

Advances in Brassinolide Regulation of Plant Growth and Development and Stress Resistance

Yangkun Zhou, Qiangtao Liao, Xianfeng Ding*, Qiaojun Jia, Ziqiang Ding

College of Life Science and Medicine, Zhejiang Sci-Tech University, Hangzhou Zhejiang
Email: *1165461886@qq.com

Received: Jun. 6th, 2020; accepted: Jun. 21st, 2020; published: Jun. 28th, 2020

Abstract

It is an effective measure to use plant hormones to regulate plant growth and the development; is an effective means to obtain high quality and high yield crops. Brassinolide, a new and environmentally friendly plant hormone, is widely used in agriculture and forestry. It promotes the growth and development of plants and maintains the normal growth of plants under stress by promoting cell division, improving photosynthetic performance, relieving oxidative stress and regulating osmotic potential of plants. At present, researches on brassinolide regulation of plant growth and development and improvement of plant stress resistance are abundant, and the regulatory mechanism of brassinolide is clearer. In this review, we summarized the role and regulatory mechanism of brassinolide in plant growth and development and stress resistance, and made a prospect of future research direction of brassinolide, in order to provide reference for further research on brassinolide.

Keywords

Brassinolide, Growth and Development, Stress Resistance, Plant Growth Regulator, Abiotic Stress

芸苔素内酯调控植物生长发育及抗逆性的研究进展

周扬锟, 廖锵涛, 丁先锋*, 贾巧君, 丁自强

浙江理工大学生命科学学院, 浙江 杭州
Email: *1165461886@qq.com

*通讯作者。

文章引用: 周扬锟, 廖锵涛, 丁先锋, 贾巧君, 丁自强. 芸苔素内酯调控植物生长发育及抗逆性的研究进展[J]. 农业科学, 2020, 10(6): 407-418. DOI: 10.12677/hjas.2020.106061

收稿日期：2020年6月6日；录用日期：2020年6月21日；发布日期：2020年6月28日

摘要

使用植物激素来调控植物生长发育是获得高品质和高产量农作物的有效手段。芸苔素内酯作为一种新型、环保的植物激素，在农林业上应用广泛，其通过促进细胞分裂、改善植物光合性能、缓解植物氧化应激、调节植物渗透势等生理过程来促进植物的生长发育和维持胁迫下植物的正常生长。目前，关于芸苔素内酯调控植物生长发育和提高植物抗逆性的研究内容丰富，芸苔素内酯的调控机制也更为明确。本文综述了芸苔素内酯对于植物生长发育和抗逆性的作用和调控机制，并对芸苔素内酯未来的研究方向做出展望，以期对芸苔素内酯的深入研究做参考。

关键词

芸苔素内酯，生长发育，抗逆性，植物生长调节剂，非生物胁迫

Copyright © 2020 by author(s) and Hans Publishers Inc.

This work is licensed under the Creative Commons Attribution International License (CC BY 4.0).

<http://creativecommons.org/licenses/by/4.0/>



Open Access

1. 引言

芸苔素内酯(brassinolide, BR)是一类在植物的生长发育中起着多重作用[1]的植物激素，由美国农业部科学家 J. W. Mitchell 等人在 1970 年首先从油菜属植物的油菜花粉中提取得到[2]。1979 年，Grove 和他的同事从油菜花粉中分离出 BR 的高纯度结晶，并对其立体结构进行了鉴定，发现这些 BR 具有类固醇的甾体核心结构并带两对邻位的羟基，而在此之前所有发现的植物激素都是非甾体。Grove 和他的同事发现了类固醇激素，将其统称为油菜素甾醇类化合物(BRs) [3]。BR 在调节细胞萌发，细胞伸长和分裂，以及叶片衰老、光形态发生、花粉管生长、花期控制、雄性生殖、质子泵活性、核酸和蛋白质合成、基因表达、光合作用等生理过程中起着重要的作用[4] [5]。

植物激素的应用是在胁迫条件下提高作物生产力的一种有前途的实用策略[6]。植物激素在植物生长调控中具有深远的作用，可以通过调节信号通路，积极参与对抗各种胁迫[7]。其中，芸苔素内酯已被广泛用于提高植物对各类生物胁迫和非生物胁迫的抗逆性[8]。近年来，BR 在农业和园艺的应用逐渐增加，以期提高作物的产量和抗逆性[9]。

BR 低廉且无害，因此在生产实践中广泛应用。本文归纳了 BR 对于植物生长发育的调节作用，和对于胁迫下植物形态和生理过程的改善作用，以期对 BR 的应用提供参考。

2. 芸苔素内酯促进生长发育

许多研究表明，BR 在促进植物生长和细胞分裂的作用显著。在 Wang 等人[10]的研究中，油菜素内酯缺乏的突变体表现出矮化和主根缩短的症状，这种症状在应用了 24-表芸苔素内酯(EBL)后得到缓解，它们的研究从植株外部形态上表明了 BR 在植物生长发育过程中起关键作用。Meudt 等人[11]则报导了 BR 促进马铃薯块茎顶端分生组织的生长。Zhiponova 等人[12]的实验表明了 BR 促进拟南芥细胞分裂和叶片扩张。Kartal 等人[13]的研究也发现了 BR 的应用通过促进细胞有丝分裂而与植物根系生长的正相关关系。

虽然 BR 促进细胞分裂的机制尚不明确,但 Hu 等人[14]认为 BR 促进 CycD3 基因的转录,从而调节细胞分裂。不仅如此, Khripach 等人[15]也观察到 BR 可以激活细胞壁松动酶来调节细胞的伸长和分裂活性。

除了促进生长的作用, Xi 等人[16]通过应用外源 BR,发现其加速了葡萄的成熟过程,并促进黄酮类化合物和花青素等次生代谢物的积累。

此外, Sayed 等人[17]报导了 BR 调节种子萌发和植物生长的双重性,较低浓度的 BR 促进了南瓜幼苗的萌发和生长,而较高浓度的 BR 则延缓了南瓜种子萌发并抑制了幼苗生长。

3. 胁迫下植物生理变化

胁迫下的氧化应激通常导致电解质渗漏和膜透性增加[18]。在非生物胁迫条件下由于类囊体电子传输,叶绿体结构被破坏等原因,植物光合性能降低。不仅如此,胁迫下 Rubp 羧化酶(Rubisco)的失活还降低了羧化效率和卡尔文循环关键酶的活性[19] [20]。同时,胁迫下叶绿素酶的活性增强而加速催化叶绿素分子降解,从而降低叶绿素含量[21]。此外,胁迫下气孔关闭导致气孔导度降低,影响植物气体交换[22],以及植物叶面积减小[23]同样降低了植物光合性能。

胁迫诱导的抑制生长与植物组织中活性氧的增加有关,这些活性氧一般包括超氧阴离子、羟基离子和过氧化氢,它们会引起脂质过氧化,从而导致植物细胞功能的紊乱[24] [25]。换言之,胁迫打破了植物活性氧积累与抗氧化防御系统之间的平衡,导致氧化应激,从而抑制植物的正常生长[26]。

温度过高或过低,土壤有效水分过少,土壤盐碱浓度过高或土壤受重金属污染等环境条件都会对植物的生长和生物量积累产生影响[27] [28] [29] [30]。胁迫下植物的株高、鲜重和干重通常会严重下降[31]。

胁迫同样影响植物激素水平,根据 Wenli 等人[32]的研究,盐胁迫使黑麦草叶片脱落酸(ABA)和赤霉素 A4 (GA4)含量增加,吲哚乙酸(IAA)、玉米素核糖苷(ZR)、吲哚丙酸(iPA)和水杨酸(SA)含量减少。

