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AsA 引发对盐胁迫下白羊草种胚线粒体 AsA-GSH 循环的影响

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摘要: 试验探究了抗坏血酸(Ascorbic acid, AsA)引发对盐胁迫下白羊草(*Bothriochloa ischaemum*)种胚线粒体 AsA-GSH 循环的影响, 以为选育耐盐白羊草种质资源新材料提供理论依据。以‘太行’白羊草种子为材料, 经 0.1 mmol·L⁻¹ 的 AsA 溶液引发 12 h 后, 采用 Na⁺ 浓度为 30 mmol·L⁻¹ 的 NaCl 和 Na₂SO₄ 溶液进行胁迫萌发试验, 分析其胚根和胚芽线粒体 AsA-GSH 循环酶活性及脂质过氧化水平的变化规律。结果表明, AsA 引发后, 白羊草胚根和胚芽线粒体中过氧化氢酶(Catalase, CAT), 谷胱甘肽转移酶(Glutathione transferase, GST), 脱氢抗坏血酸还原酶(Dehydroascorbate reductase, DHAR)和单脱氢抗坏血酸还原酶(Monodehydroascorbate reductase, MDHAR)活性显著上升($P < 0.05$), 超氧化物歧化酶(Superoxide dismutase, SOD), 抗坏血酸过氧化物酶(Ascorbate peroxidase, APX), 谷胱甘肽过氧化物酶(Glutathione peroxidases, GPX)活性及丙二醛(Malondialdehyde, MDA)和 H₂O₂ 含量显著下降($P < 0.05$)。盐胁迫下, APX 和 GPX 是调控白羊草种胚线粒体耐盐的关键酶, 而 AsA 引发后则以 CAT, MDHAR 和 DHAR 为关键酶。隶属函数分析结果表明, 0.1 mmol·L⁻¹ 的 AsA 引发对 30 mmol·L⁻¹ NaCl 胁迫下白羊草胚根线粒体 AsA-GSH 循环酶活性的提升效果最好。

关键词: 白羊草; 盐胁迫; 抗坏血酸引发; 线粒体; AsA-GSH 循环

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Influences of AsA Priming on AsA-GSH Cycle in Mitochondria of *Bothriochloa ischaemum* under Salt Stress

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Abstract: To provide a theoretical basis for the breeding of salt-tolerant germplasm resources in *Bothriochloa ischaemum*, this experiment investigated the effects of ascorbic acid (AsA) priming on the AsA-GSH cycle in the embryonic mitochondria of *B. ischaemum* under salt stress. Seeds of ‘Taihang’ *B. ischaemum* were used as experimental materials, and were primed with 0.1 mmol·L⁻¹ AsA solution for 12 h, then were germinated in NaCl and Na₂SO₄ solutions containing 30 mmol·L⁻¹ Na⁺. The changes in AsA-GSH cycle enzymes activities and lipid peroxidation levels in their mitochondria of radicle and plumule were analyzed. The results showed that the activities of catalase (CAT), glutathione transferase (GST), dehydroascorbate reductase (DHAR) and monodehydroascorbate reductase (MDHAR) in the mitochondria of radicle and plumule of *B. ischaemum* were increased significantly after AsA priming ($P < 0.05$), while the activities of superoxide dismutase (SOD), ascorbate peroxidase (APX) and glutathione peroxidases (GPX), as well as the contents of malondial-

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dehyde (MDA) and H_2O_2 , were decreased significantly ($P < 0.05$). Under salt stress, APX and GPX were the key enzymes regulating salt tolerance of embryonic mitochondria in *B. ischaemum*, but CAT, MDHAR and DHAR were served as the core regulatory enzymes after AsA priming. The membership function analysis indicated that priming with $0.1 \text{ mmol} \cdot \text{L}^{-1}$ AsA had the best effect on enhancing the activities of mitochondrial AsA-GSH cycle enzymes in the radicle of *B. ischaemum* under $30 \text{ mmol} \cdot \text{L}^{-1}$ NaCl stress.

Key words: *Bothriochloa ischaemum*; Saline stress; Ascorbic acid priming; Mitochondria; AsA-GSH cycle

土壤盐渍化是世界性生态环境问题,全球盐渍化土壤总面积已达 13.81 亿 hm^2 , 占全球陆地面积的 10.7% , 且仍在逐渐扩增^[1]。土壤盐渍化造成的植物种子萌发和幼苗建成过程受阻已成为当前限制农牧业产出和遗传资源创新利用成效的关键因素^[2]。然而,种子萌发时期因种胚代谢活跃而抗逆性较弱,成为限制植物在盐渍环境中建植的关键时期。盐胁迫不仅会直接破坏植物种胚膜系统结构,抑制其能量代谢,还会造成活性氧(Reactive oxygen species, ROS)的过量积累而导致其细胞膜系统产生脂质过氧化损伤,进而抑制植物种子萌发及其幼苗建成,最终影响植物的产量和品质^[3]。因此,提高植物种子在盐胁迫下的活力水平,对保障盐地植物产量和质量具有重要意义。

