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镉胁迫对入侵植物节节麦幼苗生长及生理生化反应的影响

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摘　要：农业土壤中的镉污染已对全球粮食安全构成严重威胁。通过盆栽控制法，研究不同浓度（0、10、20、30 mg/kg）镉胁迫对节节麦幼苗生长及生理生化反应的影响，旨在为节节麦入侵机制研究及小麦耐受性基因潜在来源的筛选提供参考。研究结果表明，镉胁迫抑制了节节麦幼苗的光合作用，导致其叶绿素 a、叶绿素 b 和总叶绿素含量降低，株高和根长均显著降低。作为响应，节节麦幼苗根系中超氧化物歧化酶（SOD）、过氧化物酶（POD）和抗坏血酸过氧化物酶（APX）的活性升高，脯氨酸含量和可溶性蛋白质含量均升高。尽管 30 mg/kg 的镉胁迫对节节麦幼苗生长指标的影响最为明显，但该浓度下根系中过氧化氢（H_2O_2）和硫代巴比妥酸（TBARS）的含量与 CK 相比差异并不显著。综上所述，节节麦能够通过自身调节适应一定浓度的镉胁迫。

关键词：节节麦；镉胁迫；保护酶活性；重金属；叶绿素含量
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Effects of Cadmium Stress on Growth and Biochemical Responses of Invasive *Aegilops tauschii* Seedlings

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Abstract: Cadmium pollution in agricultural soils has become a serious threat to global food security. This study investigated the effects of different concentrations (0, 10, 20, and 30 mg/kg) of cadmium stress on the growth and biochemical responses of *Aegilops tauschii* seedlings through a pot-based controlled experiment, aiming to provide insights for researching its invasion mechanism and screening potential sources of wheat tolerance genes. The results showed that Cd stress inhibits photosynthesis in *A. tauschii* seedlings, leading to a significant reduction in chlorophyll a and b, and total chlorophyll content, as well as in plant height and root length. In response to Cd stress, the activities of superoxide dismutase, peroxidase and ascorbate peroxidase were significantly elevated, as was the content of proline and soluble proteins, in the roots of *A. tauschii.* Although the 30 $mg \cdot kg^{-1}$ Cd treatment had the most pronounced impact on growth parameters, no significant differences in H_2O_2 and TBARS levels were observed in *A. tauschii* roots at this concentration compared to the control. In summary, *A. tauschii* can tolerate a certain degree of Cd stress through self-regulation mechanisms.

Key words: *Aegilops tauschii*; Cadmium stress; Protective enzyme activity; Heavy metal; Chlorophyll content

随着工矿企业废弃物排放量的增加以及农田中化肥农药的大量使用，人类赖以生存的土壤及水源正遭受日益严重的重金属污染[1]。与镍、铜等植物生长发育所必需的元素不同，镉、铅等为非必需元素，极低的浓度就能造成植物形态、生理及生化功能失调[2]。此外，镉主要以化合物的形式存在，较易被植物根系吸收，可以直接从土壤中转移至植物的可食用部分，危害人类健康[3-4]。小麦对包括重金属在内的各种生态胁迫较为敏感[5]。小麦的野生近缘种作为非生物胁迫

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耐受性理想基因的潜在来源越来越受到重视。此外,重金属污染可能会改变外来入侵植物的形态及生理表现,对其入侵过程及竞争力产生一定的影响[6-7]。了解重金属胁迫对入侵植物功能特性的影响,可为其成功入侵的驱动机制研究提供参考。

节节麦(*Aegilops tauschii* Coss.)为世界十大恶性杂草之一,原产于西亚及东欧等地[8]。作为小麦的野生近缘种,节节麦拥有丰富的抗性基因,与小麦的D染色体组完全同源,其优异基因可通过交换或自由重组的形式转移至小麦[9-10]。为此,国内外的相关研究主要围绕其遗传多样性、抗性基因挖掘等进行开发利用。其次,作为入侵植物,节节麦已入侵扩散至中国多个小麦主产省,并已由区域性恶性杂草上升为恶性杂草,成为中国冬小麦种植区危害最重的恶性杂草之一[11]。受到防治策略及预防不力的影响,节节麦的入侵已严重危害到我国小麦的生产安全[12]。截至目前,有关节节麦重金属胁迫的适应性研究尚未见报道,通过探讨镉胁迫对节节麦幼苗生长及生理生化反应的影响,旨在为其入侵机制研究及小麦耐受性理想基因潜在来源的筛选提供参考。

