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·专题论坛·

植物响应联合胁迫机制的研究进展

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摘要 自然界中，植物通常面对多重联合胁迫。在全球气候变化日益加剧的背景下，多重联合胁迫对植物生长发育及作物产量形成的不利影响日益显著。阐明植物响应和适应联合胁迫的生理与分子机制，对人们理解植物对自然环境的适应机理，及培育耐受联合胁迫的新品种有重要意义。研究表明，植物响应联合胁迫的机制是特异的，不能简单地从单一胁迫响应叠加来推断。植物遭受联合胁迫时，各种生理、代谢和信号途径相互作用，使得植物响应联合胁迫非常复杂。该文综述了植物响应联合胁迫的生理与分子机理的最新进展，并阐述了植物响应联合胁迫的研究方法。

关键词 联合胁迫，逆境，植物生长发育，产量，组学

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因固着生活，植物在整个生长过程中不可避免地会遇到多种生物和非生物胁迫。为了适应复杂多变的环境，植物进化出复杂的生理生态及分子机制来感知和抵御各种胁迫。目前，控制环境下植物对单一胁迫的响应与适应机制研究已有大量报道，而有关植物对多种胁迫组成的联合胁迫(combined stresses)的生理及分子机制知之甚少。因此，研究植物响应与适应联合胁迫的机制，比较联合胁迫与单一胁迫间的异同，对阐明植物对自然环境的适应机理、建立植物抵御联合胁迫的调控网络及培育耐受联合胁迫的作物具有重要的理论和实践意义。

随着全球气候变化的日益加剧，极端气候频现，一种或多种环境胁迫(如干旱、热害、盐渍、冷害、营养缺乏，以及病原菌和害虫)对植物生长发育乃至作物产量形成的不利影响越来越明显(Lobell et al., 2009; Van Ittersum, 2013; IPCC, 2014)。以美国为例，1980–2012年间，干旱单一胁迫造成的损失为500亿美元，而同时期内干旱和热害联合胁迫造成的农业损失约为2 000亿美元(http://www.ncdc.noaa.gov/billions/events)。有些作物能耐受单一胁迫，但遭受联合胁迫时，生长受到明显抑制。例如，小麦(*Triticum aestivum*)在水源充足的条件下耐热性较好，而在干旱条件下其耐热性较差(Parent et al., 2017)。故培育耐受干旱和热害联合胁迫的小麦品种具有重要意义。未来迫切需要培育耐受联合胁迫的作物新品种，以更好地保障粮食安全。

从胁迫时间上，联合胁迫分为连续胁迫(consecutive or sequential stress)和平行胁迫(simultaneous or parallel stress)两种(Zhang and Sonnewald, 2017)。连续胁迫指多种胁迫在发生时间上有一定的先后顺序，而平行胁迫指在同一时间内发生多种胁迫。从胁迫类型上，其可分为非生物胁迫之间、生物胁迫之间以及非生物与生物胁迫之间的联合胁迫。植物应对一些胁迫的响应信号机制之间存在一定的交互作用。例如，含有DRE元件的*rd29A*基因能够整合干旱、盐以及冷胁迫诱导的信号通路(图1) (Roychoudhury et al., 2013)。这种胁迫响应通路之间的内在联系，使得植物应对两种或多种胁迫的响应通常是特异的，不能够简单地从单一胁迫响应叠加来推断(Ramegowda and Senthil-Kumar, 2015; Zhang and Sonnewald, 2017)。联合胁迫发生时，植物各种生理、代谢和信号途径相互作用，对植物可能是正向、负向和中性的影响，但也有可能是新的未知的变化(Pandey et al., 2015; Prasch and Sonnewald,

