果 树 学 报 2019,36(11):1558-1565
Journal of Fruit Science

DOI:10.13925/j.cnki.gsxb.20190124

采前硝普钠喷洒增强厚皮甜瓜果实的采后抗病性

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摘 要:【目的】研究果实发育期硝普钠(Sodium Nitroprusside,SNP)多次喷洒对采后厚皮甜瓜抗病性、后熟和能量代谢的影响。**【方法】**以'玛瑙'厚皮甜瓜为试材,在果实幼果期(花后14 d)、膨大前期(花后21 d)、膨大后期(花后28 d)和成熟期(采前2 d)4个时期分别采用0.5 mmol·L^{-1} SNP进行喷洒,以清水喷洒作为对照,观察处理对采后果实损伤接种粉红单端孢发病率及病斑直径的影响,测定果实采收及贮藏期间的呼吸速率和乙烯释放量,分析果实苹果酸脱氢酶和琥珀酸脱氢酶活性以及能荷水平的变化。**【结果】**SNP喷洒有效抑制了采后损伤接种果实的发病率和病斑直径,贮藏6 d时,分别低于对照47.4%和37.4%。SNP处理降低了果实采收时的乙烯释放量,以及贮藏期间果实的呼吸强度和乙烯释放量,并使果实呼吸和乙烯跃变峰的出现推迟了2 d。此外,SNP处理还显著提高了果实贮藏期间苹果酸脱氢酶和琥珀酸脱氢酶的活性,延缓了ATP的下降速率,提高了ADP的含量,维持了果实较高的能荷水平。**【结论】**果实发育期SNP多次喷洒可有效提高厚皮甜瓜果实的采后抗病性,该作用与一氧化氮延缓果实后熟,增加能量供应,提高能荷水平密切相关。

关键词:厚皮甜瓜;硝普钠;采前喷洒;抗病性;后熟;能量代谢

中图分类号:S662 **文献标志码:**A **文章编号:**1009-9980(2019)11-1558-08

Pre-harvest sodium nitroprusside sprays enhance resistance against diseases in harvested muskmelons

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Abstract:【Objective】Muskmelon is an important cash crop, due to its unique appearance and intrinsic quality. However, postharvest rots of the muskmelon fruit are serious. Several fungi are involved in the decay of muskmelon fruit. Among them, pink rot caused by *Trichothecium roseum* is a major fungal disease in China. Although pink rot can be effectively controlled by application of chemical fungicides, the excessive use of chemical fungicides will lead to pesticide residues in fruit, pathogen resistance and environmental pollution. Therefore, a new strategy needs to be developed for controlling the rots of postharvest muskmelon fruit. In this study, we evaluated the effects of sodium nitroprusside (SNP) sprays during fruit development on disease resistance against pink rot in harvested muskmelon fruit, and explored their effect on fruit ripening and energy charge level.【Methods】The cultivar 'Manao' was used as material. The plants were sprayed with SNP at 0.5 mmol·L^{-1} for four times at the stage of young fruit (14 days after flowering), the early stage of enlargement (21 days after flowering), the late stage of enlargement (28 days after flowering) and the mature stage (2 days before harvest). Fruit with the same maturity, uniform size, with no pests and diseases were selected as experimental materials. The fruit surface was cleaned with running water, then dipped in 2% sodium hypochlorite solution for 2 mins for surface disinfection, and finally rinsed and stored at ambient temperature (25±2 ℃; RH 55%-60%). *T. roseum* for inoculation was cultivated in potato dextrose agar (PDA) and preserved in 4 ℃. The effects of

收稿日期:2019-03-27 接受日期:2019-08-18

基金项目:公益性行业(农业)科研专项(201303075)

