Plants to a Simulated Palaeozoic CO_2 Decline. *Nature Communications*, **3**, Article No. 835. https://doi.org/10.1038/ncomms1831