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二烯丙基二硫对大白菜自毒作用的缓解效应

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摘要 为探究二烯丙基二硫(diallyl disulfide, DADS)对大白菜自毒作用的缓解效应, 以大白菜品种‘金麒麟’为试验材料, 利用水培试验设置6组处理: CK1(1/2 Hoagland营养液)、CK2(重茬液处理)、D1(1 μmol/L DADS+重茬液)、D5(5 μmol/L DADS+重茬液)、D10(10 μmol/L DADS+重茬液)、D15(15 μmol/L DADS+重茬液), 每个处理设置12个组培瓶, 每个培养瓶培养4株幼苗, 共48株幼苗, 测定不同处理下大白菜幼苗生长性状、生理生化指标。结果显示, 施用不同浓度DADS对自毒作用下大白菜幼苗的生长均具有促进作用, 以5 μmol/L DADS缓解效果最好; 与CK2大白菜重茬液处理相比, D5(5 μmol/L DADS)处理大白菜幼苗的地上与地下部鲜质量分别显著增加19.42%和23.40%, 根系活力显著增加45.29%, 总根长和根尖数也随之增加, 减轻了自毒作用对根系结构的损伤; 同时叶片叶绿素含量增加; 与CK2处理相比, 大白菜幼苗的渗透调节物质含量明显增加, 抗氧化酶SOD、POD和CAT活性分别增加30.75%、27.44%和17.68%, MDA含量显著降低20.58%; 组织学染色显示, D5处理过氧化氢和超氧阴离子的积累明显减少。综上, 外源施用DADS可通过降低氧化胁迫, 促进根系生长, 从而有效地缓解大白菜根系分泌物的自毒作用, 以施加5 μmol/L DADS的缓解效应最显著。

关键词 大白菜; 根系分泌物; 自毒作用; 连作障碍; 二烯丙基二硫

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大白菜(*Brassica rapa* L. ssp. *pekinensis*), 原产于中国, 栽培历史悠久, 种植面积与市场销量大, 是我国第二大蔬菜作物^[1], 具有耐储运、食用方式多样以及营养丰富的特点, 深受人们的喜爱。近年因为连茬种植以及区域化的种植习惯, 导致连作障碍严重发生, 病虫害加剧、生长缓慢, 严重影响大白菜的产量品质和经济效益。研究表明, 造成其连作障碍的主要原因之一是根系分泌物产生的自毒作用^[2]。

在特定时刻, 植物的生长发育能与环境因子发生相互作用, 化感作用(allelopathy)是指植物向环境中释放化学物质对自身或其他动植物以及微生物受体的生长发育产生有利或不利的影响, 这类化学物质称作化感物质^[3]。化感物质会影响植物体的细胞结构、各项生理代谢过程以及土壤理化性质。自毒作用(autotoxicity)作为化感作用的一种特殊形式, 是

指植物根系分泌或植株残茬降解后向环境中释放化学物质, 严重危害自身或者种内植物, 同时也是植物适应种内竞争的表现^[4]。二烯丙基二硫(diallyl disulfide, DADS)是大蒜素分解后的有机硫化合物, 广泛存在于大蒜根系分泌物、鳞茎提取物以及地上部挥发物中^[5-7]。DADS是大蒜根系分泌物和秸秆水浸提液中的主要化感物质^[5-6]。利用GC-MS技术鉴定青蒜挥发物主要成分是DADS, 适当浓度的青蒜挥发物与DADS对黄瓜幼苗的生长有促进作用^[7]。DADS可调控植物的抗氧化酶活性和非酶类活性物质, 清除活性氧, 发挥抗氧化保护作用, 最终缓解非生物胁迫造成的膜脂过氧化^[8]。DADS可通过调节番茄内源激素含量和*EXP*s基因表达来调控根系生长和叶绿素含量, 提高POD、SOD与PAL酶活性, 调控GSSG与GSH代谢, 进而提高植株抗性; 同时还可改变番茄根系分泌物含量来缓解连作障碍^[9]。

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DADS处理黄瓜可使根系有丝分裂相关基因 $CDKA$ 和 $CDKB$ 表达上调,调控根系内源激素含量,促进根系生长^[10]。

关于DADS影响黄瓜、番茄等作物的生长生理代谢过程已有相关研究,而在芸薹属蔬菜上,外源施加DADS对大白菜自毒作用缓解效应尚不清楚。为探究DADS对大白菜自毒作用的缓解效应,本研究利用水培试验,设置6组DADS浓度处理,测定各处理大白菜幼苗的生长性状、生理指标,并通过组织染色显示过氧化氢和超氧阴离子积累情况,探讨DADS对大白菜幼苗自毒作用的影响机制,以期为大白菜绿色生产提供理论依据和参考。

