# 油菜素内酯调控植物响应非生物逆境胁迫的生理机制

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**摘要：**油菜素内酯属于甾体类激素中的油菜素甾醇类物质，是其生物合成中产生的活性副产物，对植物生长发育具有重要的调节作用。在非生物胁迫条件下，外源施用油菜素内酯可以增强植物的抗氧化系统，增加渗透物质水平，维持内源激素平衡，稳定离子和水分平衡，改善气体交换属性和光合作用，最终减轻逆境危害并促进植物生长。该文综述油菜素内酯对非生物胁迫下植物生长、生理调节的影响及调控途径，对油菜素内酯提高植物抗逆境能力的未来研究方向进行展望。

**关键词：**油菜素内酯；光合作用；抗氧化系统；渗透调节系统；激素平衡

## The physiological mechanisms of exogenous brassinolide regulating abiotic stresses in plants: a review

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**Abstract:** Brassinolide is one of brassinosterols, a group of steroid hormones. It is an active by-product of brassinosterols’ biosynthesis and plays an important role in regulating plant growth and development. Under abiotic stress, exogenous application of brassinolide can enhance plant antioxidant system, increase osmotic material level, maintain endogenous hormone balance, stabilize ion and water balance, improve gas exchange properties and photosynthesis, and therefore reduce stress damages and promote plant growth. In this paper, the effects of brassinolide on plant growth and physiological regulation under abiotic stresses were reviewed, and the possible research directions of brassinolide in promoting plant resistance to stresses were proposed

**Key words:** brassinolide; photosynthesis; antioxidant system; osmotic adjustment system; endogenous hormone balance

逆境胁迫是影响作物生产质量的一个重要因素，植物遭受的胁迫可分为生物胁迫和非生物胁迫2种类型。其中，生物胁迫是由真菌、细菌等病原生物（李卓等，2018；康保珊等，2022）和昆虫（杨硕等，2015）引起的胁迫；非生物胁迫包括高盐、干旱、重金属污染和温度等胁迫。非生物胁迫往往会造成植物光合作用受到抑制，渗透调节失衡，养分吸收紊乱（易家宁等，2020），激素比例失调（宋珊珊等，2021），活性氧增多，氧化还原失衡，质膜损伤等负面效应（牟祚民等，2019），显著抑制植物生长，最终显著影响作物产量和品质（董建梅等，2021）。例如干旱胁迫下，大麦根长、干鲜重以及叶绿素含量显著下降，丙二醛（malondialdehyde，MDA）和活性氧（reactive oxygen，ROS）含量增多（Gill et al.，2017）；盐胁迫下，番茄叶片的相对含水量、光合色素、辅助色素、气体交换参数和叶绿素荧光受到影响，MDA和$H_2O_2$含量显著升高（Ahmad et al.，2018）；低温胁迫下，种子萌发和出苗时间显著延长，净光合速率和气孔导度等减小；锌胁迫下，根长、根鲜重和光合作用等均显著减弱（Sousa et al.，2020；Sun et al.，2020）。

植物激素是植物内源小分子化学物质，以极低的浓度调节植物生长发育，往往在非生物胁迫下植

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物信号转导过程中起着重要作用（Voß et al.，2014；Kazan，2015）。油菜素甾醇类物质是一类具有广泛生物活性的甾体类激素，被称为第六类植物激素。油菜素内酯是油菜素甾醇类物质生物合成过程中产生的活性副产物，对植物生长发育具有重要的调节作用，能促进细胞扩张和分裂，调节衰老、花粉发育、果实成熟（Grove et al.，1979；Mandava，1988；Yokota & Mori，1992），以及提高对干旱、盐、高温和重金属等非生物胁迫的耐受性（Krishna，2003）。非生物胁迫条件下，油菜素内酯通过改善植物的生理调节系统，如光合作用、渗透调节系统、抗氧化调节系统、内源激素信号响应等，来促进胁迫下植物的生长（Ahmad et al.，2018；Su et al.，2020；Zhong et al.，2020）。近年来，油菜素内酯衍生物被广泛应用于农业生产中，例如24-表油菜素内酯、28-高油菜素内酯、28-表高油菜素内酯、油菜素甾酮、丙酰油菜素内酯和14-羟基芸苔素甾醇等，其中以28-高油菜素内酯和24-表油菜素内酯应用最广泛。