1 材料与方法

1.1 试验材料

供试节节麦(*A. tauschii*)种子来源于洛阳市洛龙区佃庄镇河南科技大学园艺与植物保护学院试验田(34°68′N, 112°62′E)。该地区属于温带季风气候,年平均气温14.86 ℃,年均降水量578.2 mm。重金属胁迫试验在河南科技大学园艺与植物保护学院园林植物实验室进行。

1.2 试验处理

采用培养皿滤纸法[13]进行种子催芽处理。选择从小穗剥离出的饱满节节麦种子,用5%次氯酸钠溶液消毒10 min,蒸馏水冲洗3次后,用滤纸吸去种子表面水分。将种子置于铺有2层滤纸的培养皿(直径为12 cm)中,每皿25粒,在昼/夜为25 ℃/15 ℃、光暗比为12 h/12 h的光照培养箱内催芽,至种子露白视为萌发。

将萌发的种子播种于装有200 g经过预处理粗砂(冲洗干净,在120 ℃烘箱内消毒120 min)的塑料杯(直径7 cm,高8 cm)中,每杯3株,添加1/2倍的Hogland营养液。在光照培养箱内培养3 d后(培养条件同种子催芽处理),用0、10、20、30 mg/kg氯化镉($CdCl_2$)进行处理,每个处理重复5次。之后,各组均通过补充1/2倍的Hogland营养液,维持基质湿度在75%~80%。

1.3 测定指标与方法

重金属施入25 d后结束试验。采用水冲刷的方法,将植株根部从基质中小心分离出来,并尽量减少细根的损失。每个处理随机选取10株幼苗,5株用于形态指标测定;5株取叶片及根系,液氮冷冻后-80 ℃超低温冰箱保存,用于生理生化指标测定。

1.3.1 形态指标测定

直尺测量幼苗株高和根长,精确到0.10 cm。其中,从茎基部到形态学最高点的长度为株高,以测定株高幼苗的最长根长度为根长[14]。

1.3.2 生理生化指标测定

依据李合生[15]的方法,测定叶绿素(叶绿素a、叶绿素b和总叶绿素)含量;采用氯化硝基四氮唑蓝(Nitro-tetrazolium chloride blue, NBT)光化还原法测定超氧化物歧化酶(Superoxide dismutase, SOD)活性;采用愈创木酚法测定过氧化物酶(Peroxidase, POD)活性;采用过氧化氢还原法测定过氧化氢酶(Catalase, CAT)活性;采用紫外分光光度法测定抗坏血酸过氧化物酶(Ascorbate peroxidase, APX)活性;采用酸性茚三酮显色法测定脯氨酸含量;采用考马斯亮蓝G-250法测定可溶性蛋白质含量;采用硫代巴比妥酸法测定硫代巴比妥酸(Thiobarbiturate, TBARS)含量;采用紫外吸收法测定过氧化氢(Hydrogen peroxide, H_2O_2)含量。参照Anderson等[16]的方法,取上清液测定还原型谷胱甘肽(GSH)含量和抗坏血酸(ASA)含量。

1.4 数据处理

利用SPSS 18.0软件通过单因素方差分析和Duncan′s多重比较进行差异显著性分析。利用Excel 2010进行数据整理并绘图。图中数据为“平均值±标准误”。

