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谷子耐盐性研究进展及展望*

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摘 要: 随着农业种植业结构调整, 谷子作为一种抗旱耐瘠薄作物在干旱盐碱地区的种植越来越受到重视。系统深入梳理谷子的耐盐性及盐胁迫下的生理生态响应特性, 对增加盐碱地区谷子产量、提高农民收入具有重要指导意义。本文从谷子的耐盐性筛选指标及评价、盐胁迫下植株生长发育变化规律和生理生态响应以及谷子耐盐基因发掘等 3 个方面, 综述了国内外研究进展。目前谷子耐盐鉴选指标单一, 主要依赖于谷子萌发期的发芽率, 而其他生理生态指标未被充分考虑; 因谷子品种和土壤盐分的不同, 谷子植株地上地下农艺性状、光合特征、清除活性氧相关酶类以及激素响应特征存在差异, 建立综合鉴选指标存在困难; 谷子耐盐基因的表达与作用发挥与环境条件, 如高盐、干旱 (PEG) 和脱落酸 (ABA) 等相关, 通过特定蛋白来增强抗氧化系统、保护细胞不受损伤以及提高抗渗透胁迫能力等提高谷子的耐盐性。在此基础上, 本文提出了建立谷子耐盐综合鉴选量化标准和平台、深入开展谷子耐盐调控机理研究、进一步研发谷子耐盐栽培技术体系是未来重要的研究方向。

关键词: 谷子; 耐盐性; 种质资源; 萌发期; 生理生态响应; 耐盐基因

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Research progress and prospects of foxtail millet salt tolerance*

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Abstract: With the adjustment of the agricultural planting structure, foxtail millet — a drought-resistant and barren-tolerant crop, has attracted increasing attention in arid and saline-alkali areas. Systematic and deep understanding of the salt tolerance as well as physiological and ecological response characteristics of foxtail millet under salt stress has important guiding significance for maximizing the excellent properties of foxtail millet, increasing its yield in saline-alkali areas, and improving farmers' income. This paper reviewed the research progress worldwide in detail from three aspects, namely, the screening index and evaluation of foxtail millet salt tolerance, the change law of plant growth and development and physiological-ecological response under salt stress, and the discovery of foxtail millet salt tolerance genes. At present, a single indicator of salt tolerance in foxtail millet is used, which mainly de-

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pends on the germination rate during germination. Other physiological and ecological indicators have not been fully considered. Because of the differences in foxtail millet varieties and soil salinity, there are differences in aboveground and underground agronomic characteristics, photosynthetic characteristics, enzymes related to scavenging reactive oxygen species, and the hormone response law of foxtail millet plants. Therefore, it is difficult to establish comprehensive evaluation indexes. The expression and function of foxtail millet salt tolerance genes are related to environmental conditions such as high salt, drought, and abscisic acid. The salt tolerance of foxtail millet was improved by synthesizing specific proteins to enhance the antioxidant system, protect cells from damage, and improve the ability to resist osmotic stress. Based on the results, we recommend that the establishment of quantitative standards and platforms for the comprehensive evaluation and selection of foxtail millet salt tolerance, the in-depth research on the regulation mechanism of foxtail millet salt tolerance, and further research and development of foxtail millet salt tolerance cultivation technology systems are important future research directions.

Keywords: Foxtail millet; Salt tolerance; Germplasm resources; Germination period; Physiological and ecological response; Salt tolerance gene

随着世界人口增长, 可利用耕地不断减少, 粮食安全受到严重威胁, 其中土壤盐碱化问题尤为突出。土壤盐碱化是指土壤中积聚盐、碱且其含量超过正常耕作土壤水平, 导致作物生长受到伤害的现象[1]。全世界盐碱地面积为 9.54 亿 hm^2, 包括 pH 分别在 7.1~8.5、8.5~9.5 和 9.5 以上的轻度盐碱化、中度盐碱化和重度盐碱化土地在内[2]。我国耕地中盐碱化面积达 920.9 万 hm^2, 占全国耕地面积的 6.62%[3], 广泛分布于我国东部沿海地区、东北、华北、西北等干旱省份[4]; 南方各省由于潮湿多雨, 土壤中水分主要通过下行运动将可溶性盐输入海洋, 因此盐碱土主要在沿海地区, 其他地区很少[3]。环渤海低平原区土壤瘠薄, 盐碱化严重, 作物生长受到严重制约。土壤盐分不仅会对植物产生渗透胁迫, 引发离子毒害[5-6], 还影响作物萌发、光合和呼吸、离子运输及养分吸收等多个过程在内的生长发育进程[7], 最终导致产量降低。当土壤含盐量 (干土) 为 0.3%~1.0% 时, 即土壤为弱盐渍土或中等盐渍土时, 农作物的产量仅为正常产量的 1/10~1/30。匡朴[8] 研究表明, 山东省盐碱地玉米 (*Zea mays* L.) 单产仅占全省玉米平均单产的 70%, 因此, 筛选鉴定耐盐的作物品种, 努力减少农作物在盐胁迫下产量和质量的损失至关重要。