现有综述大多集中于探究油菜素内酯与其他植物激素联合调控逆境胁迫下的植物生长（Banerjee & Roychoudhury，2018；Jiroutova et al.，2018），鲜少有系统讨论油菜素内酯促进非生物逆境下植物生长的报道。本文主要总结油菜素内酯介导植物生理调节系统参与调控非生物胁迫，概述非生物胁迫下外施油菜素内酯对植物生长和生理调节的影响及作用机制，并展望其研究和应用前景，以期为油菜素内酯的分子抗逆研究及大田抗逆应用提供生理基础。

## 1 油菜素内酯对非生物胁迫下植物生长的影响

### 1.1 促进非生物胁迫下植物生长并改善作物品质

非生物胁迫显著抑制植物生长，如番茄和黄瓜等作物地上和地下生物量减少，刺槐等树种相对含水量降低（岳健敏等，2017；Anwar et al.，2018；Shah et al.，2020）。油菜素内酯缺陷突变体具有矮化特性，外施油菜素内酯使其恢复正常表型，这表明油菜素内酯在植物生长和发育中起着关键作用，能使生长不良的植物恢复正常生长，提高植物对各种非生物胁迫的应对能力（Wang et al.，2007）。外施油菜素内酯能显著促进重金属胁迫下水稻幼苗的生长（Sharma P et al.，2016）；使盐胁迫下豌豆植株鲜重和干重分别增加 12.0%~20.0% 和 15.0%~27.0%（Shahid et al.，2014），并且恢复苹果幼苗叶片形态（Su et al.，2020）。Wu et al.（2014）研究表明，0.1 μmol/L 油菜素内酯使高温胁迫下茄子株高、茎粗、地上部和根鲜重分别增加了 26.2%、42.6%、55.3% 和 43.3%。Sun et al.（2020）研究认为低温胁迫下，油菜素内酯可促进玉米幼苗干重和鲜重的积累。Mahesh et al.（2013）研究表明，油菜素内酯能促进干旱胁迫下萝卜种子萌发。

此外，油菜素内酯对提高作物产量与质量具有良好的效果。张奥深等（2016）研究表明，冷害胁迫下外施油菜素内酯能减轻低温冻害对冬小麦生产造成的产量损失。在盐碱胁迫下，外施油菜素内酯能提高大豆（Otie et al.，2021）和番茄产量（Soylemer et al.，2017）；显著增加甜菜块根中蔗糖的贮存量，减少还原糖和有害氮的积累，改善块根品质（刘丹，2019）；也使多年生黑麦草和高羊茅的总刈割产量损失分别降低 35% 和 12%，并改善草坪草质量（Mutlu et al.，2015）。高温胁迫下，外施油菜素内酯可以降低葡萄花色苷含量的减少量，在一定程度上缓解葡萄果实着色不良的现象，弥补品质损失（张睿佳等，2015）。干旱胁迫下，外施油菜素内酯能有效提升菜豆单荚种子数、百粒重、单株荚果数等产量指标，与对照相比，外施 4 mmol/L 油菜素内酯使单株荚果数增加 20.93%，百粒重增加 15.93%（Mohammadi et al.，2019）。