许多研究表明,植物生长调节剂的应用可以有效缓解环境胁迫对植物生长的影响。有证据表明 BR 在提高植物对干旱、低温、高盐和重金属污染等环境胁迫的耐受性上具有显著作用[28] [33] [34]。

3.1. 抗旱性

许多的研究表明了干旱条件下外源 BR 的应用可以改善植株的生长,显著恢复农作物产量[35] [36] [37]。

Hu 等人[38]的研究发现外源 BR 可以改善干旱条件下辣椒的净光合速率(Pn)、蒸腾速率(E)和气孔导度(Gs)从而提高其光合性能。Lima 和 Lobato 的研究[39]同样观察到喷洒 100nM 外源油菜素内酯的植株与水分亏缺的对照组相比 Pn、E 和 Gs 三个量分别提高了 96%、24%和 33%,他们还进一步指出干旱条件下 Pn、E 和 Gs 的改善是因为外源 BR 的应用可以提高 PS II 效率并增加碳固定,在他们的实验中,喷洒 100 nM 外源油菜素内酯的植株叶绿素 a、叶绿素 b 和总叶绿素含量分别显著增加了 26%、58%和 33%。此外,外源油菜素内酯对于干旱胁迫下暗适应态的最大荧光产额(Fm)、PSII 光化学的有效量子产率(Φ PSII)、电子传递速率(ETR)和光化学猝灭系数(qP)的影响显著,它们分别增加了 32%、74%、72%和 112%。Zhao 等人[40]发现干旱胁迫下 Rubisco 活化酶(RCA)的 38~39 kDa 亚基丰度下降,但在应用外源油菜素内酯后恢复,从而提高了 Rubisco 初始活性。

BR 在清除活性氧和调节氧化还原方面起着重要的作用。孙石昂等人[41]比较了 24-表芸苔素内酯、28-高芸苔素内酯和 28-表高芸苔素内酯对干旱胁迫下玉米幼苗抗旱性的调控作用,实验结果表明,三种 BR 在不同浓度下均能提高干旱胁迫下玉米幼苗叶片中的 SOD、POD、CAT 保护酶活性,从而增强植株清除活性氧的能力,同时降低 MAD 含量,从而提高植株抗逆性。BR 还可以在干旱胁迫下下调过氧化氢

生产基因的表达而减少植物体内过氧化氢产量[42]。Peng 等人[43]的研究发现磷脂酶 D α 1 的过表达提高了拟南芥的抗旱性, 而油菜素内酯被认为是磷脂酶的调节因子, 调控磷脂酸的生成[44]。

清除活性氧(ROS)的另一个循环是 AsA-GSH 循环, Talaat 等人[35]的研究发现, 在干旱胁迫下, AsA 和 DHA 浓度增加, 但 AsA/DHA 比值降低, 并推测这可能是由于 DHAR 和 MDHAR 活性降低所致, 在应用了 BR 后, 植物的 AsA/DHA 比值恢复, 此外, BR 还调节参与 AsA-GSH 循环的酶的活性, 从而保持抗坏血酸的氧化还原状态。他们的研究还发现在干旱胁迫下, GSH/GSSG 比值降低, 而 BR 正调控干旱胁迫下生长的植株 GSH/GSSG 比值。

BR 还通过提高水势、渗透势和压力势来维持干旱胁迫下植物的相对含水量[45]。Yu 等人[46]的研究结果显示, 干旱条件下 BR 的应用引起水关系的改善, 这可能是糖等渗透调节物质的高积累所致。Talaat 等人[35]的研究也同样表示了 BR 诱导脯氨酸和甘氨酸的高积累, 减少植物组织的水分损失, 从而提高了植物组织中的水分含量。在 Khamsuk 等人[47]的研究中, BR 在干旱胁迫下提高了脯氨酸累积, 从而减少细胞膜损伤和氧化应激, 最终辣椒的相对含水量提高了 71%。

3.2. 抗冻性

Jie 等人[48]通过 RNA 测序, 发现外源 BR 使受低温胁迫的辣椒上调了 335 个基因的表达, 其中有 29 个基因与辣椒的光合能力有关。有研究发现, 外源应用 BR 后叶绿素含量的恢复可能是由于 BR 信号转导对转录和翻译过程的调节作用, 从而最终促进叶绿素生物合成或减少叶绿素分子的分解[49] [50]。而 Anwar 等人[27]的研究显示, BR 提高了低温胁迫下的植株光合色素的含量, 气孔导度, 胞间 CO₂ 含量从而提高植株光合能力。他们的研究还发现, BR 可提高抗氧化酶(SOD、POD、GR、CAT 和 APX)活性, 从而调节植物防御系统, 以减少低温胁迫的不良影响, 受低温胁迫而水平增加的 ROS 和 MAD 也被外源 BR 抑制, 提高了植物细胞膜稳定性。不仅如此, 外源 BR 也影响各植物激素的表达, 其中, 脱落酸(ABA)、吲哚乙酸(IAA)、ZR、和 BR 水平上升, 而茉莉酸(JA)、赤霉素 A4(GA4)下降。内源 BR 含量大幅上升的原因是控制 BR 生物合成的关键基因 DWF 基因受到外源 BR 的调控, CsDWF1、CsDWF2、CsDWF4 表达上升而 CsDWF3 表达下降。

3.3. 耐盐性

BR 对于缓解盐胁迫也有显著作用, Yuan 等人[51]的研究结果显示盐胁迫显著降低了黄瓜植株的茎重和根重, 而 BR 的应用一定程度克服了盐胁迫, 改善了植物的鲜重和干重。BR 还能提高胁迫下植物根瘤的数量, 从而提高作物产量。根据 Ali 等人[52]的研究结果, 用 BR 处理过的鹰嘴豆种子在盐胁迫下根瘤数量较对照组提高了 30%, 豆血红蛋白含量和固氮酶活性分别提高 28% 和 30%, 收获后, 种子产量比对照组提高了 26%。

BR 从多个方面调节盐胁迫下植物的光合性能。Xia 等人[53]的研究表明外源应用的 BR 可以上调 rbcL, rbcS 等光合基因的表达, 从而提高二磷酸核酮糖羧化酶(Rubisco)以及其它参与卡尔文循环酶的活性。其结果就是植物在盐胁迫下的气体交换参数增加[54]。此外, 在盐毒性作用下, BR 通过保护叶绿体的膜和细胞的超微结构来减少叶绿素的降解[55]。同时, 应用 BR 后叶绿素酶编码基因的下调也有助于减少叶绿素降解[56]。谷胱甘肽氧化还原稳态的维持对于 CO₂ 同化起着重要作用, 而 BR 参与维持谷胱甘肽稳态也可能提高光合性能[57]。类胡萝卜素可以加强清除活性氧的过程从而保护不利环境条件下植物的光合系统[58], Anket S 等人[56]的研究发现 BR 的应用提高了类胡萝卜素含量。

BR 的应用降低了盐胁迫下水稻幼苗的脂质过氧化以及电解质渗漏。这是由于应用了 BR 后, 植物体内 O₂⁻、H₂O₂ 生物合成显著下降[59]。Miguel 等人[60]的研究发现了 BR 降低了盐胁迫下苜蓿的 MAD 含

