响应植物逆境胁迫的线粒体蛋白研究进展

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摘要: 线粒体是真核细胞的重要细胞器, 在植物生长发育以及植物对逆境胁迫的响应方面起着重要的作用。除了线粒体呼吸系统蛋白如线粒体电子传递链(mETC)复合物、交替氧化酶(AOX)和解偶联蛋白(UCP), 越来越多的线粒体蛋白如PPR、线粒体热激蛋白(HSC)、一氧化氮合酶相关蛋白(NOA)等被报道参与植物对逆境胁迫的调控过程。本文依次综述了参与植物逆境胁迫的呼吸系统蛋白、PPR蛋白、谷胱甘肽和谷氨酸蛋白酶类蛋白、分子伴侣相关蛋白等线粒体蛋白, 并阐述了线粒体蛋白参与的胁迫种类及其分子调控的初步机制, 为进一步揭示线粒体蛋白调控植物逆境胁迫的分子机制提供参考。

关键词: 线粒体蛋白; 逆境胁迫; 分子调控

线粒体作为一种具有半自主复制能力的细胞器在细胞呼吸作用、细胞自噬和细胞代谢等细胞过程中都起着至关重要的作用, 在动物中已经得到了广泛的关注和研究(Zhou等2016)。最新的研究表明, 线粒体与肥胖(Williams等2016)、先天性免疫(West等2015)、寿命(Zhang等2016)等人类健康问题有着直接的关系。

研究发现, 植物线粒体参与减数分裂(Brownfield等2015)、细胞代谢(Dekkers等2013)、程序性细胞死亡(Yi等2015)等生长发育过程的调控以及植物对逆境胁迫的响应(Pastore等2007), 表明线粒体是植物中重要的细胞器。为了深入阐明线粒体的功能, 越来越多的线粒体基因组完成测序。与动物线粒体基因组相比, 植物线粒体基因组结构复杂(Liberatore等2016), 且基因组较大(Liberatore等2016; Wu等2015)。然而有趣的是, 大部分植物线粒体基因组保留的编码蛋白基因数目在25~40个之间(Sloan等2012), 大多数线粒体蛋白是由核基因编码的(Gray等1999)。线粒体蛋白质组学研究表明定位于线粒体的蛋白为线粒体蛋白(Kruft等2001), 据预测拟南芥(*Arabidopsis thaliana*)中约有2 000种线粒体蛋白(Taylor等2009), Heazlewood等利用液相色谱串联质谱(liquid chromatography-tandem mass spectrometry, LC-MS/MS)的方式, 鉴定了400多种线粒体蛋白, 其中约20%的蛋白功能是未知的(Heazlewood等2004)。Taylor等(2009)的研究发现了61个响应胁迫的线粒体蛋白, 尽管这些蛋白的丰度受到逆境胁迫的诱导, 但其在逆境胁迫中的具体功能及作用机理还有待于深入研究。研究认为线粒体蛋白在植物对逆境胁迫响应过程中发挥重要的作用, 如线粒体呼吸系统蛋白通过调节细胞内氧化还原反应平衡调控胁迫对植物的伤害(Dutilleul等2003; Schertl和Braun 2014), 线粒体分子伴侣相关蛋白能够调节植物体内的激素水平进而参与调控植物对胁迫的响应过程(Bekh-Ochir等2013; Park和Kim 2014)等。线粒体蛋白生物学功能的改变, 通常会影响线粒体的功能, 进而影响植物对逆境胁迫的响应过程。本文对近年来报道的参与植物逆境胁迫响应的线粒体蛋白进行了梳理和归纳(表1)。

1 线粒体蛋白与植物逆境胁迫关系

低温、盐、干旱等非生物胁迫以及真菌、病毒等生物胁迫严重影响植物的生长发育, 并对农作物生产力产生限制作用(Xiong等2002; Pu等2016)。由于植物具有不能自由移动的特性, 使得植物必须持续忍受周围各种环境的刺激, 为此植物进化了多种适应性机制以应对外界胁迫(Mittler等2004)。

