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## AM 真菌提高植物抗逆性的机制

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**摘要:**丛枝菌根(arbuscular mycorrhizae, AM)真菌是自然界中最广泛的植物共生真菌,可以提高宿主对生物和非生物逆境的抗性。AM 真菌能通过改善养分吸收、增加渗透调节物质的积累,提高抗氧化酶类活性、强化渗透调节作用并维持植物内源激素平衡,增加生长素的合成,调节碳氮代谢,刺激胁迫诱导基因表达,增强植物根系及菌丝本身对重金属元素的固持作用等提高植物对非生物逆境(如干旱、高低温、重金属、盐碱)的抗性;并能通过构建菌丝网络,形成对根部入侵病原真菌的机械屏障,增强抗病性相关酶活性,合成与抗病性相关的次生代谢产物,增强抗病、虫相关基因的表达,菌丝传递抗虫防御信号,能提高邻近植株的抗虫性,增强植物的抗病虫能力。本文归纳了近几年来国内外有关 AM 真菌影响植物抗逆性及其作用机理的研究进展,并对 AM 真菌在促进植物抗逆性方面的研究作了展望。

**关键词:**AM 真菌;植物;生物逆境;非生物逆境;抗性;机制;生理生化反应

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### Research progress on the mechanism of AM fungi for improving plant stress resistance

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**Abstract:** Arbuscular mycorrhizae (AM) fungi could increase plant resistance to biotic and abiotic stresses. AM fungi could improve plant resistance to abiotic stresses, including drought, high or low temperature, heavy metal, and salt. The mechanism includes improving plant nutrient absorption, the accumulation of osmotic adjustment substances and activities of antioxidative enzymes, strengthening the effects of osmotic adjustment and maintaining the balance of plant hormones, and increasing auxin synthesis, and regulating carbon and nitrogen metabolism. AM fungi could also induce plant defense gene expression and enhance the capacity of plant roots and mycelium to hold heavy metal. The mechanism of AM fungi for defense against plant disease and insects may include building the mycelium network that can form mechanical barriers for the pathogen that is invading, enhancing the activities of resistance-related enzymes, synthesizing secondary metabolites associated with disease and insect resistance, promoting the expression of genes related to diseases and pests, and transmission by mycelium of the signal of insect resistance defense to improve the insect resistance of adjacent plants. We summarize the effects of AM fungi on plant stress resistance and the mechanisms found both at home and abroad in recent years.

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**Key words:** arbuscular mycorrhizal; plant; biotic stress; abiotic stress; resistance; mechanism; physiological and biochemical responses

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丛枝菌根(arbuscular mycorrhizae, AM)是由球囊菌门真菌(*Glomeromycota*)与陆生植物的根形成的一种共生体,在世界范围内分布十分广泛。90%的维管植物都能形成AM真菌,120余种AM真菌可以和超过200 000种植物共生<sup>[1]</sup>。AM真菌可以活化土壤中的无机营养元素,促进宿主植物对养分(如N、P、K、Zn等)的吸收<sup>[2-6]</sup>,改善宿主的营养状况<sup>[7]</sup>;促进水分代谢,增强植物抗旱性<sup>[8]</sup>;提高宿主植物对低温、高温的耐受性<sup>[9-10]</sup>;同时AM真菌亦可增强植物耐盐碱的能力<sup>[11]</sup>,减轻土壤重金属污染对植物造成的危害<sup>[12]</sup>;提高植物抗病性<sup>[13]</sup>、抗虫性<sup>[14]</sup>,提高植物品质及其产量,对于植物适应各种逆境胁迫具有重要意义。

AM真菌在植物不同物种间的竞争中也有重要作用,可以引起群落的演替,促进物种多样性变化,影响生态系统的群落结构变化,促进系统中的碳循环及氮循环,从而在一定程度上影响全球气候的变化<sup>[15-17]</sup>。菌根生物技术的应用十分广泛,它在牧场草地修复、干旱地区土壤的改良、开垦荒山、植树造林以及保护自然生态资源、维持生态系统的稳定等方面均有重要作用<sup>[18]</sup>。AM真菌可以促进地表垃圾分解,抑制土壤微生物群落的生长,因此菌根生物技术也可广泛应用于环境修复,且这类技术具有适应性强的优点,即使在各种不利生态环境条件下,也能很好地应用,从而能更好地维持生态系统平衡<sup>[19-21]</sup>。因此加大对AM真菌的研究,尤其是利用AM真菌与植物共生对植物抗逆性的影响,对于实现农业可持续发展、促进生物多样性保护具有重要意义。

## 1 AM真菌对植物抗非生物逆境的抗性机制

### 1.1 抗旱

自然界诸多环境因子都会限制或影响植物进行正常生理生化代谢,水分是最普遍的胁迫因子之一<sup>[22-23]</sup>。水分缺失会导致植物叶面积减小,气孔关闭,根系呼吸作用加强,植株叶片光合速率和光合能力下降,严重时甚至造成植被大面积死亡;干旱地区土壤贫瘠,植被退化,生物多样性较少,生态系统稳定性降低,生态环境持续恶化,易遭受破坏且难以修复<sup>[24]</sup>。所以,提高植物体对干旱胁迫的耐受性可以促进植物群落多样性变