量和膜损伤。Rady 等人[61]也报道了 BR 应用于盐胁迫的菜豆, 降低了电解质渗漏同时提高了膜稳定性指数。

BR 降低植物在盐胁迫下的氧化应激主要通过强化植物抗氧化防御系统起作用。植物抗氧化防御系统有助于清除有害的活性氧, 从而减轻氧化爆发的负面影响[24]。Goda 等人[62]的研究发现 BR 调控拟南芥过氧化物酶编码基因 ATP2 和 ATP24a 的表达。Ding 等人[63]的研究发现 BR 提高了盐胁迫下植物体内超氧化物歧化酶、过氧化氢酶等抗氧化酶的活性, 增加了抗坏血酸、谷胱甘肽等抗氧化剂含量从而提高清除植物体内活性氧能力。Ahammed 等人[64]报道了 BR 不仅促进谷胱甘肽 S-转移酶和谷胱甘肽还原酶的活性, 还提高了还原型谷胱甘肽含量, 但不改变氧化型谷胱甘肽的含量, 从而降低植物受到的氧化损伤。

渗透调节物质是低分子量的有机溶质, 包括某些氨基酸、多胺、糖、季铵盐等多种化合物[65]。这些成分在植物细胞质中累积, 通过调节 Na^+ 和 Cl^- 来维持细胞渗透势[66]。根据 Talaat 与 Shawky [67]的研究, BR 的应用促进了小麦腐胺以及精胺、亚精胺的合成。渗透调节物质中的脯氨酸具有稳定亚细胞结构, 清除自由基的能力[68], 同时作为分子伴侣维持蛋白质结构, 增强酶活性[69]。根据 Abbas 等人[70]的研究, 辣椒在盐胁迫下脯氨酸含量升高, 而 BR 的应用进一步提高了脯氨酸含量, 进而增强植株抗逆性。Talaat 等人[67]的实验观察到盐胁迫下 BR 的应用也提高了小麦脯氨酸含量。甜菜碱也是重要的渗透调节物质, 有利于提高植物抗逆性, Talaat 等人[67]的实验同样观察到 BR 的应用促进了盐胁迫下小麦甜菜碱的生物合成。除此之外, 此项研究还观察到了外源 BR 促进盐胁迫下小麦糖的生物合成。同样, Ramadan [71]的研究也发现盐胁迫下 BR 处理过的玉米种子所形成的植株总糖合成显著增加。

盐胁迫通常增加了植物体内 Na^+ 和 Cl^- 的含量, 导致了离子毒性而打破离子平衡[72]。胞浆 K^+/Na^+ 比值被广泛认为是评判植物耐盐性的关键特征之一[73]。根据 Azhar 等人[74]的研究, 盐胁迫造成大麦根茎大量的 K^+ 损失, 从而显著降低胞浆 K^+/Na^+ 比值, 但是 BR 可以减小 NaCl 引起的根茎 K^+ 泄漏 ($P < 0.05$)。他们的研究还指出 BR 是通过控制去极化激活的 GORK 通道来提高植物的耐盐性。此外, Dong 等人[75]也报道了应用 BR 可提高小麦根和叶的 K^+/Na^+ 和 $\text{Ca}^{2+}/\text{Na}^+$ 比值, 从而减轻 Na^+ 的毒性。

除上述方面外, 还有很多其它研究表明 BR 对于调节植物耐盐性有作用。Wenli 等人[32]的研究发现了 BR 在盐胁迫下调节抗氧化活性的同时还调节叶片植物激素 ABA 和 GA4、IAA、ZR、iPA 和 SA 含量, 从而提高盐胁迫的耐受性。而 Sharma 等人[76]的研究显示了盐胁迫下 BR 的应用提升了植物体内蛋白质含量, 并且不同程度提升了多种氧化应激标志基因的表达。Zhang 等人[77]则研究了内源性 BR 在盐胁迫中的作用, 他们的研究结果显示内源性 BR 可以降低盐胁迫诱导基因 COR78 和 P5CS1 的表达。这些研究表明了 BR 对植物转录翻译的显著影响。

3.4. 耐重金属毒性

镉、砷、镍、锌、铬和铝等重金属离子通过诱导植物一系列代谢改变, 如活性氧的产生和蛋白质变性, 从而抑制植物生长[30] [78]。Andrzej Bajguz [79]的研究发现了外源施加的 BR 在 10-6-10-4M 范围内对藻类细胞中的重金属有明显的阻断作用。BR 可作用于细胞膜的电学性质和酶活性来影响细胞膜的通透性, 进而影响重金属离子的吸收[34]。除此之外, 也有许多研究表明 BR 可以调节植物对单一或者复合的重金属胁迫的抗逆性。

3.4.1. 镉胁迫

Vassilev 和 Yordanov 报道了[80]镉通过限制卡尔文循环中 ATP 和 NADPH 的使用来抑制光合过程。此外, 镉的毒性还会造成氧化应激, 诱导活性氧的产生从而改变细胞膜通透性, 最终抑制植物生长[81]。Anuradha 等人[82]的研究揭示了在萝卜幼苗中, BR 通过提高游离脯氨酸水平从而减轻镉胁迫。Kapoor 等人[83]的研究发现了 BR 的提高了镉胁迫下萝卜 POD, SOD 和 APOX 等抗氧化酶的活性。Janeczko 等

人[84]的研究则发现了 BR 的应用使得油菜子叶镉的积累降低了 14%。Hayat 等人[85]报道了 BR 的应用改善了镉胁迫下芸苔属植物的碳酸酐酶活性, 叶绿素含量, 净光合速率以及渗透调节。

3.4.2. 铜胁迫

高浓度的铜诱导通过哈伯-韦斯反应和芬顿反应产生大量自由基, 从而造成氧化应激[86], 从而导致一系列氧化损伤。Fariduddin 等人[87]报道了 BR 显著改善了铜胁迫下芸苔属植物的形态, 增加了生物量的积累。Fariduddin 等人[88]的另一项研究则发现黄瓜在盐胁迫和铜胁迫共同作用下, 生物量的积累、叶绿素含量、碳酸酐酶活性、净光合速率以及 PSII 初级光化学的最大量子产量均显著下降, 而在应用了 BR 后这些指标得到改善, 除此以外植物多种抗氧化酶活性和脯氨酸含量同时上升, 增强了植物的抗逆性。

3.4.3. 铝胁迫

Pereira 等人[89]的实验发现了铝对植物生长, 以及一些特定的酶, 如 δ -氨基乙酰丙酸脱水酶(ALA-D)活性的抑制作用。除此之外, 铝还会干扰根尖和侧根的细胞分裂、降低根系呼吸和酶活性、干扰植物营养平衡、且能通过增强 DNA 双链的刚性来抑制 DNA 复制[90]。Ali 等[91]的研究表明 BR 的应用降低了铝胁迫对绿豆幼苗的毒性, 改善了幼苗生长、光合以及其它生理过程。Madhan 等人[92]的研究发现 BR 的应用促进了铝胁迫下木豆种子的萌发和幼苗的生长。幼苗体内过氧化氢酶、过氧化物酶、超氧化物歧化酶和抗坏血酸过氧化物酶等抗氧化酶的活性也随着 BR 的应用而提高, 脯氨酸等渗透调节物质水平也同时提高, 维持了幼苗渗透平衡。

3.4.4. 镍胁迫

过量的镍对植物的光合作用、蒸散作用等生理过程以及抗氧化酶活性以及渗透调节物质水平产生影响, 还会产生活性氧并造成脂质过氧化[93] [94]。Kanwar 等人[95]报道了外源 BR 抑制了芥菜根茎对镍的吸收, 恢复了受镍胁迫的芥菜生长。他们的研究结果还表明外源 BR 可提高植物体内的 SOD、CAT、POD、APOX 等氧化酶活性, 改善植物形态和生理过程。Soares 等人[96]则报道 BR 降低了镍在植物根中的积累, 并且改善了渗透调节物质水平, 提高了植物光合色素含量以及 Rubisco 活性。