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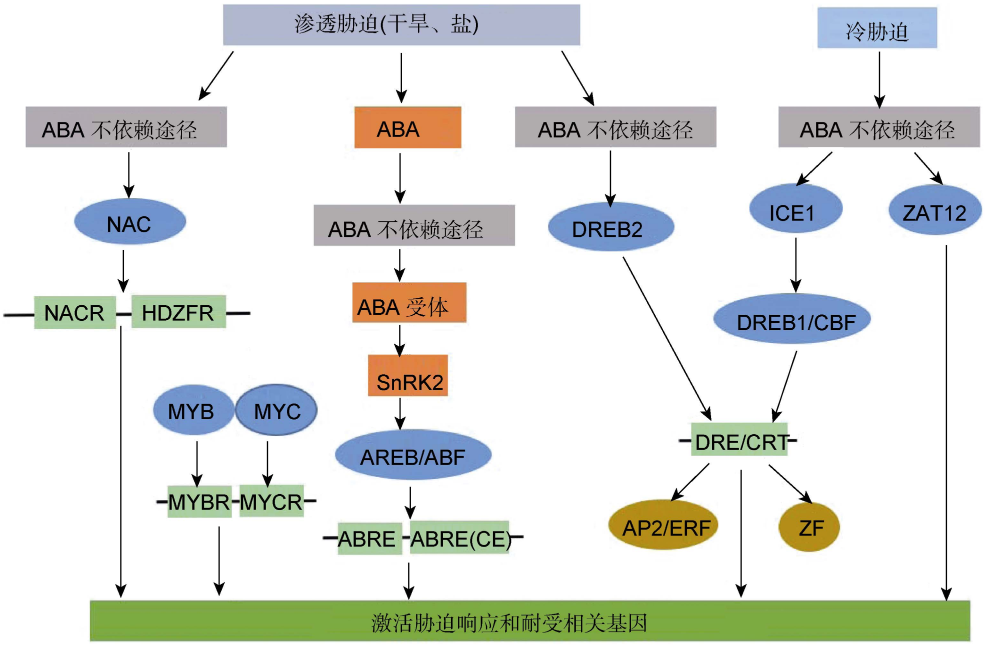

图1 植物响应非生物胁迫(干旱、盐和冷害)的ABA依赖与ABA不依赖途径的交互作用网络(改自Roychoudhury et al., 2013)

Figure 1 Cross-talk network in ABA-dependent and ABA-independent pathways during abiotic stress (drought, salinity and low temperature) (modified from Roychoudhury et al., 2013)

2013), 使得植物响应联合胁迫异常复杂。联合胁迫之间的正向或负向互作受多种因素影响, 包括不同作物、基因型或胁迫类型、处理时间及强度等(Suzuki et al., 2014) (表1)。

1 联合胁迫的负向相互作用

自然界中, 植物同时响应多种胁迫时, 胁迫之间的响应是拮抗的, 造成对植物更严重的不利影响, 称为联合胁迫的负向相互作用(negative interactions)。干旱和高温胁迫作为联合胁迫负向作用的代表, 已在多种植物中进行了研究。结果表明, 植物对干旱和高温胁迫的响应相互拮抗。高温胁迫下, 植物能增加气孔导度从而通过蒸腾作用降低叶片温度。干旱胁迫通常导致气孔关闭。当干旱和高温同时发生时, 植物不能打开气孔, 叶片温度会相对较高, 从而对植株生长发育造成更严重的伤害(Vile et al., 2012)。相对于单一的干旱或高温胁迫, 联合胁迫对小麦穗数、叶绿素含量、产量和收获指数造成了更严重的负面影响(Prasad et al., 2011; Mahrookashani et al., 2017)。植物处于高温和盐联合胁迫时, 蒸腾速率的提高会导致盐离子吸收效率更高, 从而造成更严重的盐胁迫伤害(Keles and Öncel, 2002; Wen et al., 2005)。微量元素营养胁迫与其它非生物胁迫联合发生时, 由于微量元素为抗活性氧酶类合成所必需, 从而加重了对植物生长发育的不利影响。上述研究结果表明, 联合胁迫的负向相互作用对植物生长发育造成了更加严重的影响(Martínez-Ballesta et al., 2008)。