综上所述，油菜素内酯能显著提高植物生长量的积累，改善植株幼苗，以适应外界非生物胁迫环境，最终达到提高作物产量与品质的目的。

### 1.2 促进非生物胁迫下植物生长的调控机理

油菜素内酯通过影响细胞分裂和伸长促进植株生长。Hu et al.（2000）研究发现，油菜素内酯有类似细胞分裂素的功能，能激活 d 型细胞周期蛋白基因，并在愈伤组织形成过程中替代细胞分裂素，促进细胞分裂，且不依赖蛋白激酶和蛋白磷酸酶。植物细胞的伸长需要细胞壁的修饰和延伸（Nicol & Höfte，1998），如 Sahni et al.（2016）研究表明，拟南芥油菜素内酯生物合成基因 *AtDWF4* 编码油菜素内酯生物合成过程中的限速酶，该基因转入甘蓝型油菜后能上调细胞壁修饰酶——木葡聚糖内葡聚糖酰化 A 酶/水解酶基因的表达，调节细胞壁修饰酶和其他蛋白质的生物合成和活性等能调节细胞伸长，有利于植物生长（Ashraf et al.，2010）。此外，油菜素内酯能通过调节 $H^+$-ATP 酶激活细胞壁松弛酶，增强细胞壁的延伸，从而促进植物生长（Cerana et al.，1983；Ahmad et al.，2018）。

油菜素内酯通过以下两方面提升非生物胁迫下作物的质量及产量，一方面是通过提升库源强度、韧皮部装载，促进同化物从源器官转移到库器官（Mohammadi et al.，2019）和矿质元素的转移，以增加干

物质的储存，增加果实的大小和重量（Soylemer et al.，2017）；另一方面油菜素内酯对光合系统（Otie et al.，2021）、抗氧化系统（Wani et al.，2019）和渗透调节及离子平衡（Mutlu et al.，2015）等生理系统的改善，从而提高作物的产量和质量。

## 2 油菜素内酯对非生物胁迫下植物光合作用的影响

### 2.1 提高非生物胁迫下植物光合作用

光合作用是植物将无机物转变为有机物的重要生理过程，与作物产量密切相关。胁迫条件下植株叶绿素a（chlorophyll a，Chla）含量、叶绿素b（chlorophyll b，Chlb）含量、暗适应状态的最大荧光产量、光系统II（photosystem II，PSII）光化学的最大量子产率和光化学猝灭系数等光合参数显著受到抑制（Lima & Lobato，2017, Li et al.，2021）。外施油菜素内酯对逆境胁迫下植物的光合作用有显著改善作用。Lima & Lobato（2017）研究表明，100 nmol/L油菜素内酯使干旱胁迫下的鼠尾草中净光合速率、气孔导度和蒸腾速率分别提高96.0%、33.0%和24.0%。油菜素内酯促进盐胁迫下番茄幼苗的色素含量、净光合速率和气孔导度分别提高35.4%、29.8%和121.4%（Ahmad et al.，2018）。0.1 mg/L油菜素内酯能显著提高低温胁迫下玉米幼苗的胞间二氧化碳浓度、净光合速率和气孔导度（Sun et al.，2020）。综上所述，油菜素内酯能有效缓解胁迫对光合作用产生的负面影响，促进植物生长。

### 2.2 促进非生物胁迫下植物光合作用的调控机理

叶绿体是光合作用的主要场所，其类囊体在光吸收、电子传递和能量转换功能中起着重要作用，植物需要维持完整的叶绿体结构才能确保光合作用的高效进行。在正常条件下，叶绿体呈椭圆形，有完整的类囊体结构并紧密分布于细胞中。胁迫会造成叶绿体质膜溶解，类囊体解体和片层紊乱等（Gill et al.，2017；Sun et al.，2020）。外施油菜素内酯能有效改善叶绿体结构，提高光合作用。Sun et al.（2020）研究表明，外施0.1 mg/L油菜素内酯能保持低温胁迫下玉米幼苗叶绿体整体结构的相对完整，使双层膜结构明显，质膜和基质紧密附着，基质面积明显增大。Gill et al.（2017）研究发现，干旱胁迫下外施1 mol/L油菜素内酯后，大麦叶绿体结构能恢复到正常状态。此外，油菜素内酯也有助于保持完整的类囊体膜，有效保护PSII，提高量子产率，增强光合作用（Lv et al.，2020）。