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SNP sprays on disease incidence and lesion diameter on the inoculated muskmelon fruit during ambient storage were evaluated. Meanwhile, the respiratory intensity, ethylene production, the activities of malate dehydrogenase (MDH) and succinate dehydrogenase (SDH), and energy change were determined at harvest and during storage.【Results】SNP sprays reduced the decay incidence of harvested muskmelon fruit inoculated with *T. roseum*, which were 47.4% and 29.1% lower than the control at 6 and 8 days after inoculation, respectively. Similarly, the lesion diameter of the treated fruit was also significantly lower than the control, which was 30.3% and 37.4% lower than the control at 2 and 6 days after inoculation, respectively. SNP sprays reduced ethylene release at harvest. However, no significant difference was found in respiration rate. SNP delayed the peaks of respiration and ethylene release by two days during storage. The respiration rate and ethylene release of treated fruit were significantly lower than the control at the early and the middle stages during storage, being 18.3% and 26.4% lower at the 6th day of storage, respectively. SNP sprays had no significant effects on MDH and SDH activities at harvest. However, the activities of MDH and SDH increased significantly during storage, being 54% and 43.5% higher than the control at the 4th and 6th days of storage, respectively. In addition, SNP delayed the decline of ATP content, increased the AMP content, and thus increased energy charge level. The ATP content at day 4 and energy charge at day 6 in the treated fruit were 73.8% and 48.5% higher than the control, respectively.【Conclusion】The disease resistance of harvested muskmelon fruit could be effectively enhanced by spraying with SNP during fruit development. This effect is closely related to NO delaying fruit ripening, increasing the activities of the key mitochondrial enzymes and maintaining high energy charge levels.

Key words: Muskmelon; Sodium nitroprusside; Pre-harvest sprays; Disease resistance; After ripening; Energy metabolism

厚皮甜瓜是重要的夏秋水果，由于其独特的外观及内在品质，深受广大消费者的青睐[1]。但厚皮甜瓜的采后腐烂非常严重，多种真菌与厚皮甜瓜的采后腐烂有关，其中由粉红单端孢（*Trichothecium-roseum*）引起的粉霉病是我国西北产区的重要病害[1]。虽然化学杀菌剂可有效控制厚皮甜瓜的采后病害，但存在农药残留、病原物产生抗药性以及环境污染等问题。因此，亟需寻求新的更加安全有效的控制措施[2]。近年来人们发现，通过激发果蔬自身的抗病性可有效减轻采后病害，多种化合物具有激发果蔬采后抗病性的功能[3]。研究发现，苯并噻重氮[4-5]、乙酰水杨酸[6]、硅酸钠[7]、壳聚糖[8]等诱抗剂均表现出对厚皮甜瓜采后病害的良好控制效果。此外，采前喷洒 harpin[9]和 acibenzolar-S-methyl[10]也能显著降低厚皮甜瓜的潜伏侵染率，有效提高果实的采后抗病性，由此表明在果实发育过程中采前喷洒也是控制厚皮甜瓜采后病害的有效策略。NO 是植物体内重要的信号分子，参与多种植物的生理过程，对大多数呼吸跃变型和非呼吸跃变型果实具有延缓成熟衰老，增强胁迫响应能力以及诱导果实采后抗病性的作用[11]。研究表明，NO 直接熏蒸或者通过 NO 外源供体硝普钠（Sodium nitroprusside，SNP）应用可增强杧果[12]和火龙果[13]对炭疽病、草莓[14]和猕猴桃[15]对灰霉病以及苹果[16]对黑斑病等多种果实的采后抗病性。此外，外源 NO 处理还能显著提高采后枇杷[17]和香蕉[18]果实的能荷水平，通过抑制乙烯的合成与释放延缓草莓[19]、杧果[20]、桃[21]和苹果[22]果实的后熟。目前虽然已有 NO 采后处理诱导果实抗病性的报道，但 NO 采前喷洒是否影响厚皮甜瓜的果实后熟及采后抗病性，能量代谢是否参与 NO 诱导果实的抗性尚未见报道。笔者以‘玛瑙’厚皮甜瓜为试材，通过果实发育期 SNP 4 次喷洒，研究采前处理对采后果实抗病性及后熟的影响，分析处理果实线粒体关键酶和能荷水平的变化，揭示能量代谢在 NO 诱导抗病性中的作用，以期为诱导厚皮甜瓜果实的采后抗病性提供技术和理论依据。

1　材料和方法

1.1　材料与仪器

供试‘玛瑙’厚皮甜瓜种子购于甘肃省民勤县金

谷源农业科技有限公司。采用种子直接穴播的方式种植于甘肃省民勤县收成乡露地大田(东经103.607 19°,北纬38.905 65°)。株距45 cm,行距100 cm,植株田间管理参照当地甜瓜种植规程进行。试验分别于2016年和2017年进行2年。果实商业成熟度(花后45 d)采收,单果套发泡网袋后装箱(每箱12个),次日运抵甘肃农业大学采后生物学与技术实验室,在室温条件(25±2 ℃,RH55%~60%)下贮藏待用。供试硝普钠(SNP)购于美国Sigma试剂公司。供试*T. roseum*由本实验室提供。

