

苹果砧木富平楸子×R3 杂交后代耐盐性评价

矫彩娣, 魏江彤, 贾旭梅, 李翠英, 李超*, 马锋旺*

(西北农林科技大学园艺学院·作物抗逆与高效生产全国重点实验室·陕西省苹果重点实验室, 陕西杨凌 712100)

摘要:【目的】评价2份苹果砧木富平楸子×R3砧木杂交后代的耐盐性,以富平楸子、M9-T337和M26砧木为对照,综合分析2个砧木株系的耐盐能力,为苹果砧木抗性育种提供参考。【方法】以富平楸子×R3砧木杂交后代k15和m2及苹果砧木富平楸子、M9-T337和M26无性繁殖的组培苗为试验材料,采用水培的方式,进行盐胁迫处理,通过测定生长量、生理指标、光合参数、抗氧化酶活性、元素及氨基酸含量等相关指标,并利用隶属函数法综合分析5种砧木资源的耐盐性。【结果】在150 mmol·L⁻¹盐胁迫下,5种砧木资源对照组生长正常,处理组叶片均出现不同程度的萎蔫和坏死,其中M26的叶片表型出现最早且最为严重,k15和富平楸子的叶片损伤程度最小;在盐胁迫第15天时,处理组净光合速率、叶绿素含量和根系活力显著降低,相对电导率、丙二醛含量和Na⁺/K⁺显著提高,超氧化物歧化酶、过氧化物酶和过氧化氢酶活性也显著增强,脯氨酸(Pro)、酪氨酸(Tyr)和苯丙氨酸(Phe)3种氨基酸含量显著上升,甘氨酸(Gly)、亮氨酸(Leu)和天冬氨酸(Asp)含量显著下降。【结论】5份砧木资源的耐盐性依次为:k15 > 富平楸子 > M9-T337 > m2 > M26。其中富平楸子×R3砧木杂交后代k15耐盐能力最强,甚至优于其抗盐性强的亲本富平楸子及生产中最常用的矮化砧木M9-T337;富平楸子×R3砧木杂交后代m2耐盐能力表现较差,但强于矮化砧木M26。

关键词: 苹果; 苹果砧木; 盐胁迫; 耐盐性评价; 隶属函数

中图分类号: S661.1

文献标志码: A

文章编号: 1009-9980(2025)05-0917-16

Evaluation of salt tolerance in hybrid progeny of apple rootstock *Malus prunifolia* × R3

JIAO Caidi, WEI Jiangtong, JIA Xumei, LI Cuiying, LI Chao*, MA Fengwang*

(College of Horticulture, Northwest A & F University/State Key Laboratory for Crop Stress Resistance and High-Efficiency Production/Shaanxi Key Laboratory of Apple, Yangling 712100, Shaanxi, China)

Abstract: 【Objective】With the influence of global climate change and human production activities, the scope of soil salinization in China is expanding. Soil salinization creates problems in apple growth and fruit yield and quality formation and has become one of the important factors restricting the development of apple industry in China. In the actual production of apples, the salt tolerance of seedlings is weak, and rootstocks can provide salt-tolerant roots for apples. The quality of rootstocks directly affects the absorption of nutrients and the adaptability of fruit trees to adversities. Therefore, rootstocks are the main determinant of salt tolerance in grafted plants. China's apple production model used to be arborization cultivation. With the continuous advancement of technology, arborization cultivation has exposed many problems and has gradually been replaced by dwarfing and dense planting. However, most of the common dwarfing rootstocks commercially available are introduced from abroad. Due to the climatic limitations of the birthplace, there are certain limitations in introducing them into domestic production, such as poor adaptability and weak stress resistance. Therefore, it is urgent to breed excellent dwarfing rootstock varieties in China. In this study, the salt tolerance of the hybrid offspring of *Malus prunifolia* × R3 was evaluated and its salt tolerance was comprehensively analyzed. The study will provide valuable

收稿日期: 2024-12-05

接受日期: 2025-02-03

基金项目: 国家苹果产业技术体系(CARS-27); 西北农林科技大学教育发展基金会公益项目(ZJ2023020)

作者简介: 矫彩娣, 女, 在读硕士研究生, 研究方向为果树栽培与生理。E-mail: 1572586368@qq.com

*通信作者 Author for correspondence. E-mail: cl8609@nwfau.edu.cn; E-mail: fwm64@nwsuaf.edu.cn

reference for the breeding of dwarf rootstocks with strong salt tolerance. 【Methods】 In this study, tissue cultured seedlings of five asexual reproduced rootstock materials were used. They were k15 and m2, which were selected from the hybrid offsprings of apple rootstock *Malus prunifolia* × R3 by drought resistance, *M. prunifolia*, M9-T337 and M26. The seedlings were transferred to the rooting medium for growth for 40 days, and transplanted into an 8 × 8 cm² nutrient pot after hardening seedlings, and potted plants were placed in incubator with a constant temperature and light condition. After the seedlings grew about 7-8 fully expanded true leaves, they were moved to a hydroponic pot containing 6.5 L of 1/2 concentration of Hoagland nutrient solution, and the nutrient solution was refreshed every 3 days. After one week of pre-adaptation, the even-sized healthy plants were selected for hydroponic salt treatment. The treatment was divided into two groups: (1) Control (CK), with 1/2 Hoagland nutrient solution; (2) Salt treatment (ST), with 150 mmol · L⁻¹ NaCl added in the nutrition solution. Nutrient solution was refreshed every 3 days over a period of 15 days. During the treatment, the photosynthetic rate was measured every 3 days. At the end of the treatment, 10 plants of each strain in the control group and the treatment group were taken to determine the plant height, leaf number, dry and fresh weight. Membrane leakage, chlorophyll, chlorophyll fluorescence, of fresh functional leaves were measured and NBT and DAB staining was observed. Fresh roots were taken to determine root activity and analyze root architecture. The fully mature leaf samples were wrapped in tin paper, immediately frozen in liquid nitrogen and stored at -80 °C. The contents of MDA, H₂O₂, O₂⁻, activities of antioxidant enzymes and amino acid content in each strain were determined. The contents of Na⁺ and K⁺ in roots, stems and leaves were determined with dry samples after dry weight determination. 【Results】 In the control group, there was no significant difference between the five rootstocks through the phenotype. In the salt treatment group, the phenotype of M26 appeared earliest, with severe wilting and necrosis of the leaves on the 9th day, followed by the m2 with brown spots of the leaves on the 10th day. Subsequently, on the 12th day of treatment, salt stress phenotype appeared in *Malus prunifolia*, k15, and M9-T337. The roots of the salt treatment group were brown, and the root area decreased compared with the control group. Compared with the control group, plant height and leaf number in each strain of the treatment group decreased, and the dry and fresh weights in the treatment group were significantly reduced. Membrane leakage and MDA content in each strain in the salt treatment group increased, while root activity decreased. Results of the NBT and DAB staining and O₂⁻ and H₂O₂ determination suggested that each strain under salt treatment accumulated a certain amount of reactive oxygen species. Activities of SOD, POD and CAT in each strain under salt treatment increased. At day 3 of salt stress treatment, P_n , T_n , G_s and C_i in each strain were decreased significantly by salt treatment. Total chlorophyll content in all strains in the salt stress group decreased, among which *M. prunifolia* had the smallest decrease and M26 had the largest decrease. F_v/F_m value in k15, *M. prunifolia* and M9-T337 decreased less than the other two lines after salt treatment, suggesting smaller degree of photosystem damage in the former two strains. Compared with the control group, the Na⁺ content in roots, stems and leaves of M26 had the highest increase, and the increase was relatively small in *M. prunifolia* and k15; the K⁺ content in each part showed different degrees of decrease after salt treatment. Among the strains, M26 had the largest decrease, while *M. prunifolia* and k15 had the smallest change. Salt stress significantly increased Na⁺/K⁺ ratio in each strain, and the increase in *M. prunifolia* and k15 was relatively small. The contents of Pro, Tyr and Phe increased significantly after salt treatment, while the contents of Gly, Leu and Asp decreased. By comprehensive analysis of growth, photosynthetic parameters, antioxidant enzyme activities, mineral element and amino acid contents and other 16 related indicators, the average membership function value of each strain

was calculated. The results showed that the average membership function value of k15 was the highest, indicating that k15 was least affected by salt stress, indicating its salt tolerance was the strongest among the five apple strains. The average membership function value of M26 was the lowest, indicating that its salt tolerance was the weakest. 【Conclusion】 The results showed that k15 showed strongest salt tolerance among the five strains and M26 had the poorest salt tolerance. Under salt stress, plant growth, root area, root activity and dry and fresh weights decreased. Membrane leakage and MDA content increased, with the accumulation of reactive oxygen species and the increase of antioxidant enzyme activities. Under salt stress, photosynthesis was significantly inhibited with decrease in chlorophylls, while Na^+ content increased significantly, K^+ content decreased, causing Na^+/K^+ imbalance; the contents of Pro, Tyr and Phe increased significantly, while the contents of Gly, Leu and Asp decreased. However, due to the differences in resistance among strains, the range of changes in different indicators differed. Through the comprehensive analysis of membership function, the order of salt tolerance of the 5 strains was: $\text{k15} > M. \text{prunifolia} > \text{M9-T337} > \text{m2} > \text{M26}$. Therefore, the hybrid k15 of *M. prunifolia* × R3 has strong salt tolerance and is expected to become a new high-quality rootstock resource.