1 材料与方法

1.1 试验材料

供试大白菜品种为‘金麒麟’,购于河北慕兰多种子有限公司。DADS和Hoagland营养液,购于上海麦克林有限公司。

1.2 大白菜水培重茬液的收集

大白菜种子于25℃下催芽1 d,之后将幼芽放入PCR板孔中,将其漂浮于1/4 Hoagland营养液中进行适应性培养7 d,移入1/2 Hoagland营养液的组培瓶中,每个培养瓶装入200 mL营养液培养4株大白菜幼苗。组培瓶外包锡箔纸避光,移入组培室进行培养。培养条件设为25℃ 6 000 lx光照14 h/19℃黑暗10 h,每周调节1次pH值,使pH保持在5.8~6.5,培养20 d后,调节培养瓶中营养液至200 mL,收集大白菜水培重茬培养液备用。

1.3 试验设计

催芽的大白菜植物材料在1/4 Hoagland营养液中适应性培养7 d,再使用1/2 Hoagland营养液与上述收集的重茬液分别处理5 d。之后向重茬液中加入不同浓度DADS,共设置6组处理:CK1(1/2 Hoagland营养液)、CK2(重茬液处理)、D1(1 μmol/L DADS+重茬液)、D5(5 μmol/L DADS+重茬液)、D10(10 μmol/L DADS+重茬液)、D15(15 μmol/L DADS+重茬液),每个处理设置12个组培瓶,每个培养瓶培养4株幼苗,共48株幼苗。每周调节pH值保持在5.8~6.5,期间每间隔4 d向组培瓶中加入等量1/2 Hoagland营养液。DADS处理10 d后进行取样并保存于-80℃冰箱中备用。

1.4 测定性状与方法

1)生长性状。将大白菜幼苗置于含少量清水的

培养皿中,拍照记录植株的生长情况。测量最大叶长、最大叶宽、株幅、地上部鲜质量和地下部鲜质量,再将植株的地上部和地下部放入信封中,并置于105℃的烘箱中杀青20 min,之后立即降低烘箱温度,维持在75℃,直到样品烘干至恒质量,用电子天平称量植株地上部干质量和地下部干质量。

2)根系性状。采用氯化三苯基四氮唑(TTC)法测定根系活力^[11];用清水洗净植株根系后进行扫描(根系扫描仪WinRhizo Basic03040415),在托盘内加入一定量的蒸馏水,将洗净完整的根系放入托盘中,使其平展后开始扫描,扫描后保存图片并分析总根长、根表面积以及根体积等形态性状。

3)生理性状。参照文献[11],利用96%乙醇研磨提取比色的方法测定叶绿素含量;采用考马斯亮蓝法测定叶片可溶性蛋白含量;采用酸性茚三酮比色法测脯氨酸含量;采用蒽酮比色法测可溶性糖含量;采用硫代巴比妥酸法测丙二醛(MDA)含量;采用氯化硝基四氮唑(NBT)光化还原法测超氧化物歧化酶(SOD)活性;采用愈创木酚比色法测过氧化物酶(POD)活性;采用紫外吸收比色法测过氧化氢酶(CAT)活性。

采用DAB组织化学染色法观察过氧化氢累积含量^[12],NBT组织化学染色法观察超氧阴离子累积含量^[13]。

1.5 数据处理

采用Microsoft Excel 2016软件进行数据整理及图表绘制,使用IBM-SPSS 24.0软件one-way ANOVA单因素方差分析方法对试验数据进行差异显著性分析。

2 结果与分析

2.1 外源DADS对自毒作用下大白菜幼苗生长的影响

由图1可见,与CK2重茬液处理相比,添加不同浓度DADS处理后的幼苗叶片大小及根系生长情况均得到改善,其中D5处理(5 μmol/L DADS)植株叶面积、总根长及根系数目增加明显。在重茬液中添加DADS可以缓解自毒作用对幼苗的伤害,且在5 μmol/L DADS处理下效果最好。

由表1可知,CK2处理比CK1处理大白菜幼苗株幅、最大叶宽和最大叶长分别显著降低了30.03%、39.90%和38.33%,地下部鲜质量和干质量分别显著降低了30.85%和20.00%。施用DADS后,均可促

进大白菜幼苗生长,随着DADS处理浓度增加呈现先上升后下降的趋势。D1、D5、D10和D15处理的地上部鲜质量分别较CK2处理增加了13.42%、19.42%、9.71%和3.53%;D1、D5和D10处理地下

部鲜质量较CK2处分别显著增加11.70%、23.40%和12.77%;D5处理对幼苗株幅、最大叶宽和最大叶长的促进作用达到最大值,分别比CK2处理增加了22.81%、20.93%和21.20%。