线粒体是种胚细胞内 ROS 产生的核心场所以及攻击的首要目标,而其自身氧化还原稳态的维持则主要通过抗坏血酸-谷胱甘肽(Ascorbate-glutathione, AsA-GSH)循环中关键酶的协同作用来实现^[4]。然而,盐胁迫造成的 AsA-GSH 循环功能失衡不仅会阻碍线粒体电子传递链的 ATP 合成,还会导致线粒体膜结构受损及关键酶蛋白失活,最终导致种子萌发性能下降,甚至种胚死亡^[5]。种子引发可以促进种子更快地激活自身抗氧化防御系统,已被证明是提高植物适应逆境胁迫能力的一种有效方法^[6]。研究发现,适宜的外源物质引发可以促进盐胁迫下膜荚黄芪(*Astragalus membranaceus*)^[7]、水稻(*Oryza sativa*)^[8]和紫花苜蓿(*Medicago sativa*)^[9]等植物种子的萌发性能。抗坏血酸(Ascorbic acid, AsA)作为植物体内普遍存在的重要生理活性物质,可通过 AsA-GSH 循环调控植物的抗氧化防御系统来增强自身抗逆性^[10],这在燕麦(*Avena sativa*)^[11]、小麦(*Triticum aestivum*)^[12]和高粱(*Sorghum bicolor*)^[13]等植物研究中已得到验证,但不同物种在盐胁迫下响应外源 AsA 引发的生理反应存在明显差异,对盐胁迫下植物种胚线粒体 AsA-GSH 循环抗氧化性能的调控机制也尚不清楚。

白羊草(*Bothriochloa ischaemum*)是禾本科孔颖草属多年生优质牧草,具有适口性好、草产量高、

抗旱、耐放牧和再生能力强等诸多优点因而被广泛认为是重要的饲草和生态草兼用乡土草资源,其种质资源的挖掘与利用也就日益受到重视。研究表明,盐胁迫可导致白羊草种胚线粒体 AsA-GSH 循环中抗坏血酸过氧化物酶(Ascorbate peroxidase, APX)和谷胱甘肽转移酶(Glutathione transferase, GST)活性下降, H_2O_2 和丙二醛(Malondialdehyde, MDA)含量显著上升,诱导线粒体脂质过氧化,从而抑制种子正常萌发和幼苗建植,降低其生态价值与种用价值^[14-15]。因此,试验以白羊草种子为材料,分析外源 AsA 引发对盐胁迫下白羊草种胚线粒体 AsA-GSH 循环抗氧化能力的影响规律,从而阐明 AsA 引发通过提升白羊草种胚线粒体 AsA-GSH 循环抗氧化性能来增强种子耐盐性萌发的生理机制,以期为提升我国盐渍化土地的使用效率和选育耐盐性白羊草种质资源提供理论依据。

1 材料与方法

1.1 试验材料

材料为山西农业大学草业学院草类植物育种与种子科学实验室于 2019 年 10 月收集的‘太行’白羊草种子,于 -20°C 冰箱中密封保存至 2021 年 8 月开展试验。种子千粒重为 0.65 g ,初始发芽率为 71% 。

1.2 试验设计

挑选大小均匀、颗粒饱满的白羊草种子置于浓度 $0.1 \text{ mmol} \cdot \text{L}^{-1}$ 的 AsA 溶液(预试验浓度为 $0.1, 0.2, 0.3, 0.4$ 和 $0.5 \text{ mmol} \cdot \text{L}^{-1}$)^[15]中引发 12 h ,快速滤出用蒸馏水冲洗 3 次,再用滤纸吸干种子表层水分, 25°C 黑暗环境下自然风干至引发前种子质量,每个铺有双层滤纸的培养皿摆放 100 粒供试种子,分别加入 4 mL Na^+ 浓度为 $30 \text{ mmol} \cdot \text{L}^{-1}$ 的 NaCl 和 Na_2SO_4 溶液(预试验浓度为 $0, 10, 30, 90$ 和 $270 \text{ mmol} \cdot \text{L}^{-1}$),称重后记录初始质量,每日定时补充蒸馏水以保持恒重。各处理设置 4 次重复。以盐胁迫下未进行 AsA 引发的处理作为对照(CK)。