对拟南芥中细胞器蛋白进行研究发现, 约有22%响应逆境胁迫的细胞器蛋白定位于线粒体(Taylor等2009), 但是参与胁迫响应的线粒体蛋白数目可能超过预测值。研究者对冷、热胁迫下植

表1 参与逆境胁迫的植物线粒体蛋白

Table 1 Summary of mitochondrial proteins involved in stresses in plants

蛋白名	物种	响应的胁迫类型	文献来源
CSMII	美花烟草(*Nicotiana sylvestris*)	干旱和持续轻度的水分胁迫	Galle等2010; Rzigui等2013
SDH	拟南芥(*Arabidopsis thaliana*)	真菌、细菌	Fuentes等2011; Gleason等2011; Jardim-Messeder等2015
COX17	拟南芥	病原菌、干旱等	Attallah等2007; Garcia等2016
ATP6	拟南芥	盐、干旱、冷	Zhang等2008
ATP6	水稻(*Oryza sativa*)	盐	Zhang等2006; Moghadam等2012
ATP6	小麦(*Triticum aestivum*)	盐	Moghadam等2012, 2013
AOX	梨(*Pisum sativum*)	盐	Martí等2011
AOX	拟南芥	盐、干旱、冷	Smith等2009; Kühn等2015; Armstrong等2008
AOX	苜蓿(*Medicago truncatula*)	盐	Jian等2016
AOX	小麦	干旱	Bartoli等2005; Vassileva等2009
AOX	烟草(*Nicotiana tabacum*)	干旱、冷、氮素营养、病菌、病毒	Wang和Vanlerberghe 2013; Wang等2011; Vanlerberghe和McIntosh 1992; Sieger等2005; Cvetkovska和Vanlerberghe 2012; Chivasa等1997; Ordog等2002; Liao等2012
AOX	菜花(*Brassica oleracea* var. *botrytis*)	热	Rurek等2015
AOX	水稻	热	Rachmilevitch等2007; Murakami和Toriyama 2008
AOX	大豆(*Glycine max*)	磷素营养	Juszczuk等2001; Gonzàlez-Meler等2001
AOX	菠菜(*Spinacia oleracea*)	氮素营养	Noguchi和Terashima 2010
UCP1	拟南芥	干旱、盐、病毒等	Begcy等2011; Barreto等2014; Pu等2016
UCP1	水稻	冷和干旱复合胁迫	Lee和Back 2016
UCP2	拟南芥	病毒	Pu等2016
UCP	番茄(*Solanum lycopersicum*)	病菌	Chen等2013
PPR40	拟南芥	盐	Zsigmond等2008, 2012
PGN	拟南芥	盐、病菌	Laluk等2011
PPR96	拟南芥	盐	Liu等2016a
SLG1	拟南芥	盐、干旱	Yuan和Liu 2012
SLO2	拟南芥	营养	Zhu等2012a
PAD2	拟南芥	干旱	Koffler等2014
GR1	水稻	盐	Kordrostami等2017
GR3	水稻	盐	Wu等2013
GPX1	水稻	盐	Kordrostami等2017
GPX3	水稻	盐、冷、干旱等	Passaia等2013
GDH	小麦	氨、低氧	Wang等2016a; Diab和Limami 2016
BIL2	拟南芥	盐、强光	Bekh-Ochir等2013
J1	拟南芥	盐、热等	Park和Kim 2014
DjB1	拟南芥	热	Zhou等2012
sHSP23.6	番茄	水涝	Hüther等2016
ClpB5	小麦	盐、热等	Muthusamy等2016
SUV3	水稻	盐	Tuteja等2013; Sahoo等2014
B12D1	水稻	水淹	He等2014
ORFH79	水稻	干旱、盐	Yu等2015
NRGA1	拟南芥	干旱	Li等2014; Wang等2014
MPT	拟南芥	盐	Zhu等2012b
CYS-C1	拟南芥	病菌、病毒	García等2013
NOA1	黄瓜(*Cucumis sativus*)	冷	Liu等2016b
SNAT5	新疆野苹果(*Malus sieversii*)	干旱	Wang等2017
MDH2	黑麦(*Secale cereal*)	铝	Abd El-Moneim等2015
TSPO	小立碗藓(*Physcomitrella patens*)	盐	Lehtonen等2012

