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UV-B增强对作物生产影响的研究回顾与展望

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摘 要:大气平流层臭氧耗损引起的地表紫外辐射(UV-B)增强是气候变化问题之一。UV-B辐射增强对作物生长、生理代谢、产量及品质的影响受到人们普遍关注。通常借助两种方法开展模拟试验研究,即平方波模型法和太阳追踪模型法。UV-B辐射增强引起作物生长受阻、分蘖数减少、株高下降、叶面积和叶绿素含量下降、光系统Ⅱ受抑、光合效率降低;UV-B辐射增强导致活性氧代谢失衡、叶片气孔器受到破坏、叶绿体结构变形、基粒片层排列紊乱;UV-B辐射增强使作物有效穗数、穗粒数、千粒重下降,导致产量下降;UV-B辐射增强对籽粒蛋白质影响因作物、品种而异。未来应加强UV-B辐射增强影响作物内源激素代谢分子机制研究、区域和全球模拟及其应对措施研究。

关键词:UV-B辐射;作物;生长;产量;品质

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Crop growth, yield and quality as affected by ultraviolet-B(UV-B) radiation elevating

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Abstract: Elevated UV-B radiation on the ground surface due to ozone depletion in the stratosphere has become one of the important issues in global change. Elevated UV-B radiation depressed plant growth, with reduced tiller numbers and plant height, decreased leaf area and chlorophyll content, depressed PS Ⅱ and photosynthetic efficiency. Elevated UV-B radiation resulted in the imbalance of reactive oxygen metabolism, damage to the stomatal apparatus of the blade, the chloroplast structural deformation, and the disorder of the arrangement of GRANA lamellae. Elevated UV-B radiation reduced the number of effective panicles, grain number per ear, thousand-seed weight, and yield. The effect of elevated UV-B radiation on protein content in seed varied with crop types and cultivars. Further researches are needed to investigate the molecular mechanism of endogenous hormone metabolism in crops as affected by elevated UV-B radiation, crop model simulation at regional and global scales, interaction of elevated UV-B radiation with other environmental factors as well as its counter measures.

Keywords: elevated UV-B radiation; crop; growth; yield; quality

20世纪以来,人类活动排入大气的氯氟烃类化合物、氮氧化合物等引起平流层臭氧(O_3)耗损是全球气候变化研究的重要问题之一。1985年,人类首次发现了南极“臭氧空洞”,随后,中纬度地区的臭氧层空洞被陆续证实。我国大气臭氧层衰减也很明显,据北京和昆明的监测结果,我国平流层O_3总量呈降低

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趋势，地区平均下降5.1%。由于平流层中的O_3是太阳紫外辐射的主要过滤器，臭氧层变薄及臭氧空洞的出现，使到达地面的太阳紫外辐射增强。研究表明，大气平流层O_3每减少1%，到达地面的太阳紫外辐射增加2% [1-4]。紫外辐射依其生物效应可分为：超强效应波段（UV-C, 200~280 nm），为灭生性辐射，即为通常所说的杀菌紫外线，但可全部被平流层O_3吸收而不能到达地面；强效应波段（UV-B, 280~320 nm），为生物有效辐射，绝大部分可被O_3吸收；弱效应波段（UV-A, 320~400 nm），很少被O_3吸收，但它对生物无杀伤作用，且可促进植物生长。从生物学角度分析，对地球生物造成直接影响的紫外辐射主要是UV-B辐射[5-8]。

臭氧层减薄引起的地表UV-B辐射增强对农作物生长、生理特性、产量和品质的影响是普遍关注的全球环境和气候变化问题。国内外迄今已针对200多种植物开展UV-B辐射增强响应研究，发现2/3以上的植物在UV-B增强后产生不同程度伤害，其中近100种为农作物，涉及小麦、水稻、玉米、大豆等，研究涉及作物生长发育、形态结构、生理生化、产量构成及品种遗传差异等方面[9-19]。研究表明，UV-B辐射增强下，作物生长发育受阻、分蘖数减少、株高变矮、叶面积和叶绿素含量下降、光系统Ⅱ活性受抑、光合作用效率降低[16-19]。利用电镜研究表明，UV-B辐射增强导致叶片气孔器受到破坏，叶绿体结构变形，基粒片层排列紊乱[20-22]。UV-B辐射增强引起作物有效穗数、穗粒数、结实率、千粒重下降，最终导致籽粒产量下降[9,12]。本文综述了近年来UV-B辐射增强对作物生长、生理特性、产量和品质影响的相关研究进展，为保障粮食安全及应对气候变化提供参考依据。