1.3 线粒体提取

选取盐胁迫发芽试验12 d的白羊草幼苗,分离其胚根和胚芽。参照Yin等^[16]的方法,进行线粒体的提取。

1.4 ASA-GSH循环测定指标

超氧化物歧化酶(Superoxide dismutase, SOD)活性的测定参照Beyer等^[17]的方法;过氧化氢酶(Catalase, CAT)活性的测定参照Aebi^[18]的方法;APX活性的测定参照Nakano等^[19]的方法;谷胱甘肽过氧化物酶(Glutathione peroxidases, GPX)活性的测定参照Flohé等^[20]的方法;GST活性的测定参照Nagalakshmi等^[21]的方法;单脱氢抗坏血酸还原酶(Monodehydroascorbate reductase, MDHAR)活性的测定参照Arrigoni等^[22]的方法;脱氢抗坏血酸还原酶(Dehydroascorbate reductase, DHAR)活性的测定参照Dalton等^[23]的方法;MDA含量的测定参照Bailly等^[24]的方法。 H_2O_2 含量测定使用南京建成生物工程研究所-南京建成科技有限公司生产的试剂盒(编号为A064-1-1)。

1.5 数据处理与分析

采用Microsoft Office Excel 2019软件对试验数据进行初步整理,利用SPSS 27.0软件进行单因素和双因素方差分析。AsA-GSH循环指标的单因素方差分析及组间多重比较采用Duncan's法进行, $P<0.05$ 表示差异显著, $P>0.05$ 表示差异不显著。隶属函数分析参考文献^[25]。

2 结果与分析

2.1 AsA引发对盐胁迫下白羊草种胚线粒体SOD活性的影响

AsA引发前后,NaCl胁迫下白羊草胚根线粒体SOD活性均显著低于胚芽线粒体($P<0.05$),而 Na_2SO_4 胁迫下白羊草胚根线粒体中SOD活性均显著高于胚芽线粒体($P<0.05$),NaCl胁迫下白羊草胚根和胚芽线粒体SOD活性均极显著高于 Na_2SO_4 胁迫($P<0.001$)。AsA引发后白羊草胚根线粒体SOD活性在NaCl和 Na_2SO_4 胁迫下均显著低于CK($P<0.05$)。

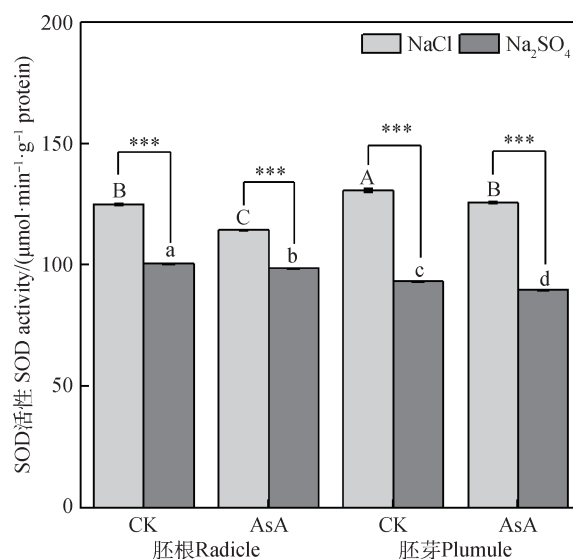


图1 AsA引发对盐胁迫下白羊草种胚线粒体SOD活性的影响

Fig. 1 Influence of AsA priming on the activities of mitochondrial SOD in the embryo of *B. ischaemum* under different salt stress

注:不同大写字母表示NaCl胁迫下不同处理的差异显著($P<0.05$),不同小写字母表示 Na_2SO_4 胁迫下不同处理的差异显著($P<0.05$)。*表示 $P<0.05$,**表示 $P<0.01$,***表示 $P<0.001$,下同
Note: Different uppercase letters indicate significant differences among treatments under NaCl stress ($P<0.05$), while different lowercase letters indicate significant differences among treatments under Na_2SO_4 stress ($P<0.05$). * indicates significant $P<0.05$, ** indicates $P<0.01$, *** indicates $P<0.001$. The same applies to the figure below

2.2 AsA引发对盐胁迫下白羊草种胚线粒体CAT活性的影响

NaCl和 Na_2SO_4 胁迫下白羊草胚根和胚芽线粒体CAT活性均无显著差异,而AsA引发后白羊草胚根线粒体CAT活性均显著高于胚芽线粒体($P<0.05$)。AsA引发前后,NaCl胁迫下白羊草胚根和胚芽线粒体中CAT酶活性均极显著高于 Na_2SO_4 胁迫($P<0.001$)。AsA引发后白羊草胚根和胚芽线粒体CAT活性均显著高于CK($P<0.05$)。

2.3 AsA引发对盐胁迫下白羊草种胚线粒体APX活性的影响

NaCl和 Na_2SO_4 胁迫下白羊草胚根线粒体APX活性均显著低于胚芽线粒体($P<0.05$);AsA引发后,NaCl胁迫下白羊草胚根线粒体APX活性显著低于胚芽线粒体($P<0.05$),而 Na_2SO_4 胁迫下其胚根