Key words: Apple; Apple stock; Salt stress; Salt tolerance evaluation; Membership function

近年来,受全球气候变化和人类生产活动的影响,我国土壤盐渍化范围不断扩大,而苹果适宜的生长环境是弱酸性或中性土壤,土壤盐渍化使苹果的生长和果实产量及品质都面临着诸多挑战,影响我国苹果产业的健康发展,这已成为限制苹果产业发展的重要因素之一^[1]。盐胁迫主要通过引起渗透胁迫、离子毒害和氧化胁迫等方式影响植物的生长和发育^[2]。遭受盐害的植株生长减缓,叶绿体结构遭到破坏,叶尖、叶缘或叶脉变黄并逐渐萎蔫脱落,主根变短,须根减少,若植物长期受到高浓度盐胁迫,植物的根系结构也会被破坏,导致根系无法正常从外界吸收营养物质,造成植株发黄腐烂、停止生长甚至死亡^[3]。此外,在盐胁迫下植物体内产生的氧化胁迫导致光合速率下降,影响植物蒸腾作用,从而影响植物水分和营养物质的运输^[4]。同时盐胁迫还会使植株遭受渗透、水分和氧化胁迫,甚至会由于调节失衡而产生离子毒害,影响植株对其他营养物质的吸收,导致营养失衡^[5]。受到盐胁迫的植物细胞内的 Na^+ 和 Cl^- 积累过量,会造成活性氧的产生与清除之间的动态平衡失衡,引起脂质过氧化和脱脂作用,伤害膜蛋白和膜脂,从而破坏膜结构^[6]。随着盐胁迫的加重,植物的生长量、干鲜质量、光合能力、碳水化合物含量和叶绿素含量等都呈现降低趋势。已有研究证实,提高植物抗氧化系统酶活性及提升抗氧化代谢水平是提高植物耐盐能力的途径之一^[7]。植物受到盐胁迫时会产生和积累渗透调节物质保证机

体渗透平衡和内部稳定,包括游离氨基酸、可溶性糖等。其中游离氨基酸脯氨酸是关键渗透调节物质之一,在植物响应逆境胁迫中起重要作用。研究表明,盐胁迫下植物体内脯氨酸含量有所增加,且外源施加脯氨酸能够改变植物的耐盐能力^[8]。

苹果实生苗的耐盐性较弱,而砧木可以为苹果提供根系,砧木品质直接影响果树对养分的吸收及对逆境的适应能力,因此砧木是不同砧穗组合耐盐能力的主要决定因素^[9]。在同一盐浓度下,当砧木的相对生长量与盐害指数成反比时,砧木的耐盐能力就越强,并且同一砧木嫁接不同品种后的耐盐能力基本一致^[10]。因此在生产实践中,通常通过嫁接耐盐性较高的砧木来增强整株的耐盐性。有研究报道,柑橘不同砧木间以及嫁接接穗后树体养分吸收及抗逆性均存在较大差异^[11]。过去,我国苹果生产常用由原产地自然条件下形成的乔化砧木,其对气候和土壤适应能力强,抗性强,寿命长,如山定子、海棠和富平楸子等^[12-13]。但由于乔化栽培存在树体骨架大,成形慢,整形修剪技术复杂,操作难度大等生产局限,逐渐被矮化密植所替代^[14]。近年来利用从国外引进的M9-T337、B9和Pajam2等矮化自根砧栽培模式在各苹果主产区逐步推广^[15],该模式相较于过去国内常用的乔化砧、矮化中间砧栽培模式,具有矮化效果显著、苗木整齐度高、节省劳动力及早果丰产性好等显著优势^[16],然而多数引进的矮化砧木源于气候相对较为

温和、土壤肥沃的西欧平原,所以并不具备很强的耐逆境胁迫等特性,从国外引进的砧木在国内的适应能力有待考查^[17]。有研究表明,国内外常用的矮化砧木M9嫁接亲和力高、对土壤适应能力强,但抗旱、抗寒性较差,在我国许多苹果栽培地区容易抽条^[18];砧木JM系矮化效果明显,适应性广,但繁殖速度慢,对自然灾害抵抗力弱,且很难通过扦插繁殖^[19-20];生产中常用的G系矮化砧木早实丰产性好、抗重茬,但根系较浅,抗逆性较差,在再植条件下树势衰弱明显^[21]。

笔者所在的苹果抗逆与品质改良创新团队前期得到了多株以富平楸子与R3(美国康奈尔大学和Geneva试验站选育的矮化砧木,亲本为M27×Robusta 5,树体生长表现良好,适应性较强^[22])为亲本的杂交1年生盆栽幼苗,经过干旱胁迫处理,从中筛选出抗旱和干旱敏感株系k15和m2^[23],分别建立外植体,并选择适宜的继代及生根培养基,成功扩繁出了两个砧木株系。为进一步探索其综合抗性,笔者以此砧木株系(k15和m2)、生产中应用广泛的砧木(M9-T337和M26)及其亲本(富平楸子)5种砧木资源为试验材料,对其耐盐性进行研究,分别测定了处理结束时的植株生长指标、生理指标、光合相关指标、Na⁺和K⁺含量、抗氧化酶活性及氨基酸含量,并利用隶属函数法对5种砧木资源耐盐能力进行综合评价,以期选育出适合我国土壤和环境的综合抗逆性较强的苹果矮化砧木。

1 材料和方法

1.1 材料

以苹果砧木富平楸子×R3的杂交后代经抗性筛选出的砧木株系k15、m2、亲本富平楸子及生产上应用广泛的砧木M9-T337和M26,5种无性繁殖的组培苗为试验材料。

1.2 方法

本试验盐胁迫处理在西北农林科技大学苹果抗逆与品质改良创新团队土肥楼水培室内进行。将上述材料扩繁至足够数量后,移至生根培养基中生长40 d,经开盖炼苗后移栽到8 cm×8 cm的营养钵中,钵内装有($V_{\text{基质}}:V_{\text{蛭石}}:V_{\text{珍珠岩}}=4:1:1$)的混合物,置于恒温光照培养箱中。待幼苗长出7~8片完全展开的真叶后,将其移至装有6.5 L 1/2浓度Hoagland营养液的水培盆中,每3 d换一次营养液。经过1周的预

适应,选取大小一致且健康的植株进行水培盐处理。处理分为两组:(1)对照(CK),1/2 Hoagland营养液;(2)盐处理(ST),NaCl浓度为150 mmol·L⁻¹。两组的pH均用H₃PO₄调至为6.5±0.2。每3 d更换1次营养液,处理时间为15 d。处理结束时,分别取鲜样、冻样和干样,用于指标测定。

1.3 生长指标测定

株高的测定:处理结束时,对照组和处理组分别取5株植株,用直尺测定株高(从根茎连接处到植株顶芽的距离)。

叶片数的测定:准确查数并记录叶片数。

干鲜质量的测定:将植株分为根、茎、叶三部分,用清水洗净并擦干,用万分之一天平测定各部分鲜质量,放入烘箱105℃杀青30 min,然后转至65℃下烘干至恒质量,再用万分之一天平测定各部分干质量。

1.4 生理指标测定

根系构型:处理结束时,将植株根部洗净并擦干,利用WinRHIZO根系扫描仪分析植株根部构型。

相对电导率测定:取相同部位新鲜功能叶,用打孔器在叶片上打10个圆片,注意避开叶脉,装入放有10 mL纯净水的15 mL离心管中,浸泡4 h,其间不断震荡混匀,利用电导率仪测量电导率,记为S₁,而后沸水浴20 min,冷却至室温后震荡混匀,再次测量电导率,记为S₂,测量纯净水的电导率,记为S₀,计算叶片相对电导率,公式如下:相对电导率(REL)/%=(S₁-S₀)/(S₂-S₀)×100。