果蔬呼吸测定仪(GXH-3051H,北京均方理化科技研究所,中国),气相色谱仪(Agilent 7820美国安捷伦科技公司,美国),生物显微镜(CX21FS1C,奥林巴斯有限公司,日本),超净工作台(SW-CJ-2FD,苏州安泰空气技术有限公司,中国),超低温冰箱(DW-HL218,中科美菱低温科技有限公司,中国),高速冷冻离心机(H-1850R,长沙湘仪离心机有限公司,中国),电导率仪(DDS-307A,上海雷磁仪器厂,中国),紫外分光光度计(UV-2450,日本岛津,日本),高效液相色谱仪(Agilent 1100,美国安捷伦科技公司,美国)。

1.2 方法

1.2.1 SNP溶液的制备及田间喷洒 将SNP直接溶于自来水中制备0.5 mmol·L^{-1}溶液(加入0.05%吐温80作为延展剂)。SNP田间喷洒参照Wang等[9]的方法。分别在果实的幼果期(花后14 d)、膨大前期(花后21 d)、膨大后期(花后28 d)和成熟期(采前2 d)喷洒植株和果实,以清水处理为对照。每升溶液喷洒20~25株。每组处理喷洒100株,重复3次。

1.2.2 果实损伤接种发病率和病斑直径的测定 孢子悬浮液的制备参照Ge等[23]的方法。*T. roseum*于28 ℃条件下PDA平板培养7 d后,加入无菌水(含0.05%的Tween80)约10 mL,用灭菌的涂布器刮下平板上的孢子,4层灭菌纱布过滤,将孢子悬浮液转入50 mL的三角瓶中,振荡15 s后再用双层纱布过滤,使用血球计数板计数并算出孢子悬浮液的浓度后稀释至所需浓度(1×10^{5}个孢子•mL^{-1})。

损伤接种果实发病率和病斑直径的测定参照Ge等[23]的方法。采收1 d后,取常温贮藏的果实,70%乙醇表面消毒后,用已灭菌的打孔器(直径3 mm,深5 mm)在果实赤道等距打孔6个,接入20 μL已制备好的孢子悬浮液,晾干2 h后室温(25±2)℃、RH55%~60%条件下贮藏,分别在接种后0、2、4、6、8、10 d统计发病率以及接种后2、6 d测量病斑直径。每组处理用果实12个,重复3次。

1.2.3 呼吸速率和乙烯释放量的测定 果实呼吸速率的测定参照Li等[24]的方法,使用果蔬呼吸测定仪进行测定。首先对空罐内CO_2及O_2的浓度进行测定,之后迅速将果实放入,待罐内CO_2及O_2的浓度达到平衡后,记录数据。每组测定用果实3个,重复3次。

乙烯释放量的测定参照Li等[24]的方法。果实准确称重后置于密闭容器中(可进行气体取样),密封8 h后,抽取0.2 mL的气体样品注入气相色谱仪进行测定,柱温为50 ℃,N_2流量8 mL·min^{-1}。FID检测器的温度230 ℃。用外标法进行定量,记录并分析数据。容器剩余体积用排水法进行测量,乙烯释放量表示为量μL·kg^{-1}·h^{-1}。每组测定用果实3个,重复3次。

1.2.4 生化测定取样 参照Yuan等[25]的方法并修改。分别在贮藏期间的0、2、4、6、8、10 d,取果实阳面赤道部分皮下约3~6 mm的皮层组织,立即用液氮冷冻并用研样机研磨成粉后装入50 mL离心管中,然后保藏于−80 ℃的超低温冰箱中待用。

1.2.5 苹果酸脱氢酶(malate dehydrogenase,MDH)和琥珀酸脱氢酶(succinate dehydrogenase,SDH)活性的测定 采用苏州科铭生物技术有限公司的试剂盒进行测定。以每克组织每分钟消耗1 nmol的NADH定义为一个酶活力单位,MDH活性表示为nmol·min^{-1}·g^{-1}。以每克组织每分钟消耗1 nmol 2,6-二氯酚靛酚定义为一个酶活性单位,SDH活性表示为nmol·min^{-1}·g^{-1}。