化、维持生态系统结构和功能的稳定。

大量研究表明,AM真菌与植物体共生可以促进宿主植物对水分的吸收与利用,提高植物对干旱胁迫的抵抗能力<sup>[25]</sup>。近年来,国内外学者已对此进行了大量的试验验证。对紫花苜蓿(*Medicago sativa*)、三叶草(*Trifolium alexandrinum*)等多种植物<sup>[26-33]</sup>的研究结果表明,在干旱胁迫条件下,摩西球囊霉(*Glomus mosseae*)、根内球囊霉(*G. intraradices*)等AM真菌可以促进植物生长,提高植物抗旱能力。在对紫花苜蓿的研究中发现,当土壤相对含水量下降到20%时,接种摩西球囊霉的植株相比未接菌植株,其地上及地下部分的干物质产量平均可增加57.93和16.47 g,可溶性糖含量增加0.018%,可溶性蛋白含量增加0.004%,丙二醛含量降低 $0.007 \mu\text{mol} \cdot \text{g}^{-1}$ <sup>[26]</sup>。有关接种AM真菌对植物体内脯氨酸含量的影响仍存在很多争议,对民勤绢蒿(*Seriphidium minchünense*)的研究发现,在水分胁迫下接种AM真菌的植株叶片脯氨酸含量低于未接菌植株<sup>[28]</sup>,但在对连翘(*Forsythia suspensa*)的研究中则发现,接种AM真菌显著增加了植株叶片脯氨酸含量<sup>[29]</sup>。AM真菌也可提高抗氧化酶类,包括超氧化物歧化酶(SOD)、过氧化物酶(POD)和过氧化氢酶(CAT)等的活性,在土壤相对含水量为30%的干旱胁迫条件下,以摩西球囊霉和缩球囊霉(*G. constrictum*)接种紫穗槐(*Amorpha fruticosa*),其SOD活性较未接种AM真菌植株最高可增加 $6.61 \text{ U} \cdot (\text{g} \cdot \text{h})^{-1}$ ,POD活性最高增加 $189.61 \mu\text{g} \cdot (\text{g} \cdot \text{min})^{-1}$ ,CAT活性最高增加 $49.38 \text{ U} \cdot (\text{g} \cdot \text{min})^{-1}$ ,而植株根系活力相应提高 $0.17 \text{ mg} \cdot (\text{g} \cdot \text{h})^{-1}$ <sup>[33]</sup>。另外,AM真菌对植物的作用还包括促进土壤团聚体的形成,改善土壤理化性质;促进生长素合成,抑制胁迫响应因子脱落酸的合成等(表1)。

AM真菌提高植物抗旱性的作用机制可以归纳为生理生化机制和分子机制。AM真菌影响植物抗旱性主要表现在植物体自身产生的生理生化反应,包括提高可溶性糖、可溶性蛋白等渗透调节物质的积累,从而提高细胞液浓度,降低细胞渗透势,防止细胞脱水,细胞水势降低,与外界形成较高的水势差,提高细胞吸水或保水能力,从而适应水分胁迫环境<sup>[26]</sup>;改变根系及

表 1 AM 真菌对干旱胁迫的响应及其机制

Table 1 Response and mechanism of AM fungi to drought stress

宿主植物 Host plant	AM 真菌 AM fungi	试验条件 Experimental condition	水分处理 Water treatment	AM 作用 AM function	参考文献 Reference
紫花苜蓿 <i>Medicago sativa</i>	摩西球囊霉 <i>G. mosseae</i> 根内球囊霉 <i>G. intraradices</i>	盆栽 Pots	80%:20%	提高可溶性糖、可溶性蛋白含量,降低丙二醛和脯氨酸含量 Improved soluble protein and soluble sugar content, reduced MDA and proline content.	[26]
枸杞 <i>Lycium barbarum</i>	缩球囊霉 <i>G. constrictum</i>	盆栽 Pots	75%~80%; 40%~50%	提高蒸腾速率和光合活性 Improved transpiration rate and photosynthesis activity.	[27]
民勤绢蒿 <i>Seriphidium minchünense</i>	摩西球囊霉 <i>G. mosseae</i>	盆栽 Pots	80%:20%	提高黄酮含量,降低脯氨酸含量 Increased flavonoids content and reduced proline content.	[28]
连翘 <i>Forsythia suspensa</i>	缩球囊霉 <i>G. constrictum</i> 集球囊霉 <i>G. fasciculatum</i>	水培 Hydroponics	正常供水 Well-watered; 干旱胁迫 Drought stress	提高脯氨酸含量与 SOD 活性 Improved proline content, SOD enzymatic activity.	[29]
三叶草 <i>Trifolium alexandrinum</i>	摩西球囊霉 <i>G. mosseae</i>	盆栽 Pots	正常供水 Well-watered; 干旱胁迫 Drought stress	促进水孔蛋白基因表达 Promoted aquaporins genes expression.	[30]
番茄 <i>Lycopersicon esculentum</i>	根内球囊霉 <i>G. intraradices</i>	盆栽 Pots	正常供水 Well-watered; 干旱胁迫 Drought stress	促进水孔蛋白基因及 <i>Slnced</i> 基因表达 Promoted aquaporins genes and <i>Slnced</i> gene expression.	[31]
大豆 <i>Glycine max</i>	摩西球囊霉 <i>G. intraradices</i> 根内球囊霉 <i>G. mosseae</i>	盆栽 Pots	正常供水 Well-watered; 干旱胁迫 Drought stress	下调 <i>gmPIP2</i> 、 <i>gmlea8</i> 和 <i>gmlea10</i> 基因的表达 Down-regulated <i>gmPIP2</i> , <i>gmlea8</i> and <i>gmlea10</i> gene expression.	[32]
紫穗槐 <i>Amorpha fruticosa</i>	摩西球囊霉 <i>G. mosseae</i> 缩球囊霉 <i>G. constrictum</i>	盆栽 Pots	30%;50%;70%	提高可溶性糖、可溶性蛋白含量,以及抗氧化酶类活性 Improved soluble protein content, soluble sugar content, and antioxidant enzymatic activity.	[33]
甜瓜 <i>Cucumis melo</i>	摩西球囊霉 <i>G. mosseae</i> 地表球囊霉 <i>G. versiforme</i> 根内球囊霉 <i>G. intraradices</i>	盆栽 Pots	80%~90%; 35%~45%	诱导 <i>MeP5CS</i> 基因表达,增加脯氨酸积累 Induced <i>MeP5CS</i> gene expression, improved proline content.	[34]
玉米 <i>Zea mays</i>	根内球囊霉 <i>G. intraradices</i>	盆栽 Pots	正常供水 Well-watered; 干旱胁迫 Drought stress	增加水孔蛋白积累量 Increased accumulation of aquaporins.	[35]