丙二醛(MDA)含量测定:按照生产厂家说明书(苏州科铭生物技术有限公司,江苏苏州),利用MDA检测试剂盒进行测定。

根系活力测定:处理结束时,取植株新鲜白根,按照生产厂家说明书(苏州科铭生物技术有限公司,江苏苏州)测定反映根系活力的脱氢酶(DHA)活性。

1.5 光合相关指标测定

光合参数测定:分别在处理的第0天、第3天、第6天、第9天和第12天利用CIRAS-3便携式光合系统仪(CIRAS, amesbury, MA, USA),测定同一位置功能叶片的净光合速率P_n、蒸腾速率T_r、气孔导度G_s和胞间CO₂浓度C_i。

叶绿素含量测定:处理结束时,取新鲜叶片洗净擦干后,用剪刀将其剪成细丝状(避开叶脉),称取0.1 g置于准备好的8 mL 80%丙酮中,暗处理24 h,

其间不断震荡,使样品充分接触丙酮。待叶片组织完全脱色变白,吸取 1 mL 于比色皿,利用 UV-2600 分光光度计,测定 663 nm、645 nm 和 470 nm 波长下的吸光值^[24]。

叶绿素荧光参数测定:处理结束时,取新鲜功能叶,暗处理 30 min,利用叶绿素荧光成像系统,测定荧光参数并拍摄荧光图片。

1.6 活性氧及抗氧化酶活性测定

活性氧积累:处理结束时,取新鲜叶片进行 NBT、DAB 化学染色,观察 H₂O₂ 和 O₂ 积累情况,并利用 H₂O₂ 和 O₂ 检测试剂盒(苏州格锐思生物科技有限公司,江苏苏州)分别测定叶片组织中 H₂O₂ 和 O₂ 含量。

抗氧化酶活性测定:将处理结束时存好的叶片冻样研磨,称取 0.1 g,利用相应试剂盒(苏州格锐思生物科技有限公司,江苏苏州)分别测定超氧化物歧化酶(SOD)、过氧化物酶(POD)和过氧化氢酶(CAT)活性。

1.7 Na⁺、K⁺含量测定

将处理结束时存好的根茎叶干样研磨过筛,称取 0.1 g 于消解管中,加入硝酸,利用微波消解炉充分消化后,去离子水定容至 50 mL,利用 M410 火焰光度计测定 Na⁺、K⁺ 含量。

1.8 氨基酸含量测定

将处理结束时的叶片冻样研磨,称取 0.1 g,浸泡于 1 mL 50% 的乙醇中,4 °C 摇匀,离心机设置为 12 000 r·min⁻¹,时间 10 min,过滤杂质,取上清液,用甲醇稀释,并保存在样品瓶中。使用高效液相色谱(HPLS-MS)系统测定氨基酸含量,色谱柱为 Inertsil

ODS-4 C18(4.6 mm × 250 mm, 5 μm),流速设定为 0.3 mL·min⁻¹。洗脱溶剂体系为含有 0.1% 甲酸的超纯水(A)和乙腈(B)^[6]。

1.9 隶属函数的综合分析

考虑到本试验的试验材料遗传背景存在差异,各项指标存在较大差异,故利用对照组和盐胁迫组各项指标的相对变化率进行隶属函数的计算,以评价其耐盐能力。

若该指标与耐盐能力呈正相关,该指标的隶属函数计算公式为: $U(X)=(X-X_{\min})/(X_{\max}-X_{\min})$;若该指标与耐盐能力呈负相关,该指标的隶属函数计算公式为: $U(X)=1-(X-X_{\min})/(X_{\max}-X_{\min})$ 。式中, $U(X)$ 为隶属函数值, X 指某一指标的相对变化率 $[(S_{\text{ST}}-S_{\text{CK}})/S_{\text{CK}} \times 100]$; $X_{\max}$ 指某一指标相对变化率的最大值, $X_{\min}$ 指某一指标相对变化率的最小值。在笔者测定的指标中,与耐盐能力负相关的指标有相对电导率、MDA 含量、过氧化氢含量和 Na⁺/K⁺,其余指标与耐盐能力均呈正相关。

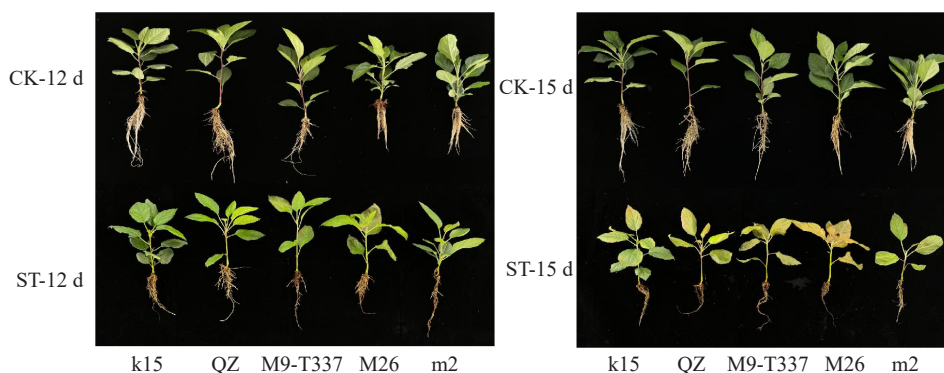
1.10 数据分析

使用 SPSS 26.0 进行数据的统计分析,并使用单因素分析和 Tukey 的多重比较($p < 0.05$)进行差异显著性分析;利用 Origin 2021 绘图。

2 结果与分析

2.1 盐胁迫下植株表型及生长指标分析

由图 1 可知,处理结束时,对照组无明显差异;盐处理组胁迫表型出现的时间存在一定差异,M26 表型出现最早,第 9 天时叶片便出现严重的萎蔫和坏死,其次是 m2 叶片在第 10 天出现褐斑,而后富平



QZ 表示富平楸子。CK-12 d 表示对照处理 12 d, CK-15 d 表示对照处理 15 d, ST-12 d 表示盐处理 12 d, ST-15 d 表示盐处理 15 d。下同。
QZ means *Malus prunifolia*, CK-12 d denotes the control for 12 d, CK-15 d denotes the control for 15 d, ST-12 d denotes the salt treatment for 12 d, and ST-15 d denotes the salt treatment for 15 d. The same below.

图 1 盐胁迫下各株系表型图

Fig. 1 Phenotypic of each strain under salt stress

楸子、k15和M9-T337在处理的第12天陆续出现盐胁迫表型,但处理结束时富平楸子和k15只是上部叶片出现明显褐斑,而M9-T337叶片已出现大面积坏死,植株萎蔫。

从干鲜质量上看,与对照组相比,处理组各株系均明显降低,其中k15降幅最小,干鲜质量分别下降43.14%和22.87%;M26降幅最大,分别显著降低71.11%和52.27%(图2-a~b)。