谷子 (*Setaria italic* L. Beauv) 在种植业结构调整、地下水压采及粮食增产中具有重要作用。谷子种植地区主要为东北地区中西部、黄淮海平原中北部和东南部等干旱半干旱和盐碱地区[9-10]。作为良地高产旱地保收的潜力作物[11], 谷子除了抗旱, 还具有耐瘠薄、强稳产性和广适应性等优势[12]。谷子发芽只需吸收本身重量 26% 的水分, 远低于玉米 (48%)、小麦 (*Triticum aestivum* L.) (45%) 和高粱 (*Sorghum bicolor* L. Moench) (40%)[13], 对水分条件要求较低, 而且谷子生育期耗水量在 193~329 mm, 蒸腾效率高于小麦、玉米[14-15]。董宝娣等[16] 研究发现, 在极端干旱致使玉米没有任何产量的环境中, 谷子可以通过调整株高, 缩短生育期来完成生命周期从而仍获得一定经济产量, 属于典型的环境友好型作物[13]。因此, 可为我国缺水区种植结构调整提供新的战略选择。目前主要在谷子抗性资源鉴定、生理生化性状分析、栽培技术构建和少量耐盐基因功能分析及预测方面开展了耐盐性研究, 相比持续开展的谷子抗旱性研究, 谷子在盐碱地的栽培生理和栽培技术研究相对滞后, 有关谷子在盐胁迫下的响应机制和调控机理研究还需系统深入探索。实际上一般常规谷子品种对盐分的敏感性较高[17], 这使得盐胁迫相较于其他逆境因素, 成为谷子在边际土地栽培过程中的突出限制因素。而杂交谷因优于常规品种的抗旱高产特征能有效缓解这种危害, 因此, 清楚理解并提高谷子在栽培技术、生理基础和分子机理方面的耐盐性, 可进一步增强谷子在战略储备作物中的竞争力[17]。为进一步系统梳理谷子耐盐性方面的研究进展, 协同提升谷子耐旱耐盐碱能力, 本文从谷子的耐盐性筛选指标及评价、盐胁迫下植株生长发育变化规律和生理生态响应以及谷子耐盐基因发掘等 3 个方面进行综述。

1 谷子种质资源耐盐性鉴选评价

目前我国已鉴定的谷子种质资源约 28 915 种[18], 品 (种) 系间、同品种 (系) 不同生育时期的耐盐性都存在显著差异。在谷子种质资源鉴定方面, 陈二影等[19] 和秦岭等[20] 对盐胁迫下种子性状指标进行综合评价。目前已鉴选出的高抗盐品种和盐敏感品种如表 1 所示[20-28]。由于谷子不同生育阶段的盐敏感性不同, 采用的鉴选方法和评价指标有差异, 不同试验结果之间也存在显著差异, 筛选出的品种少有重合。有关谷子耐盐性种质资源鉴选的研究方法, 按照研究时期可分为萌发期、苗期和全生育期的盐胁迫鉴定法。由于萌发期最易受到外部环境影响[29], 且萌发

成功与否决定之后能否继续生长发育, 因此大多数研究时期又主要集中于萌发期。鉴选标准与研究时期的分散性导致谷子种质资源耐盐鉴选评价体系难以完善。

表 1　谷子耐盐性鉴选内容

Table 1　Contents of salt tolerance evaluation of foxtail millet

处理时期 Treatment period	栽培条件 Cultivation condition	品种数量 Varieties number	盐类型 Salt type	鉴选适宜盐浓度 Suitable salt concentration	鉴定指标 Appraisal index	耐盐性分级 Salt tolerance classification	参考文献 Reference
萌发期 Germination period	培养皿 Petri dish	27	NaCl	3 g·kg^{-1}	发芽率及其相对盐害率 Germination rate, relative salt damage rate of germination	‘张杂3号’为耐盐型 ‘Zhangza 3’ is salt tolerant type.	[21]
	培养皿 Petri dish	63[24], 54[19], 100[28], 260[30]	NaCl	1.0%~1.5%	发芽率、发芽势、根长和芽长的相对值及盐害率 Relative values and salt damage rates of germination rate, germination energy, root length, bud length	‘济谷16’和‘汾特11’等20份为高耐盐型, ‘鲁谷1号’和‘豫谷15’等23份为盐敏感型 20 varieties such as ‘Jigu 16’ and ‘Fente 11’ are high salt tolerant types; 23 varieties such as ‘Lugu 1’ and ‘Yugu 15’ are salt sensitive types.	[20,24,28,30]
	培养皿 Petri dish	100[22], 11[23], 14[26], 25[31], 10[32], 14[33]	NaCl	100~250 mmol·L^{-1}	发芽率、发芽势、根长、芽长及其相对值和盐害率、相对活力指数、Na^+含量和K^+含量 Germination rate, germination energy, root length, bud length and their relative values and salt damage rates, relative vigor index, Na^+ and K^+ contents	‘晋育红谷’和‘公矮6号’等16份为高耐盐型, ‘龙谷27’和‘龙谷25’等11份为盐高度敏感型 16 varieties such as ‘Jinyuhonggu’ and ‘Gong’ai 6’ are high salt tolerant types, and 11 varieties such as ‘Longgu 27’ and ‘Longgu 25’ are highly salt sensitive types.	[22-23,26,31-33]
	培养皿 Petri dish	4	Na_2CO_3	0, 25, 50, 75, 100 mmol·L^{-1}	相对发芽率、相对盐害率 Relative germination rate, relative salt damage rate	—	[34]
	培养皿 Petri dish	20	Na_2SO_4 : NaCl : $NaHCO_3$: Na_2CO_3= 4 : 1 : 4 : 1	60~100 mmol·L^{-1}	发芽指数、活力指数、相对根长、相对芽长、盐碱害指数 Germination index, vigor index, relative root length, relative bud length, saline-alkali damage index	‘9324-8-3’ ‘坝谷214’和‘晋谷23’为耐盐碱型, ‘大同30’ ‘大白谷’和‘九根齐’为盐碱高敏感型 ‘9324-8-3’ ‘Bagu 214’ and ‘Jingu 23’ are saline alkali resistant types, and ‘Datong 30’ ‘Dabaigu’ and ‘Jiugenqi’ are highly saline-alkali sensitive types.	[27]
	培养皿 Petri dish	53	NaCl : $NaHCO_3$= 4 : 1	100 mmol·L^{-1}	相对发芽率、根长盐害率、芽长盐害率、根冠比盐害率 Relative germination rate, salt damage rate of root length, salt damage rate of bud length, specific salt damage rate of root-shoot ratio	‘鲁谷10’和‘济谷22’为强耐盐碱型, ‘豫谷31’ ‘豫谷32’和‘保谷23’为极不耐盐碱型 ‘Lugu 10’ and ‘Jigu 22’ are strong salt-alkali resistant types, while ‘Yugu 31’ ‘Yugu 32’ and ‘Baogu 23’ are extremely salt-alkali resistant types.	[25]
苗期 Seedling stage	培养皿 Petri dish	14[26], 25[31]	NaCl	50, 150 mmol·L^{-1}	根长、芽长及其相对值和盐害率 Root length, shoot length and their relative values and salt damage rates	—	[26,31]
	盆栽 Pot culture	3	NaCl	0.5%~1.0%	气孔状态、叶表面变化、相对电导率和叶绿素荧光参数、生物量、超氧化物歧化酶 Stomatal state, leaf surface changes, relative conductivity and chlorophyll fluorescence parameters, biomass, superoxide dismutase	—	[28]
全生育期 Whole growth period	盆栽 Pot culture	155	NaCl	100 mmol·L^{-1}	籽粒产量、地上部生物量、收获指数、穗部收获指数 Grain yield, aboveground biomass, harvest index, spike harvest index	—	[35]
	大田 Field	8	盐碱地 Saline soil	3.20 g·kg^{-1}	穗重、单穗粒重、干物质重、地上部含水量 Panicle weight, grain weight per panicle, dry matter weight, water content of shoot	‘济谷22’和‘济谷21’为耐盐碱型 ‘Jigu 22’ and ‘Jigu 21’ are salt and alkali resistant types.	[19]