续表 1

宿主植物 Host plant	AM 真菌 AM fungi	试验条件 Experimental condition	水分处理 Water treatment	AM 作用 AM function	参考文献 Reference
小叶锦鸡儿 <i>Caragana microphylla</i> 蒙古扁桃 <i>Prunus mongolica</i>	摩西球囊霉 <i>G. mosseae</i> 根内球囊霉 <i>G. intraradices</i>	盆栽 Pots	55% ; 35%	提高植株生物量与根系活力,降低叶片水分饱和亏(WSD)含量 Increased plant biomass and root activity, reduced leaf WSD content.	[36]
肾脏紫云英 <i>Anthyllis cytisoides</i>	土壤 AM 真菌 Soil AM fungi	水培 Hydroponics	50%~70%	提高抗氧化酶类活性 Increased antioxidant enzymatic activity.	[37]
马铃薯 <i>Solanum tuberosum</i>	根内球囊霉 <i>G. intraradices</i>	大田 Field	正常供水 Well-watered; 干旱胁迫 Drought stress	提高硝酸还原酶活性 Increased nitrate reductase enzymatic activity.	[38]
菜豆 <i>Phaseolus vulgaris</i>	土壤 AM 真菌 Soil AM fungi	盆栽 Pots	正常供水 Well-watered; 干旱胁迫 Drought stress	增加 9-顺式-环氧类胡萝卜双加氧酶(NCED)的 mRNA 丰度 Increased NCED enzyme mRNA abundance.	[39]

叶片形态,降低叶片电解质透出率,增加气孔导度,提高根系导水性,增加叶绿素积累,促进植物光合作用<sup>[27]</sup>;提高抗氧化酶类活性,增强宿主的活性氧(ROS)清除能力,降低 H<sub>2</sub>O<sub>2</sub> 的积累,减轻对原生质膜的伤害,保护生物膜的完整性,有效减轻干旱胁迫对植物的伤害<sup>[23,31]</sup>;AM 真菌可以分泌具有良好胶水性质的球囊霉素,有效增加土壤的渗透性及稳定性,而 AM 真菌菌丝则可以与土壤微粒结合,构建土壤团聚体的结构骨架,促进稳定性较高的土壤团聚体的形成,改善土壤理化性质,从而实现植物耐旱性能的提升<sup>[40]</sup>;AM 真菌菌丝网络构成了高效的营养物质吸收和转运系统,可以提高植物养分吸收效率,增强宿主植物的资源获取能力,促进植物营养代谢,从而促进水分吸收与利用,提高宿主抗旱性<sup>[41]</sup>。而究其本质,AM 真菌提高植物抗旱性主要是通过上调或者下调胁迫应答基因表达,以及诱导新的抗逆基因表达等来实现的,如特异性调节水孔蛋白基因、编码脱水素的基因 *gmPIP2*、*gmlea8* 和 *gmlea10* 等相关基因的表达,其中水孔蛋白基因控制着水孔蛋白的合成,这种蛋白可以形成一个具有高度选择性的独立水通道,从而促进植物体水分的吸收与运输;而基因 *gmPIP2*、*gmlea8* 和 *gmlea10* 均可编码脱水素,这是植物体内的一种晚期胚胎富集蛋白(late embryogenesis-abundant proteins, LEA),具有很强的亲水性,可以维持细胞膜结构及功能的稳定,

保护蛋白质和螯合金属离子,因此与植物响应干旱胁迫密切相关<sup>[30-32]</sup>。目前,有关 AM 真菌对植物干旱胁迫的影响及其抗性机制的研究主要集中于植物个体水平的生理生化层面,而对于菌根植物适应干旱胁迫的分子机制还缺乏系统深入的研究。

## 1.2 温度

温度是影响植物生长发育的一个重要因素,温度过高或过低都会影响植物正常的生理过程甚至引起植物体死亡,因此研究如何提高植物对温度胁迫的抗性极其重要。近年来,国内外专家学者对水稻(*Oryza sativa*)、君迁子(*Diospyros lotus*)<sup>[9-10,42-51]</sup>等多种植物进行了研究,发现 AM 真菌可以有效增加宿主植物对高温、低温胁迫的抗性(表 2)。以地表球囊霉(*G. versiforme*)接种君迁子,发现地表球囊霉可以促进宿主苗木的生长,增强枝干的营养贮藏水平,并显著提高了君迁子一年生苗的抗冻性<sup>[10]</sup>。与未接种植株相比,接种处理后君迁子苗高增加 50.7%,地上部干重为未接种植株的 4.4 倍;苗木木质部的淀粉含量增加 4.56%,韧皮部的全氮含量增加 0.15%,韧皮部的可溶性糖含量增加 1.76%;冻害指数下降 21.7%。摩西球囊霉和根内球囊霉也具有同样的作用,只是处理效果较地表球囊霉稍差,这可能与植物对不同菌种的依赖性有关。在对玉米的接种试验中发现,15 °C 的低温胁迫条件下,扭形球囊霉(*G. tortuosum*)可以提高叶片中碳水