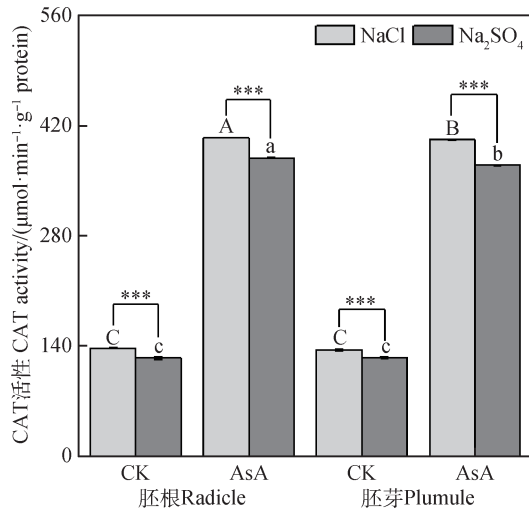


图2 AsA引发对盐胁迫下白羊草种胚线粒体CAT活性的影响

Fig. 2 Influence of AsA priming on the activities of mitochondrial CAT in the embryo of *B. ischaemum* under salt stress

线粒体APX活性与胚芽线粒体无显著差异。NaCl胁迫下白羊草胚芽线粒体APX活性极显著高于Na₂SO₄胁迫时($P < 0.01$), AsA引发后,其胚芽线粒体APX活性则在NaCl胁迫时极显著高于Na₂SO₄胁迫($P < 0.001$), AsA引发前后, Na₂SO₄胁迫下白羊草胚根线粒体APX活性极显著高于NaCl胁迫($P < 0.001$)。AsA引发后,白羊草胚根和胚芽线粒体APX活性均显著低于CK($P < 0.05$)。

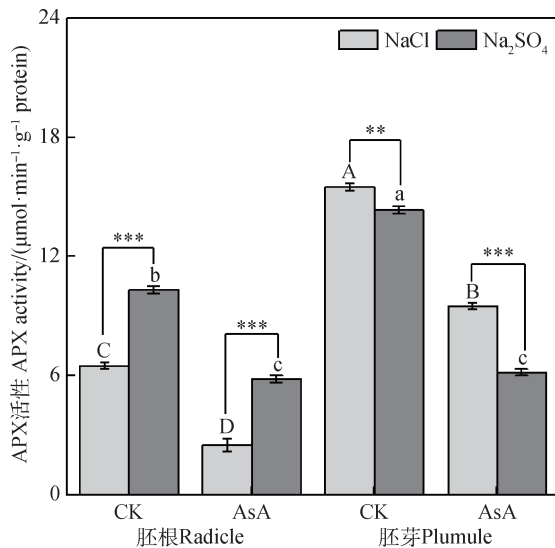


图3 AsA引发对盐胁迫下白羊草种胚线粒体APX活性的影响

Fig. 3 Influence of AsA priming on the activities of mitochondrial APX in the embryo of *B. ischaemum* under salt stress

2.4 AsA引发对盐胁迫下白羊草种胚线粒体GPX活性的影响

NaCl和Na₂SO₄胁迫下白羊草胚根线粒体GPX活性显著高于胚芽线粒体($P < 0.05$),而AsA引发后,在NaCl胁迫时白羊草胚根线粒体GPX活性显著高于胚芽线粒体($P < 0.05$),在Na₂SO₄胁迫时白羊草胚根线粒体GPX活性显著低于胚芽线粒体($P < 0.05$)。AsA引发前后,白羊草胚根线粒体GPX活性在NaCl胁迫时极显著高于Na₂SO₄胁迫时($P < 0.001$),而白羊草胚芽线粒体GPX活性则在NaCl胁迫时极显著低于Na₂SO₄胁迫时($P < 0.001$)。AsA引发后,白羊草胚根和胚芽线粒体GPX活性均显著低于CK($P < 0.05$)。

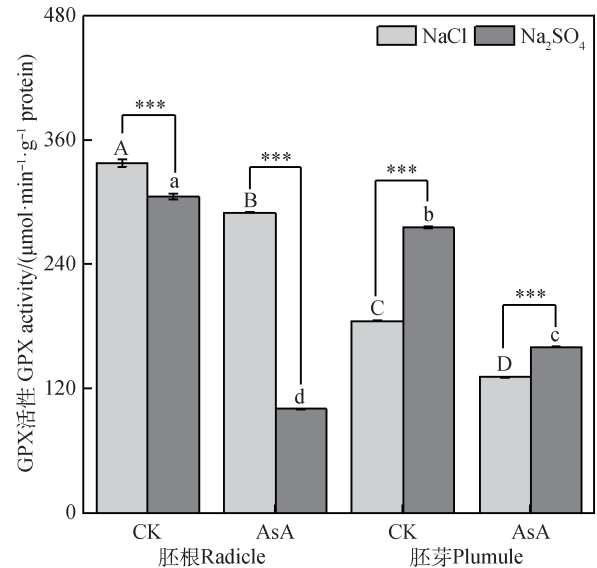


图4 AsA引发下盐胁迫对白羊草种胚线粒体GPX活性的影响

Fig. 4 Influence of AsA priming on the activities of mitochondrial GPX in the embryo of *B. ischaemum* under salt stress