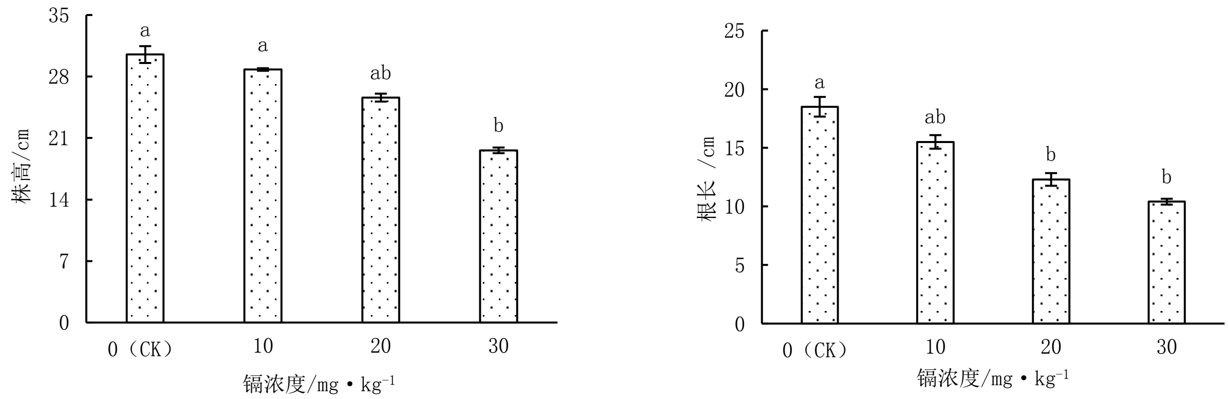
2 结果与分析

2.1 镉胁迫对节节麦幼苗株高和根长的影响

由图1可知,镉胁迫对节节麦幼苗的株高和根长具有显著影响,均随镉浓度的增加而下降。株高在0~20 mg/kg镉胁迫条件下无显著变化,在30 mg/kg镉胁迫时与CK和10 mg/kg镉胁迫处理相比显著下降。根长与株高变化趋势基本一致,在20~30 mg/kg镉胁迫条件下与CK相比显著下降。

2.2 镉胁迫对节节麦幼苗叶绿素含量的影响

由图2可知,镉胁迫对节节麦幼苗的叶绿素含量具有一定影响,叶绿素a、叶绿素b和总叶绿



注：小写字母不同表示差异显著（P<0.05），下同。

Note: Different small letters indicate significant differences at P<0.05. The same below.