表 2 AM 真菌对温度胁迫的响应及其机制

Table 2 Response and mechanism of AM fungi to temperature stress

宿主植物 Host plant	AM 真菌 AM fungi	试验条件 Experimental condition	AM 作用 AM function	参考文献 Reference
水稻 <i>Oryza sativa</i>	根内球囊霉 <i>G. intraradices</i>	盆栽 Pots	上调与多胺合成代谢相关基因表达 Up-regulated polyamine synthesis and metabolism related gene expression.	[9]
君迁子 <i>Diospyros lotus</i>	摩西球囊霉 <i>G. mosseae</i> 地表球囊霉 <i>G. versiforme</i> 根内球囊霉 <i>G. intraradices</i>	大田 Field	活化无机营养元素,分泌有活性的转化酶,提高植株营养贮藏水平 Activated inorganic nutrition, secreted active invertase, and promoted nutrition storage of plant.	[10]
枳 <i>Poncirus trifoliata</i>	摩西球囊霉 <i>G. mosseae</i>	盆栽 Pots 15 °C ; 25 °C ; 35 °C	增加可溶性蛋白含量, SOD、CAT 活性,根系抗氧化活性 Increased soluble protein content, SOD and CAT enzymatic activity, antioxidant activity of root.	[42]
玉米 <i>Zea mays</i>	扭形球囊霉 <i>G. tortuosum</i>	盆栽 Pots 25 °C ; 35 °C ; 40 °C	增加叶绿素含量、叶绿素荧光,促进光合作用 Improved chlorophyll content and chlorophyll fluorescence, promoted photosynthesis.	[43]
玉米 <i>Zea mays</i>	幼套球囊霉 <i>G. etunicatum</i>	盆栽 Pots 25 °C ; 35 °C ; 40 °C	增加叶绿素含量、蒸腾速率及气孔导度 Improved chlorophyll content, transpiration rate, and stomatal conductance.	[44]
玉米 <i>Zea mays</i>	幼套球囊霉 <i>G. etunicatum</i> , 扭形球囊霉 <i>G. tortuosum</i> , 细凹无梗囊霉 <i>Acaulospora scrobiculata</i> , 根内球囊霉 <i>G. intraradices</i>	盆栽 Pots 15 °C ; 25 °C	调节碳氮代谢,改善植株生理特征 Regulated carbon and nitrogen metabolism, improved plant physiological characteristics.	[45]
玉米 <i>Zea mays</i>	扭形球囊霉 <i>G. tortuosum</i>	生长室 Growth chamber 15 °C ; 25 °C	增加可溶性糖、蔗糖和果糖含量 Increased the content of soluble sugar sucrose and fructose.	[46]
黄瓜 <i>Cucumis sativus</i>	摩西球囊霉 <i>G. mosseae</i>	营养钵 Nutrition pot 昼/夜 Day/night: 25 °C / 15 °C ; 15 °C / 10 °C	增加可溶性蛋白含量与抗氧化酶活性,降低叶片膜脂过氧化水平 Increased soluble protein content and antioxidant enzymatic activity, reduced blade membrane lipid peroxidation.	[47]
黄瓜 <i>Cucumis sativus</i>	摩西球囊霉 <i>G. mosseae</i>	盆栽 Pots 昼/夜 Day/night: 25 °C / 18 °C ; 15 °C / 10 °C	增强三磷酸腺苷(ATP)活性,降低 H <sub>2</sub> O <sub>2</sub> 积累 Improved ATP enzymatic activity, reduced H <sub>2</sub> O <sub>2</sub> accumulation.	[48]

续表 2

宿主植物 Host plant	AM 真菌 AM fungi	试验条件 Experimental condition	AM 作用 AM function	参考文献 Reference
黄瓜 <i>Cucumis sativus</i>	摩西球囊霉 <i>G. mosseae</i>	盆栽 Pots 昼/夜 Day/night: 25 °C/15 °C; 15 °C/10 °C	增加酚类物质、类黄酮积累,促进抗逆相关基因表达 Improved phenol content, flavonoid content, promoted stress-related gene expression.	[49]
牡丹 <i>Paeonia suffruticosa</i>	摩西球囊霉 <i>G. mosseae</i> 地表球囊霉 <i>G. versiforme</i>	盆栽 Pots 25 °C; 30 °C; 35 °C; 40 °C	增强细胞膜稳定性,降低叶绿素分解 Increased cell membrane stability, reduced chlorophyll decomposition.	[50]
切花月季 <i>Rosa hybrida</i> 切花菊花 <i>Chrysanthemum morifolium</i>	透光球囊霉 <i>G. diuiphauam</i> 地表球囊霉 <i>G. versiforme</i>	盆栽 Pots 昼/夜 Day/night: 25 °C/18 °C; 35 °C/28 °C; 10°C/5°C	增强 SOD、POD、CAT、GR、APX 等酶活性,提高清除过氧化物的能力 Reinforce SOD, POD, CAT, GR, APX enzymatic activity, improved clear peroxide ability.	[51]

化合物的含量,其中可溶性糖增加 44%,还原性糖含量增加 95%;另外,植物氮代谢也会受到一定影响,接种后玉米叶片及根部的总氮和硝态氮含量均增加,硝酸还原酶(NR)、谷氨酰胺合成酶(GS)等氮代谢酶的活性也显著提高<sup>[45]</sup>。40 °C 高温胁迫下,幼套球囊霉(*G. etunicatum*)可增强根系活力,减缓叶绿素分解速度,提高水分的利用效率,提高植物细胞质膜的稳定性,从而减缓高温对细胞膜的伤害程度<sup>[44]</sup>(表 2)。

AM 真菌提高植物对温度胁迫的抗性其机制主要包括:调节碳氮代谢,促进植物体内碳水化合物的积累,促进氮素吸收,增加植物体内蛋白质氨基酸的合成,从而缓和低温对玉米生长的抑制作用<sup>[45]</sup>;增强 SOD、POD、CAT、谷胱甘肽还原酶(GR)、抗坏血酸专一性过氧化物酶(APX)等抗氧化酶类活性,降低膜脂过氧化水平,维持植物细胞质膜的稳定性,提高宿主植物清除  $O_2^{\cdot-}$  和  $H_2O_2$  等过氧化物的能力,减缓对细胞膜的伤害<sup>[42,48,51]</sup>;减缓叶绿素分解,提高叶绿素含量及叶绿素荧光,促进光合作用,提高气孔导度,加快蒸腾速率,促进植物体内水分循环,增强植物抗逆性<sup>[43-44]</sup>;另外,在受到温度胁迫时,AM 真菌可刺激多种胁迫诱导基因(如多胺合成代谢相关基因和植株根系中的 *Os01g0701500D27*、*D17*、*D10* 等基因)的表达,这些基因均与植物对温度胁迫的应答有关,特异性诱导此类基因表达可有效提高宿主植物对温度胁迫的抵抗能力<sup>[9,49]</sup>。