物线粒体蛋白质组进行研究, 发现一些线粒体蛋白如线粒体电子传递链(mitochondrial electron transport chain, mETC)复合物I~V、交替氧化酶(alternative oxidase, AOX)、解偶联蛋白(uncoupling protein, UCP)等的表达水平受到冷或热胁迫的影响, 预示着这些蛋白可能参与了植物对温度胁迫的响应过程(Qin等2009; Tan等2012; Taylor等2005; Yin等2009)。同样地, 日本研究者为了提高水淹胁迫下大豆(*Glycine max*)的产量, 借助蛋白质组学和代谢组学对水淹胁迫下大豆线粒体功能进行研究, 发现与三羧酸循环相关的蛋白表达量表现上调, 而内膜转运蛋白和电子呼吸链相关的蛋白表达量表现下调(Komatsu等2011)。可知, 植物线粒体蛋白与逆境胁迫的关系密切。

2 植物线粒体呼吸系统蛋白与逆境胁迫

逆境胁迫通常会引起植物体内活性氧(reactive oxygen species, ROS; 如过氧化氢、羟基自由基等)的积累(Jacoby等2011), 而线粒体呼吸系统与ROS的产生有直接关系(Møller 2011; Colombatti等2014)。植物体内不同的信号途径对ROS的积累起着不同的调控作用, 研究表明mETC复合物I、II和III是产生ROS的位点(Møller等2007; Gleason等2011), 而AOX、UCP等分别通过调控辅酶Q的还原状态以及跨膜电位的产生等负调控ROS的产生(Pastore等2007; Vanlerberghe 2013; Schertl和Braun 2014)。可见, 植物线粒体呼吸系统蛋白通过调控ROS参与植物对逆境胁迫的响应。

2.1 mETC复合物I~V蛋白

mETC由4个呼吸链蛋白复合物(I~IV)和ATP合酶复合物(V)组成。研究发现, mETC复合物I~III通过产生ROS参与植物对逆境胁迫的响应(Møller等2007; Gleason等2011; Jardim-Messeder等2015), 复合物IV通过自身氧化态和还原态的转变响应逆境胁迫(Dhage等1992), 而复合物V则通过产生ATP参与植物对逆境胁迫的响应(Zhang等2008)。可以看出, mETC复合物参与植物逆境胁迫的调控方式不尽相同, 预示着它们可能参与不同种类的逆境胁迫。

对美花烟草(*Nicotiana sylvestris*)中mETC复合物I缺陷CMSII突变体(mitochondrial complex I-de-ficient CMSII mutant)进行研究发现, 该复合物通过调控光合作用参与干旱(Galle等2010)和持续轻度的水分胁迫(Rzigui等2013)。模式植物拟南芥中研究发现, 只有当突变体中复合物I的丰度降低时, 十二半胱氨酸蛋白(twin cysteine proteins, At12Cys)的表达量才增加; 表观遗传学和生物化学手段检测结果发现, *At12Cys*突变体表现出对干旱和高光胁迫抗性增强的表型(Wang等2016b)。mETC复合物II-琥珀酸脱氢酶(succinate dehydrogenase, SDH)催化琥珀酸氧化为延胡索酸(*trans*-butenedioic acid), 同时将泛醌(ubiquinone, UQ)还原为泛醇(ubiquinol, UQH$_2$), 从而将三羧酸循环和电子传递系统联系起来。拟南芥*SDH1-1/sdh1-1*杂合突变体(Fuentes等2011)和SDH1-1底物结合位点点突变(mutant *disrupted stress response 1*, *dsr1*)突变体(Gleason等2011)中SDH的生物学活性都降低, 前者通过增加气孔导度而具有较高的CO$_2$同化速率, 同时维持植物中碳/氮的平衡状态, 增加氮吸收率, 从而有利于氮限制条件下植物更好地生长; 后者通过减少线粒体ROS的产生, 影响了水杨酸(salicylic acid, SA)介导的抗氧化酶等相关基因的上调表达, 从而表现出对特定真菌和细菌病原物敏感性增强的表型。进一步研究发现mETC复合物II能够调节植物体内ROS的产生并参与植物的生长发育以及植物对胁迫响应的调控过程(Jardim-Messeder等2015)。与mETC复合物I和II响应植物的非生物胁迫不同, 复合物IV除了参与机械损伤(Attallah等2007)、干旱(Garcia等2016)等非生物胁迫, 还参与病原菌侵染(Attallah等2007)的生物学胁迫过程。