3.4.5. 铬胁迫

Parr 和 Fred [97]的研究表明镉离子抑制了矮菜豆的萌芽。与其它重金属一样, 镉毒性也会产生大量的自由基和活性氧, 从而抑制植物生长[98]。Anket 等人[99]研究发现, BR 的应用显著减少了水稻中铬的积累, 改善了水稻的生长发育。Arora 等人[100]发现 BR 调节了抗氧化剂和蛋白质的生物合成, 从而减轻铬胁迫。

3.4.6. 锌胁迫

锌浓度过高会导致光合色素分解, 使叶片黄化, 抑制根生长和发生, 同时产生活性氧造成氧化损伤并打破营养平衡, 抑制植物生长[101] [102]。Ramakrishna 和 Rao [103]报道了应用 BR 可以提高锌胁迫下萝卜幼苗的抗氧化酶活性, 从而减轻活性氧对植物的损伤, 同时幼苗体内的脯氨酸水平上升, 幼苗抗逆性得到提高。它们的研究还指出应用了 BR 后 MAD 含量下降, 脂氧合酶活性和电解液泄漏得到改善。

4. 总结与展望

BR 作为一种活性的信号化合物在不同的代谢和生理过程中, 改善植物胁迫下的生长发育, 在植物生长和抗逆性方面有重要的作用。BR 通过激活多种抗氧化酶, 提高抗氧化物含量来减少活性氧对植物的损伤。不仅如此, BR 也能保护光合色素的超微结构不被降解, 从而增加光合作用和其他叶片的气交换。应用 BR 还可以增加各类渗透调节物质的积累, 特别是脯氨酸, 以调节胁迫下植物的渗透势。在不同的应

用方法中,通过种子处理和叶面喷雾应用 BR 比根应用更方便有效。此外,也有研究认为 BR 具有低浓度促进生长,高浓度抑制生长的双重性。BR 对于不同基因表达水平上具有调节作用,但是相关研究较少,还有研究表明外源芸苔素内酯影响植物体内多种激素水平,表明芸苔素内酯与其它植物激素间存在相互作用关系,但其机制尚不明确,也还需要深入研究。

基金项目

浙江省重点研发计划项目“药食同源植物黄精品质提升关键技术研究及功能食品开发”(2020C02039)。

参考文献

- [1] Clouse, S.D. (1996) Molecular Genetic Studies Confirm the Role of Brassinosteroids in Plant Growth and Development. *The Plant Journal*, **10**, 1-8. <https://doi.org/10.1046/j.1365-313X.1996.10010001.x>
- [2] Mulqueen, P. (2003) Recent Advances in Agrochemical Formulation. *Advances in Colloid & Interface Science*, **106**, 83-107. [https://doi.org/10.1016/S0001-8686\(03\)00106-4](https://doi.org/10.1016/S0001-8686(03)00106-4)
- [3] Grove, M.D., Spencer, G.F., Rohwedder, W.K., Mandava, N. and Cook, J.L.C. (1979) Brassinolide, a Plant Growth-Promoting Steroid Isolated from *Brassica napus* Pollen. *Nature*, **281**, 216-217. <https://doi.org/10.1038/281216a0>
- [4] Yang, C.J., Zhang, C., Lu, Y.N., Jin, J.Q. and Wang, X.L. (2011) The Mechanisms of Brassinosteroids' Action: From Signal Transduction to Plant Development. *Molecular Plant*, **4**, 588-600. <https://doi.org/10.1093/mp/ssr020>
- [5] Clouse, S.D. (2011) Brassinosteroid Signal Transduction: From Receptor Kinase Activation to Transcriptional Networks Regulating Plant Development. *Plant Cell*, **23**, 1219-1230. <https://doi.org/10.1105/tpc.111.084475>
- [6] Chen, Z., Wang, Z., Yang, Y., Li, M. and Xu, B. (2018) Abscisic Acid and Brassinolide Combined Application Synergistically Enhances Drought Tolerance and Photosynthesis of Tall Fescue under Water Stress. *Scientia Horticulturae*, **228**, 1-9. <https://doi.org/10.1016/j.scienta.2017.10.004>
- [7] Ahanger, M.A., Ashraf, M., Bajguz, A. and Ahmad, P. (2018) Brassinosteroids Regulate Growth in Plants under Stressful Environments and Crosstalk with Other Potential Phytohormones. *Journal of Plant Growth Regulation*, **37**, 1007-1024. <https://doi.org/10.1007/s00344-018-9855-2>
- [8] Fariduddin, Q., Yusuf, M., Ahmad, I. and Ahmad, A. (2014) Brassinosteroids and Their Role in Response of Plants to Abiotic Stresses. *Biologia Plantarum*, **58**, 9-17. <https://doi.org/10.1007/s10535-013-0374-5>
- [9] Vriet, C., Russinova, E. and Reuzeau, C. (2012) Boosting Crop Yields with Plant Steroids. *The Plant Cell*, **24**, 842-857. <https://doi.org/10.1105/tpc.111.094912>
- [10] Wang, L., Xu, Y.Y., Li, J., Powell, R.A., Xu, Z.H. and Chong, K. (2007) Transgenic Rice Plants Ectopically Expressing Atbak1 Are Semi-Dwarfed and Hypersensitive to 24-Epibrassinolide. *Journal of Plant Physiology*, **164**, 655-664. <https://doi.org/10.1016/j.jplph.2006.08.006>
- [11] Meudt, W.J., Thompson, M.J. and Bennett, H.W. (1983) Investigations on the Mechanism of the Brassinosteroid Response. III. Techniques for Potential Enhancement of Crop Production [Barley, Bean]. *Meeting Plant Growth Regulator Society of America*, **10**, 312-318.
- [12] Zhiponova, M.K., Vanhoutte, I., Boudolf, V., Betti, C., Dhondt, S., Coppens, F., *et al.* (2013) Brassinosteroid Production and Signaling Differentially Control Cell Division and Expansion in the Leaf. *New Phytologist*, **197**, 490-502. <https://doi.org/10.1111/nph.12036>
- [13] Kartal, G., Temel, A., Arican, E. and Gozukirmizi, N. (2009) Effects of Brassinosteroids on Barley Root Growth, Antioxidant System and Cell Division. *Plant Growth Regulation*, **58**, 261-267. <https://doi.org/10.1007/s10725-009-9374-z>
- [14] Hu, Y., Bao, F. and Li, J. (2010) Promotive Effect of Brassinosteroids on Cell Division Involves a Distinct cycd3-Induction Pathway in Arabidopsis. *Plant Journal for Cell & Molecular Biology*, **24**, 693-701. <https://doi.org/10.1046/j.1365-313x.2000.00915.x>
- [15] Khripach, V., Zhabinskii, V. and Groot, A.D. (2000) Twenty Years of Brassinosteroids: Steroidal Plant Hormones Warrant Better Crops for the XXI Century. *Annals of Botany (London)*, **86**, 441-447. <https://doi.org/10.1006/anbo.2000.1227>
- [16] Xi, Z.M., Zhang, Z.W., Hou, S.S., Luan, L.Y., Gao, X., Ma, L.N. and Fang, Y.L. (2013) Regulating the Secondary Metabolism in Grape Berry Using Exogenous 24-Epibrassinolide for Enhanced Phenolics Content and Antioxidant Capacity. *Food Chemistry*, **141**, 3056-3065. <https://doi.org/10.1016/j.foodchem.2013.05.137>