植物光合作用对联合胁迫的响应通常也表现出负向作用。以干旱和高温联合胁迫为例。高温胁迫下, 棉花(*Gossypium* spp.)的光合速率和气孔导度均下降, 叶片温度升高。干旱和高温复合胁迫下, 其影响程度更加严重(Carmo-Silva et al., 2012), 原因是干旱胁迫下, 叶片的气孔通常处于关闭状态, 导致CO_2可利用浓度降低, 进而限制了光合作用(Chaves et al., 2003)。高温胁迫主要通过改变电子传递能力和RuBisCO酶活性抑制光合作用(Salvucci and Crafts-Brandner, 2004; Way and Oren, 2010)。

需要指出的是, 连续胁迫中, 植物对变换两种胁迫的先后顺序的响应通常相似。例如, 在拟南芥

表1 联合胁迫之间的相互作用

Table 1 Interactions of combined stresses

	联合胁迫类型	植物	文献
负向相互作用	干旱+盐	大麦(*Hordeum vulgare*)	Ahmed et al., 2013
	干旱+热	小麦(*Triticum aestivum*), 大麦, 烟草(*Nicotiana tabacum*), 拟南芥(*Arabidopsis thaliana*), 高粱(*Sorghum bicolor*), 高羊茅(*Festuca arundinacea*), 棉花(*Gossypium* spp.), 柑橘(*Citrus reticulata*)	Craufurd and Peacock, 1993; Jiang and Huang, 2001; Rizhsky et al., 2002, 2004; Prasad et al., 2011; Vile et al., 2012
	干旱+冷害	甘蔗(*Saccharum officinarum*)	Sales et al., 2013
	干旱+UV辐射	拟南芥, 白三叶(*Trifolium repens*), 云杉(*Picea asperata*), 油菜(*Brassica napus*), 柳树(*Salix babylonica*), 杨树(*Populus*)	Hofmann et al., 2003; Poulson et al., 2006; Turtola et al., 2006; Sangtarash et al., 2009; Duan et al., 2011; Bandurska et al., 2013
	干旱+高光	拟南芥	Giraud et al., 2008
	干旱+重金属	红枫(*Acer rubrum*)	de Silva et al., 2012
	盐+高温	小麦	Keleş and Öncel, 2002; Wen et al., 2005
	盐+臭氧	欧洲白桦(*Betula pendula*), 鹰嘴豆(*Cicer arietinum*)	Welfare et al., 2002; Kasurinen et al., 2012
	高温+臭氧	欧洲白桦, 杨树	Hartikainen et al., 2009; Kasurinen et al., 2012
	高温+UV辐射	西芹(*Apium graveolens*)	Walter, 1989
	高温+高光	向日葵(*Helianthus annuus*)	Hewezi et al., 2008; Mittler and Blumwald, 2010
	冷害+高光	盐藻(*Populus tremula*)	Haghjou et al., 2009
	UV辐射+重金属	豌豆(*Pisum sativum*)	Srivastava et al., 2012
正向相互作用	干旱+臭氧	苜蓿(*Medicago truncatula*), 欧洲白桦, 欧洲山毛榉(*Fagus sylvatica*)	Pääkkönen et al., 1998; Löw et al., 2006; Iyer et al., 2013
	干旱+高CO_2	高粱	Ottman et al., 2001; Brouder and Volenec, 2008
	盐+高温	番茄(*Solanum lycopersicon*)	Rivero et al., 2014
	盐+高CO_2	莴苣(*Lactuca sativa*)	Pérez-López et al., 2013
	盐+硼	玉米(*Zea mays*)	Martínez-Ballesta et al., 2008
	臭氧+高CO_2	大豆(*Glycine max*)	Booker and Fiscus, 2005; Ainsworth et al., 2008
	高CO_2+高光	莴苣	Pérez-López et al., 2013

(*Arabidopsis thaliana*) (Zandalinas et al., 2016a)、大麦(*Hordeum vulgare*) (Rollins et al., 2013)、烟草(*Nicotiana tabacum*) (Rizhsky et al., 2002)和柑橘(*Citrus reticulata*) (Zandalinas et al., 2016b)中, 无论先进行干旱胁迫再进行高温胁迫; 还是先进行高温胁迫再进行干旱胁迫, 它们对这两种胁迫的先后处理表现出的生理响应相似, 均在联合胁迫下受到比单一胁迫更严重的损伤, 表明不同植物应对干旱和高温联合胁迫的响应机制相对保守。

