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野豌豆属牧草抗非生物胁迫研究进展

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摘要: 野豌豆属(*Vicia*)牧草兼具饲用价值与生态功能。随着全球气候变化, 低温、干旱、盐碱及重金属等非生物胁迫对野豌豆属牧草的生长发育、产量形成以及安全利用构成了严峻挑战。近年来, 围绕野豌豆属牧草抗逆生理与分子调控机制的研究不断推进, 在野豌豆属牧草适应逆境渗透调节、抗氧化防御、激素信号调控、离子稳态维持及相关基因网络调控等方面取得了良好进展。然而, 现有研究多集中于单一胁迫条件, 研究也多集中在箭筈豌豆(*Vicia sativa*)等少数物种, 对野豌豆属植物响应多重胁迫、抗逆性状遗传基础及系统调控机制的认识仍显不足。本文系统综述了野豌豆属牧草在低温、干旱、盐碱和重金属胁迫等非生物胁迫下的研究进展, 重点归纳其适应逆境的主要生理调节特征与分子调控模式, 并结合多组学整合、复合胁迫解析及根际微生物互作等研究趋势, 对未来抗逆改良与分子育种方向进行了展望, 以期对野豌豆属牧草抗逆种质创新与资源高效利用提供参考。

关键词: 野豌豆属; 非生物胁迫; 抗逆性; 分子调控; 牧草育种

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Research Progress on Abiotic Stress Responses of *Vicia* Forage Species

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Abstract: Vetch (*Vicia*) forage species possess significant forage value and ecological functions. In the context of global climate change, abiotic stresses such as low temperature, drought, salinity, and heavy metal contamination pose severe challenges to their growth, development, yield formation, and safe utilization. Considerable research progresses on the stress resistance physiology and molecular regulatory mechanisms of vetch forage have been reported in recent years. Notable advances have been made in understanding their adaptive responses to stresses through osmotic regulation, antioxidant defense, hormonal signaling, ion homeostasis, and related gene regulatory networks. However, most existing studies have focused on single stress conditions and are limited to a few species such as common vetch (*Vicia sativa*). Knowledge regarding the responses of vetch plants to combined stresses, the genetic basis of stress-resistant traits, and systematic regulatory mechanisms remains insufficient. This review systematically summarized research progress on vetch forage under abiotic stresses, including low temperature, drought, salinity, and heavy metal stress. It highlighted key physiological adaptive features and molecular regulatory patterns, and discussed future directions for stress resistance improvement and molecular breeding in light of emerging research trends such as multi-omics integration, combined stress analysis, and rhizosphere microbial interactions. The aim is to provide insights for the development of stress-resistant germplasm and the efficient utilization of vetch forage resources.

Key words: *Vicia*; Abiotic stress; Stress tolerance; Molecular regulation; Forage breeding

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在全球气候变化背景下,低温、干旱、盐碱等非生物胁迫已成为制约牧草生产力与草地生态系统稳定性的关键环境因素^[1-2]。我国高山草原地区畜牧业长期面临豆科牧草短缺问题,尤其在冬春季节蛋白饲料供应不足,严重制约着草地畜牧业发展^[3]。近年来,随着气候变化加剧及边际土地利用需求增加,干旱、低温、盐碱、重金属等非生物胁迫对牧草的地理分布和生产潜力构成严峻挑战,豆科牧草抗逆机制研究也随之成为学界关注的热点^[2]。

野豌豆属(*Vicia* L.)植物在生产上主要作为粮用作物与饲用牧草,该属牧草具有固氮能力强、营养价值高、饲喂价值优良、适应性广等优势,是我国高原牧区重要的蛋白饲料来源^[4-10]。对该属植物的研究大多集中于粮用作物蚕豆(*Vicia faba*),而对饲用牧草抗逆性的系统性研究较少,特别是在适应非生物逆境的分子调控网络、关键功能基因挖掘及抗逆性状遗传改良等方面的研究仍待深化。

近年来,围绕野豌豆属牧草应对非生物胁迫的研究不断推进,但总体上仍以单一胁迫和少数物种研究为主,对多重胁迫协同作用、抗逆性状的遗传基础及系统调控机制认识不足。因此,对该领域研究进展进行系统梳理与综合评述,明确未来研究重点,对推动野豌豆属牧草抗逆育种具有重要理论和实践意义。

