文章编号：1005-0906(2021)04-0056-06 DOI: 10.13597/j.cnki.maize.science.20210408

亚精胺提高玉米幼苗抗寒性的研究

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摘　要：以玉米品种农大108为试验材料,当玉米幼苗2叶1心时,一部分在常温下(25℃/18℃)培养,另一部分在低温下(10℃/4℃)培养,以叶片喷施0.4 mmol/L亚精胺为处理组,喷施蒸馏水为对照组,研究亚精胺在玉米幼苗冷胁迫过程中的作用。结果表明,低温胁迫抑制了幼苗生长,加剧了叶片中超氧自由基和过氧化氢的产生,提高了膜脂过氧化水平,降低了叶绿素含量。叶片喷施亚精胺,显著缓解了冷胁迫导致的生长抑制、叶绿素含量下降、活性氧积累和膜脂过氧化,提高了幼苗可溶性糖和脯氨酸含量,使抗氧化酶活性显著提高。此外,亚精胺处理提高了冷胁迫条件下幼苗热激蛋白HSP70和HSP90的mRNA和蛋白表达水平。结果表明,外源亚精胺能提高玉米幼苗的抗寒性。

关键词：玉米;亚精胺;膜脂过氧化;抗氧化酶活性;热激蛋白;抗寒性

中图分类号：S513.01 **文献标识码**：A

Study on Promotion of Cold Resistance of Maize Seedlings by Spermidine

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Abstract: Spermidine(Spd) is an important plant growth regulator and plays a vital role in the environmental stress tolerance of crops. In this study, maize seedling was sprayed with 0.4 mmol/L spermidine on the two leaves and one heart leaf stage as the treatment group and distilled water as the control group. The effects of Spd against chilling stress were investigated in maize seedlings. Low temperature treatment inhibited seedling growth, while the production of superoxide radical($O_2^{\cdot-}$) and hydrogen peroxide(H_2O_2) and the level of membrane lipid peroxidation were increased, and the content of chlorophyll was decreased in chilled maize leaves. However, leaves spraying with Spd markedly alleviated chilling stress-induced growth inhibition, chlorophyll content decrease, ROS accumulation and membrane lipid peroxidation. The content of soluble sugar and proline in seedlings was increased.The antioxidant enzymes avtivities were significantly enhanced in Spd supplied seedlings under chilling condition. In addition, we found that spermidine treatment increased mRNA and protein expression levels of heat shock proteins HSP70 and HSP90 in seedlings under cold stress. In conclusion, exogenous spermidine could improve the cold resistance of maize seedling.

Key words: Maize; Spermidine; Membrane lipid peroxidation; Antioxidant enzymes avtivities; Heat shock proteins; Cold resistance

玉米(*Zea mays* L.)属禾本科玉米属,我国玉米产区主要位于北方地区。对低温非常敏感的玉米幼苗,在自然条件下生长,在高于冰点但低于12℃的温度下,常常会出现生理生化功能紊乱,称为冷害[1,2]。冷害是影响玉米生长发育、产量和品质的主要限制因素之一[3]。冷寒的发生在很大程度上与活性氧(ROS)如超氧自由基($O_2^{\cdot-}$)、羟基自由基(·OH^-)和过氧化氢(H_2O_2)的产生有关[4]。ROS的过度积累会导致脂质过氧化、组织损伤甚至细胞死亡。农作物已经进化出抗氧化系统,包括抗氧化酶和非酶抗氧化系统,以防止或减轻ROS的损害[5]。热激蛋白(HSPs)

录用日期：2020-10-12

基金项目：江苏高校优势学科建设工程三期资助项目

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是重要的分子伴侣,在许多正常的细胞过程中负责蛋白质的折叠、组装、易位和降解,稳定蛋白质和膜,并在应激条件下协助蛋白质重新折叠[6],表明HSPs与高等植物对温度胁迫(包括低温胁迫)的适应反应有关[7]。提高作物抗逆性可以提高作物产量,提高植物抗逆性的方法之一是使用化学物质或生长调节剂进行外源处理,这些化学物质或生长调节剂已被证明能够有效缓解应激诱导的损伤[8]。多胺(Polyamines,PAs)是植物体代谢过程中产生的一类具有生物活性的小分子量脂肪族含氮碱,腐胺(二胺,Putrescine,Put)、亚精胺(三胺,Spermidine,Spd)和精胺(四胺,Spermine,Spm)是植物体内最常见的3种多胺[9]。多胺参与了植物的多种功能,如刺激细胞分裂、调节生长发育、延缓植物衰老、提高植物抗逆性等[10,11]。研究表明,非生物胁迫,包括干旱、盐、热、缺氧、UV-B、重金属、机械伤害可以导致PAs的积累[12,13]。大量证据表明,外源施用PAs可以保持植物细胞膜的完整性,降低应激引起的生长抑制,增加抗氧化酶活性,减少ROS积累[14,15]。PAs也被证明可以介导植物对低温胁迫的抗性[16]。本文研究外源亚精胺对玉米幼苗抗寒性的影响,为生产上应用亚精胺提高玉米幼苗的抗寒性提供理论依据。