2 联合胁迫的正向相互作用

相对于单一胁迫, 有些胁迫联合发生反而会对植物产生有利的影响, 称为联合胁迫的正向相互作用(positive interactions)。高温和干旱胁迫负面影响了拟南芥生物量、光合效率、叶绿素荧光、气孔导度以及叶绿素合成等, 但提高环境CO_2浓度可显著缓解高温和干旱胁迫造成的生物量降低、光合作用受抑制、叶绿素含量下降及H_2O_2和氧化还原蛋白合成上调等负面影响。这种缓解现象可能是由于在高浓度CO_2下提高了碳固定, 进而上调了抗氧化物质(多酚、ASC和CAT)的合成。Zinta等(2014)通过组学分析表明, 高浓度CO_2缓解胁迫影响也可能与抑制光呼吸从而抑制H_2O_2的合成有关。在苜蓿(*Medicago truncatula*)中, 干旱降低植物的气孔导度, 促进抗坏血酸盐和谷胱甘肽的合成, 进而提高植物对臭氧(O_3)的耐受性(Iyer et al., 2013)。

联合胁迫之间的正向或负向相互作用因植物种类不同而异。盐和高温联合胁迫对小麦造成了负向作用(Keles and Öncel, 2002)。然而，在番茄(*Solanum lycopersicon*)中，盐和高温联合胁迫却能缓解单一盐胁迫对番茄的影响。盐胁迫下，气孔关闭导致光合效率下降；而叶片中积累的果糖和葡萄糖等反馈抑制光合作用。高温胁迫主要影响光合作用中心电子传递以及二氧化碳同化等，如RuBisCO酶活、类囊体膜和光系统(PS II)反应中心均受到不同程度的影响。在盐和高温联合胁迫下，番茄积累大量的甜菜碱和海藻糖来应对联合胁迫，从而具有较高的光合效率和叶片水势。甜菜碱等物质的积累可以维持高K^+浓度，从而保证了较低的Na^+/K^+比值，使植株免受盐胁迫的损伤(Rivero et al., 2014)。此外，甜菜碱还可保护PSII免受高温诱导的失活(Allakhverdiev et al., 2003)，以及抑制盐诱导的K^+流出(Cuin and Shabala, 2005)。海藻糖被证明在保持植物光合能力和PSII效率上具有重要作用(Lunn, 2007)；并有助于细胞抵抗氧化胁迫(Garg et al., 2002; Chen and Murata, 2008)。同时，在盐和高温联合胁迫下，H_2O_2的积累与蛋白氧化损伤受到抑制，进而保护植物免受氧化胁迫(Rivero et al., 2014)。

连续胁迫中，一种胁迫的预处理通常会对后续胁迫具有缓解作用。研究表明，提前光处理能够诱导抗活性氧过程，从而缓解高温造成的生理胁迫。抗坏血酸过氧化物酶(ascorbate peroxidase 2)作为重要抗氧化酶在植物抗活性氧代谢中起主导作用。提前光处理拟南芥光敏色素B突变体(*phyB*)并不能缓解其高温胁迫损伤，外源施加抗坏血酸的抗氧化剂则能够恢复其表型。这些结果表明，光预处理引起的phyB介导的抗活性氧过程有利于植物适应高温胁迫(Han et al., 2019)。