### 1.3 盐碱、重金属

中国盐渍土的分布范围广、面积大、类型多,总面积约 1 亿  $hm^2$ <sup>[52]</sup>。土壤盐碱化不仅可限制植物体的正常生长发育,还会造成严重的生态环境问题<sup>[53]</sup>。土壤重金属污染不仅对植物生长造成很大危害,还会造成生态环境质量恶化<sup>[54]</sup>。所以土地盐碱化治理以及消除土壤重金属污染是全球面临亟待解决的资源与生态环境难题。高羊茅(*Festuca arundinacea*)、羊草(*Leymus chinensis*)等 10 种植物与 AM 真菌共生的研究结果<sup>[55-64]</sup>表明(表 3),盐碱条件下接种摩西球囊霉可显著提高高羊茅叶片抗氧化酶活性,在 1.6% 的盐胁迫时,接种植株的 SOD、POD 和 CAT 活性分别比未接种植株提高了 11.2%、8.3% 和 10.9%;接种摩西球囊霉还可提高抗坏血酸含量,在 0.8%、1.2% 和 1.6% 的盐胁迫时,接种植株的抗坏血酸含量分别比未接种植株提高了 9.1%、12.4% 和 19.5%;在 1.2% NaCl 胁迫下,接种摩西球囊霉的高羊茅叶片与未接种处理相比,丙二醛含量和膜透性分别降低 35.4% 和 25.6%;在 0.8%、1.2% 和 1.6% 的盐胁迫时,接种植株的可溶性糖含量分别比未接种处理提高 24.2%、16.7% 和 8.8%,脯氨酸含量分别比未接种处理降低 31.3%、30.5% 和 28.9%<sup>[58]</sup>。镉胁迫条件下,接种摩西球囊霉可增加水稻植株生物量,促进生长,经测定接种处理的植株地上干重与未接种对照相比,增加幅度为 10.76%~59.48%;接种 AM 真菌能显著提高光能利用率,促进植物光合作用;接种摩西球囊霉后,保证水

表3 AM真菌对盐碱、重金属胁迫的响应及其机制  
Table 3 Response and mechanism of AM fungi to salt and heavy mental stress

宿主植物 Host plant	AM 真菌 AM fungi	试验条件 Experimental condition	AM 作用 AM function	参考文献 Reference
番茄 <i>Lycopersicon esculentum</i>	根内球囊霉 <i>G. intraradices</i>	盆栽 Pots NaCl:0.1%, 0.2%,0.4%,0.8%	下调根部相关基因的表达 Down-regulated expression of the related genes on roots.	[55]
水稻 <i>Oryza sativa</i>	根内球囊霉 <i>G. intraradices</i>	盆栽 Pots	增强独脚金内酯相关基因表达 Promoted strigolactones related gene expression.	[56]
水稻 <i>Oryza sativa</i>	摩西球囊霉 <i>G. mosseae</i> 根内球囊霉 <i>G. intraradices</i>	盆栽 Pots Cd:0, 1, 2, 5, 10, 15, 20 mg · kg <sup>-1</sup>	提高超氧化物歧化酶活性 Increased superoxide dismutase enzymatic activity.	[57]
高羊茅 <i>Festuca arundinacea</i>	摩西球囊霉 <i>G. mosseae</i>	盆栽 Pots 盐浓度 Salinity: 0, 0.8%, 1.2%, 1.6%	增强抗氧化防御系统,维持内源激素平衡 Enhanced antioxidant defense system, maintained plant hormone balance	[58]
翅莢木 <i>Zenia insignis</i>	摩西球囊霉 <i>G. mosseae</i> 根内球囊霉 <i>G. intraradices</i>	盆栽 Pots	菌丝网络可固持重金属,抑制转运 Mycelial network could immobilize heavy metals and inhibit transport.	[59]
紫花苜蓿 <i>Medicago sativa</i>	层状球囊霉 <i>G. lamellosum</i> , 沾屑多样孢囊霉 <i>A. mellea</i> , 密色无梗囊霉 <i>G. mosseae</i> , 摩西球囊霉 <i>G. intraradices</i> , 根内球囊霉 <i>G. etunicatum</i> , 幼套球囊霉 <i>G. constrictum</i> , 缩球囊霉 <i>Diversispora spurcu</i> , 聚丛球囊霉 <i>G. aggregatum</i>	盆栽 Pot pH=6.02 Cd:7.5 mg · kg <sup>-1</sup> Zn:300 mg · kg <sup>-1</sup>	增强植物根系与菌丝对重金属元素的固持作用,抑制 Cd 的转运 Enhanced the capacity of plant root and mycelium to hold heavy metal, inhibited Cd transport.	[60]
大豆 <i>Glycine max</i>	摩西球囊霉 <i>G. mosseae</i>	盆栽 Pots 电导率 Conductivity: 0, 6, 12 ds · m <sup>-1</sup>	提高可溶性糖含量,降低丙二醛含量 Improved soluble sugar content and reduced MDA content.	[61]
番茄 <i>Lycopersicon esculentum</i>	摩西球囊霉 <i>G. mosseae</i>	盆栽 Pots NaCl:0,0.5%,1%	促进植物生长,保持阴阳离子平衡 Promoted plant growth, kept the balance of cation and anion.	[62]
玉米 <i>Zea mays</i>	摩西球囊霉 <i>G. mosseae</i>	盆栽 Pots pH 8.4	抑制 PP2C 蛋白表达,促进 PEPC 蛋白表达 Decreased PP2C protein expression, increased PEPC protein expression.	[63]
羊草 <i>Leymus chinensis</i>	摩西球囊霉 <i>G. mosseae</i>	温室 Glass house NaCl:0, 100, 200 mmol · L <sup>-1</sup>	增加光合速率,促进植物生长 Increased photosynthetic rate and promoted plant growth.	[64]