1　材料与方法

1.1　试验设计

试验用玉米品种为农大108。将玉米种子于蒸馏水中28°C条件下浸泡24 h,然后将玉米种子播种于塑料钵中,钵中土壤为花园土壤和蛭石的混合物(二者比例2:1),每钵5粒种子。将塑料钵置于温室中,温室条件,光强160 μmol/(m^2·s)PAR,光周期16 h/8 h,昼夜温度25℃/18℃,相对湿度70%。当幼苗2叶1心时,以叶片喷施0.4 mmol/L[17]亚精胺为处理组,叶片喷施蒸馏水为对照组,喷洒时以叶片湿润而不滴水为度。1 d喷施1次,连续喷施3 d。然后将处理组和对照组幼苗分成两部分,一部分放在常温下(25℃/18℃)培养,另一部分放在低温下(10℃/4℃)培养。生理生化指标的测定在处理3 d后进行,每个指定测定3个重复。

1.2　测定指标与方法

玉米幼苗叶片中超氧阴离子原位定位染色采用氮蓝四唑(NBT)组织染色法[18],在过氧化物酶存在时,H_2O_2与二甲基联苯胺(DAB)反应生成深棕色的多聚产物,根据颜色深浅判断过氧化氢的含量[19];电解质渗出率的测定依据Sun等的方法[20]进行,并做了一些修改,取离体叶片0.5 g,在25℃的双蒸馏中浸泡2 h,测定电导率(C1),然后在95℃下加热1 h,测量叶片的总电导率(C2),质膜相对透性以MP=C1/C2×100%表示;叶绿素含量的测定采用Arnon法[21];MDA含量按照Liu等报道的方法测定;游离脯氨酸含量按Bates等的茚三酮法[22]测定;用蒽酮法[23]测定可溶性糖含量。

取叶片0.5 g,在液氮中研磨成粉末,然后加入2 mL(pH值7.0) 50 mmol/L磷酸盐缓冲液[内含1 mmol/L EDTA和1%聚乙烯吡咯烷酮(PVP)],4℃,10 000 r/min离心20 min,取上清测定抗氧化酶的活性。超氧化物歧化酶(SOD)活性按王爱国等的方法[24]测定;抗坏血酸过氧化物酶(APX)的活性按王学奎的方法[25]测定;过氧化氢酶(CAT)活性按南京建成生物工程公司试剂盒说明进行测定;谷胱甘肽还原酶(GR)活性的测定根据Schaedle的方法[26]进行;HSP70和HSP90的mRNA和蛋白表达的测定按Liu的方法进行。

用SPSS17.0数据处理系统对试验数据进行统计分析。

2　结果与分析

2.1　亚精胺对低温胁迫下玉米幼苗生长的影响

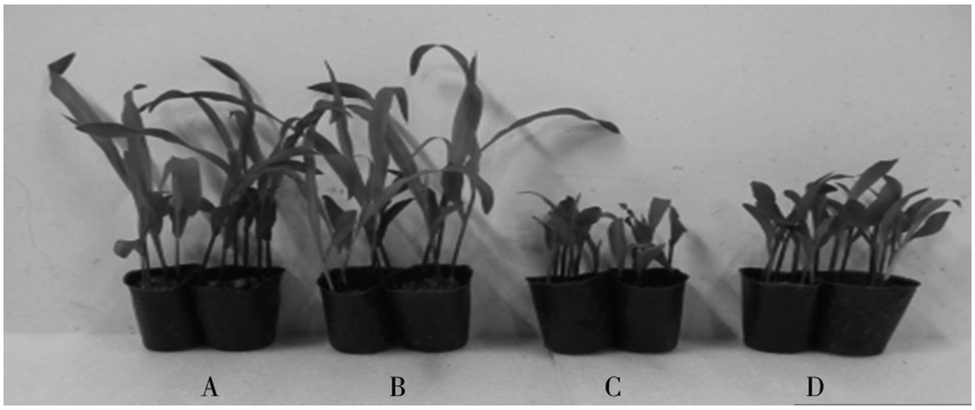
低温胁迫使玉米幼苗植株矮小,生长受到抑制,叶片变紫,边缘呈水渍状,随着胁迫时间的延长,叶片叶缘出现萎蔫症状或出现冻害斑点(图1)。亚精胺可以缓解低温胁迫对玉米幼苗生长的抑制作用。低温胁迫显著降低了玉米幼苗叶片的干重(表1),亚精胺处理缓解了冷胁迫导致的玉米叶片干重的下降。