联合胁迫的正向还是负向相互作用需要具体情况具体分析，不能一概而论。有研究表明，非生物胁迫因子可提高或削弱植物对病原菌的抗性。热胁迫导致活性氧积累，增强水稻(*Oryza sativa*)对稻瘟病的抗性(Averyanov et al., 2000)；干旱和盐胁迫处理也能提高植物对病原菌的抗性(Achuoa et al., 2006)。而生物胁迫使得植物对非生物胁迫的耐受性降低。例如，有研究表明，病毒处理的植物在联合干旱和热胁迫下，其防卫基因表达下调(Prasch and Sonnewald, 2013)，且高温促进病原菌扩散(Luck et al., 2011; Madgwick et al., 2011)；Ghandi等(2016)研究发现，受黄曲叶病毒侵染的番茄对热胁迫敏感，且热胁迫敏感的增强与植物热激蛋白或因子下调密切相关，表明非生物胁迫可能弱化植物对生物胁迫的抗性。此外，也有生物胁迫促进非生物胁迫的报道。例如，侵染内生真菌的小麦对干旱以及热胁迫的耐受性增强(Hubbard et al., 2014)；大麦感染内生真菌*Piriformis indica*后提高了其盐胁迫的耐受性和抗病性(Waller et al., 2005)。高温能够促使拟南芥提前开花，并抑制其对丁香假单胞菌(*Pseudomonas syringae*) PstDC-3000 (avrRpt2)的抗性(Liu et al., 2019)。可见，非生物胁迫弱化还是增强生物胁迫的抗性依赖于单个胁迫的本质、时间、程度以及它们之间的相互作用。

3　植物对联合胁迫的其它效应

研究表明，生物和非生物联合胁迫发生时，严重的非生物胁迫通常主导植物对联合胁迫的响应。例如，严重的干旱胁迫和线虫侵染时，在联合胁迫中96%表达上调的基因同时也受到干旱诱导，而只有2%的基因受线虫感染上调(Atkinson et al., 2013)。此外，也有关于生物胁迫主导非生物胁迫响应的报道。拟南芥在干旱、灰霉病(*Botrytis cinerea*)真菌侵染以及菜粉蝶(*Pieris rapae*)取食连续胁迫时，转录组显示基因表达主要受菜粉蝶取食调控(Coolen et al., 2016)。显然，这些联合胁迫就不能够简单地区分为正向或负向相互作用。

4　利用组学方法解析植物响应联合胁迫机制

4.1　植物响应联合胁迫的信号通路和调控网络解析

后基因组时代，利用基因组信息，结合表型组学、转录组学、蛋白组学及代谢组学，筛选、鉴定和分离植物重要性状调控基因或元件，选择最佳调控通路，实现对植物定向分子设计，是当前研究的前沿与热点。在联合胁迫下，植物通常整合不同的信号(如激素、钙离子、活性氧)及糖代谢等信号通路来响应联合胁迫，是一个系统性响应(Schenke et al., 2011; Prasch and Sonnewald, 2013)。因此，应用多组学方法解析植物响应联合胁迫的关键信号通路及应对联合胁迫的调控网络，对阐明植物应对联合胁迫的生理及分子机理显得非常重要。

Rasmussen等(2013)对处于多重胁迫(包括冷害、高温、高光、盐和病毒侵染)下的拟南芥植株进行转录组分析，发现其在不同联合胁迫下转录水平的响应有显著差异。约25%的基因在单一不同胁迫下表现出相似的转录水平，而在联合胁迫下转录水平明显不同。这些基因主要与植物的系统性防卫机制、细胞程序性死亡及水杨酸合成途径有关。另外，约29%的基因在不同单一胁迫下差异表达，但在联合胁迫下表达水平与正常组水平无差异。这些基因主要参与次级信号(如生长素(IAA)和苯基丙酸类物质)合成和生长调控(乙烯和生长素信号通路)过程。约28%的基因能够受这些胁迫的某个单一胁迫特异地调控，而不受其它单一胁迫的影响。这些基因主要参与类囊体膜的构建和高光胁迫响应，说明其调控通路主要涉及光合作用过程。

Iyer等(2013)对苜蓿进行了研究，发现其在基因转录水平特异性地响应单一的干旱或O_3胁迫以及二者的联合胁迫。干旱条件下，有关脱落酸(ABA)信号和脯氨酸合成，以及响应高光、高温和氧化胁迫的基因转录上调；而O_3特异性地诱导葡萄糖、蔗糖和葡聚糖代谢相关基因。在联合胁迫下，茉莉酸(JA)信号通路和固有免疫相关基因转录上调，一些转录因子(WRKY和MYC3)特异性上调。转录因子WRKY主要响应JA、生物和非生物胁迫的一类转录因子(Gao et al., 2011)。JAZ1和JAZ2的抑制子MYC3也参与JA信号通路(Figueroa and Browse, 2012; Kazan and Manners, 2012)。