1.2.6 ATP、ADP和AMP含量的测定及能荷的计算 参照Liu等[26]的方法并修改。准确称量3 g冷冻组织粉末置于离心管中,加入6 mL提前预冷的高氯酸溶液提取10 min,6 000 r·min^{-1},4 ℃条件下离心15 min,然后用1 mol·L^{-1}的KOH快速将溶液pH调至6.6~6.8,随后冰浴条件下放置30 min使高氯酸沉淀,再次离心10 min,取上清液并定容至6 mL。流动相为pH 7.0的磷酸钾缓冲溶液(0.1 mol·L^{-1})与甲醇的缓和溶液(99.9∶0.1),流动相与提取液在上机前需经0.45 μm滤膜过滤。采用高效液相色谱仪进行分析,色谱条件为:Eclipse Plus C18柱(5 μm×4.6 mm×250 mm,USA),检测波长254 nm,流速1 mL·min^{-1},进样量20 μL,柱温30 ℃,柱压64 bar。根据ATP、ADP、AMP标准品的保留时间以及所制作的标准曲

线对样品峰进行定量分析，结果以mg·L^{-1}表示。能荷按以下公式计算：EC=(ATP+1/2ADP)/(ATP+ADP+AMP)。

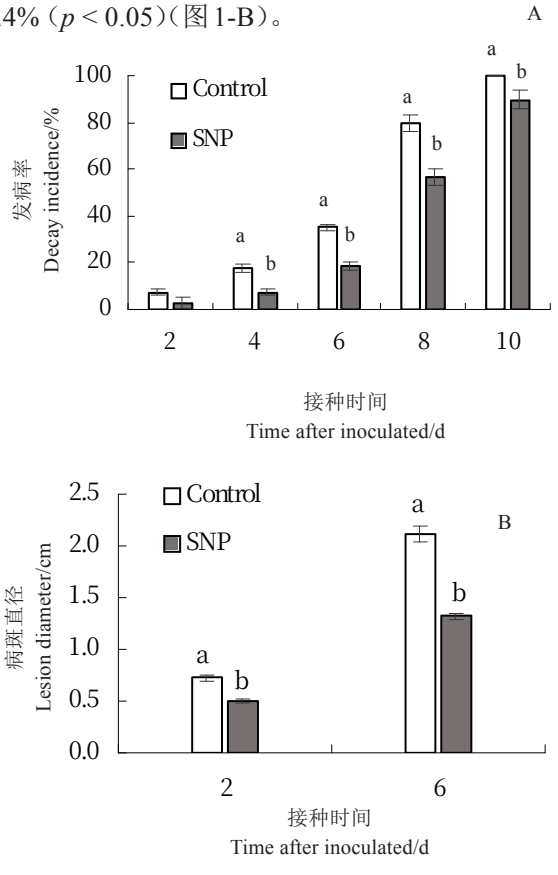
1.3　数据分析

上述所有测定至少重复3次。采用Excel 2007计算平均值与标准偏差，Origin8.5进行制图，SPSS 17.0进行差异显著分析($p < 0.05$)。

2　结果与分析

2.1　采前SNP喷洒对采后果实损伤接种发病率和病斑直径的影响

无论处理还是对照果实损伤接种后的发病率均显著上升，但处理果实的发病率显著低于对照，接种6 d和8 d后分别低于对照47.4%和29.1%($p < 0.05$)(图1-A)。同样，处理果实的病斑直径也显著低于对照，接种2 d和6 d后分别低于对照30.3%和37.4%($p < 0.05$)(图1-B)。



竖线表示标准误差。不同字母表示差异显著($p < 0.05$)。下同。

Bars indicated standard error (±SE). Different letters indicate significant differences ($p < 0.05$). The same below.

图1　采前SNP喷洒对采后果实采后损伤接种发病率（A）和病斑直径（B）的影响

Fig. 1 Effect of multiple preharvest SNP spays on incidence (A) and lesion diameter (B) of harvested muskmelons inoculated with *T. roseum*

2.2　采前SNP喷洒对采后果实呼吸速率和乙烯释放量的影响

采收时，处理和对照果实的呼吸速率无明显差异。贮藏期间，处理和对照果实的呼吸速率均呈先上升后下降的单峰型变化，但处理果实的呼吸峰值迟于对照2 d出现。此外，处理果实呼吸速率在贮藏前6 d均低于对照，贮藏6 d时显著低于对照18.3%($p < 0.05$)(图2-A)。采收时，SNP喷洒降低了果实的乙烯释放量，且显著低于对照31.2%($p < 0.05$)。贮藏期间，处理和对照果实的乙烯释放量均呈先上升后下降的单峰型变化势，但处理果实的乙烯释放峰值迟于对照2 d出现。此外，处理果实的乙烯释放量在贮藏前6 d均低于对照，贮藏6 d时低于对照26.4%($p < 0.05$)(图2-B)。