本文基于 Web of Science 数据库和中国知识基础设施工程(China National Knowledge Infrastructure, CNKI)数据库,以“野豌豆”“箭筈豌豆”“苕子”“vetch”,以及“干旱”“水分”“低温”“盐碱”“重金属”等中英文为关键词,查阅了1990年—2025年11月期间发表的文献,文章数量见图1,并逐一筛选获得文献。在此基础上,围绕野豌豆属牧草响应低温、干旱、盐碱和重金属胁迫的研究进展进行归纳总结,概述其适应非生物逆境的主要生理调节与分子调控特征,并结合多组学整合、复合胁迫解析和根际互作等研究趋势,对未来抗逆改良与分子育种方向进行展望,以期对野豌豆属牧草的资源利用和抗逆育种提供参考。

1 野豌豆属牧草抗寒调控机制

在多种非生物胁迫类型中,低温是限制我国高寒草地地区牧草安全越冬和稳定产量的环境因子之一^[11]。低温胁迫通过破坏细胞膜结构、抑制光合

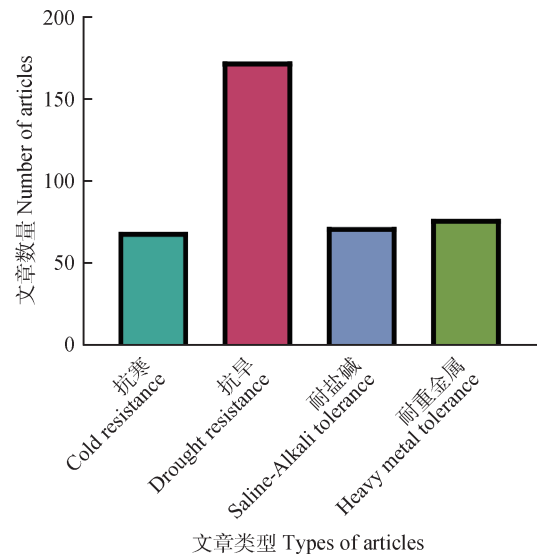


图1 野豌豆属牧草在不同非生物逆境下抗逆性研究文章数量
Fig. 1 Number of research articles on stress resistance of *Vicia* forage species under different abiotic stresses

系统功能及酶促代谢活动,引发膜脂过氧化与活性氧(Reactive oxygen species, ROS)过量积累,从而影响植物正常生长发育进程^[12]。因此,系统解析野豌豆属植物的抗寒调控机制,对于提升其生产利用价值具有重要意义。

在低温胁迫条件下,野豌豆属植物通过激活抗氧化防御系统缓解氧化损害^[13-15]。研究表明,箭筈豌豆(*Vicia sativa*)经低温处理后细胞膜结构受到损伤,同时与 H_2O_2 清除相关基因(如 *VsAPX1*, *VsGR1*, *VsCAT2* 和 *VsCAT3*)上调表达,从而减轻细胞氧化胁迫^[16]。同时,脱落酸(Abscissic acid, ABA)受体基因 *VsPYL5* 的诱导表达通过调控离子稳态与活性氧平衡,提升植株的耐寒能力^[17]。该属其他物种亦表现出类似响应特征,如山野豌豆(*Vicia amoena*)在低温胁迫下超氧化物歧化酶(Superoxide dismutase, SOD)活性显著增强,表明抗氧化防御是野豌豆属植物抵御低温损伤的共性机制^[18]。

除抗氧化防御体系外,渗透调节是该属植物抵御低温胁迫的另一重要生理策略。低温条件下,箭筈豌豆通过积累脯氨酸和可溶性糖等渗透调节物质维持细胞膨压和膜结构稳定性,类似的渗透调节响应同样出现在山野豌豆中^[16, 18]。在分子层面,脯氨酸合成相关基因(如 *P5CS*)在低温诱导下被诱导上调,而其降解相关基因表达受到抑制,促进细胞内脯氨酸的持续积累^[16]。

植物生理调节过程受到复杂信号转导与基因

调控网络的控制^[19-24]。低温胁迫可诱导箭筈豌豆生长素信号相关基因(如 *Aux/IAA*)表达,同时下调 *GH3* 基因表达,通过促进生长素积累,提升抗寒能力^[25]。在低温驯化过程中, Ca^{2+} 信号通路及多种激素信号与转录因子之间的互作发挥着关键作用^[16]。研究表明,冷驯化能通过调控光合相关基因(*LCHA5*, *FNR*)和生长调节基因(*IAA14*)的表达,维持细胞稳态,显著提升箭筈豌豆耐寒性^[26]。