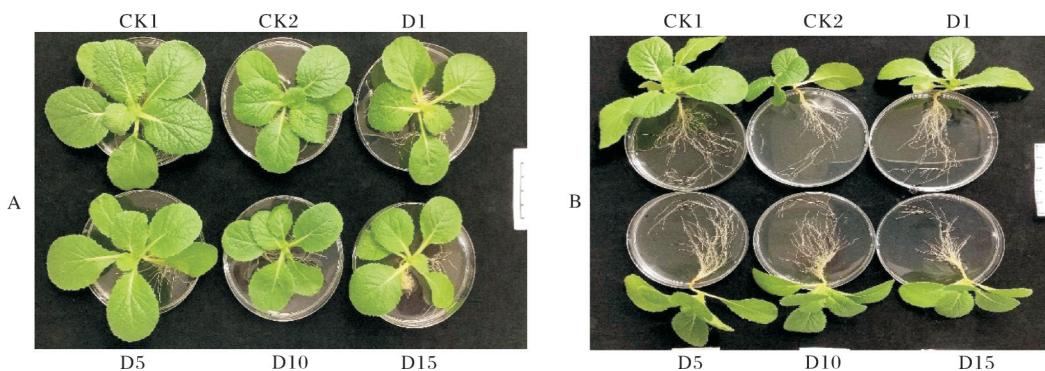


图1 外源DADS对自毒作用下大白菜幼苗叶片(A)和根系(B)的影响

Fig. 1 Effects of exogenous DADS on blade (A) and rootsy (B) of Chinese cabbage seedling under autointoxication

表1 外源DADS对自毒作用下大白菜幼苗生长的影响

Table 1 Effects of exogenous DADS on the growth of Chinese cabbage seedling under autointoxication

| 处理 Treat- ments | 地上部鲜质量/ (g/plant) Shoot fresh weight | 地上部干质量/ (g/plant) Shoot dry weight | 地下部鲜质量/ (g/plant) Root fresh weight | 地下部干质量/ (g/plant) Root dry weight | 株幅/cm Crown diameter | 最大叶宽/cm Maximum leaf width | 最大叶长/cm Maximum leaf length |
|-----------------------|---|--|--|---|-------------------------|----------------------------------|-----------------------------------|
| CK1 | 1.521±0.072a | 0.147±0.009a | 0.123±0.005a | 0.0124±0.0007a | 11.470±0.369a | 3.864±0.151a | 5.089±0.184a |
| CK2 | 1.133±0.044e | 0.104±0.006d | 0.094±0.006c | 0.0102±0.0006c | 8.821±0.167e | 2.762±1.112d | 3.679±0.106d |
| D1 | 1.285±0.072bc | 0.118±0.003bc | 0.105±0.003b | 0.0107±0.0004bc | 10.403±0.230bc | 3.166±0.101bc | 4.280±0.093b |
| D5 | 1.353±0.053b | 0.126±0.005b | 0.116±0.002a | 0.0118±0.0003ab | 10.833±0.274b | 3.340±0.036b | 4.459±0.077b |
| D10 | 1.243±0.034cd | 0.112±0.005cd | 0.106±0.004b | 0.0109±0.0006bc | 10.000±0.415cd | 2.978±0.173cd | 3.945±0.147c |
| D15 | 1.173±0.021de | 0.104±0.004d | 0.095±0.006c | 0.0103±0.0006c | 9.517±0.240d | 2.943±0.146cd | 3.848±0.079cd |

注:表中同列各个数据后不同小写字母表示差异显著水平($P<0.05$)。下同。Note: In the table, data with different lowercase letters indicated significant differences among the treatments ($P<0.05$). The same as below.

2.2 外源DADS对自毒作用下大白菜幼苗根系的影响

由图2可见,重茬液处理(CK2)显著抑制大白菜根系生长(根直径除外),外源DADS处理可以不同程度促进大白菜幼苗根系的生长,随着外源DADS处理浓度增大均呈现先上升再降低的趋势,D1、D5、D10、D15处理显著高于CK2处理各性状,且D5处理下各性状均达到峰值,根系活力、总根长、根表面积、根体积、根尖数、根系分枝数、根系交叉数分别比CK2处理提高了45.29%、34.41%、42.60%、53.45%、50.00%、57.79%、48.30%。施用DADS的各处理根部直径与CK2处理无显著差异。