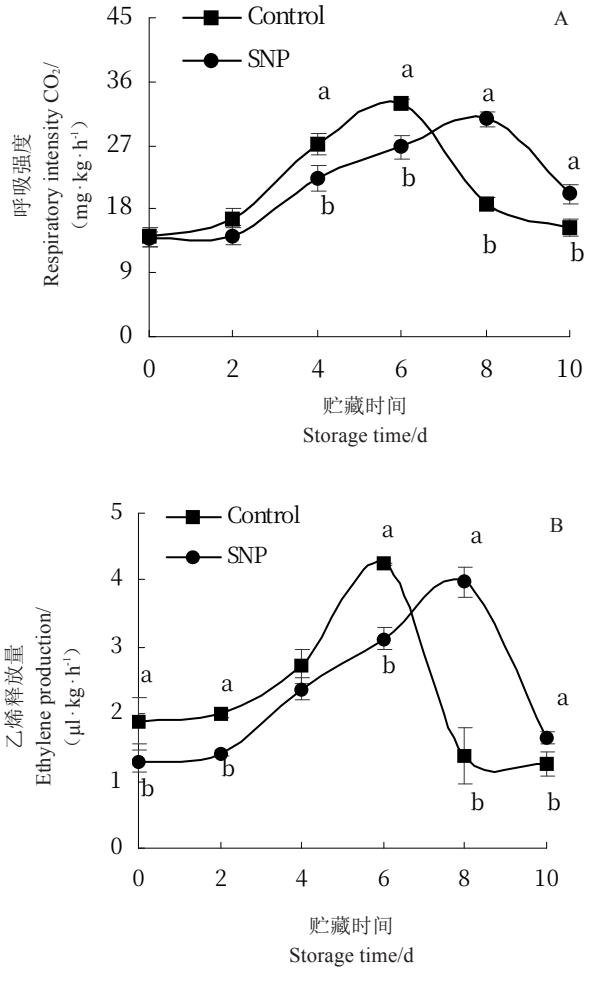


图2　采前SNP喷洒对采后果实贮藏期间呼吸速率（A）和乙烯释放量（B）的影响

Fig. 2 Effect of multiple preharvest SNP spays on respiratory intensity (A) and ethylene production (B) of harvested muskmelon fruit during storage

2.3 采前SNP喷洒对采后果实MDH和SDH活性的影响

采收时，处理和对照果实的MDH和SDH活性无显著差异。贮藏期间，处理和对照果实的MDH活性均呈现先小幅下降后逐渐上升的趋势，但处理显著高于对照，贮藏4 d时高于对照54.0%（$p < 0.05$）（图3-A）。贮藏期间，处理和对照果实的SDH活性均呈单峰型变化，但处理整体高于对照，贮藏6 d和8 d时分别高于对照43.5%和71.1%（$p < 0.05$）（图4-B）。