稻安全生产的土壤镉含量阈值扩增至  $0.21 \text{ mg} \cdot \text{kg}^{-1}$  [57]。

在盐碱胁迫下,AM 真菌可以提高植物对盐碱的耐受性,缓解对植物体造成的伤害。其抗性机制主要包括提高植物生物量,促进植物生长,增加气孔导度,提高光合色素的积累,促进植物光合作用,加快宿主体内的物质循环与能量转运 [64]; 改变宿主植物体内的渗透调节物质,如增加可溶性糖、可溶性蛋白、氨基酸等的含量及组成,降低丙二醛含量,有效调节植物组织内的渗透平衡,从而提高植物体耐盐碱能力 [61,65]; 提高抗氧化酶类(包括 SOD、POD 和 CAT 等)活性和抗氧化剂(抗坏血酸)含量,增强植物抗氧化防御系统,降低氧化胁迫对植物造成的伤害,保证细胞内正常生理生化反应及代谢得以顺利进行; 扩大植物根系的吸收范围,提高矿质养分的吸收速率、强化渗透调节作用并维持植物内源激素平衡,减缓离子毒害 [58]; AM 真菌也可以通过调节与耐盐碱相关的基因表达,如独脚金内酯(strigolactone, SL)合成相关基因、根部编码 *PIP* 和 *TIP* 的基因等,增强植物对盐碱胁迫的抗性效应 [55-56]。

在重金属胁迫下,AM 真菌可以提高脯氨酸含量,激活超氧化物歧化酶活性,减少氧化胁迫对机体造成的生理伤害,保障细胞代谢及生理生化反应,进而提高对重金属胁迫的抵御能力 [57]; 增强植物根系及菌丝本身对重金属元素的固持作用,抑制其转运,减轻对地上部造成的损伤 [66]; 增加根系细胞中金属螯合物质的含量,促进重金属元素在植物根系的固持,抑制转运,减少地上部植物组织内的重金属含量,提高植物耐重金属性 [59]; 诱导相关抗性基因或蛋白(如 PEPC 蛋白合成相关基因)的表达,提高植物对重金属污染的耐受性 [63]。

## 2 AM 真菌对植物抗生物逆境的抗性机制

### 2.1 病害

病害是草地生产的重要限制因子之一,病原菌入侵可引致草地植物病害,使草地退化、衰败,不仅造成牧草严重减产,还会影响草地生态系统的持久力和稳定性 [67]。AM 真菌可通过与病原菌互作,减轻病害发生,提高植物抗病性 [68]。表 4 中总结了包括黄瓜(*Cucumis sativus*)、西瓜(*Citrullus lanatus*)在内的多种植物与病原菌、AM 真菌形成共生体系,从而影响宿主植物抗病性的研究结果 [69-79]。尖孢镰刀菌(*Fusarium oxysporum*)可引起黄瓜枯萎病,在黄瓜育苗时接

种地表球囊霉可有效减轻尖孢镰刀菌的侵染,经试验测定,双接种地表球囊霉和尖孢镰刀菌可使植株的病情指数较单接种尖孢镰刀菌处理降低 37.5%; 另对 4 周龄的黄瓜幼苗双接种尖孢镰刀菌和地表球囊霉,两周后测得植株根系丙二醛含量较相应单接种尖孢镰刀菌处理降低了 35% [69]。地表球囊霉同样对尖孢镰刀菌引起的西瓜枯萎病有较好的抑制作用,研究表明在西瓜苗床播种时接种地表球囊霉可以降低根内镰刀菌繁殖体数量,平均比未接种对照减少约 59.7% [70]。AM 真菌除了可以减轻镰刀菌属(*Fusarium*)、疫霉菌属(*Phytophthora*)等根部病原真菌引起的植物病害,还可以抵抗病原线虫的入侵,对线虫病害也有一定防治效果。采用分根培养系统对番茄进行试验,接种摩西球囊霉与南方根结线虫(*Meloidogyne incognita*)于同一根室,AM 真菌的侵染率受到抑制,病情指数下降 34; 接种摩西球囊霉与南方根结线虫于不同根室,病情指数下降 14 [76]。另有研究发现,聚生球囊霉(*G. fasciculata*)可以抑制大豆胞囊线虫(*Heterodera glycines*)卵囊增长,减少产卵数及幼虫数量,显著降低其病情指数,减轻病害发生程度 [77]。AM 真菌与病原菌及病原线虫的互作可以有效抑制病原物对植株的侵染、减轻发病率、减少植株死亡率,保证植物正常生长。

AM 真菌与病原菌的互作机理是复杂的、多种机制协同作用的结果,主要包括:降低病原菌繁殖体数量,且 AM 真菌与病原菌存在竞争关系,可以减少病原菌侵染位点,显著降低死株率、发病率和病情指数,降低病害发生程度 [70]; 促进植物细胞皮层加厚,并构建菌丝网络,形成对根部入侵病原真菌的机械屏障,AM 真菌的泡囊和丛枝结构也能阻止病原菌菌丝穿过,增强病原真菌侵入根系的难度,减低病原真菌对根系的侵染率 [80-81]; 增强 SOD、POD、苯丙氨酸解氨酶(PAL)等多种酶的活性,合成抗细菌和抗真菌的次生代谢产物(主要包括植保素、酶类、酚类化合物和氨基酸类化合物等),保护植物体不受病原菌侵染 [82-83]; 促进植物体对养分元素的吸收与利用,减少病原菌入侵对植物体造成的伤害,增强植物抗性效应 [84-85]。

其他机理还包括介导植物抗逆信号转导,如 Pozo 等 [86] 研究发现,*G. mosseae* 和 *G. intraradices* 可通过诱导植物产生水解酶,减轻植物病害症状。进一步研究发现,植物根系分泌独脚金内酯,诱导 AM 真菌菌丝伸展及侵染植物,AM 真菌侵染初期,诱导植物水杨酸(SA)含量增加,增强植物系统获得抗病性(SAR),