- [17] Sayed, H.F., Ibrahim, H.K., El-Shafey, A.S. and Hassan, H.M. (2009) Effects of Pre-Soaking *Cucurbita pepo* L. (*C. pepo*) Seeds in Two Different Concentrations of Epibrassinolide (eb) on Seed Germination and Seedling Growth. *Australian Journal of Basic and Applied Sciences*, **3**, 4465-4477.
- [18] Ekinci, M., Yildirim, E., Dursun, A. and Turan, M. (2012) Mitigation of Salt Stress in Lettuce (*Lactuca sativa* L. var. *crispa*) by Seed and Foliar 24-Epibrassinolide Treatments. *HortScience: A Publication of the American Society for Horticultural Science*, **47**, 631-636. <https://doi.org/10.21273/HORTSCI.47.5.631>
- [19] Nogues, S. and Baker, N.R. (2000) Effects of Drought on Photosynthesis in Mediterranean Plants Grown under Enhanced uv-b Radiation. *Journal of Experimental Botany*, **51**, 1309-1317. <https://doi.org/10.1093/jexbot/51.348.1309>
- [20] Lefebvre, S., Lawson, T., Fryer, M., Zakhleniuk, O.V., Lloyd, J.C. and Raines, C.A. (2005) Increased Sedoheptulose-1, 7-Bisphosphatase Activity in Transgenic Tobacco Plants Stimulates Photosynthesis and Growth from an Early Stage in Development. *Plant Physiology*, **138**, 451-460. <https://doi.org/10.1104/pp.104.055046>
- [21] Reddy, M.P. and Vora, A.B. (1986) Changes in Pigment Composition, Hill Reaction Activity and Saccharides Metabolism in Bajra (*Pennisetum typhoides* S & H) Leaves under NaCl Salinity. *Photosynthetica*, **20**, 50-55.
- [22] Gupta, P., Srivastava, S. and Seth, C.S. (2017) 24-Epibrassinolide and Sodium Nitroprusside Alleviate the Salinity Stress *Inbrassica juncea* L. cv. Varuna through Cross Talk among Proline, Nitrogen Metabolism and Abscisic Acid. *Plant and Soil*, **411**, 483-498. <https://doi.org/10.1007/s11104-016-3043-6>
- [23] Rodriguez, P., Torrecillas, A., Morales, M.A., Ortuno, M.F. and Sanchez-Blanco, M.J. (2005) Effects of NaCl Salinity and Water Stress on Growth and Leaf Water Relations of *Asteriscus maritimus* Plants. *Environmental & Experimental Botany*, **53**, 113-123. <https://doi.org/10.1016/j.envexpbot.2004.03.005>
- [24] Tanveer, M. and Shabala, S. (2018) Targeting Redox Regulatory Mechanisms for Salinity Stress Tolerance in Crops. *Salinity Responses and Tolerance in Plants*, **1**, 213-234. https://doi.org/10.1007/978-3-319-75671-4_8
- [25] Verma, S. and Mishra, S.N. (2005) Putrescine Alleviation of Growth in Salt Stressed *Brassica juncea* by Inducing Antioxidative Defense System. *Journal of Plant Physiology*, **162**, 669-677. <https://doi.org/10.1016/j.jplph.2004.08.008>
- [26] Mittler, R. (2002) Oxidative Stress, Antioxidants and Stress Tolerance. *Trends in Plant Science*, **7**, 405-410. [https://doi.org/10.1016/S1360-1385\(02\)02312-9](https://doi.org/10.1016/S1360-1385(02)02312-9)
- [27] Anwar, A., Bai, L., Miao, L., Liu, Y., Li, S., Yu, X., et al. (2018) 24-Epibrassinolide Ameliorates Endogenous Hormone Levels to Enhance Low-Temperature Stress Tolerance in Cucumber Seedlings. *International Journal of Molecular Sciences*, **19**, 2497. <https://doi.org/10.3390/ijms19092497>
- [28] Tanveer, M., Shahzad, B., Sharma, A. and Khan, E.A. (2019) 24-Epibrassinolide Application in Plants: An Implication for Improving Drought Stress Tolerance in Plants. *Plant Physiology, and Biochemistry: PPB*, **135**, 295-303. <https://doi.org/10.1016/j.plaphy.2018.12.013>
- [29] Qasim, M., Ashraf, M., Ashraf, M.Y., Rehman, S.U. and Rha, E.S. (2003) Salt-Induced Changes in Two Canola Cultivars Differing in Salt Tolerance. *Biologia Plantarum (Prague)*, **46**, 629-632. <https://doi.org/10.1023/A:1024844402000>
- [30] Anjum, S.A., Tanveer, M., Hussain, S., Ashraf, U., Khan, I. and Wang, L. (2017) Alteration in Growth, Leaf Gas Exchange, and Photosynthetic Pigments of Maize Plants under Combined Cadmium and Arsenic Stress. *Water, Air, & Soil Pollution*, **228**, 13. <https://doi.org/10.1007/s11270-016-3187-2>
- [31] Siddiqui, M.H., Mohamed, H., Al-Wahaibi, F.M. and Sahli, A.A.A. (2014) Nano-Silicon Dioxide Mitigates the Adverse Effects of Salt Stress on *Cucurbita pepo* L. *Environmental Toxicology and Chemistry*, **33**, 2429-2437. <https://doi.org/10.1002/etc.2697>
- [32] Wu, W., Zhang, Q., Ervin, E.H., Yang, Z. and Zhang, X. (2017) Physiological Mechanism of Enhancing Salt Stress Tolerance of Perennial Ryegrass by 24-Epibrassinolide. *Frontiers in Plant Science*, **8**, 1017. <https://doi.org/10.3389/fpls.2017.01017>
- [33] Krishna, P. (2003) Brassinosteroid-Mediated Stress Responses. *Journal of Plant Growth Regulation*, **22**, 289-297. <https://doi.org/10.1007/s00344-003-0058-z>
- [34] Shahzad, B., Tanveer, M., Che, Z., Rehman, A., Cheema, S.A., Sharma, A., et al. (2018) Role of 24-Epibrassinolide (ebl) in Mediating Heavy Metal and Pesticide Induced Oxidative Stress in Plants: A Review. *Ecotoxicology and Environmental Safety*, **147**, 935-944. <https://doi.org/10.1016/j.ecoenv.2017.09.066>
- [35] Talaat, N.B., Shawky, B.T. and Ibrahim, A.S. (2015) Alleviation of Drought-Induced Oxidative Stress in Maize (*Zea mays* L.) Plants by Dual Application of 24-Epibrassinolide and Spermine. *Environmental and Experimental Botany*, **113**, 47-58. <https://doi.org/10.1016/j.envexpbot.2015.01.006>
- [36] Anjum, S.A., Wang, L.C., Farooq, M., Hussain, M. and Zou, C.M. (2011) Brassinolide Application Improves the Drought Tolerance in Maize through Modulation of Enzymatic Antioxidants and Leaf Gas Exchange. *Journal of Agronomy and Crop Science*, **197**, 177-185. <https://doi.org/10.1111/j.1439-037X.2010.00459.x>
- [37] Xiong, J., Kong, H., Akram, N., Bai, X., Ashraf, M., Tan, R., et al. (2016) 24-Epibrassinolide Increases Growth, Grain