2.5 AsA引发对盐胁迫下白羊草种胚线粒体GST活性的影响

NaCl和Na₂SO₄胁迫下白羊草胚根线粒体GST活性均显著高于胚芽线粒体($P < 0.05$), AsA引发后无显著差异。AsA引发前后,白羊草胚根线粒体GST活性在Na₂SO₄胁迫时极显著高于NaCl胁迫时($P < 0.01$),而其胚芽线粒体GST活性在Na₂SO₄和NaCl胁迫时无显著差异。AsA引发后,白羊草胚根和胚芽线粒体均显著高于CK($P < 0.05$)。

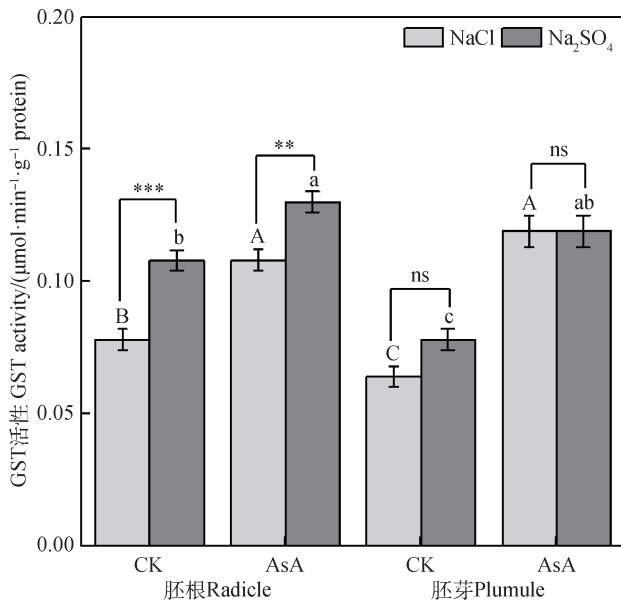


图5 AsA引发下盐胁迫对白羊草种胚线粒体GST活性的影响

Fig. 5 Influence of AsA priming on the activities of mitochondrial GST in the embryo of *B. ischaemum* under salt stress
注: ns表示无显著差异 ($P>0.05$)。下同

Note: ns indicates no significant difference ($P>0.05$). The same applies to the figure below

2.6 AsA引发对盐胁迫下白羊草种胚线粒体MDHAR活性的影响

NaCl和Na₂SO₄胁迫下白羊草胚根线粒体MDHAR活性均显著高于胚芽线粒体 ($P<0.05$), AsA引发后则在NaCl胁迫时显著高于胚芽线粒体 ($P<0.05$), 在Na₂SO₄胁迫时显著低于胚芽线粒体 ($P<0.05$)。NaCl胁迫下白羊草胚根线粒体MDHAR活性显著高于Na₂SO₄胁迫 ($P<0.05$), AsA引发后极显著高于Na₂SO₄胁迫 ($P<0.01$), 胚芽线粒体MDHAR活性在AsA引发前后均极显著低于Na₂SO₄胁迫时 ($P<0.01$)。AsA引发后, 白羊草胚根和白羊草胚芽线粒体MDHAR活性均显著高于CK ($P<0.05$)。

2.7 AsA引发对盐胁迫下白羊草种胚线粒体DHAR活性的影响

NaCl和Na₂SO₄胁迫下白羊草胚根线粒体DHAR活性均显著高于胚芽线粒体 ($P<0.05$), AsA引发后白羊草胚根线粒体DHAR活性则在NaCl胁迫下显著低于胚芽线粒体 ($P<0.05$)。Na₂SO₄胁迫下白羊草胚根和胚芽线粒体DHAR活性均极显著高于NaCl胁迫 ($P<0.001$); AsA引发后, 白羊草胚根线粒体DHAR活性在