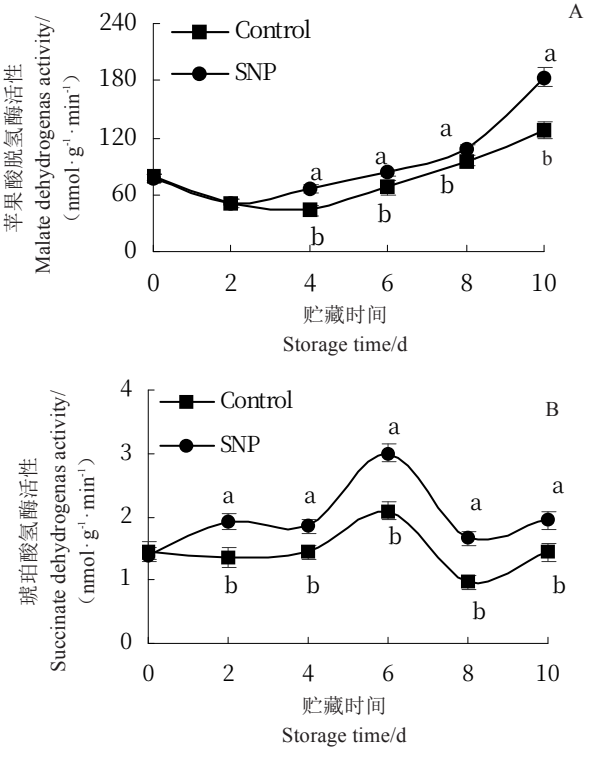


图3 采前SNP喷洒对采后果实贮藏期间苹果酸脱氢酶（A）和琥珀酸脱氢酶（B）活性的影响

Fig. 3 Effect of multiple preharvest SNP spays on the activities of MDH（A） and SDH （B） of harvested muskmelons during storage

2.4 采前SNP喷洒对采后果实ATP、ADP、AMP以及EC的影响

采收时，处理和对照果实的ATP含量无明显差异。贮藏期间，处理和对照果实的ATP含量总体呈先升高后缓慢下降再升高的趋势，但处理果实的ATP含量显著高于对照，贮藏4 d时高于同期对照73.8%（$p < 0.05$）（图4-A）。采收时，处理果实的ADP含量低于对照，但采收后却显著高于对照，贮藏4 d时高于对照2.56倍（$p < 0.05$）（图4-B）。处理和对照果实的AMP含量在采收时无明显差异。贮

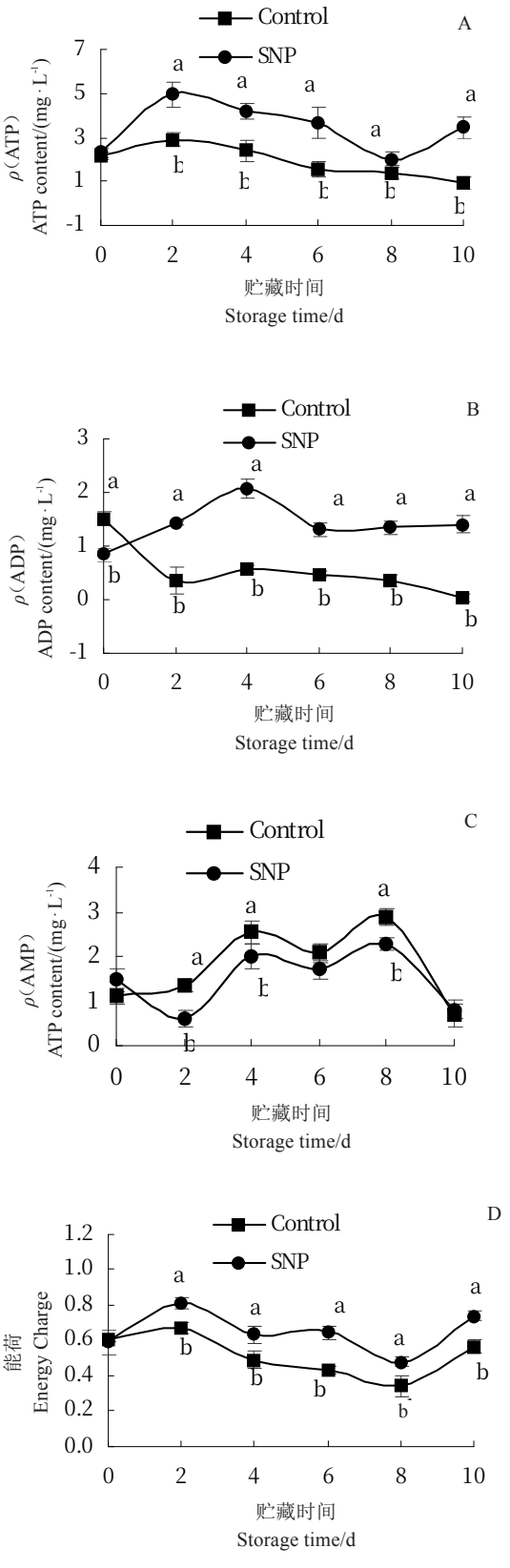


图4 采前SNP喷洒对采后果实贮藏期间ATP（A）、ADP（B）、AMP（C）含量和EC的影响

Fig. 4 Effect of multiple preharvest SNP spays on the contents of ATP（A）, ADP（B）, AMP（C）, and EC of harvested muskmelons during storage