随着多组学技术的应用,研究者进一步从系统层面揭示了野豌豆属植物抗寒性的分子基础。转录组和代谢组联合分析表明,“兰箭”系列春箭筈豌豆通过提高抗氧化物质积累,降低离子渗透率及调控糖类和氨基酸代谢,从而增强低温适应能力^[27]。游离氨基酸与多胺的积累,以及 ABA 信号与赤霉素(Gibberellin, GA)信号交互作用,有助于植物在低温条件下维持生长平衡^[28-29]。苯丙烷类代谢途径通过类黄酮、木质素等次生代谢物的合成,增强细胞抗氧化防御活性和膜结构完整性,也是箭筈豌豆冷适应的重要分子基础之一^[16]。此外,花青素积累可能与低温响应信号调控密切相关^[30]。

2 野豌豆属牧草抗旱调控机制

水分是制约植物生长的关键环境因素^[31-33]。持续或间歇性的水分亏缺会引发渗透胁迫和活性氧积累,破坏细胞膜结构与蛋白质功能,干扰核酸稳定性并导致代谢紊乱^[33]。在长期进化过程中,植物逐步形成形态调节、生理防御与分子调控相协同的抗旱适应体系^[31]。

在形态结构方面,野豌豆属植物在干旱响应中表现出明显差异,为抗旱育种提供了丰富的遗传资源^[34-35]。部分野豌豆属植物通过增加叶片栅栏组织厚度、提高气孔密度并调控气孔开度,降低蒸腾失水^[36]。同时,干旱会导致茎导管直径与叶片韧皮部厚度减小,影响水分运输效率^[37]。研究表明,箭筈豌豆地上生物量、株高及气孔导度与其耐旱性显著相关,可作为抗旱性评价的重要表型指标^[38-39]。

野豌豆属植物亦能通过维持细胞水分状态、氧化稳态和积累渗透调节物质来增强抗旱能力^[37,39]。例如, *Vicia michauxii* 在严重干旱条件下仍能维持较高的叶片相对含水量(Relative water content, RWC)和光系统 II 最大光化学效率(Maximum variable fluorescence, F_v/F_m),表现出较强的耐旱潜

力^[34]。植物在响应干旱时,超氧化物歧化酶、过氧化物酶(Peroxidase, POD)、抗坏血酸过氧化物酶(Ascorbate peroxidase, APX)及谷胱甘肽还原酶(Glutathione reductase, GR)等抗氧化酶活性显著增强,能够缓解活性氧过量积累引发的氧化损伤^[40-41]。

在分子调控层面,野豌豆属牧草对干旱胁迫的响应由多基因协同作用的复杂调控网络所驱动。相关研究表明,在中至重度干旱条件下, *sod*, *aq1* 和 *bzip* 等与抗氧化防御、水分运输及胁迫信号调控相关的基因表达发生显著变化,其表达水平和幅度受胁迫强度及基因型差异的共同影响^[42]。不同基因型在这些关键基因的调控策略上表现出明显差异,被认为是野豌豆属牧草耐旱性分化的重要分子基础^[42]。转录组分析进一步表明,干旱胁迫下的分子响应主要涉及活性氧稳态调控、细胞壁相关代谢过程以及 ABA 信号通路的激活^[43]。同时,与干旱胁迫响应相关的转录因子,包括 *DOF*, *DREB*, *WRKY33*, *MYB13* 和 *BTF3* 等家族成员,其表达也呈现显著变化^[43]。此外,水通道蛋白基因 *VsPIP1;2* 和 *VsPIP2;2* 是调控箭筈豌豆抗旱性的关键候选基因^[44]。

3 野豌豆属牧草耐盐碱及重金属调控机制

第三次全国国土调查结果显示,全国盐碱地面积达 $1.15 \times 10^8 \text{ hm}^2$, 是重要的后备耕地资源,选育和推广耐盐碱的牧草品种,对于提高盐碱地的生产力至关重要^[45-46]。盐胁迫主要通过引发渗透胁迫、离子毒害和营养失衡抑制植物生长^[47-49],而碱胁迫则在此基础上叠加了高 pH 对细胞结构和代谢体系的损伤^[50]。植物通常通过渗透调节、离子稳态、pH 平衡及抗氧化防御等多种方式适应盐碱环境^[51]。