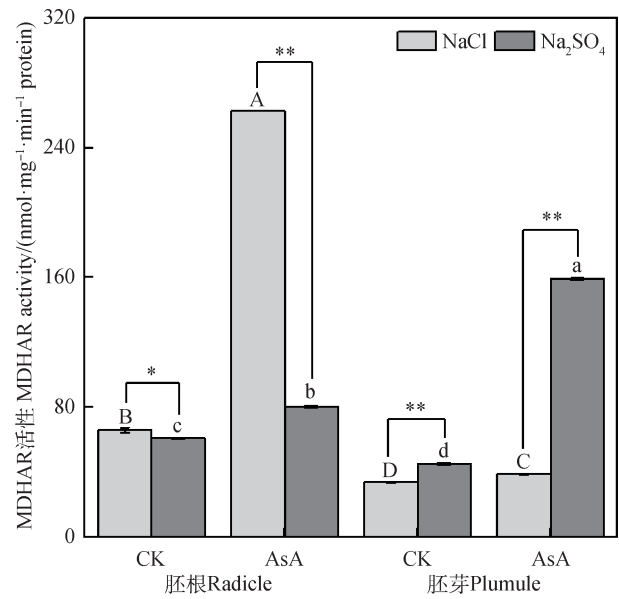


图6 AsA引发下盐胁迫对白羊草种胚线粒体MDHAR活性的影响

Fig. 6 Influence of AsA priming on the activities of mitochondrial MDHAR in the embryo of *B. ischaemum* under salt stress

Na₂SO₄胁迫下极显著高于NaCl胁迫时 ($P<0.001$), 其胚芽线粒体DHAR活性在NaCl胁迫下极显著高于Na₂SO₄胁迫 ($P<0.001$)。AsA引发后, 白羊草胚根线粒体DHAR活性均显著高于CK ($P<0.05$)。

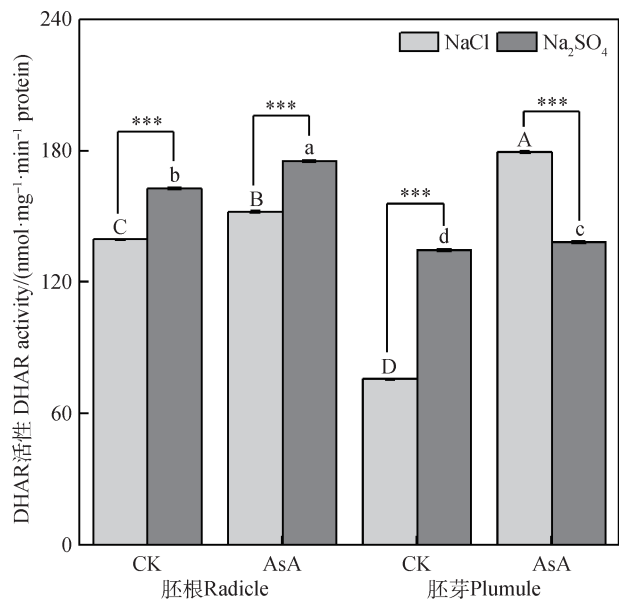


图7 AsA引发下盐胁迫对白羊草种胚线粒体DHAR活性的影响

Fig. 7 Influence of AsA priming on the activities of mitochondrial DHAR in the embryo of *B. ischaemum* under salt stress

2.8 AsA 引发对盐胁迫下白羊草种胚线粒体 MDA 含量的影响

NaCl 和 Na₂SO₄ 胁迫下白羊草胚根与胚芽线粒体 MDA 含量无显著差异;AsA 引发后,白羊草胚根线粒体 MDA 含量在 Na₂SO₄ 胁迫下显著高于胚芽线粒体 ($P<0.05$)。盐胁迫下,白羊草胚根和胚芽线粒体 MDA 含量在 NaCl 和 Na₂SO₄ 胁迫间无显著差异,AsA 引发后,白羊草胚根线粒体 MDA 含量在 NaCl 和 Na₂SO₄ 胁迫间无显著差异,白羊草胚芽线粒体 MDA 含量在 NaCl 胁迫下极显著高于 Na₂SO₄ 胁迫 ($P<0.01$)。AsA 引发后白羊草胚根和胚芽线粒体均显著低于 CK ($P<0.05$)。

2.9 AsA 引发对盐胁迫下白羊草种胚线粒体 H₂O₂ 含量的影响

NaCl 和 Na₂SO₄ 胁迫下白羊草胚根线粒体 H₂O₂ 含量均显著高于胚芽线粒体 ($P<0.05$);AsA 引发后,白羊草胚根线粒体 H₂O₂ 含量均显著低于胚芽线粒体 ($P<0.05$)。NaCl 胁迫下白羊草胚根和胚芽线粒体 H₂O₂ 含量均极显著高于 Na₂SO₄ 胁迫 ($P<0.01$),AsA 引发后则在 NaCl 胁迫下极显著低于 Na₂SO₄ 胁迫 ($P<0.01$)。AsA 引发后,白羊草胚根和胚芽线粒体 H₂O₂ 含量均显著低于 CK ($P<0.05$)。

2.10 隶属函数分析

隶属函数综合评价值越高,耐盐性越强。NaCl 胁迫下白羊草胚根线粒体耐盐性最弱,经 AsA 引发后,其耐盐性显著增强且在所有处理中最优(表 1)。盐胁迫下,APX 和 GPX 为白羊草种胚线粒体耐盐性关键酶,AsA 引发后,CAT,GST,MDHAR 和 DHAR 为白羊草耐盐性关键酶。AsA 引发对 NaCl 胁迫下白羊草胚根线粒体的抗氧化酶活性提升效果最好。