光合作用是多种酶参与调控的复杂过程，油菜素内酯能通过提高Rubisco酶和硝酸还原酶等关键酶的活性改善逆境下植株的光合作用（Yu et al.，2004）。类胡萝卜素负责传递和吸收光能，保护叶绿体。八氢番茄红素合酶是类胡萝卜素生物合成途径中的关键酶，外施油菜素内酯能提高八氢番茄红素合酶活性，促进类胡萝卜素合成（Sharma A，2016）。

在胁迫条件下，油菜素内酯能上调与光合作用相关基因的表达。5-氨基乙酰丙酸（5-aminolevulinic acid，ALA）是叶绿素生物合成的第1个前体，影响叶绿素生物合成速率，在ALA向叶绿素转化过程中有许多中间体，如镁原卟啉IX和原叶绿素酸脂，外施油菜素内酯能上调编码这些中间体的转录产物（Granick & Sassa，1971；Zhao et al.，2019）。Li J et al.（2016）研究表明，外施油菜素内酯能上调编码Chla/Chlb结合蛋白，以及依赖三磷酸腺苷的锌金属蛋白酶、PSII核心复合蛋白、PSII反应中心W蛋白等叶绿体蛋白修饰酶基因的表达。

油菜素内酯也可以通过促进$Ca^{2+}$、$Mg^{2+}$的吸收促进胁迫植株合成叶绿素（Lechowski & Białczyk，1993；Choudhary，2012；Alam et al.，2019）。综上所述，油菜素内酯通过改善光合器官结构、促进光合酶合成和提高光合酶活性及关键矿质元素吸收等途径增强逆境胁迫下的植物光合作用，促进植物生长。

## 3 油菜素内酯对非生物胁迫下植物渗透调节系统的影响

### 3.1 改善非生物胁迫下植物渗透调节系统

渗透调节物质主要包括有机渗透调节物质和无机离子，其中有机渗透调节物质包括氨基酸、可溶性糖、蛋白质、多胺和一些非酶抗氧化剂（Yancey，2005），对胁迫下植物生长具有重要的调节作用。例如，脯氨酸（proline，Pro）是干旱胁迫下植物的碳源和氮源，为植物提供能量（Behnamnia et al.，2009），能稳定蛋白质和细胞膜等亚细胞结构，清除自由基及稳定氧化还原电位（Liu et al.，2009），也能作为分子伴侣增强不同酶的活性（Szabados & Savouré，2010）。甘氨酸-甜菜碱（glycine betaine，GB）能清除自由基和维持氧化还原电位，减少脂质过氧化并维持膜结构（Ashraf & Foolad，2007）。无机离子主要包括$K^+$、$Na^+$、$Ca^{2+}$、$Mg^{2+}$、$Cl^-$、$NO_3^-$等，对维持植物细胞液渗透压、离子稳态和营养吸收平衡至关重要。

Li et al.（2008）研究表明，油菜素内酯能提高干旱胁迫下刺槐幼苗的Pro和可溶性糖含量，玉米Pro

和GB含量（Talaat et al., 2015）；盐胁迫下黄瓜和小麦的Pro含量（Fariduddin et al., 2013; Talaat & Shawky, 2013），菜豆和大麦的GB含量（Ali et al., 2006），玉米和小麦的可溶性糖含量（Talaat & Shawky, 2013; Agami, 2013）；高温胁迫下茄子幼苗的Pro和可溶性糖含量（Wu et al., 2014）；而且能降低盐胁迫下苜蓿幼苗不同器官中$Na^+$、$Cl^-$及$Cu^{2+}$的含量，提高$K^+$、$Ca^{2+}$、$Mn^{2+}$、$Zn^{2+}$等离子的含量。因此，油菜素内酯通过提高渗透物质含量，维持渗透势及水分平衡，促进非生物胁迫下植物生长（寇江涛，2016）。