箭筈豌豆在盐胁迫下通过维持较高的 K^+/Na^+ 比值,并上调 *NHX7*, *HKT1*, *AKT2*, *HAK17* 离子转运基因的表达,维持离子平衡^[52]。同时,脯氨酸的积累以及超氧化物歧化酶、过氧化氢酶(Catalase, CAT)和抗坏血酸过氧化物酶等抗氧化系统的激活,有效缓解了盐胁迫诱导的氧化损伤^[52]。在盐碱胁迫下 ABA 受体基因 *VsPYL5* 通过调节离子和活性氧稳态发挥核心调节作用^[17]。此外,不同植物组织的抗盐机制具有特异性,抗氧化酶活性、丙二醛含量及脯氨酸积累水平差异显著^[53]。

除盐碱胁迫外,土壤中重金属胁迫同样是影响

牧草生产安全的重要环境因素。植物在生长过程中需要吸收微量元素,但镉(Cd)、汞(Hg)、砷(As)、铅(Pb)和铬(Cr)等非必需元素即使在低浓度下也具有强毒性^[54]。研究表明,镉胁迫会显著抑制箭筈豌豆的营养吸收和生长,植株往往通过积累渗透调节物质以缓解由镉毒诱导的水分胁迫^[55]。广布野豌豆(*Vicia cracca*)在污染环境中表现出典型的氧化应激反应,如脂质过氧化增强与光合效率下降^[56]。因此,系统阐明牧草对重金属的耐受与调控机制,对安全利用牧草具有重要意义。

野豌豆属植物演化出多种解毒机制,主要包括区隔化、螯合与抗氧化防御:(1)细胞壁固定:箭筈豌豆应对铜胁迫主要依靠根部细胞壁富集铜元素并限制其向地上部迁移^[57]。其咖啡酰辅酶A O-甲基转移酶基因(*VsCCoAOMT*)通过促进木质化作用将铜离子隔离至细胞壁^[58]。在铝胁迫下,根系响应也涉及细胞壁果胶修饰、 Na^+/K^+ 通道调控、 Ca^{2+} 信号传导及激素信号调节等多重机制以限制铝进

入^[59]。(2)细胞内整合:*VsPCS1*和*Vsγ-ECS*基因通过促进谷胱甘肽(Glutathione, GSH)及植物螯合肽(Phytochelatins, PCs)合成以增强镉整合^[60-61];广布野豌豆的抗性也可能源于体内丰富的金属螯合剂与金属硫蛋白的协同作用^[62]。(3)抗氧化防御:针对重金属胁迫引发的氧化应激,野豌豆属植物激活了高效的抗氧化系统。镍胁迫会引发箭筈豌豆发生氧化应激,而植株在低浓度镍胁迫下可通过提高过氧化氢酶(CAT)活性及脯氨酸含量来缓解伤害^[63]。抗坏血酸(AsA)循环则通过调节脱氢抗坏血酸还原酶(DHAR)与APX活性,维持抗坏血酸水平,从而减轻氧化损伤^[64]。研究还发现,在镉胁迫下,耐性品种通过提高漆酶活性来降低毒害,而敏感品种则表现出活性氧积累^[65]。这些多层次的反应在转录组层面得到了印证,例如镉胁迫下细胞壁合成、谷胱甘肽代谢及金属转运相关基因的表达普遍上调^[66]。