1 UV-B辐射增强的模拟研究方法

探究平流层O_3耗损所引起的UV-B辐射增强对作物的影响，通常借助特定装置开展模拟研究。用于研究UV-B辐射增强效应的试验，主要是通过在冠层上部架设UV-B灯管来增加辐射强度。辐射剂量根据试验所在地环境UV-B强度和当地大气O_3衰减趋势来确定。UV-B辐射系统有两种模型：一种为平方波模型，选取以中午为中心的时间段开灯辐射，并保持灯管与植物冠层的距离，这种系统由于具有设置简单、便于操作、运行经济的特点而得到了较广泛的应用[15-20]；另一种为太阳追踪模型或可调式辐射系统，通过连续监测环境中UV-B辐射和植物受到的UV-B辐射强度，根据阳光中UV-B强度的变化来自动调整UV-B灯管的辐射强度，但由于其设备技术复杂、费用高等因素，迄今只有少数报道采用这种模拟系统[14,23]。UV-B辐射增强试验一般分为室内试验和大田试验。为尽可能真实地反映自然环境中作物对UV-B辐射增强的响应，一般多趋向于采用大田试验。采用室内试验时，要尽量模拟田间可见光、UV-A以及其他一些影响因子，室内试验的优势是可同时进行多因子复合试验及便于控制环境因子开展机理性研究[23]。

2 UV-B辐射增强对作物生长的影响

UV-B辐射增强通过改变植株体内生长激素含量，削弱顶端优势[9-14]。UV-B辐射与光敏色素和蓝光受体相互作用，影响节间伸长[5,20]，从而降低株高[14,18,24-25]。UV-B辐射增强对株高的抑制效应因品种而异。Kataria等[14]发现，滤除UV-B辐射可显著提高4个小麦品种株高，但品种间存在差异。陈建军等[20]对20个大豆品种的研究发现，UV-B辐射增加降低了17个大豆品种株高，但提高了3个品种株高。

叶片是对环境胁迫较为敏感的植物器官，它会通过形态结构的改变来适应各种环境变化[26]。植株叶片会通过减小尺寸、增加厚度、增加表面蜡质含量等来避免或减轻UV-B辐射对植物叶片的穿透性和伤害程度[22-23]。植物还会增加叶表皮毛的数目以增加对UV-B辐射的散射和反射，降低对UV-B的吸收[27]。研究发现，叶片总厚度与紫外吸收物质（类黄酮、生物碱、花色素苷等）总量存在相关关系[28]，植物通过增加叶片内紫外吸收物质含量来减少UV-B进入叶片组织内部[29]，从而减轻UV-B辐射对叶肉细胞的伤害[30]。孟凡来等[31]研究发现，甘薯叶片紫外吸收物质含量随UV-B辐射增加而显著增加。但是，UV-B辐射强度超过植物忍耐阈值时，植物叶片呈现褪绿、变黄、卷曲等症状，叶脉间会出现不均匀的条状和块状斑点[32]。Li等[33]在对水稻的研究中发现，传统水稻品种可通过改变叶片空间分布（叶顶基距、叶倾角）、增加叶片蜡质含量等来适应UV-B辐射增强。

UV-B辐射增强会通过降低作物株高和绿叶数等减少作物光合有效面积，从而降低地上部干物质累积[16,34-35]，同时还会抑制地下部根系生长[36-37]。UV-B辐射增强抑制根系生长的原因在于：（1）诱使叶片产生信号分子（ROS、NO等）运输到根部抑制根生长[38]；（2）减少叶片中生长激素含量，降低生长激素通过韧

皮部运输到根部，从而抑制根系生长[39-40]。滤除UV-B辐射可提高6个大豆品种地下部根系生物量[35]。UV-B辐射增加还引起作物生物量分配发生变化，大豆在总生物量降低的情况下，会将较多的生物量分配至籽粒，而向叶片分配的量降低[20]。

3 UV-B辐射增强对作物生理代谢的影响

有关UV-B辐射增强对植物生理代谢的影响，集中于UV-B感光体UVR8和UVR8介导的信号传导途径上。UVR8是位于细胞质和细胞核中的β螺旋蛋白，在UV-B辐射下，UVR8与组成型光形态建成1蛋白发生作用，开启UV-B光反应信号[41]。