2.2　亚精胺对低温胁迫下玉米幼苗叶片超氧阴离子和过氧化氢的影响

亚精胺对正常温度条件下生长的玉米叶片中超氧阴离子和过氧化氢含量的影响不明显(图2、图3)。低温胁迫使玉米幼苗叶片中超氧阴离子和过氧化氢含量增加,亚精胺处理可使玉米幼苗叶片中超氧阴离子和过氧化氢积累减少,表明亚精胺可减少低温胁迫下玉米叶片中超氧阴离子和过氧化氢的积累。

2.3　亚精胺对低温胁迫下玉米幼苗叶片生理生化指标的影响

低温胁迫显著降低了玉米幼苗叶片的叶绿素含量,显著提高了电解质外渗、MDA含量、脯氨酸含量、可溶性糖含量(表1),导致抗氧化酶SOD、APX和CAT活性明显升高。亚精胺处理缓解了冷胁迫导致的玉米叶片叶绿素含量的下降,降低了电解质外渗和MDA含量,提高了玉米幼苗叶片脯氨酸和可溶性糖含量,显著提高了抗氧化酶SOD、CAT和GR的活性。



注:A为常温+蒸馏水;B为常温+亚精胺;C为低温+蒸馏水;D为低温+亚精胺。下图同。

Note: A, Normal temperature + Distilled water(ND); B, Normal temperature + Spermidine(NP); C, Low temperature + Distilled water(LD); D, Low temperature+ Spermidine(LP). The same below.

图1 亚精胺对低温胁迫下玉米幼苗生长的影响

Fig.1 Effect of spermidine on the growth of maize seedlings under low temperature stress

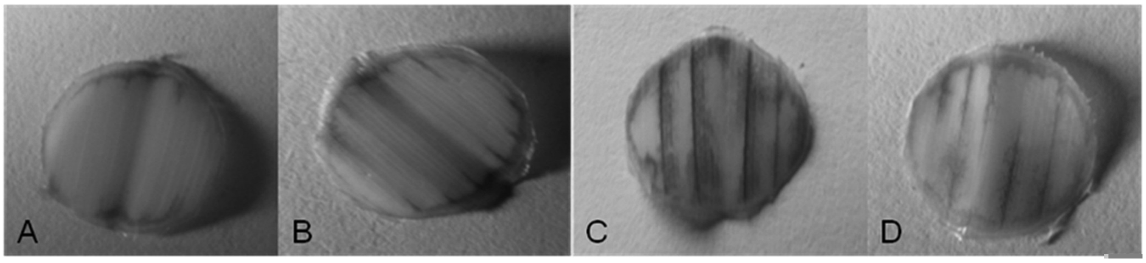


图2 亚精胺对低温胁迫下玉米叶片中超氧阴离子含量的影响

Fig.2 Effect of spermidine on super oxygen anion content in maize seeding leaves under low temperature stress