水稻(*Oryza sativa*) (Zhang等2006; Moghadam等2012)、拟南芥(Zhang等2008)以及小麦(*Triticum aestivum*) (Moghadam等2012, 2013)中的研究均发现, mETC复合物V参与植物对盐胁迫的响应, 并从两个方面得到验证: 一方面, 盐胁迫引起小麦和水稻中ATP合酶6 kDa亚基基因(ATP synthase 6 kDa subunit gene, *ATP6*)表达水平升高(Moghadam等2012, 2013); 另一方面, 过表达水稻和拟南芥复合物V的*ATP6*转基因株系对盐胁迫的耐受性增强(Zhang等2006, 2008)。除了响应盐胁迫, 复合物V还参与干旱、冷等非生物胁迫过程(Zhang等2008)。

上述结果说明, mETC复合物蛋白参与植物逆

境胁迫响应的调控方式以及逆境胁迫类型存在差异。然而, mETC复合物蛋白在逆境胁迫下的表达、活性或功能还受到哪些因素(如蛋白、信号分子、代谢物)的调控及调控方式如何仍不清楚。

2.2 能量耗散系统AOX和UCP蛋白

植物线粒体中至少有两条功能相关的能量耗散途径: 一条途径通过偶联辅酶Q的氧化过程将分子氧还原成水, 该途径与AOX蛋白有关(Vanlerberghe和McIntosh 1997); 另一条途径通过解偶联底物的氧化过程将ADP磷酸化成ATP并以热量的形式释放出来, 该途径与UCP蛋白有关(Pecqueur等2009)。研究发现, 过表达AOX或UCP能够增强植物对逆境胁迫的耐受性(Vanlerberghe 2013; Smith等2009; Brandalise等2003), 可知线粒体能量耗散系统蛋白AOX和UCP参与植物对逆境胁迫的响应。

植物AOX家族蛋白由*AOX1*和*AOX2*亚家族编码, 其中AOX1蛋白存在于所有植物中, 并参与植物对逆境胁迫的响应, 而AOX2仅存在于双子叶植物中, 主要参与植物生长发育过程的调控(Considine等2002; Clifton等2006; Saisho等2001)。研究发现, AOX广泛参与了盐、干旱、温度等非生物胁迫以及细菌、病毒等生物胁迫的生物学过程(Vanlerberghe 2013; Vanlerberghe和McIntosh 1997)。

AOX通过调控线粒体的呼吸作用(Martí等2011)和ROS积累量(Smith等2009; Jian等2016; Mhadhbi等2013)等方式增强植物对盐胁迫的耐受性。研究发现, 干旱能够引起AOX呼吸途径在线粒体呼吸作用中的比例增加(Ribas-Carbo等2005), 使植物以AOX含量增加(Bartoli等2005; Vassileva等2009)或活性增强(Galle等2010; Kühn等2015)的方式调控呼吸作用、光合作用和叶绿素合成来维持细胞平衡。此外, 严重干旱胁迫后*AOX*突变体的恢复能力减弱(Wang和Vanlerberghe 2013)。低温可以通过诱导AOX的基因转录(Wang等2011)、蛋白表达(Vanlerberghe和McIntosh 1992)以及蛋白活性增强(Armstrong等2008)的方式, 使AOX参与植物对低温胁迫的响应。对温度胁迫下菜花(*Brassica oleracea* var. *botrytis*)线粒体蛋白组学进行研究, 发现热胁迫能够引起AOX活性以及*AOX1a*和*AOX1d*转录水平的升高(Rurek等2015)。而组成型过表达AOX的水稻植株对高温胁迫的耐受性增强, 可能