叶绿素是作物光合作用的物质基础，其含量高低可作为衡量UV-B辐射增强对作物伤害程度的重要指标。UV-B辐射增强通过多种途径影响叶绿素含量，包括：（1）影响叶绿体中参与暗反应的关键酶——1,5二磷酸核酮糖羧化酶，使羧化速率下降；（2）使叶绿体膜上镁-三磷酸腺苷酶活性下降，导致叶绿体基质pH降低，叶绿体膜组分改变[42]；（3）破坏类囊体光系统，使叶绿素发生光氧化或破坏叶绿体结构[43-44]。叶绿素含量减少直接降低叶片的光能吸收效率和传递速率，干扰光能在PSⅠ和PSⅡ间的分配和转换[45]。UV-B辐射增强常导致叶绿素含量下降[46]。但也有研究认为，UV-B辐射增强可通过延迟叶片落黄，提高叶绿素含量[47-48]，如权佳锋等[47]发现，UV-B辐射增强使烤烟中部叶的叶绿素a、b含量高于对照。

UV-B辐射增强通过影响植物类囊体膜中的光化学反应、卡尔文循环中酶过程、影响气孔开度阻碍CO_2供应、破坏氨基酸残基、损伤氧介导的植物细胞膜中不饱和脂肪酸等影响光合作用[34, 49-52]。其中，UV-B辐射增强对光合系统Ⅱ（PSⅡ）的影响，主要是通过损坏植物PSⅡ水氧化锰决定簇，破坏光合电子传递，降低PSⅡ反应中心捕获激发能的效率[5, 53]，破坏PSⅡ中酪氨酸电子供体与D1和D2蛋白反应中心，导致PSⅡ活性降低，从而降低光合能力[5]。UV-B辐射增强对气孔的影响是由UVR8介导的NO途径调控[54]，增加H_2O_2的生成和产生，诱使细胞质碱化，导致气孔关闭[55]。研究发现，UV-B辐射增强20%会抑制大麦[16,56-57]、小麦[58]、水稻[59]、花生[60]、棉花[61]等作物的净光合速率。UV-B辐射对光合作用的影响还与辐射剂量及时间有关。祁虹等[61]研究发现，UV-B辐射增强20%处理的棉花叶片净光合速率高于UV-B辐射增强40%。王娟等[62]研究发现，0.616 $mW\cdot cm^{-2}$的UV-B辐射处理烤烟23 d会提高烤烟净光合速率，而处理33 d则会降低烤烟净光合速率。此外，UV-B辐射增强还通过改变叶片水分运输和分配，使叶片表面气孔开度减小，气孔阻力增大，根系生长和根系活力受抑，从而降低蒸腾速率[16-63]。

UV-B辐射增强导致植物体内活性氧（ROS）产生，积累过多的O^{2-}、OH^-和H_2O_2等自由基，引起活性氧代谢系统紊乱[64-65]，从而增加植物氧化应激效应[66]。ROS积累与UVR8、COP1和HY5/HYP转录因子信号传导途径有关，低剂量UV-B辐射可诱使植物产生ROS保卫机制，激活植物应急信号途径[54]。酶促和非酶促抗氧化剂的产生是植物对非生物胁迫的适应性反应。UV-B辐射增强会提高植物酶促抗氧化剂（如超氧化物歧化酶、过氧化氢酶、过氧化物酶）活性，增加非酶促抗氧化剂（如抗坏血酸、生育酚、谷胱甘肽、脯氨酸）的积累[67-69]，从而清除过多的自由基，使植物体内的自由基维持在正常的生理水平[70]。研究发现，UV-B辐射增强会使小麦[71]、水稻[46]、玉米[72]、土豆[73]等多种作物抗氧化酶活性增加，以提高作物对UV-B辐射增强耐受力。然而，高剂量UV-B辐射会使抗氧化剂不足以清除过量产生的ROS，导致DNA、蛋白质和光合作用机制受损，光合基因下调[74]。此外，不同作物抗氧化酶活性对UV-B辐射增强响应并不相同。研究发现，UV-B辐射增加使苦瓜超氧化物歧化酶、过氧化氢酶、过氧化物酶活性升高[75]，而使玉米抗坏血酸过氧化物酶和谷胱甘肽过氧化物酶活性升高[76]。UV-B辐射增强会使烟草过氧化物酶活性高于其他抗氧化剂[68]。