大多数研究者进行萌发期耐盐性鉴定主要是利用培养皿试验, 分析不同浓度盐溶液下发芽率、芽长、根长及其相对值和盐害率等指标的差异性。不同的研究者使用的盐溶液类型、确定的适宜盐浓度和鉴定指标有一定差异 (表 1)。多数研究者用于试验的盐溶液类型主要为 NaCl 溶液, 鉴选浓度一般为 100~250 mmol·L^{-1}[29], 根据发芽状况的相对值和盐害率等各指标差异性确定耐盐性的鉴选指标。也有研究者选用混合盐碱溶液进行耐盐性鉴定, 如郭瑞锋等[27] 利用 Na_2SO_4∶NaCl∶$NaHCO_3$∶Na_2CO_3=4∶1∶4∶1 的混合盐碱溶液, 以 20 份山西谷子为材料进行萌发期的耐盐性试验, 确定 60~100 mmol·L^{-1} 的混合盐碱溶液浓度为鉴选受试谷子的适宜盐浓度范围, 有效鉴定指标为发芽与活力指数、根长与芽长相对值, 及盐碱害指数; 另有陈二影等[25] 在 NaCl∶$NaHCO_3$=4∶1 混合盐碱胁迫下对 53 份谷子品种进行萌发期的耐盐鉴定试验, 发现此混合盐碱溶液鉴选谷子耐盐的适宜浓度为 100 mmol·L^{-1}, 相对发芽率、根长盐害率、芽长盐害率和根冠比盐害率在划分耐盐性等级方面具有显著差异性, 被确定为有效鉴定指标。可以看出, 与单一 NaCl 溶液胁迫下的谷子萌发试验确定的盐最适浓度范围 100~250 mmol·L^{-1} 相比, 混合盐碱胁迫下的最适筛选浓度较低, 有效鉴定指标都较为常规。虽然不同研究者确定鉴选指标有一定差异, 但是相对发芽率、根长和芽长的相对盐害率均被确定为有效鉴选指标。

对谷子其他时期的耐盐鉴选试验鲜少报道, 且主要集中于苗期。部分研究在谷子萌发期试验基础上延长至幼苗期, 通过观察鉴定谷子苗期在盐胁迫下的生长指标差异从而筛选耐盐品种, 对谷子苗期初期的根长、芽长、株高、盐害率及相对值进行测定, 初步鉴定其苗期耐盐性[26,31]。与培养皿试验不同, 有的研究者苗期进行的耐盐性试验是盆栽试验, 盐胁迫溶液为 NaCl 溶液, 其测定指标侧重于生理指标[20,28]。袁雨豪等[28] 对 2 个谷子品种进行 1% NaCl 胁迫, 发现气孔状态、叶表面变化、叶绿体超微结构变化、相对电导率及叶绿素荧光参数可以作为筛选谷子苗期耐盐性的有效指标。秦岭等[20] 对 3 个谷子品种进行 0.5% 的 NaCl 胁迫, 筛选出生物量和活性氧清除系统酶类等指标来鉴定耐盐性谷质。对全生育期进行盐处理的试验比较少, 陈二影等[19] 在 3.20 g·kg^{-1} 的盐碱地条件下, 选取 8 个谷子品种进行大田处理的谷子耐盐性试验, 发现盐害影响产量主要通过降低或减少穗重、单穗粒重、干物质重和地上部含水量对产量造成危害, 这 4 个指标可鉴定大田尺度下谷子的耐盐碱性。