2.3 外源DADS对自毒作用下大白菜幼苗叶绿素含量的影响

外源DADS处理对自毒作用下大白菜幼苗的叶绿素含量测定结果(表2)显示,CK2处理的叶绿素含

量均显著低于CK1处理,施加外源DADS后幼苗叶绿素含量先升后降,总体高于CK2,其中D5处理作用最好,大白菜幼苗叶绿素a、叶绿素b、类胡萝卜素和叶绿素(a+b)分别比CK2处理提高18.97%、20.39%、17.16%和19.42%。

2.4 外源DADS对自毒作用下大白菜幼苗渗透调节物质和MDA含量的影响

由图3可见,施用DADS后,对比CK2处理,大白菜叶片可溶性蛋白、可溶性糖和脯氨酸含量随浓度增加呈先升后降趋势,以D5处理(5 μmol/L)最高,其可溶性蛋白、可溶性糖和脯氨酸含量分别高于CK2处理12.97%、16.72%和36.63%。

自毒作用导致CK2处理的大白菜幼苗MDA含量比CK1显著升高,而外源施用DADS均可降低MDA积累,随浓度增加呈先降后升趋势,D1、D5和D10处理的MDA含量分别比CK2处理降低了8.96%、20.58%

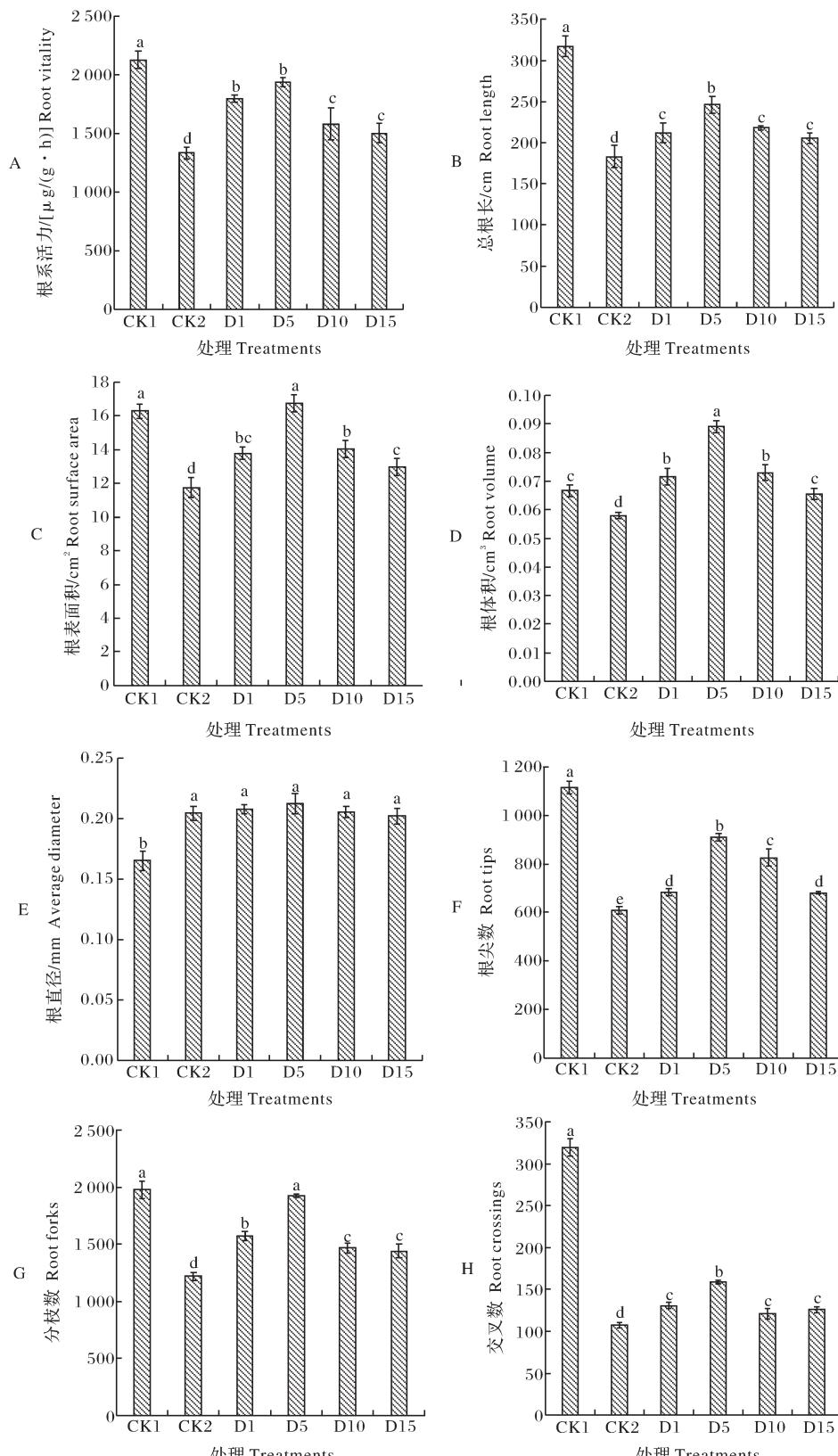


图2 各处理大白菜幼苗的根系活力(A)、总根长(B)、根表面积(C)、根体积(D)、根直径(E)、根尖数(F)、分枝数(G)和交叉数(H)