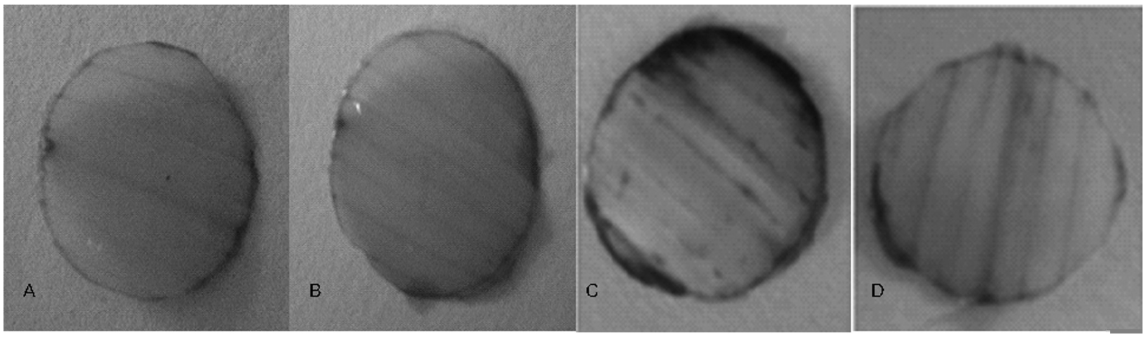


图3 亚精胺对低温胁迫下玉米幼苗叶片过氧化氢含量的影响

Fig.3 Effect of spermidine on hydrogen peroxide content in maize seedling leaves under low temperature stress

表1 亚精胺对低温胁迫下玉米幼苗叶片生理生化指标的影响

Table 1 Effect of spermidine on leaf dry weight, electrolyte leakage, MDA, chlorophyll, soluble sugar, proline, antioxidant enzymes activity in maize seeding leaves under low temperature stress

测量指标 Measurement	常温+蒸馏水 ND	常温+亚精胺 NP	低温+蒸馏水 LD	低温+亚精胺 LP
干重(g)	1.34±0.12 a	1.41±0.09 a	0.66±0.07 c	1.08±0.08 b
电解质渗出率(%)	16.50±3.10 c	17.30±2.50 c	51.80±5.30 a	29.20±4.20 b
丙二醛含量(nmol/g·FW)	4.31±0.42 d	3.81±0.41 d	14.50±1.40 a	8.35±0.98 c
叶绿素含量(mg/g·FW)	1.67±0.12 a	1.69±0.14 a	0.71±0.21 c	1.26±0.24 b

续表1　Continued 1

测量指标 Measurement	常温+蒸馏水 ND	常温+亚精胺 NP	低温+蒸馏水 LD	低温+亚精胺 LP
可溶性糖含量(mg/g·FW)	1.81±0.11 d	1.94±0.15 d	4.54±0.46 c	7.14±0.32 a
脯氨酸含量(μg/g·FW)	60.10±5.12 d	66.20±4.98 d	80.40±7.040 c	109.00±8.65 a
超氧化物歧化酶活性(U/mg·protein)	176.30±13.30 c	188.50±11.20 c	250.60±14.80 b	332.40±24.50 a
抗坏血酸过氧化物酶[nmol ASA/(min·mg·protein)]	155.00±21.40 c	192.00±17.20 b	202.00±31.10 ab	249.00±20.50 a
过氧化氢酶活性[nmol H_2O_2/(min·mg·protein)]	809.40±98.20 d	839.20±89.40 d	1 178.40±143.40 c	1 754.70±157.20 a
谷胱甘肽还原酶活性[nmol NADPH/(min·mg·protein)]	46.30±8.10 a	55.40±5.20 b	46.70±4.60 a	61.20±6.20 bc

注:同一行内不同字母代表差异显著性(P<0.05)。

Note: Different letters in the same line represent significant differences(P<0.05).

2.4　亚精胺对低温胁迫下玉米幼苗叶片HSP70 mRNA、HSP90 mRNA和蛋白表达的影响

HSPs被认为是冷胁迫早期反应的关键元素,因此进一步检测Hsp70和Hsp90这两种HSPs的基因表达和蛋白含量。RT-PCR和western blot结果表明,冷害增强了玉米叶片Hsp70和Hsp90基因表达和蛋白质含量的提高(图4、图5)。亚精胺处理显著提高了冷胁迫下玉米叶片中Hsp70和Hsp90的基因表达水平和蛋白含量。

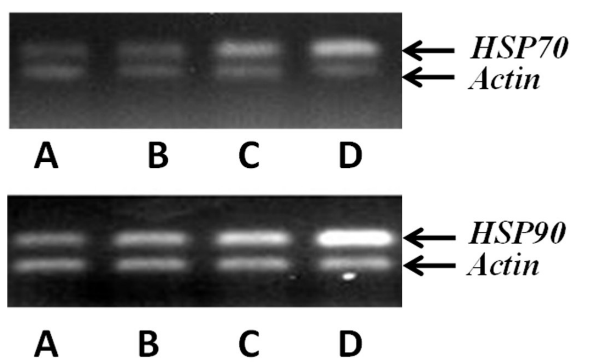


图4　亚精胺对低温胁迫下玉米幼苗叶片HSP70 mRNA和HSP90 mRNA表达的影响

Fig.4　Effect of spermidine on HSP70 mRNA and HSP90 mRNA expression in maize seeding leaves under low temperature stress