从以上分析可知, 在大量的谷子耐盐性鉴选试验中, 由于研究品种与试验条件等差异, 不同研究人员确定的有效鉴选指标重合度并不高, 并且, 盐胁迫下谷子生理生化性状虽有研究, 但并没有将其列为筛选指标。少量指标无法全面筛选优质耐盐谷种, 因此扩大筛选指标范围, 明确并综合运用更多具有广泛应用性的主要鉴定指标, 是亟待解决的问题。

2 盐胁迫下谷子生理生态响应

2.1 地上-地下农艺性状响应

根系作为土壤中与盐接触的最直接器官, 盐浓度过高导致根部细胞水势降低, 产生渗透胁迫、离子失衡和毒害, 使其无法正常吸收运输营养元素[36-39]。盐胁迫下作物根长、根面积等生长参数受盐胁迫影响而下降, 根系结构成分改变, 主根和侧根的生长速度均有减缓, 对养分的吸收能力下降, 因此整体形成受抑制[7,40]。谷子根系盐胁迫的相关研究主要集中在萌发期。其中, 根长受盐害影响最大。陈二影等[25] 研究不同盐碱浓度下谷子萌发指标发现, 根长的盐害率均值为 77.6%。盐胁迫对根系细胞内 pH 也有一定影响, 抗盐品种 pH 变化小于盐敏感品种。李小波等[40] 用 150 mmol·L^{-1} NaCl 溶液对‘豫谷 2 号’(抗盐) 和‘安 04’(盐敏感) 进行盐胁迫, 测定谷子根组织细胞的荧光强度, 发现细胞内 pH 与绿色荧光通道和蓝色荧光 ECFP 通道的荧光强度比值呈正相关关系, 盐敏感品种‘安 04’根细胞内 pH 提高 7.28%, 比抗盐品种增加 6.15%。表明谷子耐盐品种根细胞内 pH 自我调节能力强于盐敏感品种, 受外界环境影响变化较小。有关盐分对谷子根系其他参数的影响研究相对较少, 谷子根系在盐胁迫下的形态参数及根系活力等生理生态响应规律少见报道。

盐胁迫抑制谷子地上部组织的生长发育, 进而影响产量。目前研究均表明, 盐胁迫条件下, 谷子成株期地上部各农艺性状一般均受到不同程度的抑制, 影响幅度与盐胁迫程度和品种抗盐性显著相关[41]。作物植株株高和生物量干重的下降幅度随盐浓度升高而增加[41]。张艳亭[42] 研究发现谷子株高及其地上部含水量与盐处理浓度均呈负相关关系, 在 0.1%~0.3% NaCl 胁迫下, 盐敏感品种‘济谷 16’株高比对照分别下降 11.69% 和 16.91%, 在 0.5%~0.7% NaCl 胁迫下, 敏感品种‘鲁谷 1 号’株高分别降低 20.01% 和 26.17%。徐心志等[43] 研究发现在 NaCl 胁迫下, 谷子幼苗株高和生物量随盐含量增加而降低, 而在 Na_2SO_4 和 $NaHCO_3$ 下则表现为“低浓度盐胁迫促

进生长, 高浓度盐胁迫抑制生长”。其中, 0.4% 的 $NaHCO_3$ 对干物质量影响最大, 较对照下降 37.0%。陈二影等[19]对 8 个谷子品种在含盐量为 3.2 g·kg^{-1} 的盐碱地田间试验中发现, 各品种产量因穗重、单穗粒重、干物质重和地上部含水量受盐害影响均呈现显著降低趋势, 其变异系数分别为 13.5%、13.5%、3.1% 和 6.0%, 产量盐害率为 20.7%~63.4%, 且与开花期地上部含水量和花前转运同化物质对籽粒的贡献率均呈显著负相关。张笛[44]研究发现盐胁迫对谷子农艺指标影响程度不同。盐胁迫对谷子的影响最主要的是产量构成因素 (单穗重、穗单粒重), 其次是穗部性状 (穗长、码行数、码粒数), 最后是形态指标 (株高、茎粗)。

2.2　生理生化指标响应

光合作用是植物利用光能, 合成有机物, 释放氧气并为自身生长发育提供能量的过程, 对植物生长至关重要。盐胁迫下谷子叶片的净光合速率、蒸腾速率和气孔导度均有降低。盐胁迫下谷子幼苗主要通过降低蒸腾作用、呼吸作用、叶绿素含量和气孔开度来适应盐胁迫条件。其原因可能是盐胁迫引起渗透胁迫, 致使水分和养分吸收受阻, 气孔开度降低、CO_2 进入叶肉细胞速率下降导致。高昆等[45]研究发现, ‘豫谷 18’幼苗的净光合速率伴随着复合盐浓度 (0~0.9%) 的升高而下降, 主要与气孔导度和蒸腾速率下降有关, 其中, 0~0.3% 盐胁迫时蒸腾速率、气孔导度下降较快, 0.6%~0.9% 时下降趋势减缓。盐胁迫下光合速率下降品种间存在显著差异。耐盐品种‘公矮 6’ ‘龙谷 35’等在盐胁迫条件下光合、蒸腾和气孔导度降低幅度基本都在 10% 以内, 受抑制程度较小, 而盐敏感品种‘晋谷 35’ ‘红粘谷’ ‘嫩选 15’在相同盐分胁迫条件下, 下降幅度基本都在 40% 以上, 受抑制程度较大。不同类型盐成分对叶片光合特性影响也有一定差异。徐心志等[43]选取中性盐 (NaCl、Na_2SO_4) 和碱性盐 ($NaHCO_3$), 研究了盐胁迫对‘豫谷 17’苗期生长、叶绿素含量和光合特性的影响, 发现叶绿素受 NaCl 影响最大, 0.2% 和 0.4% 处理下分别比对照下降 24.1% 和 34.0%; 不同类型盐成分处理的谷子叶片净光合速率 (P_n) 均随盐含量增加而降低, 盐含量为 0.2% 和 0.4% 时, NaCl 处理下降 33.5% 和 59.1%, Na_2SO_4 和 $NaHCO_3$ 处理分别下降 47.8%、80.2% 和 38.9%、85.5%。也有研究[46-52]认为盐胁迫降低光合作用主要是 Na^+ 通过破坏气孔、叶绿体结构和功能以及降低酶活来影响光合作用。