Fig. 2 Roots vitality(A), total length(B), surface area(C), volume(D), diameter(E), tips(F), forks(G) and crossings(H) of the Chinese cabbage seedling under different treatments

表2 不同处理大白菜幼苗叶绿素含量

Table 2 Chlorophyll content of Chinese cabbage seedling under different treatments

mg/g

| 处理 Treatment | 叶绿素a含量 Chlorophyll a content | 叶绿素b含量 Chlorophyll b content | 类胡萝卜素含量 Carotenoid content | 叶绿素(a+b)含量 Chlorophyll (a+b) content |
|-----------------|---------------------------------|---------------------------------|-------------------------------|---|
| CK1 | 1.193±0.021a | 0.423±0.004a | 0.232±0.004a | 0.809±0.011a |
| CK2 | 0.870±0.012e | 0.304±0.005e | 0.169±0.008d | 0.587±0.007e |
| D1 | 0.988±0.019c | 0.350±0.008bc | 0.186±0.005c | 0.669±0.013c |
| D5 | 1.035±0.035b | 0.366±0.015b | 0.198±0.006b | 0.700±0.025b |
| D10 | 0.962±0.021cd | 0.338±0.008cd | 0.178±0.002cd | 0.650±0.014cd |
| D15 | 0.935±0.012d | 0.326±0.002d | 0.181±0.007c | 0.631±0.007d |

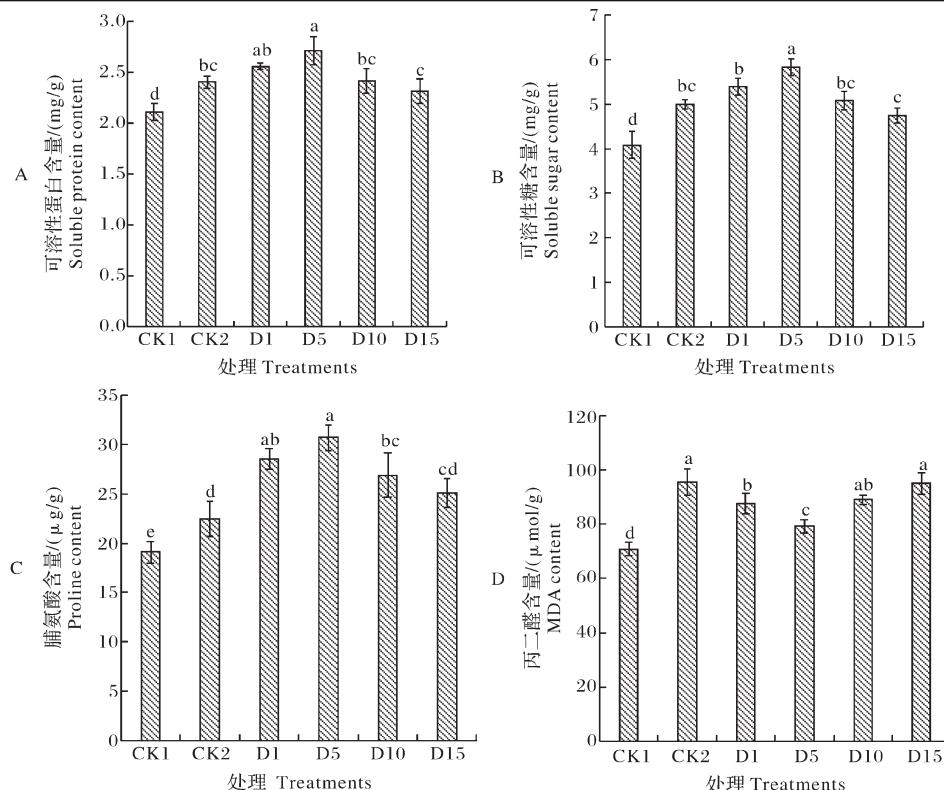


图3 不同处理大白菜幼苗渗透调节物质和MDA含量

Fig. 3 The osmotic regulation substances and the MDA content of Chinese cabbage seedling under different treatments