是由于AOX途径成为呼吸作用的主要途径造成的(Rachmilevitch等2007; Murakami和Toriyama 2008)。同样地, 在磷(Juszczuk等2001; Gonzàlez-Meler等2001)和氮(Sieger等2005; Noguchi和Terashima 2010)营养胁迫条件下AOX含量或活性增加, 从而提高了植物对营养胁迫的耐受性。

此外, 当植物遭受细菌病原物侵袭时, AOX通过调节超氧阴离子(O_2^-)信号通路影响植物对细菌感染的反应(Cvetkovska和Vanlerberghe 2012)。研究发现, AOX通过水杨基羟肟酸 (salicylhydroxamic acid, SHAM)敏感途径(Chivasa等1997)、病毒诱导的HR (hypersensitive response) (Ordog等2002)以及建立SAR (systemic acquired resistance) (Liao等2012)等参与抗病毒反应。

对过表达拟南芥*UCP1*的转基因烟草(*Nicotiana tabacum*)进行研究, 发现UCP1通过减少逆境胁迫引起的ROS积累量从而增强转基因株系对干旱、盐等非生物胁迫的耐受性(Begcy等2011; Barreto等2014)。Pu等(2016)对*ucp1*和*ucp2*突变体进行研究发现, 突变体表现出对芜菁皱缩病毒(*Turnip crinkle virus*, TCV)感染抵抗能力减弱的表型, 该表型与光合特性的损坏、细胞氧化还原能力的改变和ROS的积累有着一定的关系。番茄(*Solanum lycopersicum*)中的研究结果也表明UCP通过降低ROS的积累量和脂质过氧化作用等, 提高转基因植株对热胁迫的耐受性以及对灰霉病(灰葡萄孢菌, *Botrytis cinerea*)的抗性(Chen等2013)。此外, 水稻中研究发现2-羟基褪黑素(2-hydroxymelatonin, 2-OHMel)预处理过的幼苗对冷和干旱复合胁迫的抗性与UCP1的表达水平升高有关(Lee和Back 2016)。

3 其他线粒体蛋白与逆境胁迫

3.1 PPR蛋白

植物PPR (pentatricopeptide repeat)家族蛋白的数量很多, 如拟南芥中含有约450个成员(Lurin等2004)。研究发现, 拟南芥线粒体PPR蛋白如PPR40 (Zsigmond等2008, 2012)、PGN (Laluk等2011)、PPR96 (Liu等2016a)、SLG1 (Yuan和Liu 2012)通过调控细胞内ROS的积累量参与植物对盐胁迫的响应。其中*PGN*突变体还表现出对番茄灰霉病菌(*B. cinerea*)和西兰花(*B. oleracea* var. *italica*)猝倒

病菌(甘蓝链格孢菌, *Alternaria brassicicola*)敏感性增强的表型(Laluk等2011), 而*SLG1*突变体则对干旱胁迫的耐受性增强(Yuan和Liu 2012)。此外, 在缺少蔗糖的营养胁迫条件下, *SLO2*突变体根长变短、晚花等表型与对照相比更加显著(Zhu等2012a)。上述结果说明, 植物线粒体PPR蛋白参与干旱、盐以及病原菌等逆境胁迫过程。