图1　镉胁迫对节节麦幼苗的株高和根长的影响

Fig.1 Plant height and root length of *A. tauschii* under Cd stress

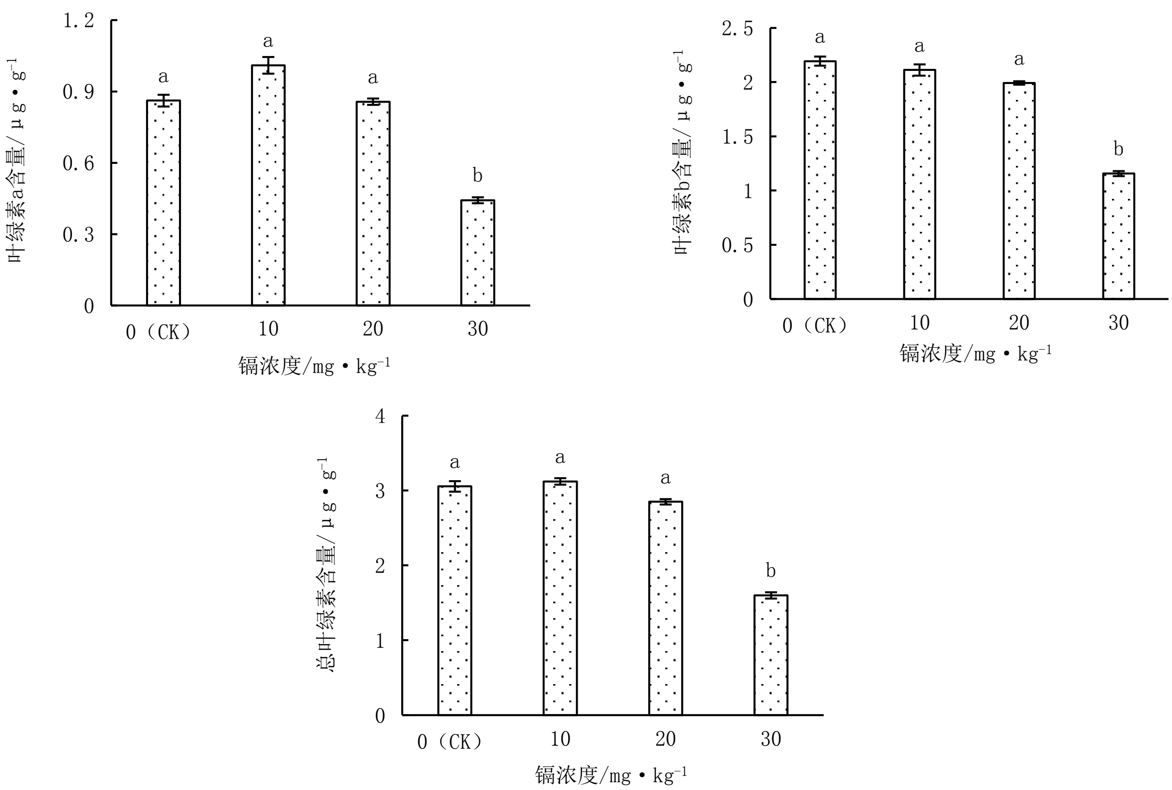


图2　镉胁迫对节节麦幼苗叶片中叶绿素a、叶绿素b和总叶绿素含量的影响

Fig.2 Content of Chl a, Chl b and Chl(a+b) in *A. tauschii* leaves induced by Cd stress

素含量均随镉胁迫浓度的增加呈下降趋势。在0~20 mg/kg镉胁迫条件下，Chl a、Chl b及Chl（a+b）含量无显著变化，当镉浓度达到30 mg/kg时，Chl a、Chl b、Chl（a+b）含量较CK分别显著降低48.63%、47.27%和47.66%。

2.3　镉胁迫对节节麦幼苗生理生化指标的影响

由图3可知，镉胁迫对节节麦幼苗根系中抗氧化酶活性具有显著影响，不同浓度镉处理下SOD、POD、CAT、APX活性变化趋势各异。SOD活性在0~10 mg/kg镉胁迫条件下无显著变化，在30 mg/kg镉胁迫条件下较CK显著增加163.32%。POD活性和APX活性与SOD活性的变化趋势不同，各处理与CK相比均无显著差异。在30 mg/kg镉胁迫条件下POD活性和APX活性分别较CK增加55.40%和43.55%。CAT活性在不同镉胁迫条件下与CK相比均无显著差异，在30 mg/kg镉胁迫条件下仅为CK的87.41%。