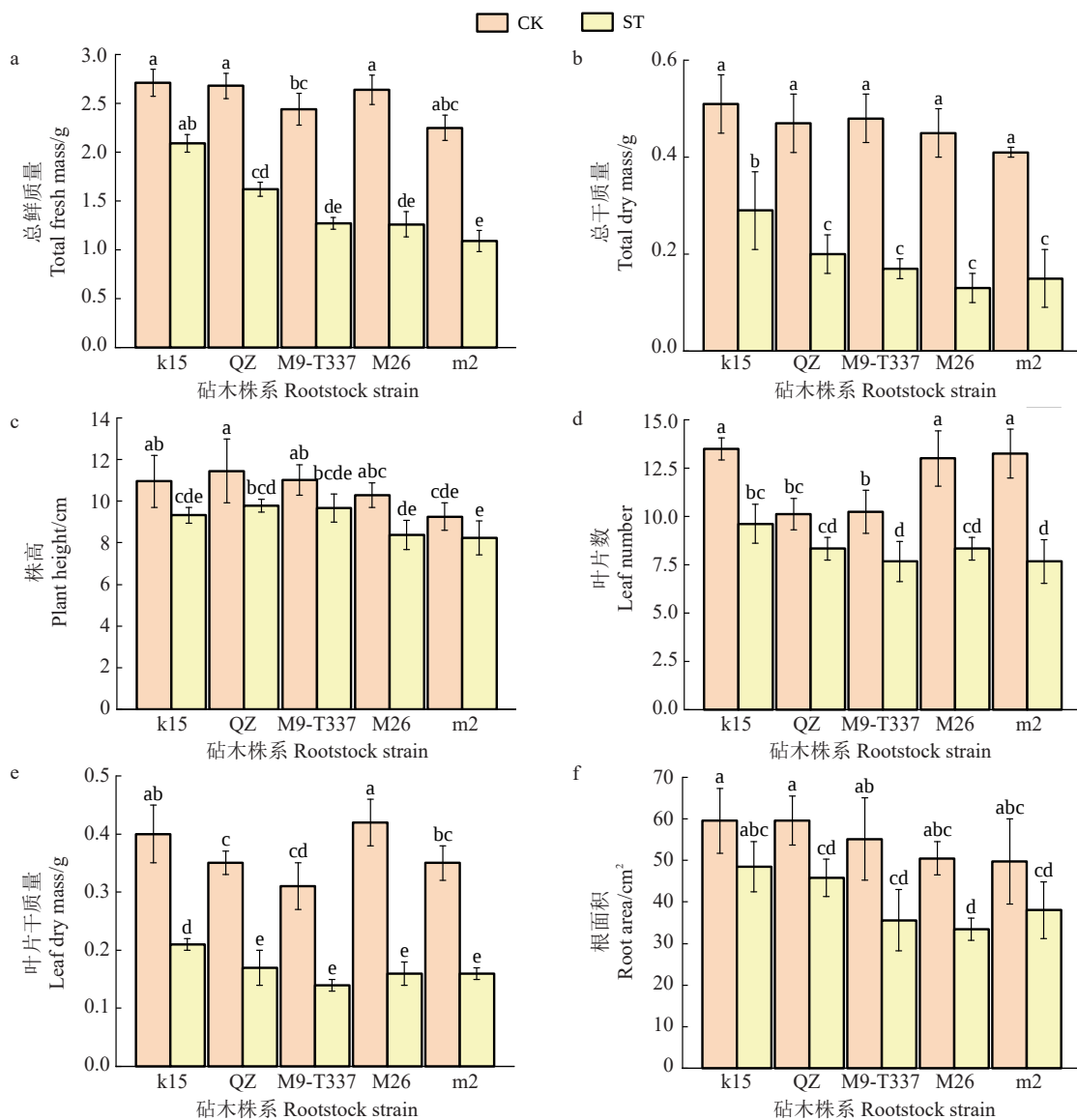
从株高、叶片数上看,与对照组相比,处理组各株系均有所下降(图2-c~d)。但值得注意的是,k15和m2相对来说节间较短(株高一定的情况下,叶片

数相对较多),说明两个砧木株系自身存在一定的矮化现象。

从根部状态看,盐处理组根系均呈褐色,但k15根系明显更密,根面积下降幅度最小,仅下降18.6%,M9-T337根面积减少幅度最大,为31.6%(图2-f)。

2.2 盐胁迫下植株生理指标分析

通过比较相对电导率、MDA含量以及根系活力,发现与对照组相比,盐处理组各株系相对电导率和MDA含量显著上升,根系活力显著降低。其中,相比于对照组,处理组k15的相对电导率上升幅度



CK 表示对照组,ST 表示盐处理组。不同字母表示各株系间存在显著差异($p < 0.05$)。下同。

CK denotes the control group, ST denotes the salt treatment group. Different letters indicate significant difference among the strains ($p < 0.05$). The same below.

图2 盐胁迫下各株系生长量变化

Fig. 2 Growth changes of each strain under salt stress

最小,为42.6%,处理组 M26 上升幅度最大,为55.1%(图3-a);盐处理后的MDA含量,富平楸子和k15显著低于其他3个株系,与对照组相比,分别显

著增加了28.7%和27.9%,M9-T337上升幅度最大,为54.3%(图3-b)。相比于对照组,处理组k15根系活力下降幅度最小,其次为m2和M9-T337,下降幅

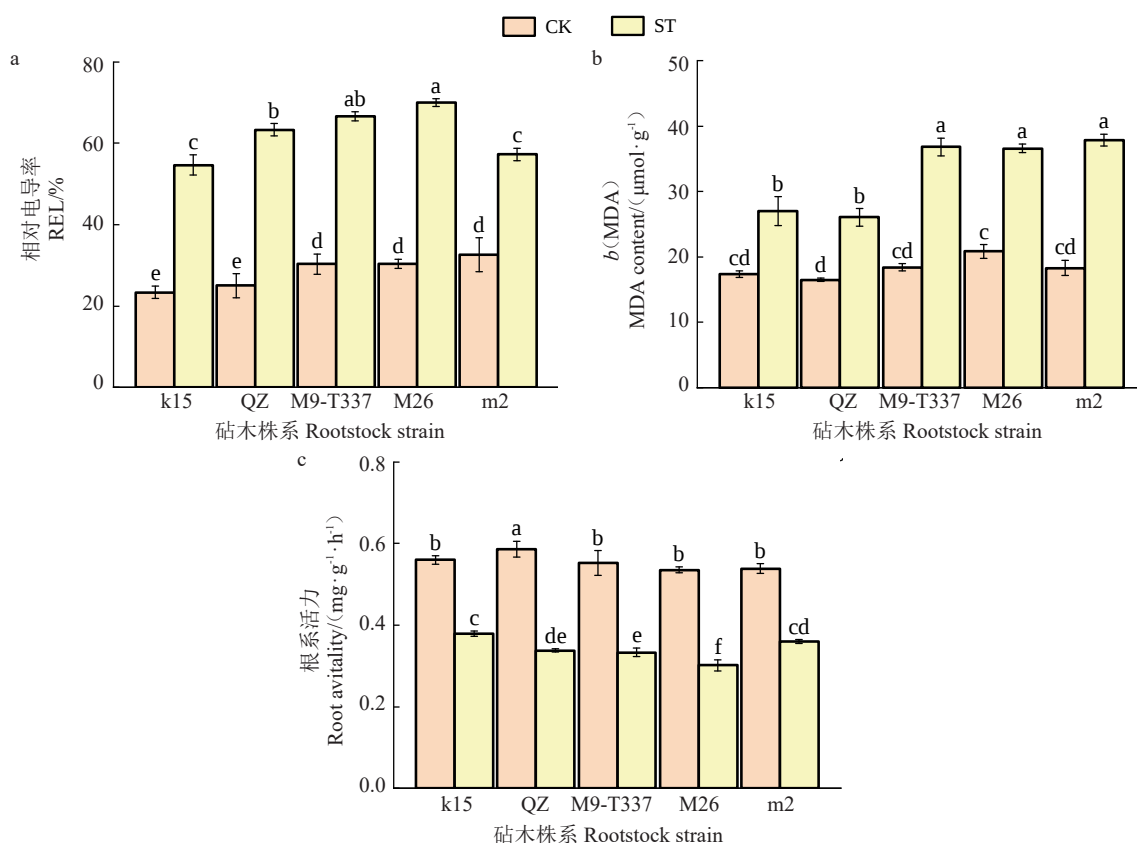


图3 盐胁迫对各株系相对电导率、MDA含量及根系活力的影响

Fig. 3 Effects of salt stress on relative electrical conductivity, MDA content and root vitality of each strain

度分别为30.9%、33.3%和40.0%(图3-c)。

2.3 盐胁迫下活性氧含量和抗氧化酶活性分析

为评价盐胁迫下各株系的抗氧化能力,对NBT和DAB进行了染色,并测定了 O_2 和 H_2O_2 含量。从NBT染色图上来看,k15、富平楸子和M9-T337蓝色斑点明显少于M26和m2(图4-a);从DAB染色来看,k15棕色斑点明显少于其他株系(图4-b);从 O_2 和 H_2O_2 含量上看,盐胁迫导致各株系均积累了一定量的 O_2 和 H_2O_2 ,其中M26积累量最多,富平楸子积累量最少(图4-c~d)。

抗氧化相关酶活性结果显示,盐胁迫处理后各株系SOD、POD和CAT活性均显著上升。5个株系的SOD活性分别显著升高33.1%、23.0%、27.6%、12.2%和11.1%(图5-a);从POD活性上看,盐胁迫下,k15的POD活性最高,m2的POD活性最低,与对照组相比,分别显著提高了42.9%和36.2%(图5-b);CAT活性分别显著升高62.6%、60.5%、48.1%、