在盐胁迫条件下, 植物体内清除活性氧的保护酶活性增强, 从而清除体内过多的活性氧, 以减少对植物的伤害。秦岭等[20]研究发现谷子叶片中的超氧化物歧化酶 (SOD)、过氧化物酶 (POD) 和过氧化氢酶 (CAT) 等清除活性氧的保护酶系统在盐胁迫下的活性随胁迫天数先上升后下降。张笛[44]研究发现在一定的盐胁迫下谷子叶片中的 SOD、POD 和 CAT 活性与对照相比均有增强, 3 种抗氧化酶活性的变化程度为: SOD>CAT>POD。抗氧化酶活性的变化程度在不同品种间存在显著性差异, 耐盐性强的谷子品种酶活性上升幅度显著大于耐盐性弱的品种, 活性氧清除能力更强。丙二醛 (MDA) 可以间接反映膜系统受盐胁迫程度。有研究[53]发现在较低浓度的 100 mmol·L^{-1} NaCl 胁迫下, 谷子耐盐品种与盐敏感品种的 MDA 含量没有显著差异; 而在较高浓度的 250 mmol·L^{-1} NaCl 胁迫下, 耐盐品种的 MDA 含量几乎保持不变, 但盐敏感品种由于膜系统受伤害严重 MDA 含量增加到两倍以上。激素对盐胁迫下谷子的特定效用少有报道, 但研究发现脱落酸 (ABA) 可诱导植物脯氨酸的大量积累, 从而维持细胞膜结构的稳定性, 提高保护酶的活性[54]; 植物生长激素 (IAA)、赤霉素 (GA_3) 等也能够缓解盐胁迫对植物的伤害[55-56], 此研究结果可作为盐胁迫下谷子激素研究的基础。

盐胁迫导致谷子生长发育改变是各项生理生化反应综合作用的结果, 目前谷子在耐盐方面的研究主要集中在种质资源的鉴选和生理生态分析方面 (表 2), 而谷子耐盐抗盐的基因发掘和调控网络还有很大的提升空间。

3　谷子部分耐盐基因发掘

植物的耐盐性属于数量性状遗传, 受多基因调控[57]。近年来通过反向遗传学及转录组分析鉴定了大量与盐胁迫直接相关或参与盐胁迫过程的基因。

目前已通过双向电泳及遗传转化等手段发现 *SiPHGPX*、*SiLEA14 和 bZIPs* 直接参与了谷子盐胁迫相关的过程。*SiPHGPX* 基因是耐盐谷子中最显著的由盐处理诱导的蛋白质基因, Sreenivasulu 等[53]研究发现盐胁迫下 *SiPHGPX* 基因在 RNA 水平和蛋白质水平上表达均上调, 这与盐胁迫下 *PHGPX* 在柑橘 (*Citrus reticulata* Blanco)[58]中蛋白水平上调和大麦 (*Hordeum vulgare* L.)[59]、豌豆 (*Pisum sativum* L.)[60]中 cDNA 水平升高的研究结果一致。*SiPHGPX* 提高谷子耐盐性主要是通过清除有机过氧化物和脂质过氧化物来对抗盐介导的氧化膜损伤, 保护细胞免受氧化应激影响[53]。与之功能相似的基因还有 *SiALDHs*, 通过间接解毒细胞活性氧 (ROS), 降低脂质过氧化引起的细

表 2 盐胁迫影响谷子生理生化指标

Table 2 Physiological and biochemical indexes of foxtail millet affected by salt stress