- Yield and Beta-ODAP Production in Seeds of Well-Watered and Moderately Waterstressed Grass Pea. *Plant Growth Regulation*, **78**, 217-231. <https://doi.org/10.1007/s10725-015-0087-1>
- [38] Hu, W.H., Yan, X.H., Xiao, Y.A., Zeng, J.J., Qi, H.J. and Ogwen, J.O. (2013) 24-Epibrassinosteroid Alleviate Drought-Induced Inhibition of Photosynthesis in *Capsicum annuum*. *Scientia Horticulturae*, **150**, 232-237. <https://doi.org/10.1016/j.scienta.2012.11.012>
- [39] Lima, J.V. and Lobato, A.K.S. (2017) Brassinosteroids Improve Photosystem II Efficiency, Gas Exchange, Antioxidant Enzymes and Growth of Cowpea Plants Exposed to Water Deficit. *Physiology and Molecular Biology of Plants*, **23**, 59-72. <https://doi.org/10.1007/s12298-016-0410-y>
- [40] Zhao, G.W., Xu, H.L., Zhang, P.J., et al. (2017) Effects of 2,4-Epibrassinolide on Photosynthesis and Rubisco Activase Gene Expression in *Triticum aestivum* L. Seedlings under a Combination of Drought and Heat Stress. *Plant Growth Regulation*, **81**, 377-384. <https://doi.org/10.1007/s10725-016-0214-7>
- [41] 孙石昂, 何发林, 姚向峰, 乔治华, 于灏泳, 李向东, 等. 芸苔素内酯可提高玉米幼苗的抗旱性[J]. 植物生理学报, 2019(6): 829-836.
- [42] Sharma, A., Thakur, S., Kumar, V., Kesavan, A.K., Thukral, A.K. and Bhardwaj, R. (2017) 24-Epibrassinolide Stimulates Imidacloprid Detoxification by Modulating the Gene Expression of *Brassica juncea* L. *BMC Plant Biology*, **17**, 56. <https://doi.org/10.1186/s12870-017-1003-9>
- [43] Peng, Y., Zhang, J., Cao, G., Xie, Y., Liu, X., Lu, M., et al. (2010) Overexpression of PLD α 1 Gene from *Setaria italica* Enhances the Sensitivity of Arabidopsis to Abscisic Acid and Improves Its Drought Tolerance. *Plant Cell Reports*, **29**, 793-802. <https://doi.org/10.1007/s00299-010-0865-1>
- [44] Pokotylo, I.V., Kretynin, S.V., Khripach, V.A., Ruelland, E., Blume, Y.B. and Kravets, V.S. (2014) Influence of 24-Epibrassinolide on Lipid Signalling and Metabolism in *Brassica napus*. *Plant Growth Regulation*, **73**, 9-17. <https://doi.org/10.1007/s10725-013-9863-y>
- [45] Farooq, M., Wahid, A., Basra, S.M.A. and Islam-ud-Din (2009) Improving Water Relations and Gas Exchange with Brassinosteroids in Rice under Drought Stress. *Journal of Agronomy and Crop Science*, **195**, 262-269. <https://doi.org/10.1111/j.1439-037X.2009.00368.x>
- [46] Yu, J.Q., Huang, L.F., Hu, W.H., Zhou, Y.H., Mao, W.H., Ye, S.F. and Nogues, S. (2004) A Role for Brassinosteroids in the Regulation of Photosynthesis in *Cucumis sativus*. *Journal of Experimental Botany*, **55**, 1135-1143. <https://doi.org/10.1093/jxb/erh124>
- [47] Khamsuk, O., Sonjaroon, W., Suwanwong, S., et al. (2018) Effects of 24-Epibrassinolide and the Synthetic Brassinosteroid Mimic on Chili Pepper under Drought. *Acta Physiologiae Plantarum*, **40**, 106. <https://doi.org/10.1007/s11738-018-2682-z>
- [48] Alejandro, C.-U., et al. (2016) Transcriptome Analysis of Pepper (*Capsicum annuum*) Revealed a Role of 24-Epibrassinolide in Response to Chilling. *Frontiers in Plant Science*, **7**, 1281. <https://doi.org/10.3389/fpls.2016.01281>
- [49] Honnerova, J., Rothova, O., Hola, D., Kocova, M., Kohout, L. and Kvasnica, M. (2010) The Exogenous Application of Brassinosteroids to *Zea mays* (L.) Stressed by Long-Term Chilling Does Not Affect the Activities of Photosystem I or 2. *Journal of Plant Growth Regulation*, **29**, 500-505. <https://doi.org/10.1007/s00344-010-9153-0>
- [50] Kalinich, J.F., Bhushan, M.N. and Todhunter, J.A. (1985) Relationship of Nucleic Acid Metabolism to Brassinolide-Induced Responses in Beans. *Journal of Plant Physiology*, **120**, 207-214. [https://doi.org/10.1016/S0176-1617\(85\)80107-3](https://doi.org/10.1016/S0176-1617(85)80107-3)
- [51] Yuan, L., Shu, S., Sun, J., et al. (2012) Effects of 24-Epibrassinolide on the Photosynthetic Characteristics, Antioxidant System, and Chloroplast Ultrastructure in *Cucumis sativus* L. under Ca(NO $_3$) $_2$ Stress. *Photosynthesis Research*, **112**, 205-214. <https://doi.org/10.1007/s11120-012-9774-1>
- [52] Ali, B., Hayat, S. and Ahmad, A. (2007) 28-Homobrassinolide Ameliorates the Saline Stress in Chickpea (*Cicer arietinum* L.). *Environmental and Experimental Botany*, **59**, 217-223. <https://doi.org/10.1016/j.envexpbot.2005.12.002>
- [53] Xia, X.J., Huang, L.F., Zhou, Y.H., Mao, W.H., Shi, K., Wu, J.X., et al. (2009) Brassinosteroids Promote Photosynthesis and Growth by Enhancing Activation of Rubisco and Expression of Photosynthetic Genes in *Cucumis sativus*. *Planta*, **230**, 1185-1196. <https://doi.org/10.1007/s00425-009-1016-1>
- [54] Fariduddin, Q., Mir, B.A., Yusuf, M. and Ahmad, A. (2014) 24-Epibrassinolide and/or Putrescine Trigger Physiological and Biochemical Responses for the Salt Stress Mitigation in *Cucumis sativus* L. *Photosynthetica*, **52**, 464-474. <https://doi.org/10.1007/s11099-014-0052-7>
- [55] Castle, J., Montoya, T. and Bishop, G.J. (2003) Selected Physiological Responses of Brassinosteroids: A Historical Approach. In: *Brassinosteroids: Bioactivity and Crop Productivity*, Springer, Berlin, 45-68. https://doi.org/10.1007/978-94-017-0948-4_2
- [56] Anket, S., Sharad, T., Vinod, K., Kanwar, M.K., Kesavan, A.K., Thukral, A.K., et al. (2016) Pre-Sowing Seed Treat-