野豌豆属牧草响应非生物胁迫的生理调控与分子机制如图2所示。

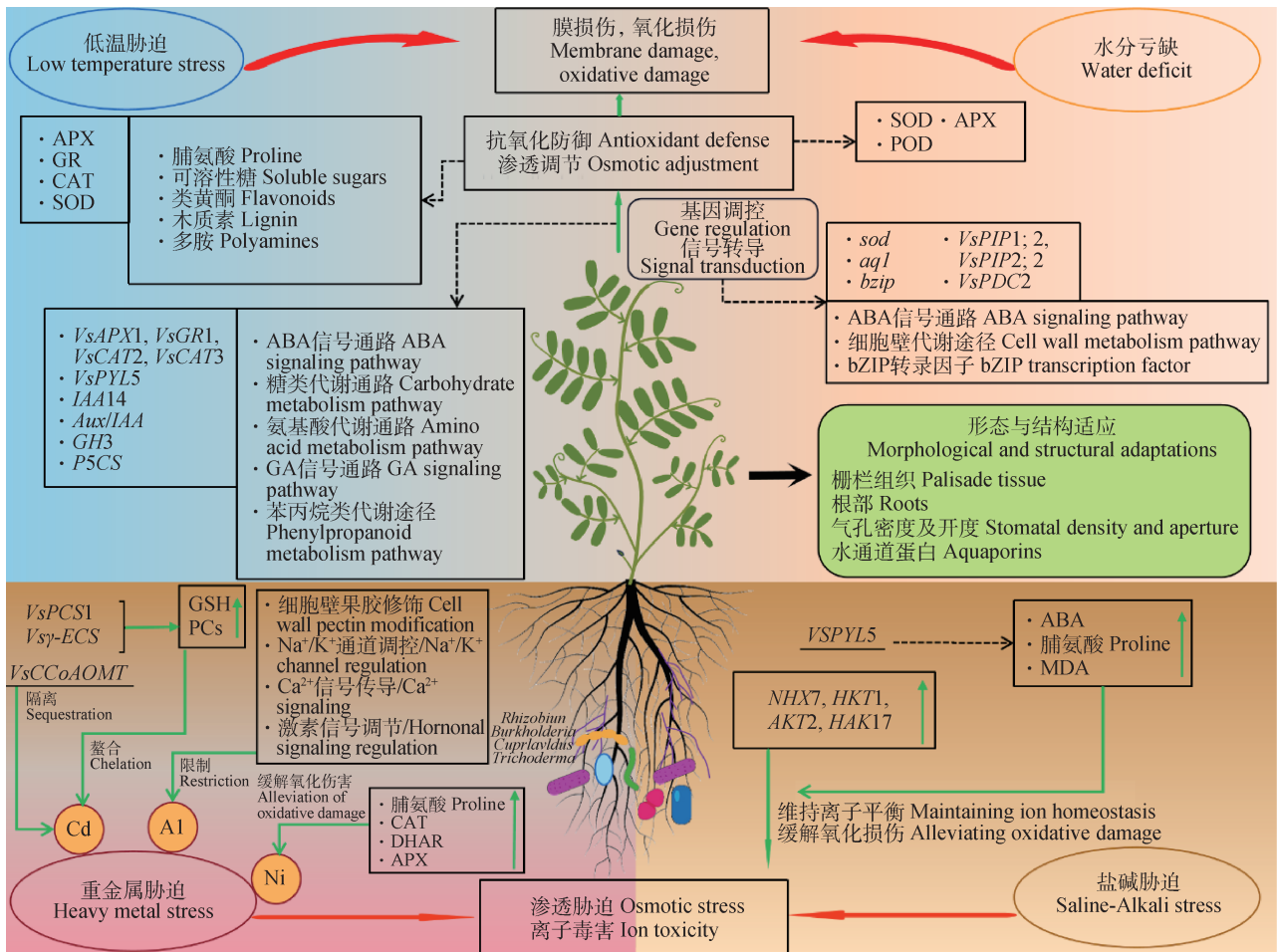


图2 野豌豆属牧草响应非生物胁迫的生理调控与分子机制

Fig. 2 Physiological regulations and molecular mechanisms of *Vicia* forage in response to abiotic stress

4 展望

近年来,围绕野豌豆属牧草在干旱、低温、盐碱及重金属等非生物胁迫下的生理响应与适应机制研究已取得一系列进展,为抗逆种质筛选奠定了基础。野豌豆属植物在抗旱^[34]、耐盐碱^[53, 57-69]及重金属耐受性^[70-71]等方面表现出明显的种间差异,反映出其丰富的遗传多样性和生态适应潜力,这种差异性为抗逆种质挖掘和功能利用提供了重要基础。然而,现有研究仍主要集中于表型鉴定与单一胁迫响应层面,对抗逆性状的遗传结构、多重胁迫协同机制以及植物-微生物互作在抗逆形成中的系统作用缺乏深入解析,限制了野豌豆属牧草在抗逆育种中的精准改良与高效利用。未来研究亟需在多组学整合与多尺度解析的框架下,系统推进抗逆机制研究与种质创新。