由图4可知，镉胁迫对节节麦幼苗根系中

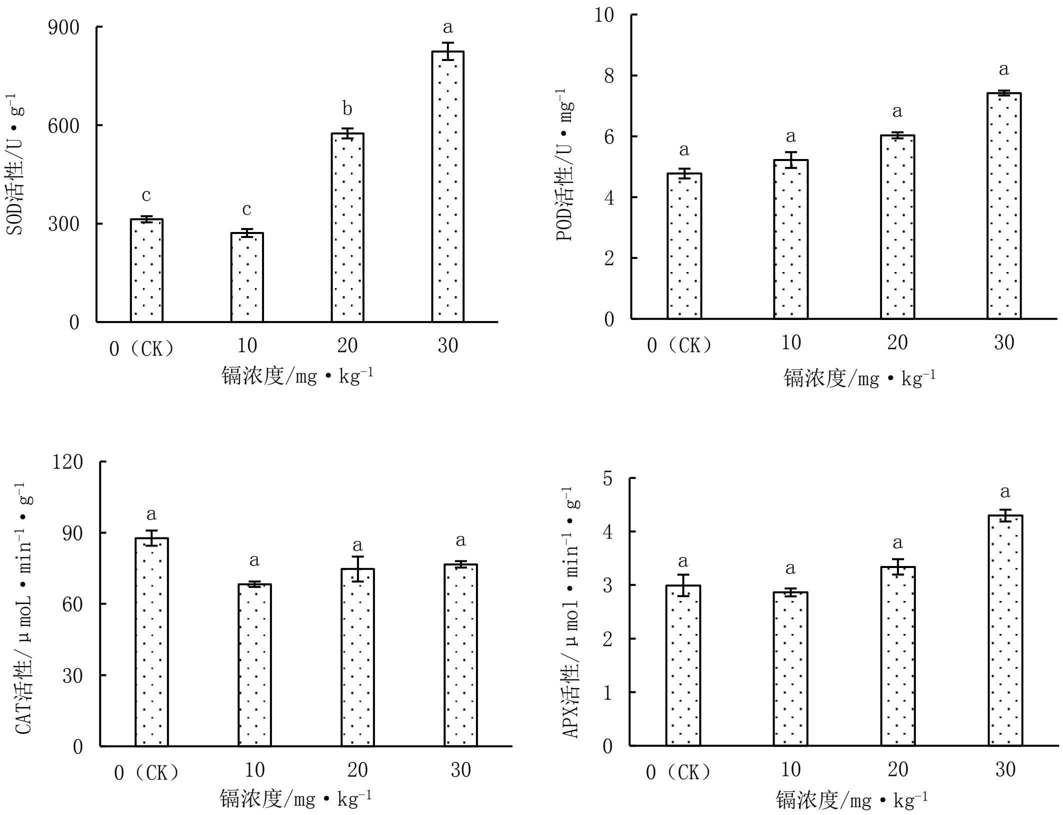


图3　镉胁迫对节节麦幼苗根系中的SOD、POD、CAT和APX活性的影响

Fig.3 Activities of SOD, POD, CAT, APX in *A. tauschii* roots induced by Cd stress

GSH含量和AsA含量具有一定的影响,但GSH含量和AsA含量并未随镉浓度增加而升高。在10 mg/kg镉胁迫条件下,GSH含量与CK差异显著,在10~20 mg/kg镉胁迫条件下,AsA含量与CK差异显著,在30 mg/kg镉胁迫条件下,GSH含量和AsA含量分别降低至CK的77.71%和91.99%,但差异不显著。

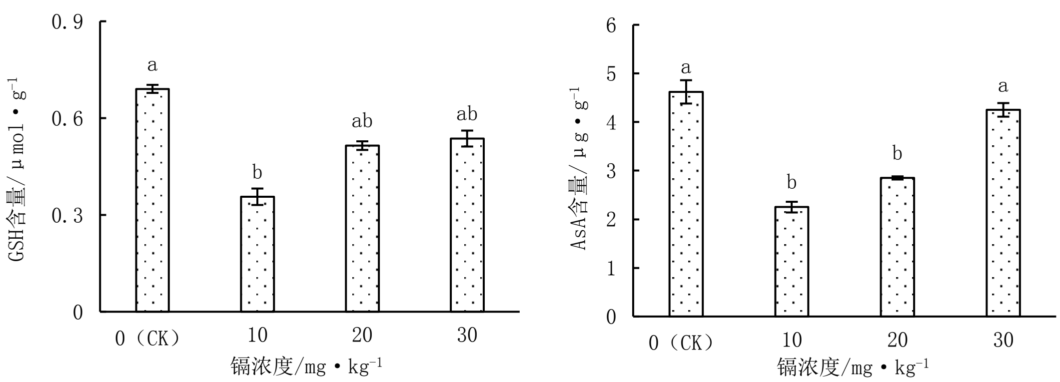


图4　镉胁迫对节节麦幼苗根系中的GSH和AsA含量的影响

Fig.4 Content of GSH and AsA in *A. tauschii* roots induced by Cd stress

由图5可知,镉胁迫对节节麦幼苗根系中H_2O_2含量和TBARS含量具有一定影响。H_2O_2含量和TBARS含量均随镉浓度(10~30 mg/kg)的增加呈增加趋势,但不同镉胁迫条件下,H_2O_2含量和TBARS含量与CK相比均无显著差异。当镉浓度达到30 mg/kg时,H_2O_2含量和TBARS含量分别较CK增加了13.21%和20.69%。