- ment with 24-Epibrassinolide Ameliorates Pesticide Stress in *Brassica juncea* L. through the Modulation of Stress Markers. *Frontiers in Plant Science*, **7**, 1569. <https://doi.org/10.3389/fpls.2016.01569>
- [57] Jiang, Y.P., Cheng, F., Zhou, Y.H., Xia, X.J., Mao, W.H., Shi, K., *et al.* (2012) Cellular Glutathione Redox Homeostasis Plays an Important Role in the Brassinosteroid Induced Increase in CO_2 Assimilation in *Cucumis sativus*. *New Phytologist*, **194**, 932-943. <https://doi.org/10.1111/j.1469-8137.2012.04111.x>
- [58] Siefermann-Harms, D. (1987) The Light-Harvesting and Protective Functions of Carotenoids in Photosynthetic Membranes. *Physiologia Plantarum*, **69**, 561-568. <https://doi.org/10.1111/j.1399-3054.1987.tb09240.x>
- [59] Guerrero, Y.R., Gonzalez, L.M., Dell'Amico, J., Nuñez, M. and Pieters, A.J. (2015) Reversion of Deleterious Effects of Salt Stress by Activation of ROS Detoxifying Enzymes via Foliar Application of 24-Epibrassinolide in Rice Seedlings. *Theoretical & Experimental Plant Physiology*, **27**, 31-40. <https://doi.org/10.1007/s40626-014-0029-8>
- [60] Lopez-Gomez, M., Hidalgo-Castellanos, J., Lluch, C. and Herrera-Cervera, J.A. (2016) 24-Epibrassinolide Ameliorates Salt Stress Effects in the Symbiosis *Medicago truncatula*-*Sinorhizobium meliloti* and Regulates the Nodulation in Cross-Talk with Polyamines. *Plant Physiology, and Biochemistry*, **108**, 212-221. <https://doi.org/10.1016/j.plaphy.2016.07.017>
- [61] Rady, M.M. (2011) Effect of 24-Epibrassinolide on Growth, Yield, Antioxidant System and Cadmium Content of Bean (*Phaseolus vulgaris* L.) Plants under Salinity and Cadmium Stress. *Scientia Horticulturae*, **129**, 232-237. <https://doi.org/10.1016/j.scienta.2011.03.035>
- [62] Goda, H., Shimada, Y., Asami, T., Fujioka, S. and Yoshida, S. (2002) Microarray Analysis of Brassinosteroid-Regulated Genes in Arabidopsis. *Plant Physiology*, **130**, 1319-1334. <https://doi.org/10.1104/pp.011254>
- [63] Ding, H.D., Zhu, X.H., Zhu, Z.W., Yang, S.J., Zha, D.S. and Wu, X.X. (2012) Amelioration of Salt-Induced Oxidative Stress in Eggplant by Application of 24-Epibrassinolide. *Biologia Plantarum*, **56**, 767-770. <https://doi.org/10.1007/s10535-012-0108-0>
- [64] Ahammed, G.J., He, B.B., Qian, X.J., Zhou, Y.H., Shi, K., Zhou, J., *et al.* (2017) 24-Epibrassinolide Alleviates Organic Pollutants-Retarded Root Elongation by Promoting Redox Homeostasis and Secondary Metabolism in *Cucumis sativus*, L. *Environmental Pollution*, **229**, 922-931. <https://doi.org/10.1016/j.envpol.2017.07.076>
- [65] Yancey, P.H. (2005) Organic Osmolytes as Compatible, Metabolic and Counteracting Cytoprotectants in High Osmolarity and Other Stresses. *Journal of Experimental Biology* **208**, 2819-2830. <https://doi.org/10.1242/jeb.01730>
- [66] Ottow, E.A., Brinker, M., Teichmann, T., Fritz, E., Kaiser, W., *et al.* (2005) *Populus euphratica* Displays Apoplastic Sodium Accumulation, Osmotic Adjustment by Decreases in Calcium and Soluble Carbohydrates, and Develops Leaf Succulence under Salt Stress. *Plant Physiology*, **139**, 1762-1772. <https://doi.org/10.1104/pp.105.069971>
- [67] Talaat, N.B. and Shawky, B.T. (2012) 24-Epibrassinolide Ameliorates the Saline Stress and Improves the Productivity of Wheat (*Triticum aestivum* L.). *Environmental & Experimental Botany*, **82**, 80-88. <https://doi.org/10.1016/j.envexpbot.2012.03.009>
- [68] Ashraf, M. and Foolad, M.R. (2007) Roles of Glycine Betaine and Proline in Improving Plant Abiotic Stress Resistance. *Environmental and Experimental Botany*, **59**, 206-216. <https://doi.org/10.1016/j.envexpbot.2005.12.006>
- [69] Szabados, L. and Savoure, A. (2010) Proline: A Multifunctional Amino Acid. *Trends in Plant Science*, **5**, 89-97. <https://doi.org/10.1016/j.tplants.2009.11.009>
- [70] Abbas, S., Latif, H.H. and Elsherbiny, E.A. (2013) Effect of 24-Epibrassinolide on the Physiological and Genetic Changes on Two Varieties of Pepper under Salt Stress Conditions. *Pakistan Journal of Botany*, **45**, 1273-1284.
- [71] Agami, R.A. (2013) Alleviating the Adverse Effects of NaCl Stress in Maize Seedlings by Pretreating Seeds with Salicylic Acid and 24-Epibrassinolide. *South African Journal of Botany*, **88**, 171-177. <https://doi.org/10.1016/j.sajb.2013.07.019>
- [72] Athar, H.U.R., Khan, A. and Ashraf, M. (2008) Exogenously Applied Ascorbic Acid Alleviates Salt-Induced Oxidative Stress in Wheat. *Environmental and Experimental Botany*, **63**, 224-231. <https://doi.org/10.1016/j.envexpbot.2007.10.018>
- [73] Shabala, S., White, R.G., Djordjevic, M.A., Ruan, Y.L. and Mathesius, U. (2016) Root-to-Shoot Signalling: Integration of Diverse Molecules, Pathways and Functions. *Functional Plant Biology*, **43**, 85-86. <https://doi.org/10.1071/FP15252>
- [74] Azhar, N., Su, N., Shabala, L. and Shabala, S. (2017) Exogenously Applied 24-Epibrassinolide (ebl) Ameliorates Detrimental Effects of Salinity by Reducing K^+ Efflux via Depolarization-Activated K^+ Channels. *Plant and Cell Physiology*, **58**, 802-810. <https://doi.org/10.1093/pcp/pcx026>
- [75] Dong, Y.J., Wang, W.W., Hu, G.Q., Chen, W.F., Zhuge, Y.P., Wang, Z.L., *et al.* (2017) Role of Exogenous 24-Epibrassinolide in Enhancing the Salt Tolerance of Wheat Seedlings. *Journal of Soil Science and Plant Nutrition*, **17**, 554-569. <https://doi.org/10.4067/S0718-95162017000300001>
- [76] Sharma, I., Bhardwaj, R. and Pati, P.K. (2013) Stress Modulation Response of 24-Epibrassinolide against Imidacloprid