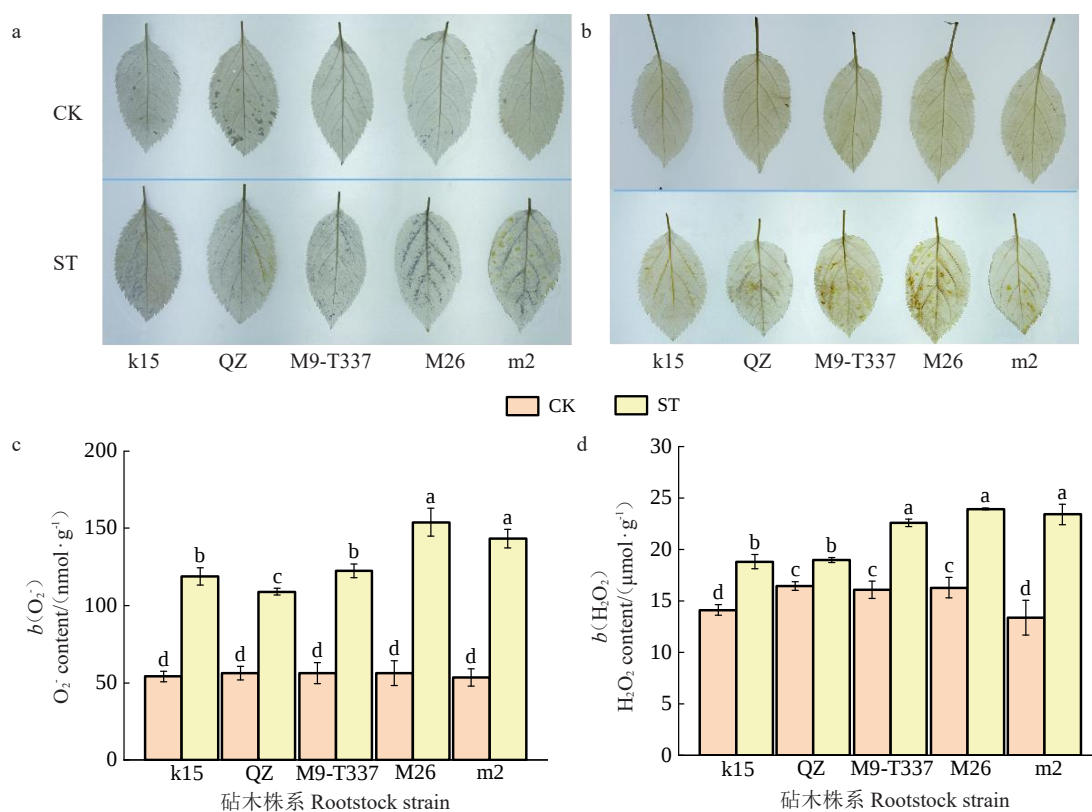
43.2%和44.5%(图5-c)。由此可以推断,盐胁迫下各株系抗氧化相关酶活性均显著上升,其中k15和富平楸子表现较为突出。

2.4 盐胁迫下植株光合相关指标分析

在盐胁迫处理过程中,每3 d测定1次光合参数。结果表明,盐胁迫组第3天,各株系 P_n 、 T_r 、 G_s 和 C_i 均出现大幅度下降,随后下降幅度有所减缓(图6)。

k15从第6天开始,光合参数 P_n 和 T_r 与其他株系出现分化,而 G_s 及 C_i 表现较为突出的是富平楸子,下降幅度相对较缓。结合两者在盐胁迫中的表现,相比于其他3个株系,k15和富平楸子表现出较强的光合能力,增强了一定的抗盐能力。

从总叶绿素含量上看,与对照组相比,盐胁迫组各株系均显著下降,k15、富平楸子、M9-T337、M26和m2下降幅度分别为32.4%、25.7%、36.4%、49.1%和47.3%,其中富平楸子降幅最小,M26降幅最大,这与处理结束时M26叶片大面积失绿相符



a 和 b 分别为植株叶片 O_2^- 和 H_2O_2 组织化学染色。

a and b mean O_2^- and H_2O_2 histochemical staining in the leaf.

图 4 盐胁迫对各株系活性氧积累的影响

Fig. 4 Effects of salt stress on the accumulation of active oxygen in each strain

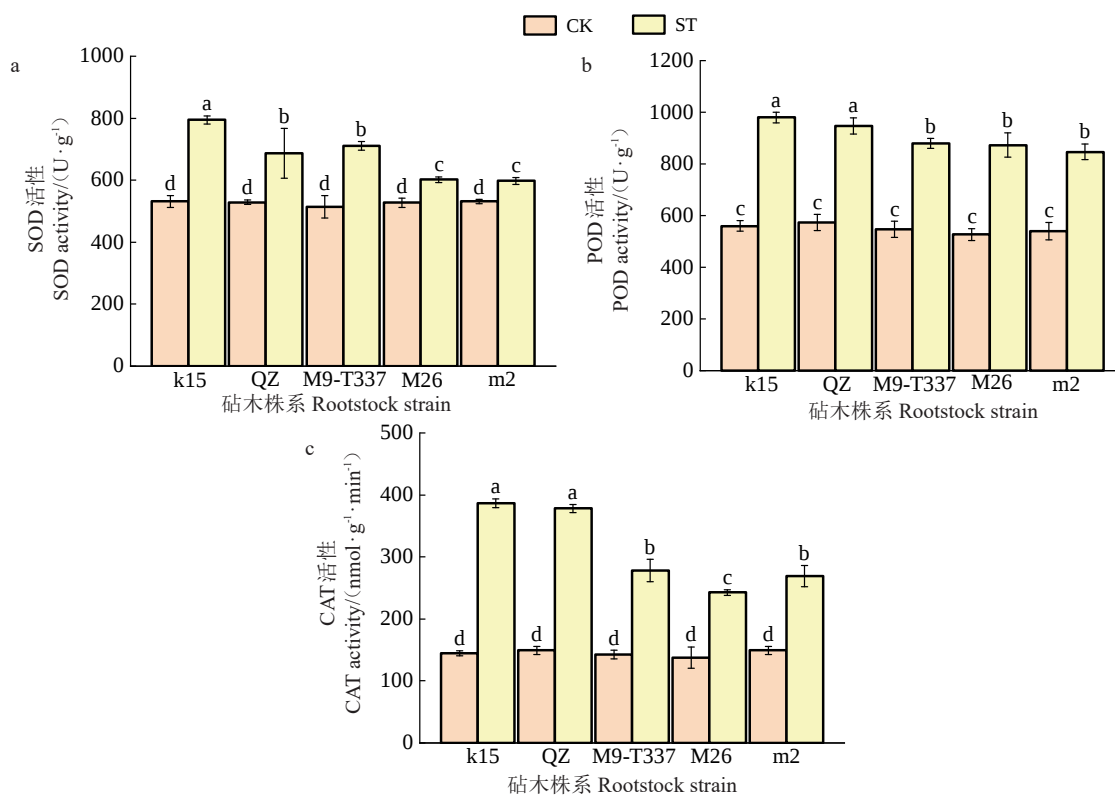
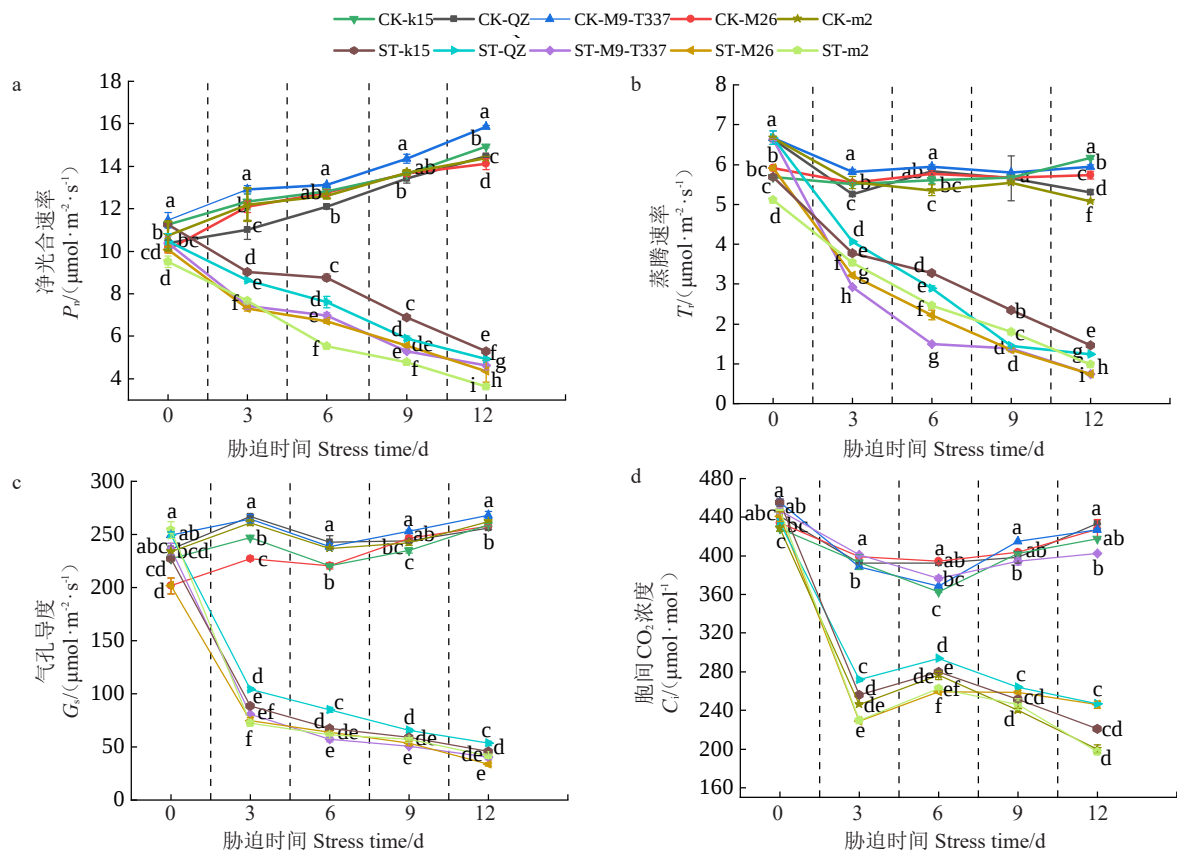