表 4 AM 真菌对植物抗病性的影响及其机制  
Table 4 Effects of AM fungi on plant disease resistance and its mechanism

宿主植物 Host plant	AM 真菌 AM fungi	试验条件 Experimental condition	病害菌 Pathogen	AM 作用 AM function	参考文献 Reference
黄瓜 <i>Cucumis sativus</i>	地表球囊霉 <i>G. versiforme</i>	盆栽 Pots	尖孢镰刀菌 <i>F. oxysporum</i>	促进植物生长及次生代谢物质积累 Promoted plant growth and accumulation of secondary metabolite.	[69]
西瓜 <i>Citrullus lanatus</i>	地表球囊霉 <i>G. versiforme</i>	盆栽、大田 Pots, Field	尖孢镰刀菌 <i>F. oxysporum</i>	改变根系分泌物, 减少病原菌侵染位点 Changed root exudates and reduced infection sites.	[70]
洋葱 <i>Allium cepa</i>	摩西球囊霉 <i>G. mosseae</i>	盆栽 Pots	尖孢镰刀菌 <i>F. oxysporum</i>	降低病原菌侵染 Reduced pathogenic infection.	[71]
仙客来 <i>Cyclame</i>	聚生球囊霉 <i>G. fasciculatu</i>	盆栽 Pots	尖孢镰刀菌 <i>F. oxysporum</i> 盘长孢状刺盘孢 <i>Colletotrichum gloeosporioides</i>	增加植株抗氧化能力 Increased plant antioxidant ability.	[72]
甜瓜 <i>Cucumis melo</i>	摩西球囊霉 <i>G. mosseae</i>	温室 Glass house	尖孢镰刀菌 <i>F. oxysporum</i>	促进养分吸收 Promoted nutrition absorption.	[73]
豌豆 <i>Pisum sativum</i>	摩西球囊霉 <i>G. mosseae</i>	盆栽 Pots	立枯丝核菌 <i>Rhizoctonia solani</i>	促进根系生长 Promoted root growth.	[13]
水稻 <i>Oryza sativa</i>	根内球囊霉 <i>G. intraradices</i>	盆栽 Pots	灰梨孢 <i>Pyricularia grisea</i>	促进效应蛋白 SP7 积累 Promoted accumulation of effects protein SP7.	[74]
番茄 <i>Lycopersicon esculentum</i>	地表球囊霉 <i>G. versiforme</i>	两室根箱系统 Two-bin system	拮抗细菌 Antagonistic bacteria	提高结合态酚含量 Improved bound phenolic content.	[75]
番茄 <i>Lycopersicon esculentum</i>	摩西球囊霉 <i>G. mosseae</i>	分根培养系统 Split-root cultivated system	南方根结线虫 <i>M. incognit</i>	抑制卵囊增长, 降低病情指数 Inhibited oocyst growth and reduced disease index.	[76]
大豆 <i>Glycine max</i>	聚生球囊霉 <i>G. fasciculatu</i>	盆栽 Pots	大豆胞囊线虫 <i>H. glycines</i>	抑制卵囊增长, 线虫产卵数下降 Inhibited oocyst growth and decreased laying eggs.	[77]
黄瓜 <i>Cucumis sativus</i>	地表球囊霉 <i>G. versiforme</i>	盆栽 Pots	南方根结线虫 <i>M. incognit</i>	增加 P 元素含量 Increased phosphorus content.	[78]
凤仙花 <i>Impatiens balsamina</i>	球囊霉属 <i>Glomus</i> 盾巨孢囊霉属 <i>Scutellospora</i> 无梗囊霉属 <i>Acaulospora</i>	盆栽 Pots	南方根结线虫 <i>M. incognit</i>	增加叶面积和脯氨酸含量, 发病率下降 Increased leaf area and proline content, incidence rate decreased.	[79]

当 AM 真菌进入植物皮层细胞内后,水杨酸含量降低,而丛枝形成阶段,植物茉莉酸(JA)含量提高,同时促进植物脱落酸(ABA)含量增加,增强植物细胞壁抗性。SA、JA 等信号传导物质还可诱导防御性基因表达,增强植物抗病能力。另外,AM 真菌可改变植物根系分泌物的化学组分,影响根际细菌群落组成,进而诱导植物茉莉酸、乙烯相关系统性抗性<sup>[87-88]</sup>。AM 真菌亦可诱导抗病相关基因的表达,增强效应蛋白如 SP7

的积累,提高植物抗病性<sup>[89-92]</sup>。AM 真菌对线虫的生长发育及其繁殖同样具有抑制作用,能够抑制线虫卵囊的增长,提高相关酶活性,降低病情指数,有效减轻病原线虫的侵染,降低线虫病害发生<sup>[76-79]</sup>。