指标类型 Index system	指标 Index	表现 Performance	参考文献 Reference
农艺性状 Agronomic characters	根系 Root system	混合盐碱胁迫下, 不同品种的根长盐害率均值达77.6%; NaCl胁迫下盐敏感品种根部细胞内pH提高7.28%, 比抗盐品种增加6.15% Under the mixed saline-alkali stress, the average root length salt damage rate of different varieties was 77.6%; under NaCl stress, the pH in the root cells of salt sensitive varieties increased by 7.28%, which was 6.15% higher than that of salt resistant varieties.	[25,40]
	株高 Plant height	0.1%~0.3% NaCl胁迫下'济谷16'较敏感, 株高降低11.69%~16.91%, 在0.5%~0.7% NaCl胁迫下, '鲁谷1号'株高降低20.01%~26.17% Under 0.1%−0.3% NaCl stress, 'Jigu 16' was sensitive, and the plant height decreased by 11.69%−16.91%. Under 0.5%−0.7% NaCl stress, 'Lugu 1' was the more sensitive, and the plant height decreased by 20.01%−26.17%.	[42]
	地上部含水量 Aboveground water content	含盐3.2 $g\cdot kg^{-1}$的大田条件下谷子成熟期的地上部含水量变幅为 35.4%~49.2% Under the field condition of salt content of 3.2 $g\cdot kg^{-1}$, the aboveground water content of millet at maturity varies from 35.4% to 49.2%.	[19]
产量要素 Yield factors	穗重、单穗粒重、千粒重 Ear weight, grain weight of per panicle, 1000-seed weight	含盐3.2 $g\cdot kg^{-1}$大田条件下谷子各品种的穗重、单穗粒重、千粒重变异系数分别为13.5%、13.5%和3.1%, 产量盐害率为20.7%~63.4% Under the field condition of salt content of 3.2 $g\cdot kg^{-1}$, the variation coefficients of panicle weight, grain weight per panicle and 1000-grain weight of millet varieties were 13.5%, 13.5% and 3.1% respectively, and the yield salt damage rate was 20.7%−63.4%.	[19]
光合特性 Photosynthetic characteristics	叶绿素、气孔导度、蒸腾速率、净光合速率 Chlorophyll, stomatal conductance, transpiration rate, net photosynthetic rate	复合盐胁迫(0~0.9%)下净光合速率由于气孔导度和蒸腾速率下降而降低, 0~0.3%时蒸腾速率、气孔导度下降较快, 0.6%~0.9%时下降趋势减缓; 在中性盐NaCl、Na_2SO_4及碱性盐$NaHCO_3$胁迫下, 叶绿素受NaCl影响最大, 0.2%和0.4%的处理分别比对照下降24.1%和34.0% Under compound salt stress (0−0.9%), the net photosynthetic rate decreased due to the decrease of stomatal conductance and transpiration rate. The transpiration rate and stomatal conductance decreased rapidly at 0−0.3%, and the downward trend slowed down at 0.6%−0.9%. Under the stress of neutral salt NaCl, Na_2SO_4 and alkaline salt $NaHCO_3$, chlorophyll was most affected by NaCl. Under the treatment of 0.2% and 0.4% NaCl, the chlorophyll decreased by 24.1% and 34.0%, respectively, compared with the control.	[43,45]
活性氧清除系统 Active oxygen scavenging system	超氧化物歧化酶(SOD)、过氧化物酶(POD)、过氧化氢酶(CAT) Superoxide dismutase (SOD), peroxidase (POD), catalase (CAT)	盐胁迫下SOD、POD和CAT活性均随胁迫天数增加先上升后下降, 且与对照相比均有增强, 变化程度为: SOD>CAT>POD Under salt stress, the activities of SOD, POD and CAT increased first and then decreased with the days of stress, and increased compared with the control. The change degree of activity was SOD>CAT>POD.	[20,22]
激素 Hormone	脱落酸、生长素、赤霉素 Abscisic acid (ABA), auxin (IAA), gibberellin (GA_3)	ABA可诱导脯氨酸的大量积累, 从而维持细胞膜结构的稳定性, 提高保护酶的活性, IAA和GA_3能够缓解盐胁迫对植物的伤害 ABA can induce a large amount of proline accumulation in plants, so as to maintain the stability of cell membrane structure and improve the activity of protective enzymes. IAA and GA_3 can also alleviate the damage of salt stress to plants.	[54-56]

胞毒性[61]。Wang 等[62]通过对谷子基因的表达分析, 发现 *SiLEA14* 在渗透胁迫、NaCl 和外源 ABA 胁迫下表达上调, 并在 *SiLEA14*启动子的−793 bp 到−77 bp 区域中鉴定出 10 个含有 ABRE-ACGT 核心的顺式元件, 进一步通过 GUS 报告基因试验表明 *SiLEA14* 启动子受到 ABA 的激活, 且转基因谷子种子在 ABA 溶液中的发芽率比野生型高。所有这些结果表明, 盐胁迫和干旱胁迫下 *SiLEA14* 的激活可能依赖于 ABA。ABRE 作为受 ABA 诱导表达的主要顺式作用元件, 被鉴定可以和 *bZIP* 转录因子 *AREB/ABF* 结合[63-66]。与之相对应的是, 许多物种中的 *bZIPs* 基因也被报道参与盐胁迫, 例如玉米 *ZmbZIP72*[67]、水稻 (*Oryza sativa* L.) *OsbZIP23*[68]、葡萄 (*Vitis vinifera* L.) *VvbZIP23*[69] 和番茄 (*Lycopersicon esculentum* Miller) *SlbZIP19* 基因[70]。谷子中与上述基因具有同源性的 *SibZIP55*、*SibZIP50*、*SibZIP39* 和 *SibZIP46* 在干旱或盐胁迫下也上调表达, 表明这些基因在谷子抵御干旱和盐胁迫等逆境过程中发挥重要作用[70]。另有秦玉海等[71]通过构建植物表达载体 *pBI121-SibZIP42*, 转化拟南芥 [*Arabidopsis thaliana* (L.) Heynh.] 并检测转 *SibZIP42* 拟南芥的耐盐性及对 ABA 处理的敏感性, 发现与野生型相比, *SibZIP42* 转基因拟南芥株系在种子萌发时期耐盐性显著提高, 可能通过 ABA 信号途径正向调控植物的耐盐性[71-72]。