3.2 谷胱甘肽和谷氨酸蛋白酶类

谷胱甘肽还原酶(glutathione reductase, GR)和谷胱甘肽过氧化物酶(glutathione peroxidase, GPX)参与水稻对盐(Wu等2013; Kordrostami等2017; Lima-Melo等2016)和干旱胁迫(Prakash等2016)的响应。研究发现, *OsGR3*的表达受到盐胁迫的诱导, 而脱水或热胁迫并未引起该基因表达水平的明显改变(Wu等2013); 同样地, 水稻中*OsGR1*和*OsGPX1*的表达水平在盐胁迫条件下也明显升高(Kordrostami等2017)。而GPX3除了参与盐胁迫, 还参与冷、干旱等(Passaia等2013)非生物胁迫过程。对拟南芥谷胱甘肽突变体*pad2-1*进行研究, 发现突变体对干旱胁迫的高度敏感可能是由于低水平的谷胱甘肽含量引起的植物抗氧化能力降低造成的(Koffler等2014)。

研究还发现, 谷氨酸脱氢酶(glutamate dehydrogenase, GDH)在小麦对氨胁迫(Wang等2016a)以及低氧胁迫(Diab和Limami 2016)中起作用, 表明其参与植物对营养胁迫的响应。

3.3 分子伴侣相关蛋白

J蛋白含有一个由大约70个氨基酸组成的高度保守的J结构域和一个HPD (His-Pro-Asp)三肽模体, 而HPD模体对于ATP酶活性的激活是必需的(Kampinga和Craig 2010)。拟南芥中已鉴定了120种J蛋白(Rajan和D'Silva 2009), 该家族成员广泛参与了发育、信号传导和胁迫抗性等生物学过程(Sedbrook等1999; Guan等2003; Shen等2011)。拟南芥中线粒体定位的J蛋白/热击蛋白40 (J-protein/Heat shock protein 40, DnaJ/Hsp40)家族成员BIL2 (Brz-insensitive-long hypocotyls 2)和AtJ1分别通过影响油菜素内酯(brassinosteroid, BR)参与植物对盐和强光胁迫的抗性过程(Bekh-Ochir等2013)以及影响脱落酸(abscisic acid, ABA)参与植物对盐、热等胁迫的响应(Park和Kim 2014)。AtDjB1也是J蛋白家族的一员, 编码409个氨基酸, 具有线粒体定位序列(Kroczynska等1996; Miernyk 2001)。研究发现AtDjB1能够通过与线粒体Hsc70-1 (mitochondrial heat-shock protein 70, mtHSC70)相互作用, 激活mtHSC70的ATP酶活性, 从而增强拟南芥对热胁迫的耐受性(Zhou等2012)。此外, 番茄中线粒体小热击蛋白(mitochondrial small heat shock proteins, MT-sHSP23.6)能够增强植物对水涝胁迫的抗性(Hüther等2016), 小麦中分子伴侣酪蛋白酶(caseinolytic proteases, Clps)家族基因*TaClpB5*在盐、热等胁迫下表达水平升高(Muthusamy等2016)等。虽然上述结果已经确定线粒体分子伴侣蛋白参与了植物对逆境胁迫的响应, 但是线粒体分子伴侣蛋白是通过结合哪些或哪几类蛋白形成调控途径的机制仍未完全清楚。

3.4 其他蛋白

水稻DNA和RNA解旋酶OsSUV3 (suppressor of Var 3)通过维持较高水平的赤霉素(gibberellin, GA)、吲哚乙酸(indole-3-acetic acid, IAA)等降低盐胁迫对水稻的生长发育和产量的影响(Tuteja等2013; Sahoo等2014)。而OsB12D1 (B12D-like protein)属于Balem (barley aleurone and embryo)蛋白家族, 研究发现OsB12D1参与水淹胁迫, 该基因过表达转基因株系的种子对水淹胁迫的耐受性显著增强(He等2014)。此外, 水稻营养组织中积累细胞质雄性不育蛋白(cytoplasmic male sterility, CMS)-ORFH79能够引起线粒体功能紊乱, 研究发现过表达诱导*orfH79*转录本剪切的*Rf* (restorer of fertility)基因不仅能够恢复线粒体的功能, 而且显著提高了水稻对干旱和盐胁迫的耐受性(Yu等2015)。