4 UV-B辐射增强对作物产量的影响

有关UV-B辐射增强（相当于臭氧耗损量的9%~50%）对作物产量影响的研究，大多基于田间模拟试验及温室盆栽试验，但结果不一。大多数研究认为，UV-B辐射增强通过降低作物光合面积、叶绿素含量来降低干物质累积，最终引起产量下降[14, 77]。UV-B辐射增强使大豆果荚数、粒数、粒重等产量构成指标下降，从而导致产量降低[78]。UV-B辐射增强引起春小麦成熟期植株干质量、穗粒数和穗粒质量下降，UV-B辐射增强使小麦发育小花数降低，以致可孕小花数、每穗粒数降低是导致产量下降的关键原因。UV-B辐射增强可降低水稻单株有效穗数、单穗总粒数、结实率、千粒重[79]。

但也有研究认为，UV-B辐射增强并不影响作物

产量。如Hakala等[80]发现，UV-B辐射增强未对小麦产量造成明显影响。少数研究认为，UV-B辐射增强会提高作物产量。此外，不同作物产量对UV-B辐射增强响应的敏感性存在差异，棉花、大豆、小麦及玉米对UV-B辐射增强响应的敏感性依次为棉花>大豆>小麦>玉米[81]。未来应进一步加强不同UV-B辐射增强对不同生态区域作物产量影响的研究，从机理上阐明引起产量差异的原因。

5 UV-B辐射增强对作物品质的影响

UV-B辐射增强对不同作物品质影响的研究，涉及花生、水稻、小麦、玉米等数十种作物[82-87]，但结果不一。UV-B辐射增强对作物籽粒蛋白质含量的影响，可能与作物种类、品种抗性及UV-B辐射强度或剂量等内外因素存在差异有关。据报道，UV-B辐射增强对小麦籽粒蛋白质含量没有显著影响[83]；或导致小麦籽粒蛋白质含量增加[88]。Gao等[87]研究发现，UV-B辐射增加9.5%使玉米籽粒蛋白质含量降低；而Yin等[84]则认为，UV-B辐射增加30%使玉米籽粒蛋白质含量提高。UV-B辐射增强显著增加水稻籽粒氮含量、脂肪酸及蛋白质含量，而对水分和支链淀粉没有影响[82]。UV-B辐射增强对可溶性糖、可滴定酸的影响因作物种类、辐射强度的不同而异[89-92]。例如，3.6 kJ·m^{-2} UV-B辐射对果实存储期间可溶性糖、可滴定酸含量无显著影响[91]，而6 kJ·m^{-2}的UV-B辐射则抑制蓝莓果实存储期间可溶性糖、可滴定酸值的增加[92]。UV-B辐射对果实蔗糖、总糖含量等品质指标影响取决于发育期，在果实二次膨大前可提高果实糖积累、可溶性固形物/总酸度比值和花青素含量，但延长UV-B辐射时间则抑制糖积累[89]。未来应进一步关注UV-B辐射增强对不同作物品质影响的研究并阐明内在机理。

6 UV-B辐射增强与其他因子对作物的耦合影响

作物生长受多种环境因子制约，研究UV-B辐射与其他胁迫因子对作物的耦合影响，有助于作物可持续生产[93]。UV-B辐射增强与其他因子耦合对作物的影响，涉及的相关因子很多，包括营养元素、温度、干旱、CO_2浓度升高、O_3浓度升高及重金属胁迫等，受篇幅所限，另文详述。

施加营养元素（如硒、硅、钾）会改变植物对UV-B辐射增强的响应，缓解UV-B辐射增强对植物的损伤[94-95]。硒与UV-B复合可刺激苯丙素代谢途径酶活性，促进酚类物质产生[96]，提高冬小麦籽粒产量和品质（如蛋白质含量和营养元素氮、铁、铜、硒含量）[97]。施硅可通过改变植物形态、调节植物内源激素、增加紫外吸收物质（总酚、类黄酮）含量等，减轻UV-B辐射增强对作物光合作用的抑制程度[37,95]。施钾可缓解UV-B辐射增强对花生、大麦叶片净光合速率、蒸腾速率、气孔导度及水分利用率的抑制作用，提高花生株荚果数、株荚果质量和产量[56,85]。

UV-B增强可降低株高、叶面积和地上部生物量，但可提高紫外吸收物质含量[98]。增温则促进作物生长，降低酚类含量[99]。UV-B辐射与温度以相反方式影响酚类含量，特别是类黄酮的含量[100]。高温和UV-B辐射的相互作用方式因温度不同而异，在适当的温度范围内（21~31 ℃），温度升高可降低UV-B辐射对小麦生长和光合作用的抑制，但当温度过高（36 ℃）时，高温与UV-B表现为协同作用，二者共同抑制植物生长和光合作用[101]。