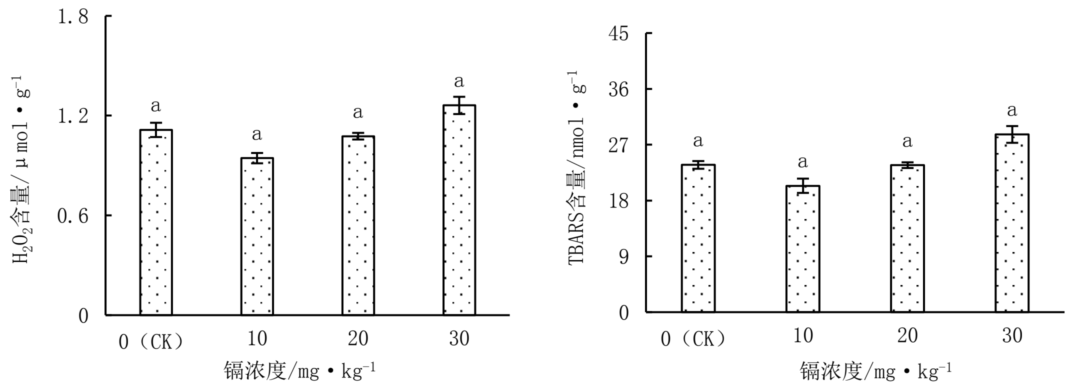


图5 镉胁迫对节节麦幼苗根系中的H_2O_2和TBARS含量的影响

Fig.5 Content of H_2O_2 and TBARS in *A. tauschii* roots induced by Cd stress

由图6可知，镉胁迫对节节麦幼苗根系中脯氨酸含量和可溶性蛋白质含量具有显著影响。脯氨酸含量随镉浓度的升高逐渐增加，在镉浓度达到30 mg/kg时，较CK增加了128.57%。可溶性蛋白质含量随镉浓度增加呈先降后升的变化趋势，但在不同浓度镉胁迫条件下与CK相比均无显著差异，在镉浓度达到30 mg/kg时较CK增加了15.75%。

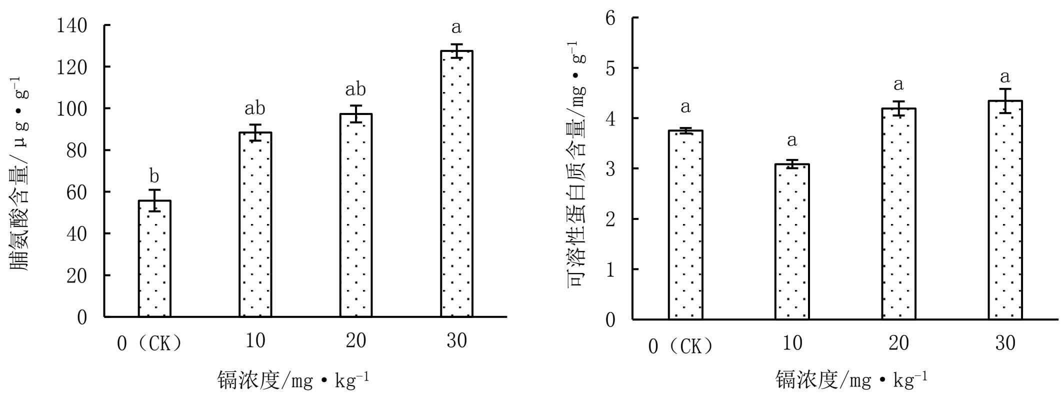


图6 镉胁迫对节节麦幼苗根系中的脯氨酸和可溶性蛋白质含量的影响

Fig.6 Content of proline, soluble protein in *A. tauschii* roots induced by Cd stress

3 结论与讨论

植物对重金属的耐受性通常是根据生长介质中由于不良金属的存在所产生的根或茎生长受限程度来评估的[17]。也有研究表明，根系生长是比叶绿素测定更为敏感的金属耐受性指标[18]。由于在生长介质中与根系的直接接触，根系生长的减少是镉胁迫的第一毒性效应[19]。本研究中，随着镉浓度的增加，节节麦幼苗的株高和根长均呈下降趋势，表明镉胁迫在一定程度上抑制了节节麦幼苗的生长发育，而这也与镉胁迫对小麦（*Triticum aestivum* L.）[20]、番茄（*Solanum lycopersicum* L.）[21]及红花（*Carthamus tinctorius* L.）[22]的影响一致。