和7.32%，其中D5处理降低最显著(图3D)。

2.5 外源DADS对自毒作用下大白菜幼苗抗氧化酶活性的影响

大白菜幼苗各处理抗氧化酶活性测定结果如图4所示,对比CK2处理,施用DADS后大白菜幼苗抗氧化酶活性随处理浓度增加呈先升后降趋势,以D5处理($5 \mu\text{mol/L}$)最高,其SOD、POD和CAT活性比CK2分别增加了30.75%、27.44%和17.68%。

2.6 外源DADS对自毒作用下大白菜幼苗活性氧积累的影响

DAB组织化学染色结果(图5)显示,CK2处理比CK1的叶片染色深,棕褐色沉淀面积明显增加,过氧

化氢累积含量较高;重茬液中添加不同浓度DADS后,棕褐色沉淀程度比CK2浅及面积小,随浓度增加呈现先浅后深的趋势,以D5处理($5 \mu\text{mol/L}$ DADS)棕褐色沉淀最浅,说明过氧化氢累积含量最少。NBT可与超氧阴离子反应生成蓝紫色沉淀物质,用于观察植物组织中的超氧阴离子的积累情况。蓝紫色沉淀物质越多,说明超氧阴离子积累量越多。CK2处理比CK1处理染色程度加深,蓝紫色斑点明显增加,表明超氧阴离子积累量较多;重茬液中添加不同浓度DADS后,棕褐色沉淀程度比CK2浅及面积小,随浓度增加呈现先浅后深的趋势,D5处理蓝紫色沉淀明显减少,斑点颜色减轻,活性氧积累明显降低(图5)。

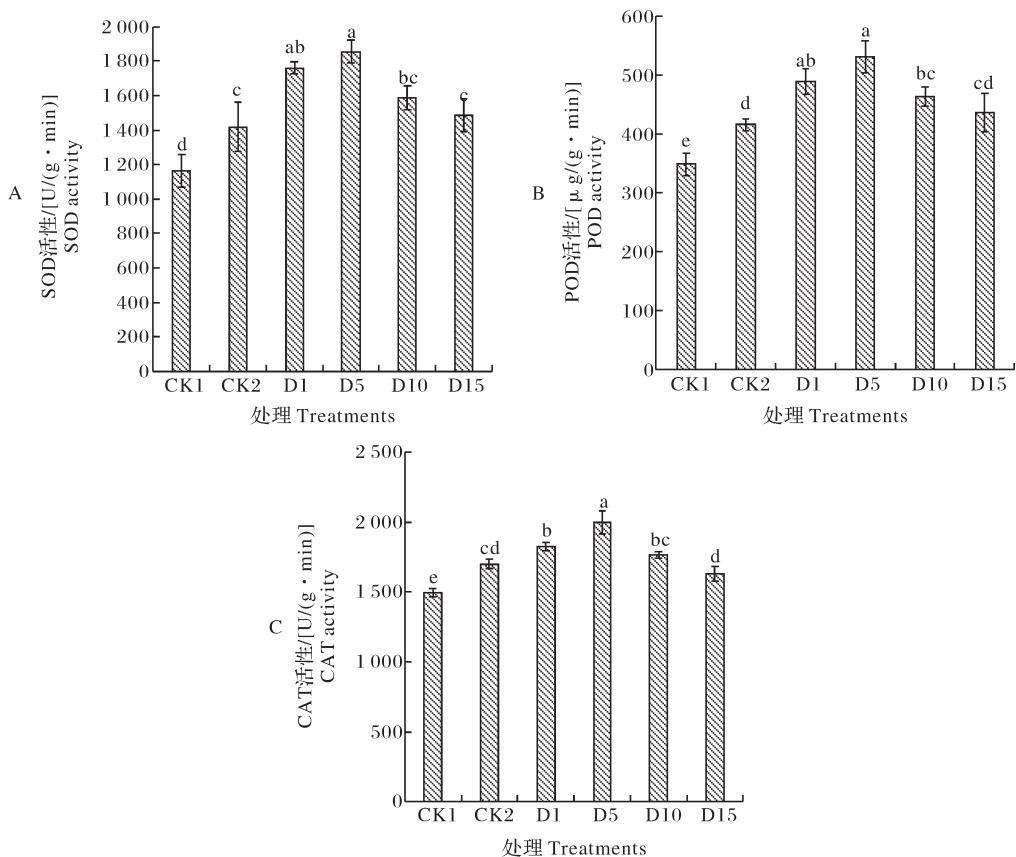


图4 不同处理大白菜幼苗SOD(A)、POD(B)和CAT(C)活性

Fig. 4 SOD(A), POD(B) and CAT(C) activities of Chinese cabbage seedling under different treatments