### 3.2 改善非生物胁迫下植物渗透调节系统的调控机理

Pro主要受Δ1-吡咯啉-5-羧酸合酶（Δ1pyrroline-5-carboxylate synthase, P5CS）和Δ1-吡咯啉-5-羧酸还原酶催化，由谷氨酸经一系列氧化还原反应合成，同时受脯氨酸脱氢酶（proline dehydrogenase, PDH）催化降解（Stewart et al., 1977; Hu et al., 1992）。Gao et al.（2016）研究表明，外施油菜素内酯能提高P5CS活性且降低PDH活性，促进Pro积累。盐胁迫下，油菜素内酯使细胞$H^+$流出大于流入，增强$H^+$-ATP酶活性，一方面使膜电位负值变小，减少保卫细胞外向$K^+$通道中$K^+$的外排（Azhar et al., 2017），另一方面激活盐过度敏感1（salt overly sensitive1, SOS1）途径，增加$Na^+$外排（Shi et al., 2000; Azhar et al., 2017）。拟南芥液泡膜$Na^+/H^+$逆向转运（vacuolar $Na^+/H^+$ antiporter in *Arabidopsis thaliana*, AtNHX）蛋白基因介导$Na^+$和$K^+$向液泡的转运，对维持$Na^+$和$K^+$平衡以及提高植物耐盐性至关重要（Apse et al., 1999; Zhang & Blumwet, 2001）。Su et al.（2020）研究表明，外施油菜素内酯能上调盐胁迫下苹果树*AtNHX*同源基因*MhSOS1*、*MhNHX1-3*、*MhNHX4-1*和*MhNHX4-2*的表达，从而降低$Na^+$含量，提高$K^+$含量。此外，外源油菜素内酯能有效平衡阳离子拮抗作用，促进无机离子的吸收，有效调控植物体内离子的运输和分配，维持细胞中的离子平衡（寇江涛，2016）。因此，油菜素内酯主要通过促进离子吸收、运输和分配的平衡，调控渗透物质相关酶活性及离子运输相关基因的表达，改善逆境下植物渗透调节，维持离子和水分平衡，促进植物生长。

## 4 油菜素内酯对非生物胁迫下植物抗氧化系统的影响

### 4.1 降低非生物胁迫下植物ROS含量

ROS在光合和呼吸过程中不断产生，并受多种机制严格控制以保持氧化还原平衡，是细胞代谢的重要调节和信号元件，在植物生长发育过程中起着关键作用（Li et al., 1998）。但逆境会破坏叶绿体和线粒体电子传递链，增加细胞中氧气的溶解度，损伤PSII中心和影响$H_2O$氧化系统等原因，产生大量ROS如超氧阴离子（$O_2^{\cdot-}$）、氢氧根离子（$OH^-$）和羟基自由基（$OH^{\cdot}$），造成氧化胁迫（Guo et al., 2006; Sharma & Dietz, 2009; Hasanuzzaman et al., 2012）。研究表明，外施油菜素内酯使低温胁迫下葡萄幼苗中的$O_2^{\cdot-}$和$H_2O_2$含量显著降低，锌胁迫下龙葵的$O_2^{\cdot-}$含量降低（Sharma et al., 2019; Sousa et al., 2020）。叶面喷施1 μmol/L油菜素内酯能使干旱胁迫下大麦叶片和根中的$H_2O_2$含量分别降低38.0%和32.0%；$OH^{\cdot}$含量分别降低56.0%和40.0%（Gill et al., 2017）。综上所述，油菜素内酯能有效清除活性氧，缓解非生物胁迫造成的氧化损伤，促进植物生长。