干旱与UV-B辐射复合使玉米和大豆总干物质量因叶绿素含量及光合速率降低而降低，其中UV-B辐射起主导作用[102]。UV-B辐射增强可保护小麦叶片免受干旱引起的枯萎和叶面卷曲，UV-B辐射和干旱复合显著缓解干旱或UV-B辐射增强单因子胁迫对小麦产量的影响[103]。UV-B辐射与干旱处理间相互影响很小，UV-B辐射的影响被水分亏缺的影响所遮蔽，UV-B与干旱复合在很大程度上可推迟葡萄果实成熟[104]。可见，UV-B辐射与干旱复合对作物影响的研究结果不完全一致，这可能与UV-B和干旱处理水平、供试土壤、作物种类及品种抗性不同等有关。

CO_2浓度升高可缓解UV-B辐射增强对冬小麦幼苗生长的抑制作用，但并不能缓解对水稻结实率及产量的抑制作用[105-106]，原因可能在于试验条件不同，前者在室内人工气候室进行，而后者则在室外半人工气候室进行。CO_2倍增和低剂量UV-B辐射能使番茄抗氧化酶活性增强，而高剂量UV-B辐射与CO_2复合则对植株伤害作用加剧[107]。原因可能在于CO_2倍增为光合作用提供充足原料，提高RuBP羧化酶活性，抑制RuBP加氧酶活性，提高光合速率，抵消低剂量UV-B辐射对PSⅡ抑制作用，但当UV-B辐射为高剂量时，CO_2浓度倍增提高的抗氧化酶效应不能缓解UV-B辐射增强对植株的伤害。可见，UV-B辐射与CO_2复合处理对作物的影响，可能与供试作物种类、试验环境条件、CO_2浓度及UV-B辐射剂量等有关。

UV-B辐射增强和O_3浓度升高显著降低大豆根

系生物量，改变叶片内源激素平衡[108]。UV-B辐射增强和O_3浓度升高复合胁迫降低冬小麦PSⅡ最大潜在光合能力，使PSⅡ光合活性显著下降[109]。UV-B辐射增强和O_3浓度升高复合胁迫下，UV-B辐射抑制希尔反应活力，降低RuBPcase活性，影响光合电子传递速率，抑制PSⅡ酶活性，使呼吸增强，净光合速率下降[110]。O_3则使细胞内外CO_2浓度差减小，光合作用消耗CO_2量减少，细胞内CO_2滞留量增加，外界CO_2更不易进入叶肉细胞，这种恶性循环最终使光合作用下降，生物量积累减少[111]。

UV-B辐射增强与砷复合可加剧砷对向日葵生长参数和光合色素含量抑制，使向日葵幼苗抗氧化酶活性提高，脯胺酸含量增加[112]。UV-B增强与镍复合胁迫对大豆幼苗光合电子传递的抑制作用高于单一处理，引起活性氧大量累积，对大豆幼苗造成损害[113]。UV-B增强与镉复合胁迫对冬小麦生长及生理存在协同效应[114]。镉明显拮抗UV-B辐射对大豆叶片POD活性诱导，使得植物体内POD活性较UV-B单独胁迫显著降低[115]。UV-B辐射增强与重金属复合胁迫，引起植物产生过量活性氧，活性氧可直接与生物分子作用引起脂质过氧化、蛋白质氧化和DNA突变[116-117]。

7 研究展望

近年来有关UV-B辐射对作物生长、产量和品质的影响研究取得了较大进展，未来有望在以下方面取得突破：(1)UV-B辐射增强影响作物光合作用及内源激素代谢的分子机制尚缺少深入研究。(2)有关UV-B辐射增强对作物影响的研究多是通过温室或田间模拟试验进行，未来可通过作物生长模型耦合气候模式开展区域及全球尺度的相关研究。(3)加强UV-B辐射增强对作物产量及品质影响的作用机制研究。(4)筛选培育对UV-B辐射适应性强的作物品种。不同作物基因型对UV-B辐射增强及其与其他因子复合作用的响应不同，有关分子机制有待探究。(5)UV-B辐射增强与其他因子耦合对作物影响的研究多是采用模拟试验，与真实环境状况仍有一定差异，如何改进田间试验条件有待进一步研究。

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