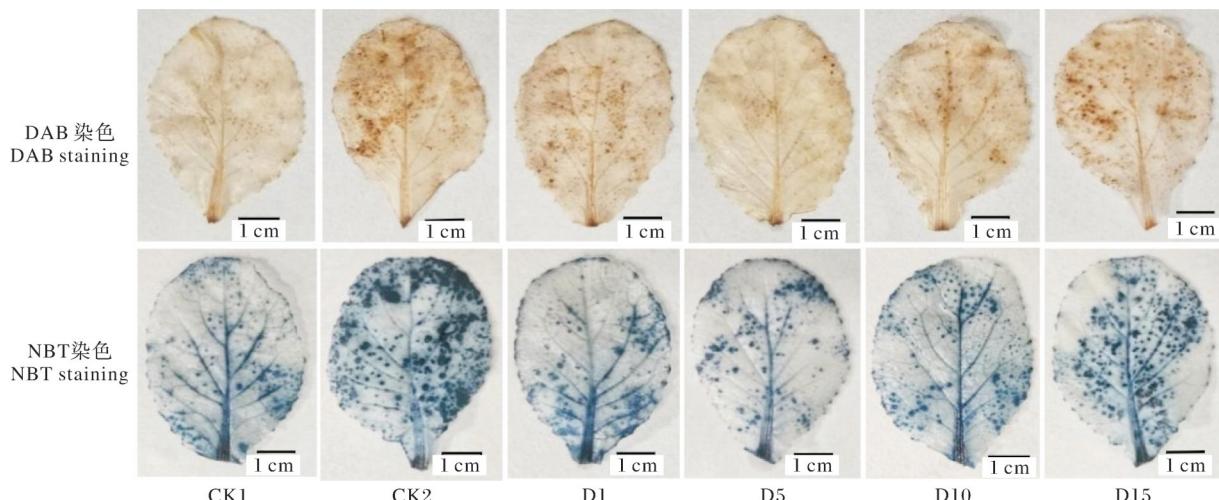


图5 不同处理大白菜幼苗组织学染色观察

Fig. 5 The histochemical staining of Chinese cabbage seedling under different treatments

3 讨 论

DADS作为一种生物刺激素可参与植物的整个生长周期,如通过增强植物的新陈代谢来提高生物量,诱导植物产生刺激反应,使其生长更快,尤其在

逆境条件下处理效果更明显^[14-15]。DADS可促进番茄幼苗防御反应的发生,使番茄的生长和发育更好^[16]。本研究中添加DADS可在一定程度上缓解大白菜幼苗的自毒作用,促进幼苗生长和生物量积累,这与前人报道的结果^[9]一致。大白菜遭受自毒作用

后,添加DADS处理的大白菜幼苗株幅、最大叶长和叶宽均增加,地上部和地下部干鲜质量均明显高于CK2处理组,尤其以5 μmol/L DADS表现最佳。

DADS与生长素的生物合成密切相关,DADS通过调控番茄和黄瓜幼苗中的生长素含量来促进细胞的有丝分裂和根系生长^[10]。Cheng等^[17]研究结果表明,DADS可以通过促进细胞分裂、调控内源激素水平和扩展蛋白基因表达来促进番茄的根系生长。本研究中,DADS可通过调控大白菜幼苗根系发育来缓解自毒作用的影响。在自毒作用胁迫下,施用DADS明显提高了大白菜幼苗的根系活力、根长和根尖数,增强了抵御自毒作用的能力,这可能与DADS参与调控植物地下部的发育有关。

DADS是大蒜素分解后的有机硫化合物。许多研究表明,在受体植物叶面喷施大蒜鳞茎水浸提液、土壤添加腐熟大蒜茎或套种大蒜均可提高植物叶绿素、类胡萝卜素含量和净光合速率^[18-20]。Cheng等^[21]报道,DADS可消减番茄的连作障碍,这可能是由于DADS处理使得番茄的光合色素增加,改善了源库关系以及水分和营养的吸收,增强了植株的光合同化作用。因此,DADS在一定程度上能保护植物的光合系统。本研究发现大白菜幼苗在遭受自毒作用时,光合作用会受到抑制,CK2处理显著降低幼苗叶片的叶绿素a、b及总叶绿素含量。施用DADS各处理的叶绿素a、b及总叶绿素含量均有不同程度的增加,说明DADS在一定程度上能保护植物光合系统遭受逆境伤害。