为阐明多重联合胁迫下植物-病原菌互作的分子机制, Prasch和Sonnewald (2013)建立了干旱、热害以及病毒多重胁迫联合控制体系，分析了单个、双重以及三重胁迫下转录组和代谢组学变化。他们鉴定了所有胁迫组合中差异表达的11个基因，同时也鉴定了三重胁迫下特异调节的23个重要基因，发现病毒侵染的植物防卫基因的表达上调，而在进一步干旱和热胁迫下，这些基因表达下调。以上表明在这些联合胁迫下，通常是编码细胞质响应蛋白的基因被诱导表达，而编码内质网响应蛋白的相关基因表达下调。

4.2 参与联合胁迫响应的重要功能基因挖掘和代谢标志物鉴定

通过组学研究，可以鉴定参与植物联合胁迫响应的特异表达功能基因或代谢标志物，为定向调控植物应对联合胁迫提供重要的理论依据。拟南芥中45个蛋白特异地响应干旱和高温联合胁迫，这些蛋白主要参与活性氧和苹果酸盐代谢及卡尔文循环；在植物抗活性系统中，细胞质APX1蛋白对耐受联合胁迫非常重要(Koussevitzky et al., 2008)。玉米(*Zea mays*)干旱和高温胁迫下的代谢组学数据显示，多种具有渗透调节功能的侧链氨基酸能够特异性响应联合胁迫(Obata et al., 2015)。Zandalinas等(2017)在柠檬响应干旱和高温的研究中，发现次级代谢物质(类黄酮等)大量积累。Gupta等(2017)通过激素代谢组实验，发现拟南芥在干旱以及丁香假单胞菌单独胁迫下，ABA和水杨酸(SA)分别起到了重要调控作用；而在联合胁迫下，ABA并未被诱导，SA和JA浓度快速上升，表明SA和JA在联合胁迫耐受性中起重要作用。

Rizhsky等(2002)研究表明，烟草(*Nicotiana tabacum*)在干旱和热激联合胁迫下明显诱导衰老基因*SAG12*和转录因子NtWRKY4的表达。使用转录组学和蛋白组学方法，专家们筛选出一些植物适应多重胁迫相关的候选基因(如*Apx1*和*Mbf1c*)，这些基因在作物抗性育种中有很大应用潜力(Koussevitzky et al., 2008; Kumar et al., 2015; Zandalinas et al., 2016a)。另外，Giraud等(2008)对拟南芥进行了研究，发现其交替氧化酶突变体(*aox1a*)在高光和干旱联合胁迫下，比野生型积累了更多(10倍以上)的花青素，且光合效率下降，超氧阴离子自由基增加，根系生长量减少。转录组和代谢组学分析表明，联合胁迫下参与花青素合成和活性氧防御，叶绿体和线粒体组分及细胞壁合成，蔗糖和淀粉代谢的转录物发生显著变化。上述研究表明在联合胁迫下，定位于线粒体的AOX1a蛋白缺失，线粒体和叶绿体信号通路平衡发生改变，叶绿体定位的抗氧化系统被显著诱导。可见, AOX1a蛋白在细胞正常的氧化还原平衡中起重要作用。

番茄在响应盐和病原菌联合胁迫时，植物激素发挥了重要作用。在ABA缺乏突变体*sitiens*中，番茄对盐胁迫的耐受性减弱，但对灰霉病的抗性增强，其抗病性增强与SA响应基因的诱导表达相关，但与JA响应基因无关。盐胁迫下，抗病性的回复与H_2O_2大量积