### 4.2 提高非生物胁迫下植物抗氧化系统调节能力

植物抗氧化系统可以清除ROS，维持氧化还原平衡。植物的抗氧化酶包括超氧化物歧化酶（superoxide dismutase, SOD）、过氧化物酶（peroxidase, POD）、过氧化氢酶（catalase, CAT）、谷胱甘肽过氧化物酶和抗坏血酸过氧化物酶（ascorbate peroxidase, APX）等。其中，SOD是消除氧化胁迫的第1道防线，将$O_2^{\cdot-}$转化为$H_2O_2$，随后被POD、CAT和APX清除至正常水平或转化为水和氧气。非酶抗氧化剂包括抗坏血酸（ascorbic acid, AsA）、生育酚、类胡萝卜素和谷胱甘肽（glutathione, GSH）等。2个系统交叉作用所形成的AsA-GSH途径在ROS清除过程中也发挥着重要作用，它主要包括APX、脱氢抗坏血酸还原酶（manodehydroascorbate reductase, MDHAR）、脱氢抗坏血酸还原酶（dehydroascorbate reductase, DHAR）和谷胱甘肽还原酶（glutathione reductase, GR）等4种关键酶和AsA及GSH两种抗氧化物质（Prachi et al., 2015）。油菜素内酯能通过提高非酶抗氧化物质含量及抗氧化酶的活性，增强胁迫下植物抗氧化系统的调节能力。研究表明，外施油菜素内酯使盐胁迫下海棠的SOD和CAT活性从1.3 U/mg和14.9 U/mg分别提高到1.4 U/mg和24.4 U/mg（Su et al., 2020），玉米幼苗SOD、POD和CAT活性分别提高15.2%、39.2%和37.6%（魏湜等，2018）；使高温胁迫下甜瓜的SOD、POD、CAT和APX活性分别增加了13.0%、59.0%、95.0%和33.0%（Zhang et al., 2014）；提高了低温胁迫下葡萄幼苗的AsA含量（Chen et al., 2019）；提高了盐胁迫下大豆GR、MDHAR、DHAR活性及总酚和总类黄酮含量，

并有效调节了AsA-GSH循环中抗氧化酶和活性物质的氧化还原状态(Alam et al.,2019)。因此,油菜素内酯能改善逆境下植物抗氧化系统,促进植物生长。

### 4.3 提高非生物胁迫下植物抗氧化系统的调节机理

油菜素内酯通过调节相关基因表达缓解逆境下植物的氧化胁迫。Cao et al.(2010)研究发现,外施油菜素内酯通过上调*det2*基因表达提高了SOD和CAT活性。重金属胁迫下,油菜素内酯能上调番茄幼苗根部SOD、GSH1、CAT1、GR1和APX(Li MQ et al.,2016)及芥菜CAT、POD、DHAR、GST和GR的表达水平(Kohli et al.,2018),进而提高抗氧化物质含量。此外,外施油菜素内酯上调有丝分裂原激活的蛋白激酶(mitogen-activated protein kinase,MAPK)基因*MAPK1*和*MAPK3*的表达,增强MAPK级联反应,更有利于植物应对胁迫环境(Nakagami et al.,2005)。在高温、干旱和盐胁迫下,外施油菜素内酯能下调$H_2O_2$的合成基因RBO表达,减少ROS(Sharma A et al.,2017)。综上所述,在非生物胁迫下,油菜素内酯能上调植物抗氧化调节系统相关基因的表达,增强其清除ROS的能力,也能下调ROS基因表达,减少其产生,进而缓解氧化胁迫,促进植物生长。

## 5 油菜素内酯对非生物胁迫下植物内源激素信号响应的影响

### 5.1 调节非生物胁迫下植物内源激素含量变化

植物激素是植物生长发育过程中的关键调节因子,在调节生长、养分分配等过程中发挥着核心作用(Sharma I et al.,2017)。例如,生长素(auxin,IAA)促进植株生长,刺激愈伤组织生成,促进形成层细胞分裂。赤霉素(gibberellin,GA)调控细胞伸长、种子萌发、植株衰老及植物对外界胁迫响应。脱落酸(abscisic acid,ABA)可调控植物生长发育进程,对植株抵御外界胁迫等十分重要。植物激素含量及种类的平衡对维持代谢平衡、缓解逆境胁迫具有重要作用(魏湜等,2018)。油菜素内酯作为一种植物激素,可以上调低温胁迫下辣椒中水杨酸(salicylic acid,SA)和茉莉酸(jasmonic acid,JA)的内源水平,降低乙烯(ethylene,ETH)的生物含量;提高高温胁迫下大豆叶片的IAA和ABA含量;促进盐胁迫下玉米叶片内源IAA和GA的合成,减少内源ABA含量(Li J et al,2016;谢云灿,2017;魏湜等,2018),有效调控非生物胁迫下植物内源激素比例平衡,促进植物生长。