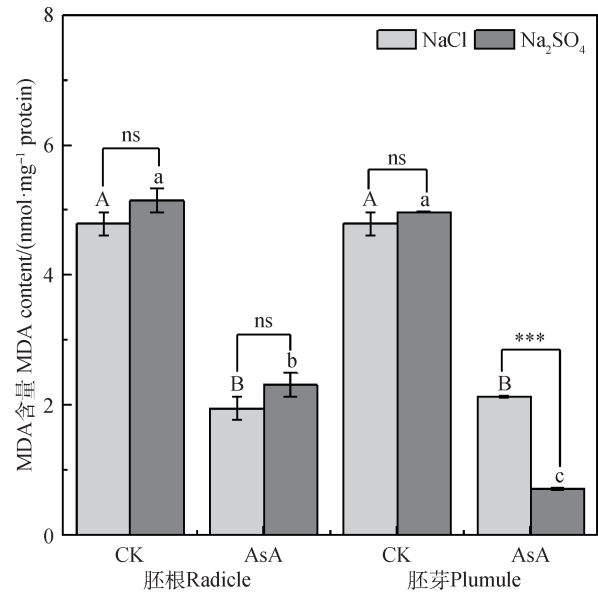


图 8 AsA 引发下盐胁迫对白羊草种胚线粒体 MDA 含量的影响

Fig. 8 Influence of AsA priming on the contents of mitochondrial MDA in the embryo of *B. ischaemum* under salt stress

表 1 AsA 引发对盐胁迫下白羊草种胚线粒体抗氧化酶活性和脂质过氧化水平隶属函数分析

Table 1 The analysis of the membership function in the activities of antioxidant enzymes and lipid peroxidation level in mitochondria of *B. ischaemum* seeds primed with AsA under salt stress

处理 Treatment												综合评价值	抗性排名	隶属度最高指标
盐胁迫 Saline stress	处理 Treatment	SOD	CAT	APX	GPX	GST	MDHAR	DHAR	MDA	H ₂ O ₂	Comprehensive score	Resistance ranking	Highest degree of membership	
NaCl	胚根 Radicle	CK	0.83	0.04	0.93	1.00	0.00	0.13	0.00	0.09	0.01	0.30	6	GPX
		AsA 引发 priming	0.63	1.00	0.00	0.60	0.80	1.00	0.48	0.86	1.00	0.81	1	CAT ,MDHAR
	胚芽 Plumule	CK	0.81	0.03	1.00	0.52	0.24	0.00	0.22	0.03	0.09	0.25	8	APX
		AsA 引发 priming	0.77	0.99	0.51	0.09	1.00	0.04	1.00	0.82	0.90	0.69	3	DHAR,GST
Na ₂ SO ₄	胚根 Radicle	CK	0.25	0.00	0.55	0.83	0.79	0.10	0.51	0.00	0.02	0.32	5	GPX
		AsA 引发 priming	0.25	0.93	0.23	0.00	0.93	0.18	0.54	0.80	0.99	0.73	2	CAT ,GST
	胚芽 Plumule	CK	0.21	0.01	0.51	0.52	0.24	0.49	0.22	0.05	0.43	0.28	7	GPX
		AsA 引发 priming	0.20	0.89	0.27	0.19	0.79	0.92	0.56	1.00	0.80	0.65	4	MDHAR

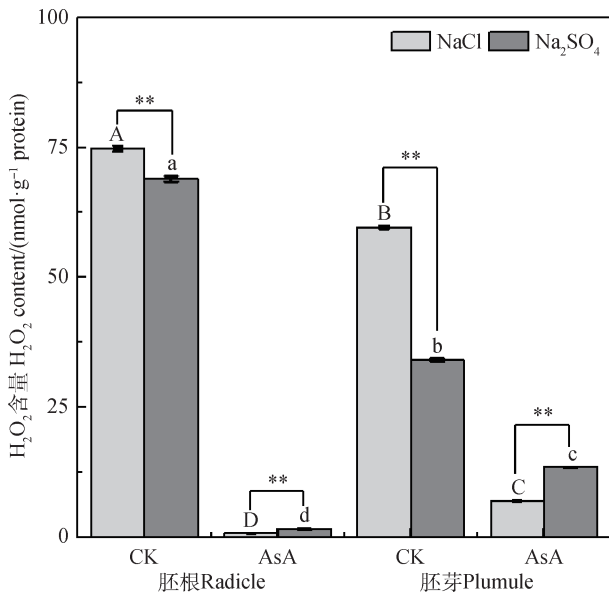


图9 AsA引发下盐胁迫对白羊草种胚线粒体H₂O₂含量的影响

Fig. 9 Influence of AsA priming on the contents of mitochondrial H₂O₂ in the embryo of *B. ischaemum* under salt stress