在抵御逆境胁迫时,植物的渗透调节能力也会提高。程芳^[9]用番茄连作地的土壤浸提液和DADS共同处理番茄幼苗,番茄叶片和根系的可溶性蛋白含量均显著增加。Ali等^[22]用适宜浓度的大蒜水提取物使茄子幼苗中的可溶性蛋白含量增加。王梦怡^[23]和肖雪梅^[24]研究认为,青蒜与春茬、秋茬黄瓜套作和大蒜与茄子套作均可降低叶片中MDA含量,本研究得到类似的结果。在重茬液中施用5 μmol/L DADS后,渗透调节物质的含量均显著高于CK2处理组,同时MDA含量显著降低,这表明DADS对细胞膜具有一定的修复和保护作用,减轻自毒胁迫对膜系统的伤害。

自毒物质在一定浓度下会使植物细胞内的活性氧积累增加,迫使植物细胞产生氧化应激反应,提高抗氧化酶活性来抵御逆境伤害。程芳^[9]研究认为,DADS可以通过提高番茄防御酶基因的表达来调节

抗氧化酶活力,减轻番茄自毒作用造成的伤害。Yang等^[25]从青蒜中提取的挥发性有机物DADS能降低超氧阴离子,还可调节抗氧化酶(SOD、CAT、POD)的活性、抗氧化物质(MDA、GSH和ASA)的含量和基因(*CscAPX*、*CsGPX*、*CsMDAR*、*CsSOD*、*CsCAT*、*CsPOD*)的表达来抵御逆境胁迫。DADS能够缓慢释放H₂S^[26],使细胞中积累少量H₂S,积累的H₂S又可以调节植物生长和调控抗氧化系统,进而减轻多种非生物胁迫对植物造成的伤害^[27-28]。在本研究中,大白菜幼苗受到自毒作用胁迫后施用DADS,保护酶SOD、POD和CAT活性较CK2处理组显著升高,H₂O₂、O₂⁻积累速率下降,减轻了氧化胁迫对幼苗造成的伤害。

综上,适宜浓度的外源DADS对大白菜幼苗的自毒作用具有缓解效应,以施加浓度为5 μmol/L的效果最为理想,可显著提高幼苗渗透调节物质含量和抗氧化酶活性,降低活性氧水平,并在一定程度上增加叶片叶绿素含量,促进大白菜幼苗的生长与干物质的积累,从而缓解自毒胁迫对大白菜幼苗的伤害。

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Effects of diallyl disulfide on mitigating autotoxicity of Chinese cabbage

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Abstract Diallyl disulfide (DADS) is a biologically active organic sulfide produced by the decomposition of allicin, which has a strong effect on inhibiting plant stress. The Chinese cabbage variety ‘Golden Kirin’ was used to study the effect of DADS on mitigating the autotoxicity of Chinese cabbage. 6 groups of treatments including CK1 (1/2 Hoagland nutrient solution), CK2 (continuous cropping solution), D1 (1 $\mu\text{mol/L}$ DADS + continuous cropping solution), D5 (5 $\mu\text{mol/L}$ DADS + continuous cropping solution), D10 (10 $\mu\text{mol/L}$ DADS + continuous cropping solution), D15 (15 $\mu\text{mol/L}$ DADS + continuous cropping solution) were set up using hydroponic experiment, with 12 tissue culture bottles in each treatment and 4 seedlings cultured in each bottle. The effects of different concentrations of DADS on the growth, physiological and biochemical trait of seedlings under the autotoxicity of Chinese cabbage were investigated. The results showed that the application of different concentrations of DADS had an effect on promoting the growth of seedlings under the autotoxicity of Chinese cabbage, with D5 having the best effect of mitigating. Compared with CK2, D5 treatment significantly increased the fresh weight of aboveground and underground parts of seedlings, and root activity of Chinese cabbage by 19.42% and 23.40%, and 45.29%. The length of total root and the number of root tip increased as well, which mitigated the damage of autotoxicity effect on root structure; meanwhile, the content of chlorophyll in leaves was increased, which promoted the photosynthesis in turn. The content of osmoregulatory substances in seedlings of Chinese cabbage significantly increased, with the activity of antioxidant enzyme SOD, POD, and CAT increasing by 30.75%, 27.44%, and 17.68%, and the content of MDA significantly decreasing by 20.58%. The results of histological staining showed that the accumulation of hydrogen peroxide anion and superoxide anion was significantly reduced by D5 treatment. It is indicated that exogenous application of diallyl disulfide (DADS) can effectively mitigate the autotoxicity of exudates from the roots of Chinese cabbage by reducing the oxidative stress and promoting the growth of root. The most significant mitigating effect was observed when 5 $\mu\text{mol/L}$ DADS was applied. It will provide a new method to mitigate the obstacles of continuous cropping caused by the autotoxicity and lay the foundation for the rational use of diallyl disulfide (DADS).

Keywords Chinese cabbage; exudates from roots; autotoxicity; obstacles of continuous cropping; diallyl disulfide (DADS)

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