### 5.2 调控非生物胁迫下植物内源激素信号响应的机理

油菜素内酯能介导JA、ETH、SA或ABA对非生物胁迫的响应和信号转导(Li XJ et al.,2016)。外施油菜素内酯后,油菜素类固醇不敏感2(brassinosteroid insensitive 2,BIN2)与ABA信号的负调节因子脱落酸不敏感1(ABA insensitive 1,ABI1)和脱落酸不敏感2(ABA insensitive 2,ABI2)相互作用,能协调拟南芥的生长和胁迫反应(Wang et al.,2018)。高温胁迫下,外施24-表油菜素内酯能显著增强ETH、ABA、JA缺乏或不敏感突变体的耐热性。低温胁迫下,油菜素内酯能与JA和SA信号通路相互作用,上调JA生物合成基因和SA相关的异抗坏血酸合酶基因,也能下调编码ETH信号成分和ETH响应转录因子基因,激活油菜素内酯信号途径,缓解冷害胁迫(Divi et al.,2010;Li J et al.,2016)。综上所述,非生物胁迫下,油菜素内酯能介导内源植物激素的信号响应,调控植物激素含量变化,促进植物生长。

## 6 展望

水分、盐渍、温度等非生物胁迫是限制农业生产的重要因素,尽管植物自身具有免疫调节系统,但在长期和严重的胁迫条件下,植物光合作用、渗透平衡及氧化还原稳态等生理过程会受到严重影响,最终破坏细胞结构,导致代谢紊乱,影响植株生长。油菜素内酯作为一种微量、高效的化学物质,能通过调节内源激素含量,增强基因表达和酶活性等方式缓解胁迫(图1)。尽管已有大量研究表明油菜素内酯对胁迫下玉米(Sun et al.,2020;赵小强等,2021;Sun et al.,2022)、小麦(Dong et al.,2017;尚宏芹和高昌勇,2018;刘丽杰等,2020)等粮食作物,葡萄(惠竹梅等,2013;彭小琴等,2015;Chen et al.,2019)、黄瓜(陆晓民等,2011;Anwar et al.,2018)等园艺作物的生长生理具有调节作用,但仍有一些重点方向值得深入研究。

首先,现有研究试验条件多为人工气候箱或温室,有必要进一步在田间条件下探索非生物胁迫条件下油菜素内酯对作物产量与质量的作用效应,以期为改善农业生产提供更好的支撑。此外还可向基因层面延伸,深入探究油菜素内酯缓解植物逆境胁迫的分子机制,特别是与其他胁迫相关激素的联合机制。植物激素种类繁多,对植物生长的作用也各不相同,外施油菜素内酯能调控内源植物激素含量为联合应用植物激素,缓解胁迫下植物生长提供了新思路。尽管已有研究涉及相关方面,如探究ABA

和油菜素内酯对干旱胁迫下高羊茅光合作用的影响(Chen et al.,2018);激动素和油菜素内酯对盐胁迫下番茄抗氧化和渗透代谢的影响(Ahanger et al.,2020);油菜素内酯和水杨酸对铅胁迫下芥菜抗氧化防御系统和基因表达的影响(Kohli et al.,2018)。但涉及的植物激素和植物类型均较少。因此可以深入研究油菜素内酯与其他类型激素的联合作用和互作机理。

其次,需要探究油菜素内酯缓解植物应对多种胁迫联合危害的效应和机理。在农业生产中,多种胁迫条件往往交错在一起,相互影响,如高温和干旱胁迫,盐碱和干旱胁迫等,但现在的研究大多只关注单一胁迫。因此可以模拟多重胁迫,揭示植株生长影响及生理生化机制,探究外源油菜素内酯对联合胁迫的改善作用,而后进行大田试验,应用于大田生产。