通过对比耐盐与不耐盐的谷子品种在盐胁迫下的遗传转录组发现 *SiRLK35* 和 *SiPEPC* 参与了谷子的干旱胁迫响应以及脱水应答过程[73-74]。*SiRLK35* 基因对不同胁迫均可以产生响应, 干旱和盐处理下响应较为明显, 其表达量在 6 h 分别达到未处理时的 38 倍和 15 倍[73]。250 $mmol\cdot L^{-1}$ NaCl 胁迫下诱导的 *SiPEPC* 表达量最高值为对照的 9.96 倍, 对逆境的响应明显[74]。已有研究结果表明 (表 3), 众多谷子基因

表 3 谷子耐盐相关基因克隆与功能分析

Table 3 Cloning and functional analysis of salt tolerance related genes in foxtail millet

基因名称 Gene name	转基因受体与亚细胞定位 Transgenic receptor and subcellular localization	诱导因素及基因功能 Inducing factors and gene function	依赖途径 Dependent approach	参考文献 Reference
SiPHGPX	无细胞定位, 基于宏阵列的胁迫特异性基因表达分析 No cell localization. Macroarray-based stress-specific gene expression analysis	受NaCl诱导, *PHGPX*基因产物在抗盐诱导的氧化损伤的防御反应中起着重要作用 Induced by NaCl, the *PHGPX* gene product plays an important role in the defense response against salt-induced oxidative damage.	—	[53]
SiALDHs	谷子和水稻同源区 Homologous region of rice and foxtail millet	渗透胁迫、低温、过氧化氢和植物激素脱落酸(ABA)诱导基因表达量增加, 对蛋白质损伤、细胞膜破坏和细胞凋亡有保护功能, 提高耐盐性 Osmotic stress, low temperature, hydrogen peroxide and plant hormone abscisic acid (ABA) induce increased gene expression, which has protective functions against protein damage, cell membrane destruction and cell apoptosis, and improves salt tolerance.	ABA依赖, 编码NAD(P)依赖性酶 ABA independent pathway, encoding NAD(P)-dependent enzyme	[61]
SiLEA14	细胞质 Cytoplasm	受渗透胁迫、NaCl和外源脱落酸诱导, 提高谷子萌发期的抗渗透胁迫能力, 提高耐盐性和耐旱性 Induced by osmotic stress, NaCl and exogenous abscisic acid, it improves the resistance to osmotic stress during the germination of millet, and improves salt and drought tolerance.	ABA依赖 ABA dependent pathway	[62]
SibZIPs	细胞核 Nucleus	受高盐、干旱(PEG)和ABA胁迫诱导, 可通过与具有调控作用的蛋白(如蛋白激酶、*NPR1*相关蛋白)互作而介导调控谷子抵御胁迫反应 Induced by high salt, drought (PEG) and ABA stress, it can mediate and regulate millet to resist stress response by interacting with regulatory proteins (such as protein kinases, *NPR1* related proteins).	ABA依赖与非依赖途径 ABA dependent and independent pathways	[71-72]
SiARDPs	细胞核 Nucleus	提高谷子耐旱耐盐性 Improve drought tolerance and salt tolerance of millet.	ABA依赖 ABA dependent pathway	[76]
SiNF-Ys	细胞质、细胞核 Cytoplasm, nucleus	受干旱、盐、甘露醇和氧化胁迫诱导, *SiNF-YA1*或*SiNF-YB8*通过增强抗氧化系统来增强胁迫耐受性 Induced by drought, salt, mannitol and oxidative stress, *SiNF-YA1* or *SiNF-YB8* enhances stress tolerance by enhancing the antioxidant system.	*SiNF-YA5* ABA非依赖, *SiNF-YA1*和*SiNF-YA8* ABA依赖 *SiNF-YA5* through ABA independent pathway, *SiNF-YA1* and *SiNF-YA8* through ABA dependent pathway	[77-78]
SiVHA-E	液泡膜 Vacuole membrane	被高盐、茉莉酸甲酯(MeJA)、水杨酸(SA)和ABA胁迫诱导表达, 提高植物耐盐性 Induced expression by high salt, methyl jasmonate (MeJA), salicylic acid (SA) and ABA stress to improve plant salt tolerance.	ABA依赖 ABA dependent pathway	[79]
SiASR4	细胞核、细胞质和细胞膜 Nucleus, cytoplasm and cytomembrane	受ABA、NaCl和PEG诱导, 提高谷子对干旱和盐胁迫的耐受性 Induced by ABA, NaCl and PEG, the tolerance of millet to drought and salt stress was improved.	ABA依赖 ABA dependent pathway	[80]
SiLTPs	表皮细胞[烟草(*Nicotiana tobacum* L.)叶]、细胞质(玉米原生质体) Epidermal cells (tobacco leaves), cytoplasm (maize protoplasts)	脱落酸(ABA)诱导基因表达量增加, 提高谷子耐盐性和耐旱性 Abscisic acid (ABA) increased gene expression and improved salt tolerance and drought tolerance of foxtail millet.	ABA依赖 ABA dependent pathway	[81]
SiNAC110	细胞核 Nucleus	被干旱、高盐等非生物胁迫诱导, 提高谷子对干旱和高盐胁迫的耐受性 It was induced by abiotic stress such as drought and high salt to improve the tolerance of millet to drought and high salt stress.	ABA非依赖 ABA independent pathway	[82]
SiRLK35	质膜 Plasma membrane	受NaCl、PEG、ABA、GA、MeJA胁迫诱导, 其中明显响应盐胁迫, 显示其对作物耐旱、抗盐及抗胁迫等方面具有重要调控作用 It was induced by NaCl, PEG, ABA, GA, MeJA stresses, and responded significantly to salt stress, indicating that it plays an important role in regulating drought tolerance, salt tolerance and stress resistance of crops.	可能ABA依赖 It may be ABA dependent pathway.	[73]
SiCBL4	细胞膜、细胞质 Cytomembrane, cytoplasm	受盐、ABA、甲基紫精醇(MV)、热休克和冷胁迫因素诱导, *CBL-CIPK*通路可被调控以提高植物耐盐性 Induced by salt, ABA, methyl viologen (MV), heat shock and cold stress, the *CBL-CIPK* pathway can be regulated to improve plant salt tolerance.	可能ABA依赖 It may be ABA dependent pathway.	[75,83]
SiCIPK24	细胞质 Cytoplasm	受盐、ABA、MV、热休克和冷胁迫因素诱导, *CBL-CIPK*通路可被调控以提高植物耐盐性 Induced by salt, ABA, MV, heat shock and cold stress, *CBL-CIPK* pathway can be regulated to improve plant salt tolerance.	可能ABA依赖 It may be ABA dependent pathway.	[83]
SiNADP-ME	叶绿体、线粒体和细胞质 Chloroplast, mitochondria and cytoplasm	被ABA、低温、PEG、NaCl胁迫诱导表达, 广泛参与谷子苗期非生物逆境胁迫应答 It was induced by ABA, low temperature, PEG and NaCl stress and widely participated in abiotic stress response of millet seedling.	可能ABA依赖 It may be ABA dependent pathway.	[84]
SiPEPCs	细胞质、细胞核和线粒体 Cytoplasm, nucleus and mitochondria	受ABA、低温、PEG、高盐胁迫诱导表达, 参与谷子对非生物逆境的应答, 可能在干旱和其他逆境胁迫信号途径中起关键作用 Induced by ABA, low temperature, PEG and high salt stress, it participates in the response of millet to abiotic stress, and may play a key role in drought and other stress signaling pathways.	可能ABA依赖 It may be ABA dependent pathway.	[74]