- in an Elite Indica Rice Variety Pusa Basmati-1. *Pesticide Biochemistry and Physiology*, **105**, 144-153. <https://doi.org/10.1016/j.pestbp.2013.01.004>
- [77] Zhang, Y., Gu, M., Shi, K., Zhou, Y.H. and Yu, J.Q. (2010) Effects of Aqueous Root Extracts and Hydrophobic Root Exudates of Cucumber (*Cucumis sativus* L.) on Nuclei DNA Content and Expression of Cell Cycle-Related Genes in Cucumber Radicles. *Plant and Soil*, **327**, 455-463. <https://doi.org/10.1007/s11104-009-0075-1>
- [78] Anjum, S.A., Ashraf, U., Khan, I., Tanveer, M., Ali, M., Hussain, I., et al. (2016) Chromium and Aluminum Phytotoxicity in Maize: Morpho-Physiological Responses and Metal Uptake. *Clean*, **44**, 1075-1084. <https://doi.org/10.1002/clel.201500532>
- [79] Bajguz, A. (2000) Blockade of Heavy Metals Accumulation in *Chlorella Vulgaris* Cells by 24-Epibrassinolide. *Plant Physiology, & Biochemistry*, **38**, 797-801. [https://doi.org/10.1016/S0981-9428\(00\)01185-2](https://doi.org/10.1016/S0981-9428(00)01185-2)
- [80] Vassilev, A. and Yordanov, I. (1997) Reductive Analysis of Factors Limiting Growth of Cadmium-Treated Plants: A Review. *General and Applied Plant Physiology*, **23**, 114-133.
- [81] Mahmood, T., Gupta, K.J. and Kaiser, W.M. (2009) Cadmium Stress Stimulates Nitric Oxide Production by Wheat Roots. *Pakistan Journal of Botany*, **41**, 1285-1290.
- [82] Sou, A. and Srou, R. (2007) The Effect of Brassinosteroids on Radish (*Raphanus sativus* L.) Seedlings Growing under Cadmium Stress. *Plant, Soil and Environment*, **53**, 465-472. <https://doi.org/10.17221/2307-PSE>
- [83] Kapoor, D., Kaur, S. and Bhardwaj, R. (2014) Physiological and Biochemical Changes in *Brassica juncea* Plants under CD-Induced Stress. *Journal of Biomedicine and Biotechnology*, **2014**, Article ID: 726070. <https://doi.org/10.1155/2014/726070>
- [84] Janeczko, A., Koscielniak, J., Pilipowicz, M., Szarek-Lukaszewska, G. and Skoczowski, A. (2005) Protection of Winter rape Photosystem 2 by 24-Epibrassinolide under Cadmium Stress. *Photosynthetica (Prague)*, **43**, 293-298. <https://doi.org/10.1007/s11099-005-0048-4>
- [85] Hayat, S., Ali, B., Hasan, S.A. and Ahmad, A. (2007) Brassinosteroid Enhanced the Level of Antioxidants under Cadmium Stress in *Brassica juncea*. *Environmental and Experimental Botany*, **60**, 33-41. <https://doi.org/10.1016/j.envexpbot.2006.06.002>
- [86] Halliwell, B. and Gutteridge, J.M.C. (1984) Oxygen Toxicity, Oxygen Radicals, Transition Metals and Disease. *Biochemical Journal*, **219**, 1-14. <https://doi.org/10.1042/bj2190001>
- [87] Fariduddin, Q., Yusuf, M., Hayat, S. and Ahmad, A. (2009) Effect of 28-Homobrassinolide on Antioxidant Capacity and Photosynthesis in *Brassica juncea* Plants Exposed to Different Levels of Copper. *Environmental and Experimental Botany*, **66**, 418-424. <https://doi.org/10.1016/j.envexpbot.2009.05.001>
- [88] Fariduddin, Q., Khalil, R.R.A.E., Mir, B.A., Yusuf, M. and Ahmad, A. (2013) 24-Epibrassinolide Regulates Photosynthesis, Antioxidant Enzyme Activities and Proline Content of *Cucumis sativus* under Salt and/or Copper Stress. *Environmental Monitoring and Assessment*, **185**, 7845-7856. <https://doi.org/10.1007/s10661-013-3139-x>
- [89] Pereira, L.B., Tabaldi, L.A., Gonçalves, J.F., Jucoski, G.O., Pauletto, M.M., Weis, S.N., et al. (2006) Effect of Aluminum on δ -Aminolevulinic Acid Dehydratase (ala-d) and the Development of Cucumber (*Cucumis sativus*). *Environmental & Experimental Botany*, **57**, 106-115. <https://doi.org/10.1016/j.envexpbot.2005.05.004>
- [90] Alexandre, V.V., Regina, C.F. and Antonio, S.V. (2005) Recent Advances in Aluminum Toxicity and Resistance in Higher Plants. *Brazilian Journal of Plant Physiology*, **17**, 129-143. <https://doi.org/10.1590/S1677-04202005000100011>
- [91] Ali, B., Hasan, S.A., Hayat, S., Hayat, Q., Yadav, S., Fariduddin, Q., et al (2008) A Role for Brassinosteroids in the Amelioration of Aluminium Stress through Antioxidant System in Mung Bean (*Vigna radiata* L. Wilczek). *Environmental and Experimental Botany*, **62**, 153-159. <https://doi.org/10.1016/j.envexpbot.2007.07.014>
- [92] Madhan, M., Mahesh, K. and Seeta, R.R.S. (2014) Effect of 24-Epibrassinolide on Aluminium Stress Induced Inhibition of Seed Germination and Seedling Growth of *Cajanus cajan*. Millsp. *International Journal of Multidisciplinary and Current Research*, **2**, 286-290.
- [93] Pandey, N. and Sharma, C.P. (2002) Effect of Heavy Metals Co^{2+} , Ni^{2+} and Cd^{2+} on Growth and Metabolism of Cabbage. *Plant Science (Oxford)*, **163**, 753-758. [https://doi.org/10.1016/S0168-9452\(02\)00210-8](https://doi.org/10.1016/S0168-9452(02)00210-8)
- [94] Gajewska, E. and Skłodowska, M. (2008) Differential Biochemical Responses of Wheat Shoots and Roots to Nickel Stress: Antioxidative Reactions and Proline Accumulation. *Plant Growth Regulation*, **54**, 179-188. <https://doi.org/10.1007/s10725-007-9240-9>
- [95] Kanwar, M.K., Bhardwaj, R., Chowdhary, S.P., Arora, P., Sharma, P. and Kumar, S. (2013) Isolation and Characterization of 24-Epibrassinolide from *Brassica juncea* L. and Its Effects on Growth, Ni Ion Uptake, Antioxidant Defense of Brassicaplants and *in Vitro* Cytotoxicity. *Acta Physiologiae Plantarum*, **35**, 1351-1362. <https://doi.org/10.1007/s11738-012-1175-8>
- [96] Soares, C., Sousa, A.D., Pinto, A., Azenha, M. and Fidalgo, F. (2016) Effect of 24-Epibrassinolide on ROS Content,

- Antioxidant System, Lipid Peroxidation and Ni Uptake in *Solanum nigrum* L. under Ni Stress. *Environmental and Experimental Botany*, **122**, 115-125. <https://doi.org/10.1016/j.envexpbot.2015.09.010>
- [97] Parr, P.D. and Jr., F.G.T. (1982) Germination and Growth Effects of Hexavalent Chromium in Orocol T1 (a Corrosion Inhibitor) on *Phaseolus vulgaris*. *Environment International*, **7**, 197-202. [https://doi.org/10.1016/0160-4120\(82\)90105-2](https://doi.org/10.1016/0160-4120(82)90105-2)
- [98] Hegedus, A., Erdei, S. and Horvath, G. (2001) Comparative Studies of h₂o₂ Detoxifying Enzymes in Green and Greening Barley Seedlings under Cadmium Stress. *Plant Science (Shannon)*, **160**, 1085-1093. [https://doi.org/10.1016/S0168-9452\(01\)00330-2](https://doi.org/10.1016/S0168-9452(01)00330-2)
- [99] Anket, S., Vinod, K., Renu, B. and Ashwani, K.T. (2016) Seed Pre-Soaking with 24-Epibrassinolide Reduces the Imidacloprid Pesticide Residues in Green Pods of *Brassica juncea* L. *Toxicological & Environmental Chemistry*, **99**, 95-103. <https://doi.org/10.1080/02772248.2016.1146955>
- [100] Arora, P., *et al.* (2011) Pre-soaking Seed Treatment of 24-Epibrassinolide Modulates Cr Stress in *Brassica juncea* L. *Terrestrial & Aquatic Environmental Toxicology*, **5**, 14-18.
- [101] Castiglione, S., Franchin, C., Fossati, T., Lingua, G., Torrigiani, P. and Biondi, S. (2007) High Zinc Concentrations Reduce Rooting Capacity and Alter Metallothionein Gene Expression in White Poplar (*Populus alba* L. cv. Villafranca). *Chemosphere*, **67**, 1117-1126. <https://doi.org/10.1016/j.chemosphere.2006.11.039>
- [102] Wang, C., Zhang, S.H., Wang, P.F., *et al.* (2009) Excess Zn Alters the Nutrient Uptake and Induces the Antioxidative Responses in Submerged Plant *Hydrilla verticillata* (L.f.) Royle. *Chemosphere*, **76**, 938-945. <https://doi.org/10.1016/j.chemosphere.2009.04.038>
- [103] Ramakrishna, B. and Rao, S.S.R. (2012) 24-Epibrassinolide Alleviated Zinc-Induced Oxidative Stress in Radish (*Raphanus sativus* L.) Seedlings by Enhancing Antioxidative System. *Plant Growth Regulation*, **68**, 249-259. <https://doi.org/10.1007/s10725-012-9713-3>