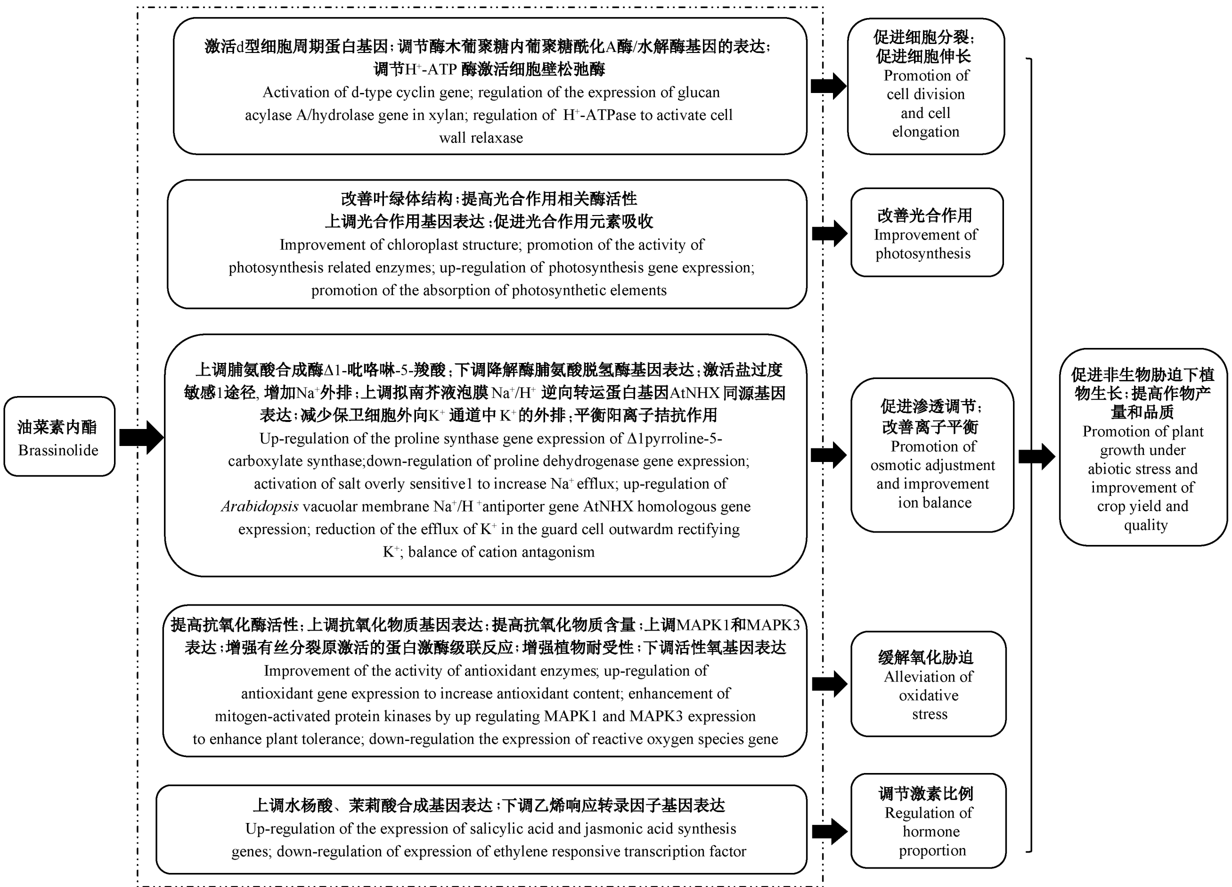


**图1 油菜素内酯调控非生物胁迫下植物生长的生理机制**

Fig. 1 Physiological mechanisms of brassinolide regulating plant growth under abiotic stresses

最后,比较不同油菜素内酯缓解逆境胁迫的差异。油菜素内酯衍生物种类丰富,目前关于缓解植物非生物逆境胁迫的研究,基本上都集中24-表油菜素内酯上,而不同油菜素内酯衍生物的效应差异研究较为缺乏。因此,可以比较油菜素内酯不同种类衍生物缓解植物逆境危害的差异,为其推广应用提供理论支撑。

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