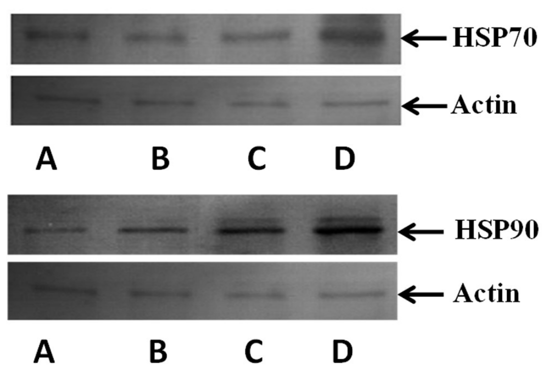


图5　亚精胺对低温胁迫下玉米幼苗叶片HSP70和HSP90蛋白表达的影响

Fig.5　Effect of spermidine on HSP70 and HSP90 protein expression in maize seeding leaves under low temperature stress

3　结论与讨论

低温胁迫通常会导致玉米生长受到抑制,光合能力下降,甚至导致细胞死亡,从而导致玉米产量的极大损失。本研究表明,低温胁迫下玉米叶片的干重和叶绿素含量显著下降,表明光合系统受损,固碳能力下降。在冷害玉米叶片中也观察到O_2^-和H_2O_2的含量明显提高,表明冷害导致活性氧(ROS)大量产

生[27]。与ROS含量上升对应的是，在冷胁迫下，玉米叶片的脂质过氧化升高，表现为电解质的渗漏和MDA含量的增加。因此，为了应对氧化应激诱导的损伤，玉米叶片中APX、SOD和CAT等抗氧化酶的活性被上调。

已有研究表明，亚精胺在介导植物对低温胁迫的反应中发挥了重要作用。亚精胺合成酶的过表达增强了转基因拟南芥对低温胁迫的耐受性。Shen[28]报道，亚精胺作为一种细胞膜稳定剂，通过抑制黄瓜NADPH氧化酶的活性，对抗由低温引起的脂质过氧化。本研究发现，亚精胺提高了冷害胁迫下玉米叶片的干重和叶绿素含量，这说明亚精胺可提高玉米幼苗的抗冷性[29,30]。在冷胁迫条件下，亚精胺显著提高了SOD、APX、CAT和GR的活性。较高的SOD活性可以催化超氧化物生成氧和H_2O_2，较高的CAT活性可以快速去除H_2O_2。这两种酶在细胞的不同部位，如叶绿体、线粒体和细胞质提供了抗氧化应激的第一道防线，除了使用抗坏血酸作为还原剂直接清除H_2O_2外，APX活性的提高有助于促进AsA-GSH循环，并在维持植物中非常重要的非酶抗氧化剂AsA的含量中发挥重要作用[31]。GR通过催化氧化型谷胱甘肽(GSSG)还原为还原型谷胱甘肽(GSH)，在植物细胞抗氧化应激中发挥重要作用。较高的GR活性有助于玉米叶片中GSSG还原为GSH。因此，亚精胺处理能诱导SOD、APX、CAT和GR的共同作用，从而有效地降低冷害胁迫下玉米幼苗叶片中高毒性超氧化物和羟自由基的形成和脂质过氧化。

热激蛋白负责蛋白质的折叠和组装，稳定蛋白质和细胞膜，并在胁迫条件下协助蛋白质重新折叠，重建细胞稳态，在植物抵御非生物胁迫中发挥关键作用。本研究发现，冷胁迫上调了两种热休克蛋白HSP70和HSP90的基因表达和蛋白丰度，表明热激蛋白是低温诱导植物表达的基因的一部分[32]。本研究表明，在低温条件下，亚精胺处理显著提高了HSP70和HSP90的基因表达水平和蛋白丰度，亚精胺预处理可以在长时间涝渍胁迫下保持玉米根系中较高的Hsp70和Hsp90丰度。热激蛋白本身可能参与保护细胞免受氧化应激[33]，因此Hsp70和Hsp90的增加能保护玉米叶片在低温胁迫下免遭细胞损伤。

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