图 5 盐胁迫对各株系抗氧化酶活性的影响

Fig. 5 Effects of salt stress on antioxidant enzyme activities of each strain



不同小写字母表示同一时间的不同株系差异显著($p < 0.05$)。

Different small letters indicate significant difference among different strains of the same time ($p < 0.05$).

图6 盐胁迫对各株系光合作用的影响

Fig. 6 Effects of salt stress on photosynthesis of each strain

(图7-b)。

叶绿素荧光图像清晰显示了各株系在盐胁迫后叶片的荧光变化情况(图7-a);同时从 F_v/F_m 值来看,对照组除M26外,几乎无差异,而盐处理后k15、富平楸子和M9-T337较其他2个株系下降幅度更小,光系统损伤程度更小(图7-c)。

2.5 盐胁迫下植株离子稳态分析

水培盐胁迫会导致植物根部积累较多的 Na^+ ,根部被迫吸收过量 Na^+ 并运输到其他部位,使得植物细胞内 Na^+ 过量积累,产生离子毒害,同时影响 K^+ 及其他营养元素的吸收,打破细胞内部的离子稳定。本试验在处理结束时测定了各部位 Na^+ 、 K^+ 含量及 Na^+/K^+ 。结果表明,对照组各株系根、茎、叶的 Na^+ 含量均较低,盐处理组均表现出显著升高,其中M26涨幅最大,富平楸子、k15涨幅相对较小(图8-a~c); K^+ 则在盐处理后表现出不同程度的降低,其中M26降幅最大,富平楸子和k15变幅最小(图8-d~f);处理后各株系总 Na^+/K^+ 显著升高,其中富平楸

子与k15涨幅相对较小,分别为95.49%和95.94%,M26涨幅最大,为97.78%(图8-g)。

2.6 盐胁迫下植株氨基酸含量分析

在植物响应盐胁迫时,氨基酸能够起到保护作用。其中脯氨酸为逆境胁迫的关键游离氨基酸,可参与渗透调节来保持机体渗透平衡。研究表明,植物遭受逆境胁迫时,脯氨酸含量有所增加,且在抗性较强的植株中增加量明显低于敏感型植株,而其他游离氨基酸浓度变化暂无明显固定规律^[25]。为分析盐胁迫下各株系氨基酸变化情况,笔者在处理结束时对氨基酸含量进行了测定。结果(表1)表明,脯氨酸(Pro)、酪氨酸(Tyr)和苯丙氨酸(Phe)3种氨基酸含量在处理呈显著上升趋势,与对照组相比,5个株系(k15、富平楸子、M9-T337、M26和m2)脯氨酸含量分别提高了29.94%、20.27%、27.36%、35.72%和31.69%,其中M26变化幅度最大,富平楸子变化幅度最小;酪氨酸含量分别提高了27.44%、18.79%、28.19%、32.39%和37.13%,其中m2变化幅度最大,

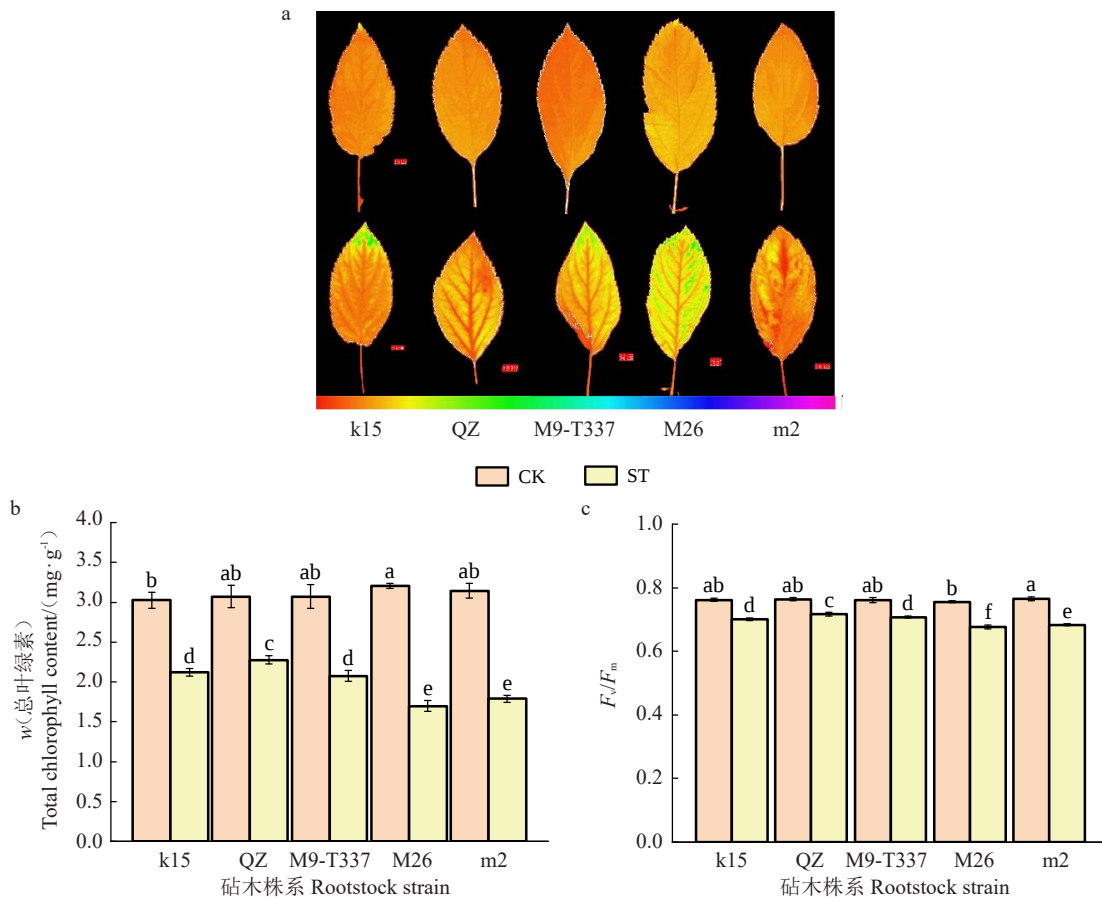


图7 盐胁迫对叶绿素含量及叶绿素荧光的影响

Fig. 7 Effects of salt stress on chlorophyll content and chlorophyll fluorescence

富平楸子变化幅度最小;苯丙氨酸含量分别提高了21.13%、32.53%、38.79%、50.94%和45.99%,其中M26变化幅度最大,k15变化幅度最小;而甘氨酸(Gly)、亮氨酸(Leu)和天冬氨酸(Asp)含量均显著下降,与对照组相比,5个株系甘氨酸含量分别降低了16.67%、7.14%、12.19%、19.69%和17.90%,其中富平楸子变化幅度最小,M26降幅最大;亮氨酸含量分别降低了19.67%、21.40%、17.72%、30.71%和46.29%,其中M9-T337变幅最小,m2降幅最大;天冬氨酸含量分别降低了23.15%、22.75%、45.33%、57.05%和37.88%,其中富平楸子降幅最小,M26降幅最大。综上所述,相比于对照组,盐胁迫组各株系氨基酸含量变化幅度最小的是富平楸子,最大的是M26和m2。