3 讨论

AsA-GSH循环是植物线粒体清除ROS维持自身氧化还原平衡的核心系统,线粒体遭受脂质过氧化应激时,该循环内关键酶会被激活启动防御,而AsA在增强植物体内AsA-GSH循环抗氧化酶活性及清除ROS方面至关重要^[26-27]。试验中,AsA引发后白羊草种胚线粒体中CAT,GST,DHAR和MDHAR活性显著提高($P<0.05$),MDA和H₂O₂含量显著下降($P<0.05$),说明AsA引发增强了白羊草种胚线粒体AsA-GSH循环的抗氧化性能,减轻了盐胁迫对白羊草种胚线粒体的脂质过氧化损伤,这与燕麦^[28]和高粱^[13]中研究结论相似,可能是AsA引发直接激活并强化了MDHAR和DHAR介导的AsA再生通路,促进线粒体AsA-GSH循环高效运转,进而提升CAT的酶促活性和GST的解毒与抗氧化能力,以协同缓解盐胁迫对线粒体膜结构的破坏^[29]。然而,SOD,APX和GPX活性却在AsA引发后显著下降($P<0.05$),这可能因AsA引发提高了种胚线粒体的抗氧化储备,有效减轻了膜脂过氧化程度,从而减少了超氧阴离子的产生速率;同时,AsA-GSH循环中AsA的充足供给减轻了种胚线粒体对盐胁迫氧化应激,导致氧化损伤程度减轻,降低了对SOD,APX及GPX的胁迫诱导需求^[30-31]。此外,张杰敏等^[32]在对盐胁迫下燕麦幼苗

线粒体的研究中发现SOD和GPX活性随AsA引发浓度的升高而降低,因而也可能是AsA引发浓度的调控效应造成SOD,APX和GPX活性下降。

试验中,AsA引发前后,NaCl胁迫下白羊草胚根和胚芽线粒体SOD,CAT,GPX活性均极显著高于Na₂SO₄胁迫($P<0.001$),Na₂SO₄胁迫下胚根线粒体GST,APX和DHAR活性以及胚芽线粒体GST和MDHAR活性高于NaCl胁迫,表明不同盐种类对白羊草种胚线粒体的损伤机制和AsA-GSH循环关键酶的影响存在差异,这与偃麦草(*Elytrigia repens*)^[33]的研究结果相似,这可能因Cl⁻与SO₄²⁻理化特性和生理功能不同,从而引发循环差异动态调控,Cl⁻因半径小易渗入线粒体,从而诱发ROS过量生成,进而诱导SOD活性上调,催化持续生成的超氧阴离子转化为H₂O₂,而H₂O₂过量积累进一步上调CAT,GPX活性,以清除线粒体内多余的H₂O₂,维持内部H₂O₂的动态平衡^[14,34];而SO₄²⁻半径大不易进入线粒体,对线粒体造成的直接氧化胁迫较弱,还可作为硫源促进GSH合成,为AsA-GSH循环提供充足还原底物,提高循环中AsA再生,GSH结合相关酶活性,保障相应酶促反应高效进行,进一步维持循环稳态^[35]。

种子萌发过程中胚根较胚芽更先受到盐胁迫,往往发挥着更关键的抵御作用^[14]。试验中白羊草胚根线粒体CAT,GPX,GST,DHAR和MDHAR活性,隶属函数综合评价值及抗逆性排名均高于胚芽线粒体,这可能因种子萌发过程中胚根较胚芽更早接触盐胁迫,感知胁迫信号,导致线粒体积累的ROS更多,为抵御盐胁迫伤害、清除过量ROS,胚根线粒体的抗氧化酶活性持续维持在较高水平,形成更强的抗氧化防御能力,从而抗逆性高于胚芽线粒体^[15],这与李尹琳等^[14]提出的白羊草幼苗胚根线粒体对盐胁迫响应较胚芽要更敏感的结论相似。

4 结论

AsA引发可显著提升盐胁迫下白羊草种胚线粒体AsA-GSH循环CAT,GST,DHAR和MDHAR活性($P<0.05$),降低MDA和H₂O₂含量,且对NaCl胁迫下胚根线粒体的调控效果最优。NaCl与Na₂SO₄胁迫对白羊草种胚线粒体AsA-GSH循环关键酶活性影响存在差异,胚根线粒体抗氧化酶活性、隶属函数综合评价值及抗逆性均显著

高于胚芽线粒体($P < 0.05$)。盐胁迫下, APX, GPX 为白羊草种胚线粒体耐盐的关键酶, 而 AsA 引发后则以 CAT, MDHAR 和 DHAR 为其耐盐的关键酶, AsA 引发可有效促进白羊草种胚线粒体 AsA-GSH 循环, 提升白羊草种胚线粒体对盐胁迫的耐受性。

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