累有关，同时H_2O_2积累诱导了植物衰老(Bai et al., 2018)。拟南芥中过表达*NCED5*基因，导致ABA含量增加2倍以上；同时增加了过表达植株对丁香假单胞菌的敏感性，ABA促进JA的积累，但与SA拮抗互作(Fan et al., 2009)，表明ABA可减弱植物对病原菌的抗性。联合胁迫中，各种信号通路的交互作用，加深了植物响应联合胁迫的复杂性，说明多重联合胁迫不可预见。寻找关键的遗传调控因子减少不同信号通路的拮抗互作，是未来重要的研究方向。

Berens等(2019)报道了在生物和非生物联合胁迫下，拟南芥平衡两个负向相互作用的遗传调控机制，及拟南芥叶片在不同生长时期平衡生长与生殖的差异优先性机理。他们发现，在高盐和干旱条件下，老叶通过调控ABA信号途径提高植物胁迫耐受性，但同时降低了植物的免疫反应；此外，他们还鉴定了SA防卫信号中的重要成员PBS3，发现其可保护新叶免于ABA介导的免疫抑制作用。该研究揭示了一种植物在自然环境条件下面对多重胁迫的策略，同时在植物机体水平证明了胁迫激素交互作用的生理重要性。

5 展望

非生物或生物胁迫的联合发生影响作物的生长发育，导致其产量下降，严重时甚至绝收。在单一胁迫研究已获得大量进展的基础上，面对粮食安全和全球气候变化，研究植物对联合胁迫的响应与适应机制将成为未来重点研究方向。综上所述，植物在表型、生理生化、基因表达(包括转录、转录后、翻译和翻译后)及代谢水平响应联合胁迫，各种生理代谢途径和信号网络交互作用，故相关机制非常复杂。目前的联合胁迫研究，主要关注植物的地上部，而对地下部(如根)的研究很少；此外，对营养生长阶段的关注更多，而对生殖生长阶段的研究较少。故今后应该加强联合胁迫过程中植物地下部和生殖生长阶段的研究。

当前，关于联合胁迫研究主要集中在转录组和代谢组水平，表型组学和蛋白组学在联合胁迫研究中的应用相对偏少。杜康兮等(2018)研究表明，表观遗传在调控植物响应非生物胁迫中起重要作用，而表观组学在联合胁迫中的研究报道较少。未来需要进一步加强运用多组学研究联合胁迫下表型组变化、生理生化调控、遗传调控以及信号(激素、活性氧及钙等)和表观遗传网络之间的互作机制，鉴定和克隆耐受联合胁迫的关键生理代谢标志物和遗传调控因子。虽然已鉴定到一些在联合胁迫中起重要调控作用的相关代谢物(如可溶性糖)和遗传调控因子(如转录因子)，但有关胁迫的重要调控因子(如microRNA)还未见报道。此外，我国有丰富的作物种质资源，结合基因组测序和全基因组关联分析，研究这些种质资源对联合胁迫响应的自然遗传变异，解析作物响应联合胁迫的分子机理和调控网络将具重要意义。总之，未来我们应该联合分子生物学家、生理生态学家、栽培学家及育种学家，加强植物对联合胁迫响应与适应机制的研究，以加深人们对植物适应环境机理的认识，更好地制定大田条件下的育种策略，及培育耐受多重胁迫环境的新品种，以保障我国的粮食安全。

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Advances in the Mechanism Underlying Plant Response to Stress Combination

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Abstract Under field conditions, biotic and abiotic stresses usually occur simultaneously, and threaten global food security. Uncovering the mechanisms underlying plant response to combinations of two or more stress conditions holds the potential to breed new crop varieties with enhanced stress tolerance. Recent studies have revealed that the response of plants to stress combinations is unique and cannot be directly extrapolated from the response of plants to each of the different stresses. The responses of plants to different combined stresses might integrate with different signaling pathways at multiple levels, including defence responses, transcription factors, hormone signaling and osmolyte biosynthesis. Here, we review the molecular and physiological responses and adaptations of plants to different stress combinations, and provide an update on multi-omics approaches to study combined stresses.

Key words stress combinations, environmental stress, plant growth and development, yield, omics

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