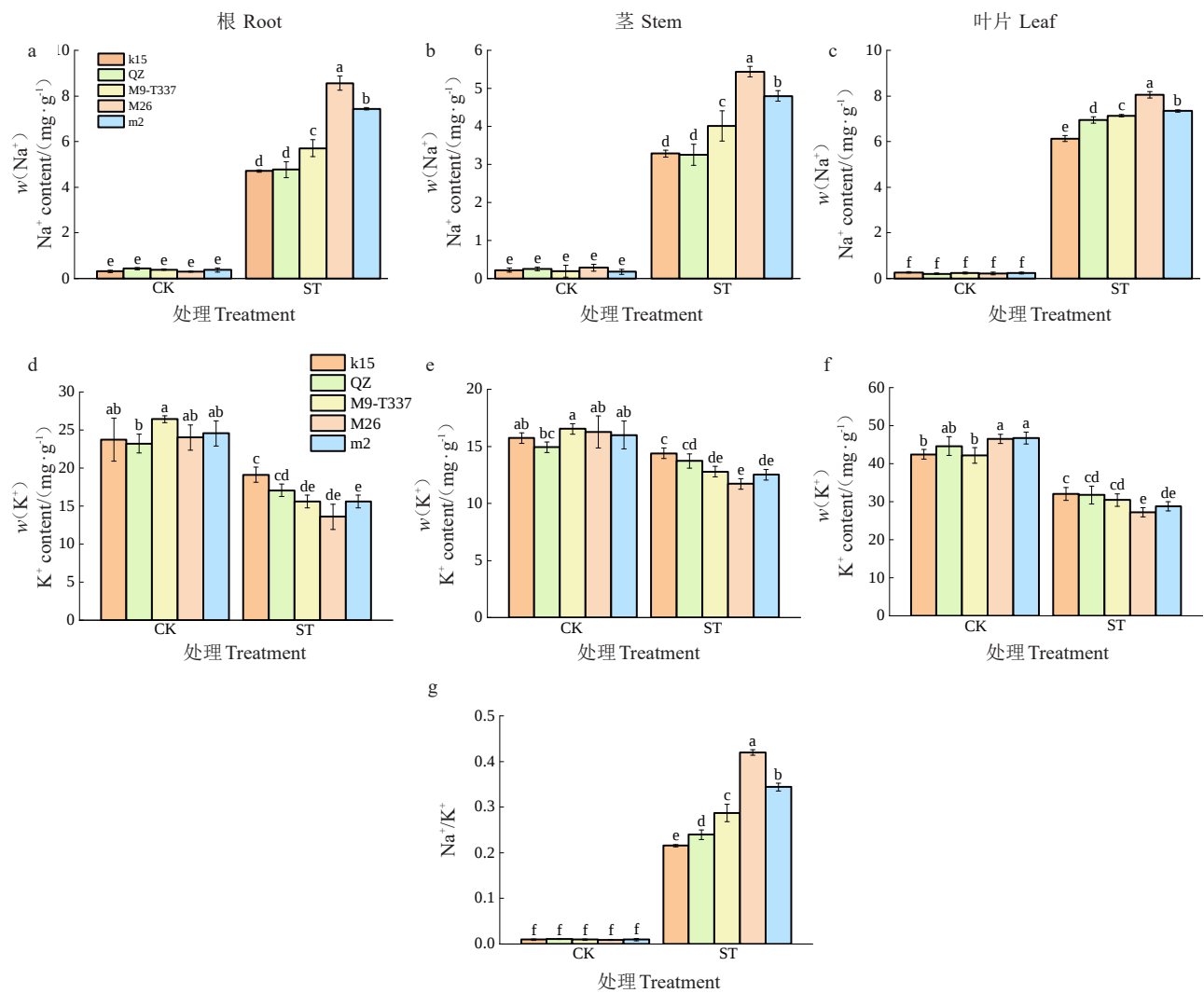
2.7 盐胁迫下各株系耐盐性综合评价

以各株系对照组与盐处理组相对变化率计算隶属函数值,以各株系隶属函数值的平均值为依据进行耐盐性综合评价,平均隶属函数值越大说明植株耐盐能力越强。通过分析相对电导率、MDA含量、

过氧化氢含量、SOD活性、POD活性、CAT活性、净光合速率、叶绿素含量、 F_v/F_m 值、 Na^+/K^+ 和氨基酸含量16项指标,计算出了各株系的平均隶属函数值。结果(表2)表明,k15的平均隶属函数值最大,表明盐胁迫下其各指标的相对变化程度最小,与其他种质资源相比耐盐能力最强。平均隶属函数值最小的是M26,表明其耐盐能力最弱。由此得出各株系耐盐能力依次为k15>富平楸子>M9-T337>m2>M26。

3 讨论

盐胁迫下植株生长受到抑制,根系发育迟缓,叶片失水、萎蔫甚至脱落^[26]。本研究中,150 mmol·L⁻¹盐胁迫处理15 d导致各个株系均出现不同程度的盐害表现。株高受到抑制,叶片出现褐斑并随着处理时间加长逐渐萎蔫脱落,根系生长迟缓并呈现褐色,新根变少^[27]。盐胁迫下植物通过提高根系活力来适应环境变化,确保根系正常吸收水分及矿质营养,植株正常生长。研究表明,在低盐浓度下或短期中高



a. 根中 Na⁺含量;b. 茎中 Na⁺含量;c. 叶片中 Na⁺含量;d. 根中 K⁺含量;e. 茎中 K⁺含量;f. 叶片中 K⁺含量;g. 总 Na⁺/K⁺。

a. The content of Na⁺ in roots; b. The content of Na⁺ in stems; c. Na⁺ content in leaves; d. K⁺ content in roots; e. K⁺ content in stems; f. K⁺ content in leaves; g. Total Na⁺/K⁺.

图 8 盐胁迫对各株系离子稳态的影响
Fig. 8 Effects of salt stress on ion homeostasis of each strain

表 1 盐胁迫对各株系氨基酸含量的影响

砧木株系及处理 Rootstock strain and treatment	Table 1 Effects of salt stress on amino acids content in each strain (μg·g ⁻¹)					
	w(脯氨酸) Pro content	w(酪氨酸) Tyr content	w(苯丙氨酸) Phe content	w(甘氨酸) Gly content	w(亮氨酸) Leu content	w(天冬氨酸) Asp content
k15-CK	87.44±1.83 e	35.42±1.07 de	43.63±0.79 c	125.52±6.05 ab	61.12±2.76 a	234.21±11.44 c
QZ-CK	99.51±4.02 c	35.81±1.13 de	41.04±1.12 cd	123.36±5.97 ab	62.42±3.33 a	243.96±7.59 c
M9-T337-CK	85.23±2.41 e	32.78±1.91 ef	35.63±1.04 e	123.64±1.06 ab	48.32±4.16 b	264.88±18.15 b
M26-CK	86.92±1.24 e	35.90±2.35 de	36.63±2.54 de	129.62±8.72 a	51.40±4.30 b	287.11±12.85 a
m2-CK	96.54±3.33 c	30.03±1.69 f	35.03±2.25 e	120.15±1.67 bc	61.37±3.90 a	237.33±12.49 c
k15-ST	113.62±3.17 d	45.14±3.32 a	52.85±4.78 ab	104.59±1.70 e	49.10±0.45 b	179.98±6.23 d
QZ-ST	119.68±2.72 b	42.54±1.45 bc	54.39±1.27 b	114.55±1.04 cd	49.06±2.04 b	188.46±9.39 d
M9-T337-ST	108.55±1.83 c	42.02±1.43 bc	49.45±1.95 ab	108.90±2.28 de	39.76±3.67 c	144.82±3.79 e
M26-ST	117.97±3.09 b	47.53±3.03 ab	55.29±3.41 a	104.10±1.25 e	35.62±1.30 d	123.30±14.18 f
m2-ST	127.13±3.56 a	41.18±2.52 c	51.14±4.46 ab	98.64±4.99 f	32.96±1.88 cd	147.43±10.31 e

表2 隶属函数值
Table 2 Membership function value

指标 Index	砧木株系 Rootstock strain				
	k15	QZ	M9-T337	M26	m2
相对电导率 REL	0.244	0.000	0.431	0.289	1.000
丙二醛含量 MDA content	1.000	0.954	0.129	0.245	0.000
过氧化氢含量 H ₂ O ₂ content	0.703	1.000	0.584	0.474	0.000
超氧化物歧化酶活性 SOD activity	1.000	0.469	0.691	0.039	0.000
过氧化物酶活性 POD activity	1.000	0.457	0.230	0.496	0.000
过氧化氢酶活性 CAT activity	1.000	0.849	0.212	0.000	0.048
净光合速率 P _n	0.338	0.441	0.429	0.000	1.000
叶绿素含量 Total chlorophyll content	0.811	1.000	0.692	0.000	0.189
F _v /F _m	0.404	0.000	0.202	0.964	1.000
Na ⁺ /K ⁺	1.000	0.992	0.658	0.000	0.449
脯氨酸含量 Pro content	0.866	1.000	0.933	0.000	0.638
酪氨酸含量 Tyr content	0.688	1.000	0.466	0.259	0.000
苯丙氨酸含量 Phe content	1.000	0.541	0.490	0.00	0.149
甘氨酸含量 Gly content	0.412	1.000	0.414	0.00	0.233
亮氨酸含量 Leu content	0.919	0.848	1.000	0.251	0.000
天冬氨酸含量 Asp content	0.988	1.000	0.371	0.000	0.527
平均得分 Average score	0.773	0.718	0.500	0.189	0.326
排序 Rank	1	2	3	5	4