拟南芥线粒体丙酮酸载体(negative regulator of guard cell ABA signaling 1, NRGA1)和磷酸盐转运蛋白(mitochondrial phosphate transporter, MPT)分别通过ABA介导的气孔运动负调控拟南芥对干旱胁迫的响应(Li等2014; Wang等2014), 以及可能通过影响GA负调控拟南芥对盐胁迫的响应(Zhu等2012b)。研究发现, 拟南芥氰丙氨酸合成酶-线粒体*CYS-C1*基因突变体通过提高ROS的积累量以及水杨酸依赖途径诱导的发病相关基因*PR1*的表达水平等增强了突变体对丁香假单胞菌番茄致病变种(*Pseudomonas syringae* pv. *tomato*, DC3000)和甜

菜曲顶病毒(*Beet curly top virus*, BCTV)的抗性 (García等2013)。

此外, 黄瓜(*Cucumis sativus*)中的一氧化氮合酶相关蛋白(nitric oxide synthase associated gene1, NOA1) (Liu等2016b)和新疆野苹果(*Malus siever-sii*)中的5-羟色胺-*N*-乙酰转移酶(serotonin *N*-acetyl-transferase, SNAT5)蛋白(Wang等2017)、黑麦(*Secale cereal*)中的苹果酸脱氢酶(malate dehydrogenase, MDH2)蛋白(Abd El-Moneim等2015)以及小立碗藓 (*Physcomitrella patens*)中的富含色氨酸的传感蛋白(tryptophane-rich sensory protein, TSPO) (Leh-tonen等2012)等分别参与冷、干旱、铝以及盐等非生物学胁迫。

由此可知, 线粒体蛋白可能通过植物激素(如 ABA、GA)、信号分子(如ROS、NO)等参与植物对逆境胁迫的响应过程, 但对其调控途径及作用机理的阐明仍需要大量的研究支持。

4 展望

干旱、盐等非生物胁迫以及病毒、病菌等生物胁迫能够影响作物的生长发育, 降低作物产量, 严重时甚至可以导致作物绝产。逆境胁迫不但影响植物的光合作用、呼吸作用, 还通过ROS对细胞膜和多种细胞器造成氧化胁迫。作为细胞内最先识别逆境胁迫的部位之一, 线粒体蛋白在维持胁迫条件下细胞的正常生命活动中发挥重要作用。因此, 研究线粒体蛋白在逆境胁迫方面所起的生物学功能有助于深入了解线粒体内复杂的网络信号途径, 进而为选育抗逆农作物新材料提供基础。目前, 研究者已经对植物响应逆境胁迫的线粒体蛋白进行了大量研究, 确定了线粒体蛋白能够通过调节呼吸作用、ROS积累量、植物激素水平等调控植物对逆境胁迫的响应机制, 但是"植物受到胁迫时线粒体蛋白之间信号是如何实现交流的?" "线粒体蛋白又是如何精确地接收并反馈相关信号?" "各信号通路之间又是如何交叉的?"等问题目前仍需深入研究探讨。对于线粒体参与植物逆境胁迫响应方面的研究仍需更多、更深入的探讨。

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Advances in mitochondrial proteins responding to stresses in plants

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Abstract: Mitochondrion is an important organelle in eukaryotic cells, which plays important roles in plant development and stress responses. More and more mitochondrial proteins, such as PPR (pentatricopeptide repeat), HSC (mitochondrial heat-shock protein) and NOA (nitric oxide synthase associated protein), have been reported to be involved in regulation of mitochondrial response to stresses, except for mitochondrial respiration proteins including mETC (mitochondrial electron transport chain) complex, AOX (alternative oxidase) and UCP (uncoupling protein). Here, we reviewed the category and molecular basis of mitochondrial proteins including proteins in respiration pathways, PPR proteins, enzymes related to glutathione and glutamate, which would provide reference for further revealing the regulation mechanism of mitochondrial proteins in response to biotic and abiotic stresses in plants.

Key words: mitochondrial proteins; stresses; molecular regulation