(1) 深化分子与基因调控机制研究

抗旱、抗寒和耐盐碱等性状多属于复杂数量性状,其形成依赖于多基因协同调控。尽管近年来已通过叶绿体基因组解析^[37]、SSR 标记开发^[37]、miRNA 调控^[72]及全基因组关联分析^[73]等手段初步定位了一批与抗逆相关的候选基因,为分子设计育种提供了重要候选靶点,但针对野豌豆属牧草的系统性全基因组研究仍相对有限。未来应依托高质量参考基因组、群体重测序与多维生物信息学分析,系统解析野豌豆属牧草在固氮能力、抗逆性及多年生特征等关键性状上的遗传基础,明确核心调控基因及其网络关系,为分子设计育种提供可靠的基因资源。

(2) 加强复合胁迫互作机制解析

自然生态系统中,多种非生物胁迫通常以复合形式共同存在^[74],而当前研究多基于单一胁迫条件展开,难以全面反映野豌豆属牧草在实际生境中的适应策略。尽管初步研究已发现箭筈豌豆在多重胁迫下存在核心共响应基因^[75],但整体机制仍不明确。未来研究应通过复合胁迫模拟实验,结合多组学技术,系统解析其生理响应、代谢重构及共响应调控机制,为培育耐复合逆境的牧草品种提供理论依据^[76]。

(3) 强化根际微生态与共生互作研究

根际微生物在植物抗逆性形成中发挥重要作用,植物可在胁迫条件下通过根系分泌代谢物选择性招募有益微生物,减轻非生物胁迫对植物的不利

影响^[77-79]。现有研究表明,根际微生物在缓解重金属胁迫、调节养分吸收与维持氧化还原稳态方面具有潜力^[80-84]。未来研究应重点关注胁迫条件下,根际微生物群落结构与功能的动态变化,以及其与宿主生理状态之间的互作机制。通过系统解析固氮菌、植物根际促生菌(Plant growth promoting rhizobacteria, PGPR)及丛枝菌根真菌(Arbuscular mycorrhizal fungi, AMF)等有益微生物在养分吸收和抗逆调控中的作用^[85-91],可为提升牧草抗逆性和促进土壤生态修复提供新的策略和理论支撑。

(4) 推进多组学整合与系统生物学研究

植物对非生物胁迫的响应涉及复杂的信号通路和基因调控网络^[92]。未来应加强转录组、蛋白质组、代谢组及表型组等多组学数据的整合分析,解析激素信号和关键代谢通路^[93-97]间的协同调控关系,建立跨层级的抗逆信号调控模型^[93-97]。结合高通量表型分析与人工智能技术,有望实现对野豌豆属种质抗逆特征的高效识别与动态监测。

(5) 推动种质创新与智能化育种应用

在气候变化背景下,抗逆育种对草业可持续发展具有重要意义^[98]。我国在野豌豆属抗寒、抗旱品种选育方面已取得积极进展,为后续育种工作提供了宝贵的种质资源和技术支持^[27]。应进一步整合分子标记辅助选择、高通量表型分析及人工智能预测模型,建立针对区域环境条件的抗逆性评价与育种决策体系^[99]。同时,可通过杂交、诱变及基因编辑等手段拓展抗逆种质多样性,加快优异基因型的定向改良与推广应用^[100]。通过大规模基因组重测序与表型数据库整合,可构建针对区域环境的抗逆性评价与育种决策系统^[101],为野豌豆属牧草的精准改良与推广提供智能化支持。

(6) 提升野豌豆属牧草抗逆性的应用技术路径

在应用层面,外源调控措施和微生物互作被证明是提升野豌豆属牧草抗逆性的重要补充途径。

通过预处理^[102-105]及优化农艺措施^[106-110](如施用生物肥料^[109]、接种微生物^[110]),可在一定程度上改善植株在干旱、低温、盐碱、重金属胁迫条件下的生理状态,增强其适应能力。与此同时,通过调控植物与微生物互作关系,可改变重金属在植物体内的吸收与分配模式,为牧草生产和污染土壤生态修复提供新的技术路径^[80]。

野豌豆属牧草抗逆研究正由单一生理响应解析向多层次机制整合与智能化育种方向转变。通

过深化遗传机制解析、强化复合胁迫研究、揭示根际微生物互作规律并推动智能化育种应用,有望全面提升其在逆境条件下的适应能力,实现优异抗逆种质的定向创新与高效利用,为草业可持续发展、生态修复及农业应对气候变化提供坚实的科学支撑。

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