广泛参与萌芽期与苗期非生物逆境胁迫应答，同已有其他作物在逆境应答方面的基因研究结果是一致的，但由于不同逆境之间存在信号交叉，同一基因应答逆境的信号系统比较复杂[75]，更多谷子耐盐基因只确定与盐胁迫有关，更深入的反应机理需要对基因功能进一步解析获悉。

4 谷子耐盐性研究重点方向

面对我国盐碱地面积不断扩大的严峻形势，结合 2019 年中央一号文件提出的扩大轮作休耕试点，明确盐碱荒地的充分利用对我国粮食安全具有重要意义。谷子作为耐逆性强、生育期宽泛的补充性杂粮作物，未来耐盐性研究重点主要集中在以下 3 个方面。

4.1 建立综合谷子种质资源耐盐鉴选评价体系

谷子耐盐性状是一个多基因控制的数量性状，由于耐盐调控机理的复杂性和多尺度性，尽管目前在谷子的耐盐性研究中开展了萌发期和整个生育期农艺性状和一定生理生化鉴选指标的研究。但是，多数采用直接鉴定法集中研究在谷子萌发期和苗期，利用一些简单的萌发指标进行鉴选，或利用生理生态指标的变化间接鉴选谷子种质资源的耐盐性强弱。可是，各农艺性状和生理生化性状对盐胁迫的响应程度最终以产量形式体现，只用苗期指标来评价鉴选谷子的耐盐性有一定的局限性。因此，应该加强谷子整个生育期生长发育和产量性状以及生理生化指标对盐胁迫响应的研究，深入加强谷子表型组学与环境的互作研究，把不同生育期的主要鉴选指标和评价方法结合起来进行综合评价。根据谷子耐盐性迥异，明确种植区域，为不同类型或不同程度的盐碱荒地充分利用提供品种理论和技术支撑。

4.2 深入开展谷子耐盐调控机理研究

谷子作为杂粮作物，过去对其生长发育过程中的耐逆性、尤其是耐盐的生理机制研究相对薄弱。大部分相关研究也是参考水稻等其他农作物展开，研究方法和结论可能存在种间差异。因此，应加强谷子耐盐碱遗传规律的研究、耐盐基因的克隆及其功能和调控网络的解析，特别是基于关联分析、连锁分析、比较遗传学等方法的谷子或野生近缘种耐盐碱等优异基因的发掘和利用，在提升谷子耐盐性的同时，也为禾谷类作物如小麦、玉米、水稻分子设计育种提供优异的基因资源，从而提升谷类作物的整体抗逆性。

4.3 进一步研发谷子耐盐栽培技术体系

大田栽培生产是所有谷子抗 (耐) 盐材料研究的终极目的。由于受土壤盐碱不均匀分布性、气候、天气等多变性、水盐胁迫伴生性、地域差异性等多因素影响，谷子田间耐盐碱研究鲜见报道。因此，应加强谷子耐盐栽培技术体系研发和谷子耐盐碱评价指标体系建设，建立鉴选耐盐碱平台，筛选培育高抗盐谷子品种；利用土壤调理剂、混合有机物料添加等增加土壤有机质、创建肥沃耕层以协同活化谷子耐盐阈值；通过播期、垄作、秸秆覆盖等耕作栽培措施，创建适水减蒸抑盐高效生产技术；研发相应的配套农机具，实现农机农艺一体化技术体系，提升谷子耐盐高效栽培的就绪度，促进谷子在边际土地的推广应用。

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