## 2.2 虫害

昆虫是生物群落中十分重要的组成部分,在植物的生长发育过程中扮演了必不可少的角色。一方面,一些植食性昆虫取食植物叶片,并将植物体作为生长

表 5 AM 真菌对植物抗虫性的影响及其机制

Table 5 Effects of AM fungi on plant insect resistance and its mechanism

宿主植物 Host plant	AM 真菌 AM fungi	试验条件 Experimental condition	昆虫 Insect	AM 作用 AM function	参考文献 Reference
垂穗披碱草 <i>Elymus nutans</i>	幼套球囊霉 <i>G. etunicatum</i>	盆栽 Pots	蝗虫 Locust	诱导产生具趋避作用的挥发性化合物 Induced avoidance effect volatile compounds production.	[94]
长叶车前 <i>Plantago lanceolata</i>	土壤 AM 真菌 Soil AM fungi	大田 Field	灯蛾 Arctiidae	诱导产生具有抑制或毒害作用的物质 Induced suppression or toxic effect substances production.	[95]
黄瓜 <i>Cucumis sativus</i>	根内球囊霉 <i>G. intraradices</i>	盆栽 Pots	甜菜夜蛾 <i>Spodoptera exigua</i>	诱导产生植物防御化学物 Induced plant defensive chemicals production.	[96]
番茄 <i>Lycopersicon esculentum</i>	摩西球囊霉 <i>G. mosseae</i>	盆栽 Pots	斜纹夜蛾 <i>Spodoptera litura</i>	菌丝网络传递防御信号 Mycelial network carries defense signals.	[97]
梯牧草 <i>Phleum pratense</i>	摩西球囊霉 <i>G. mosseae</i> 根内球囊霉 <i>G. intraradices</i>	盆栽 Pots	蚜虫 <i>R. padi</i> 寄生蜂 <i>A. rhopalosiphi</i>	降低虫口数量,增加植物生物量 Reduced insect quantity, increased plant biomass.	[98]
香根菊 <i>Baccharis halimifolia</i>	摩西球囊霉 <i>G. mosseae</i> 根内球囊霉 <i>G. intraradices</i>	大田 Field	三叶斑潜蝇 <i>Liriomyza trifolii</i>	降低昆虫寄生性 Reduced insect infestation.	[99]
矢车菊 <i>Centaurea cyanus</i>	摩西球囊霉 <i>G. mosseae</i> 根内球囊霉 <i>G. intraradices</i>	大田 Field	传粉昆虫 Pollinating insects	增加昆虫访问频率,促进传粉 Increased insect access frequency and promoted pollination.	[14]
百脉根 <i>Lotus japonicus</i>	株状巨孢囊霉 <i>G. margarita</i>	户外玻璃箱 Outdoor glass box	二斑叶螨 <i>Tetranychus urticae</i>	减少雌虫数量 Reduced quantity of females.	[100]
水稻 <i>Oryza sativa</i>	根内球囊霉 <i>G. intraradices</i>	盆栽 Pots	水稻象甲 <i>Lissorhoptrus oryzophilus</i>	昆虫产卵量增加 Increased insects laying eggs.	[101]

场所,植物正常生长发育受阻,产量及品质降低,严重时甚至可导致植被大面积死亡,危害农林牧业发展,造成严重经济损失。另一方面,一些天敌昆虫可以捕食害虫,减少其对植物的取食及为害,传粉昆虫有助于植物花粉的传播,而有的昆虫还可以携带并传播植物种子。研究AM真菌-植物-昆虫这三者之间的相互作用,对于植物害虫的防治和有益昆虫的保护具有重要指导意义。大量研究表明,AM真菌具有调控植物与昆虫互作的效应<sup>[93]</sup>。在对垂穗披碱草(*Elymus nutans*)、长叶车前(*Plantago lanceolata*)等植物与昆虫相互作用的研究<sup>[94-101]</sup>表明(表5),幼套球囊霉可以诱导植物产生含量与组分更多的挥发性化合物,主要是萜烯类、醇类、酯类和少量烷烃类物质,通常这类物质是作为植物-昆虫营养关系中信息传递的媒介<sup>[94]</sup>。Hempel等<sup>[98]</sup>用摩西球囊霉和根内球囊霉接种梯牧草(*Phleum pratense*),研究植物、蚜虫(*Rhopalosiphum padi*)与寄生蜂(*Aphidius rhopalosiphii*)的相互关系,发现接种AM真菌可增加植物生物量5.2%,降低蚜虫的虫口数量47%。对矢车菊(*Centaurea cyanus*)的研究<sup>[14]</sup>则发现AM真菌也可以吸引授粉昆虫,增加其在植株上的访问频率,促进植物传粉。

AM真菌与昆虫的作用机制包括两个方面。一是直接毒杀作用,AM真菌侵染植物后产生的毒性代谢物,对害虫具有抑制或毒杀效果<sup>[102]</sup>;二是间接影响,AM真菌侵染植物后,通过影响植物的营养代谢来影响昆虫的发育及繁殖,也可通过调节害虫天敌间接影响害虫,控制害虫的种群数量<sup>[99]</sup>;诱导植物产生挥发性化合物,如E-2-己烯-1-醇、芳樟醇、苯甲醛、香芹酚

等,这类物质对害虫具有趋避作用,可以保护植物,减少昆虫取食,提高植物抗虫性<sup>[94,97]</sup>;另外,一旦害虫取食植物,AM真菌可以通过强大的菌丝网络在邻近植株间传递抗虫防御信号,使邻近植株及时进入防御状态,减少害虫取食<sup>[97]</sup>。AM真菌菌丝网络传递信号的功能极为稳定可靠,因此在害虫防治以及有益昆虫保护等方面应用前景十分广泛。

### 3 展望

随着国家“粮改饲”及种植业结构调整政策的进一步深入,草地农业在食物安全及生态环境建设中的重要性日益突出。草地多分布在干旱、高寒、土壤贫瘠地区,逆境胁迫严重影响植物的生长发育,造成牧草减产和草地退化。因此,提高草类植物对逆境的抗性,对于提高牧草产量,促进系统种群多样性以及维持草地生态系统稳定极其重要。目前有关于AM真菌与植物互作的研究主要集中于少数几个AM真菌属,如病害多限于球囊霉属的研究,鉴于不同AM真菌对植物抗逆性影响不同,应加强对菌根真菌多样性及丰富度对草地植物抗逆的影响及机理的研究;同时,目前的研究多为人工模拟单一逆境,应加强AM真菌-草地植物对多种逆境因子响应的研究<sup>[103-105]</sup>。机理方面,AM真菌提高植物抗逆机理包括促进植物养分吸收、生长,调节植物生理、生化代谢,诱导信号介导,基因及蛋白表达等诸多方面,应关注不同抗性机理的相关性,强化现代分子生物学技术和细胞学技术应用,推动AM真菌在促进植物抗逆机理方面的研究。

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