藏期间，处理和对照果实的AMP含量均呈双峰型波动，但处理始终低于对照，贮藏8 d时低于对照20.9%（$p < 0.05$）（图4-C）。采收时处理和对照果实的EC无明显差异。贮藏期间，处理和对照果实的EC均缓慢下降，但处理显著高于对照，贮藏6 d时高于对照48.5%（$p < 0.05$）（图4-D）。

3　讨　论

作为重要的信号分子，NO能够通过延缓成熟衰老和提高能荷水平增强采后果实的抗病性[11,27]。本研究我们发现，果实发育期多次喷洒NO外源供体SNP可显著提高厚皮甜瓜果实的采后抗病性。NO采前喷洒提高厚皮甜瓜采后抗病性的现象与NO延缓果实后熟、提高MDH和SDH活性以及维持果实体内较高的能荷水平密切相关。

厚皮甜瓜属于典型的呼吸跃变型果实，完成后熟后果实迅速进入衰老阶段，导致果实对采后病害的防御能力急剧下降。在果实的成熟过程，果皮中预先形成的抗菌化合物含量的持续降低有助于潜伏侵染真菌的发展[28]，延缓成熟衰老是提高果实采后抗病性的关键因素[25]。研究表明，NO处理能够通过抑制果实乙烯的合成和减缓呼吸速率延缓果实的成熟衰老，并诱导果实的采后抗病防卫反应[29]。本研究我们发现，果实发育期SNP喷洒显著降低了厚皮甜瓜果实的呼吸速率和乙烯释放量并推迟了峰值的出现，延缓了果实的后熟，有效提高了果实的采后抗病性。该结果与前人采用NO处理在草莓[19]、杧果[12,20]、桃[21]以及苹果[22]等果实上观察到的结果基本类似。Zhu等[19]研究发现，适当浓度的SNP处理能够通过降低乙烯生物合成过程中的前体物质1-氨基环丙烷-1-羧酸（ACC）的含量和关键限速酶ACC合酶（ACC synthease，ACS）和ACC氧化酶（ACC oxidase，ACO）的活性来抑制草莓果实乙烯的生物合成并降低呼吸速率。低浓度的NO处理能抑制植物线粒体细胞色素C氧化酶的活性，而高浓度的NO会结合线粒体中呼吸酶的铁硫簇，破坏酶的结构，使其失活。因此，不同浓度的NO皆能有效的抑制呼吸作用，但前者是可逆的过程，后者则是不可逆的过程[30]。Hu等[12]应用0.1 mmol·L^{-1}的SNP也显著降低了杧果果实成熟期间乙烯释放量和呼吸速率并推迟了峰值的出现，有效提高了果实对炭疽病的采后抗性。

果实的采后抗病性与能量状态密切相关，能量的供应不足会导致果实抗病能力显著降低[31-32]。最近的研究表明，增加果实组织的ATP含量或者能荷水平有助于提高荔枝[33]、桃[34]等果实的采后抗病能力并延缓成熟衰老。果蔬细胞中许多呼吸代谢关键性酶如糖酵解、三羧酸循环的活性调节都依赖于能荷的变化，线粒体是合成ATP的重要场所，MDH和SDH均为线粒体内膜上的关键酶，MDH在三羧酸循环中至关重要，可催化苹果酸形成草酰乙酸，其活性与能量代谢密切相关，而SDH是连接氧化磷酸化与电子传递的枢纽之一，在三羧酸循环中通过催化琥珀酸转变为延胡索酸，参与ATP的合成[17]。Wang等[18]的结果表明SNP处理能显著提高香蕉果实的ATP含量、能荷水平以及线粒体关键酶SDH的活性。本研究发现，SNP处理显著的增强了MDH和SDH的活性，提高了果实贮藏期间的能荷水平，诱导了果实的采后抗病性。该结果与前人采用外源激发子处理提高枇杷[17,35]，杧果[36]，梨[37]和桃[38]等果实的能荷水平的结果类似。虽然本研究发现采前SNP多次喷洒可通过延缓后熟，激活能量代谢和提高能荷水平增强厚皮甜瓜果实的采后抗病性。但该药物对果实采后抗病性的诱导可能还涉及其他多种机制，尚待进一步揭示。

4　结　论

果实发育期多次喷洒SNP可有效诱导厚皮甜瓜果实的采后抗病性，降低果实损伤接种后的发病率。该作用与NO延缓果实后熟、提高线粒体关键酶活性以及维持较高的能荷水平密切相关。

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