光合作用是植物生长发育的基础，而叶绿素含量的变化在一定程度上可以反映植物光合作用的变化规律。已有的研究表明，镉胁迫抑制了植物叶片中光合色素的合成，加速了光合色素的降解，导致光合色素含量下降[23-24]。本研究中，节节麦幼苗的Chl a、Chl b、Chl（a+b）含量均随镉浓度的增加而不断下降，这与在小麦[25]、玉米（*Zea mays* L.）[26]中的研究结论一致。此外，由于重金属胁迫导致的叶绿素含量减少及由此造成的光合作用受抑，致使植物生长受阻[27]。当镉胁迫浓度达到30 mg/kg时，节节麦幼苗的Chl a、Chl b及Chl（a+b）含量较CK降幅达到显著水平，这表明此浓度的镉致使节节麦幼苗光合作用受抑制而导致其生长受阻最为显著，而这也与上述株高和根长的变化情况相符。

为了应对非生物胁迫降低氧化损伤，植物进

化出由SOD、POD、CAT和APX等抗氧化酶，以及GSH、AsA和酚类化合物组成非酶类抗氧化剂[28]。抗氧化酶活性及非酶抗氧化水平的增加有助于缓解氧化应激反应[29]。本研究结果发现，节节麦幼苗根系中的SOD、POD和APX 的抗氧化酶活性均随镉浓度的增加而增加。但当镉浓度达到30 mg/kg时，CAT活性仅为CK的87.41%，这与节节麦似乎并不依靠CAT清除活性氧自由基有关，而这也与小麦对镍胁迫的研究结论类似[30]。非酶抗氧化活性氧（ROS）清除机制中，AsA作为干预外部氧化剂损伤的第一道防线，在清除H_2O_2方面发挥着核心作用[31]。GSH通过调节氧化还原平衡，最大限度降低植物地上和地下部分的金属自由离子浓度，在细胞对金属胁迫的耐受性中发挥着重要作用[32]。本研究中，镉浓度达到30 mg/kg时，GSH含量和AsA含量仅为CK的77.71%和91.99%，这可能与节节麦自身具有较高重金属胁迫适应性有关，较低的非酶抗氧化水平就可满足清除镉胁迫造成的过量ROS需要。

非生物胁迫引起的以H_2O_2为代表的ROS和以TBARS为代表的膜脂过氧化反应，均会通过强烈的氧化行为造成不可逆的细胞损伤[33]。已有的研究表明，镉胁迫会造成小麦体内H_2O_2、MDA含量的增加[24,34-35]。本研究中，随着镉胁迫浓度的升高，节节麦幼苗根系中H_2O_2、TBARS含量不断增加，但当镉胁迫浓度为30 mg/kg时，H_2O_2、TBARS含量与CK差异均不显著，这可能是由于节节麦通过自身调节，较大程度地抑制镉胁迫造成ROS产生及膜脂过氧化。此外，在浓度为10~20 mg/kg镉胁迫中的H_2O_2、TBARS含量均低于CK，这可能是节节麦抗氧化系统调节的结果，与前人的研究结论相符[36-37]。

作为渗透保护剂之一，脯氨酸可直接参与ROS解毒及脂膜氧化还原等过程[38]，其含量与植物对重金属胁迫的适应能力呈正相关[29]。本研究中，脯氨酸含量随镉浓度的增加而增加，并在镉浓度达到30 mg/kg时，与CK差异显著，表明节节麦通过脯氨酸含量的增加来应对镉胁迫，这也与玉米[26]、水稻（*Oryza sativa* L.）[39]及小麦[34]的研究结论一致。可溶性蛋白质是植物体内重要的渗透调节剂，其含量被认为是重金属胁迫下植物细胞氧化胁迫的良好指标[40]。本研究中，可溶性蛋白质含量随镉浓度的增加而增加，这可能是因为适度范围内的镉胁迫促进了节节麦幼苗根系中蛋白质合成，这与镉胁迫对小麦[41]的影响研究结论一致。

总之，一方面，镉胁迫导致节节麦幼苗叶片的Chl a、Chl b及Ch1（a+b）含量下降，一定程度抑制了幼苗光合作用而导致其生长受阻，体现在根长及株高的明显降低；另一方面，依据保护酶（SOD、POD和APX）活性、非酶性抗氧化剂（GSH、AsA）及渗透调节物质（脯氨酸和可溶性蛋白质）含量的提升，节节麦通过自身调节能够较大程度地抑制H_2O_2、TBARS的过量产生，从而适应一定浓度的镉胁迫。

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