盐浓度下,植物根系活力提高,且提高幅度与耐盐能力呈正相关,当盐浓度超过一定承受范围时,根系活力会大幅下降^[28]。本研究中,由于 150 mmol·L⁻¹ 盐浓度超过苹果植株耐受能力,各株系根系活力均呈下降趋势。处理结束时,M26 盐害表现最为严重,其次为 M9-T337 和 m2。相比之下,k15 和富平楸子盐害表型出现较晚,且盐害程度相对较轻,与前人的研究结果相近^[29]。

遭受盐胁迫的植株内部生理出现紊乱,抗性较强的株系则可以通过自身调节作用减轻损伤^[30-31]。相对电导率和 MDA 含量能够反映生物膜的损伤程度,可作为植物耐逆境胁迫能力的关键生理指标^[32]。MDA 作为膜脂过氧化的产物,其含量反映了植物膜脂过氧化程度,盐胁迫下 MDA 过量积累,破坏生物膜结构和功能,导致膜通透性增强,电解质外渗,电导率增大^[33-34]。植物耐受性越强,相对电导率和 MDA 含量越稳定。笔者测定了各株系相对电导率及 MDA 含量,结果表明,盐胁迫下各株系的相对电导率及 MDA 含量均有所上升,但 k15 和富平楸子的涨幅明显更小,侧面反映出两者较强的耐受性。

植物在盐胁迫下,细胞内会产生过量的活性氧,这些活性氧若没有及时清除便会引起氧化胁迫^[35]。有研究证实,提高植物体内抗氧化系统酶活性及增

强抗氧化代谢能力是提高植物抗盐能力的途径之一^[36]。耐盐能力较强的植株可以通过启动抗氧化系统消除过量的活性氧,使活性氧与抗氧化酶保持动态平衡,以减轻盐害^[37]。笔者通过 NBT 和 DAB 染色来分析活性氧含量,判断各株系 O₂ 和 H₂O₂ 积累情况,结果表明,k15、富平楸子和 M9-T337 的 O₂ 含量显著低于 M26 和 m2;k15 和富平楸子的 H₂O₂ 含量显著低于其他株系。k15 在盐胁迫下体内 O₂ 和 H₂O₂ 积累均较少,这可能与 k15 自身较好的抗氧化调节能力有关。关于抗氧化酶活性变化与逆境胁迫的关系,有不同的研究结果。研究表明,植物抗氧化相关酶活性会随逆境胁迫加重而提高,并存在阈值^[38];也有研究报道,保护酶活性会随胁迫程度增加而下降^[39]。不同砧木逆境胁迫下的响应机制不同,需要的保护酶也不同,且变化规律差异较大^[40]。本研究在盐胁迫处理 15 d 后,5 个株系中 POD、SOD 和 CAT 活性上升幅度最大的均为 k15,由此可以推断,150 mmol·L⁻¹ 盐胁迫下各植株都启动了保护酶系统,且保护酶活性与植株抗性呈正相关,k15 表现出较强的耐盐能力。

光合作用是植物生长的必要条件,盐胁迫下光合能力强弱间接体现植株耐盐能力^[41]。本试验的结果表明,盐胁迫组从第 3 天开始,各株系 P_n、T_c、G_s 和

C_i均出现大幅度下降,随着处理时间延长下降幅度有所减缓,这可能与植株建立了稳态耐受机制有关。研究表明,植物受到盐害时,短期内光合作用受气孔因素限制而降低;随着盐害时间变长,植物光合器官受到破坏,限制因素逐渐转为非气孔因素^[42]。当植物净光合速率下降、胞间二氧化碳浓度升高时,光合作用受到非气孔因素的限制而下降^[43]。由此可以推测,本研究第6天开始光合能力下降可能是受到非气孔因素的影响,光合器官受到破坏。株系k15从第6天开始,净光合速率和蒸腾速率与其他株系出现分化,而从气孔导度和胞间CO₂浓度上看,富平楸子较其他4个株系表现最突出,下降幅度相对较缓。结合两者在盐胁迫中的表现,相比于其他3个株系,k15和富平楸子表现出较强的光合能力,增强了其抗盐能力。研究表明,盐胁迫下,小麦由于吸收不到充足的水分和矿质元素,叶绿素降解酶活性增强,叶绿素含量大幅降低,叶片失绿^[44]。本研究在处理结束时测定了叶绿素含量及荧光参数。从总叶绿素含量上看,M26下降幅度最大,这与处理结束时M26叶片大面积失绿萎蔫的表型相符。叶绿素荧光参数可以作为分析植物受光抑制程度的重要指标^[45]。通过分析 F_v/F_m 值,盐处理后k15、富平楸子、M9-T337较M26和m2两个株系下降幅度小,表明其受光抑制程度较低。

植物根系处于高盐环境下,会引起细胞内离子浓度发生改变,植物会顺着电化学梯度从外界吸收大量的Na⁺,从而产生离子毒害^[46]。当细胞内Na⁺浓度过高时会置换结合内膜上的Ca²⁺,导致细胞膜功能遭到破坏,同时细胞内K⁺等有机溶质外渗,导致植物生长代谢受到影响^[47-49]。研究表明,碱蓬之所以具有较好的耐盐能力,是因为根系通过渗透调节将体内的盐分转运、区域化,降低细胞内盐浓度,同时增加液泡内Na⁺浓度,保持细胞正常吸水,调节离子平衡^[50-51]。可见,耐盐能力强的植株根系能够通过类似排盐、拒盐机制维持内部Na⁺/K⁺稳定。由此推断,盐胁迫下,Na⁺/K⁺越稳定,植株耐盐能力越强。笔者通过分析各部位Na⁺、K⁺含量及Na⁺/K⁺,结果表明,富平楸子和k15的Na⁺和K⁺含量以及Na⁺/K⁺变化幅度较小,侧面反映出其较强的耐盐能力。

植物体内氨基酸在逆境胁迫中发挥重要作用,如植物遭受逆境胁迫时会通过脯氨酸的积累来提高自身耐受性^[52]。研究表明,不同物种间脯氨酸含量

与植物抗逆性强弱的关系存在差异,如耐热性强的不结球白菜高温胁迫下积累更多的脯氨酸^[53],番茄幼苗耐盐能力则与脯氨酸含量呈负相关^[54]。本研究5个株系中M26的脯氨酸含量涨幅最大,富平楸子涨幅最小,可见脯氨酸含量与植株抗盐能力呈负相关,这与前人在苹果抗盐性评价中的结果存在差异^[55],该研究认为抗盐性较强的砧木优系盐胁迫后脯氨酸含量增加幅度大,这可能与不同砧木自身的脯氨酸代谢方式有关,具体机制还有待研究。此外,本研究中酪氨酸(Tyr)和苯丙氨酸(Phe)含量在盐处理后呈现显著上升趋势,而甘氨酸(Gly)、亮氨酸(Leu)和天冬氨酸(Asp)含量均显著下降。植物响应逆境胁迫时氨基酸代谢机制较为复杂,单一组分变化无法作为抗盐性评价的绝对依据^[56],需综合分析。

4 结 论

150 mmol·L⁻¹的水培盐处理下5个株系中k15表现出较强的耐盐能力,M26耐盐性较差。盐胁迫下,各植株生长量下降,生长受到抑制,根面积减小,干鲜质量下降;相对电导率和MDA含量显著升高,根系活力显著降低;植物体内活性氧积累,抗氧化酶活性升高;叶绿素含量降低,光合作用明显受到抑制;Na⁺含量显著升高,K⁺含量下降,Na⁺/K⁺失衡;脯氨酸(Pro)、酪氨酸(Tyr)和苯丙氨酸(Phe)3种氨基酸含量显著升高,甘氨酸(Gly)、亮氨酸(Leu)和天冬氨酸(Asp)含量显著降低。但由于各株系抗性存在差异,不同指标变化率有所不同。通过隶属函数综合分析,最终得出各株系耐盐能力顺序为:k15 > 富平楸子 > M9-T337 > m2 > M26。因此,苹果砧木富平楸子×R3杂交后代k15的耐盐能力较强,有望成为新的优质砧木资源。

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