促进稻麦同化物转运和籽粒灌浆的途径与机制

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摘要 协调植株衰老、光合作用与光合同化物向籽粒转运的关系是谷类作物的一个科学难题. 研究解决这一难题, 对阐明促进谷类作物同化物向籽粒转运和籽粒灌浆的调控途径与机制, 解决目前生产上部分稻麦品种或是在高氮水平下茎、鞘中同化物向籽粒转运率低、籽粒灌浆慢和充实不良等问题具有十分重要的理论和实践意义. 本文概述了促进稻麦同化物向籽粒转运和籽粒灌浆的栽培途径和生理机制, 重点介绍了3个重要发现: (1) 稻麦花后适度土壤干旱可以协调植株衰老、光合作用与同化物向籽粒转运的关系, 促进籽粒灌浆, 提高收获指数、产量和水分利用效率; (2) 花后适度土壤干旱通过提高脱落酸(abscisic acid, ABA)与乙烯、赤霉素(GAs)比值, 有效促进籽粒灌浆; 在水稻(*Oryza sativa*)和小麦(*Triticum aestivum*)活跃灌浆期, 籽粒充实需要较高的内源ABA水平、较高的ABA与乙烯比值及ABA与GAs比值; (3) 通过适度土壤干旱或施用低浓度ABA适度增加体内ABA水平, 可以增强茎和籽粒中糖代谢关键酶活性, 增加同化物在源端的装载与在库端的卸载能力, 进而促进同化物向籽粒转运和淀粉在籽粒中的合成与累积. 今后建议从信号传导等方面深入研究调控谷类作物同化物转运和籽粒灌浆的分子机理.

关键词 水稻, 小麦, 适度干旱, 同化物转运, 籽粒灌浆, 生理机制

水稻(*Oryza sativa*)和小麦(*Triticum aestivum*)是提供人类食用的两种最大谷类作物, 中国是世界上这两大作物的最大生产国与消费国^[1,2]. 提高水稻和小麦产量, 对保证我国乃至世界粮食安全具有十分重要的作用^[3,4]. 水稻和小麦的籽粒灌浆是产量形成的最后阶段, 籽粒充实的优劣直接决定了粒重和产量的高低^[5,6]. 水稻和小麦等谷类作物籽粒灌浆所需的光合同化物来自两个方面: 花后光合作用和开花前储存在茎和其他器官(主要为叶鞘)的非结构性碳水化合物(non-structure carbohydrate, NSC)^[7-9]. 在通常情况下, 水稻和小麦花前储存在茎(含叶鞘, 下同)中NSC对籽粒产量的贡献约占最后籽粒重量的

1/6~1/3, 其量的多寡主要取决于生长条件和氮素供应水平^[9-11]. 杨建昌^[12]曾观察到, 花前储存在茎中的NSC不仅是籽粒灌浆物质的一部分, 而且是启动灌浆的重要物质基础, 其转运速率和转运量影响了籽粒灌浆速率, 进而影响粒重和最终产量. 因此, 促进同化物向籽粒转运是促进稻麦籽粒灌浆和提高产量的重要途径. 但同化物向籽粒转运与植株衰老过程有密切关系, 植株衰老与光合作用又是“此消彼长”的一对矛盾^[13,14]. 植株衰老过快, 光合作用会严重降低, 影响籽粒充实. 相反, 植株不能适时衰老, 同化物就不能顺畅地向籽粒转运, 进而延缓籽粒灌浆、降低灌浆速率、造成籽粒充实不良. 在生产上, 部分稻

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麦品种或在高氮水平下茎、鞘中同化物向籽粒转运率低、籽粒充实不良是突出问题,由此造成的产量损失在20%以上^[15-18]。因此,协调稻麦植株衰老、光合作用与物质转运的关系对于促进籽粒充实非常重要,但也是作物学研究领域长期未解决的一个难题,存在着尚待揭示与解答的主要科学问题。

科学问题1:协调稻麦植株衰老、光合作用与同化物向籽粒转运关系的途径。通过何途径可以协调植株衰老、光合作用与同化物向籽粒转运关系?如何通过栽培途径或方法做到既可以不明显抑制叶片光合作用,又可以适时、适度地启动植株的衰老过程,促进同化物向籽粒转运,加速籽粒灌浆,进而提高产量?

科学问题2:促进同化物向籽粒转运和籽粒灌浆的生理调控机制。协调稻麦植株衰老、光合作用与同化物向籽粒转运之间关系的生理调控途径是什么?植物激素如何调控这种关系,其调控机制是什么?

探明以上科学问题,对于阐明促进谷类作物同化物向籽粒转运和籽粒灌浆的调控途径与机制、解决目前生产上部分稻麦品种或在高氮水平下同化物向籽粒转运率低、籽粒灌浆慢和充实不良等问题具有十分重要的理论和实践意义。围绕以上两个科学问题,本文概述了促进稻麦同化物向籽粒转运和籽粒灌浆的栽培途径和生理机制,并对存在的问题和今后的研究重点进行了讨论。

1 促进同化物向籽粒转运和籽粒灌浆的水分调控途径

植株衰老、光合作用和同化物向籽粒转运受植株水分状况调控^[19-21]。通常,稻麦花后遭受干旱胁迫会使植株早衰、物质生产减少、灌浆期缩短、粒重降低。虽然干旱胁迫可以增加茎中储存的NSC向籽粒转运,加速籽粒灌浆,但因茎中NSC向籽粒转运增加之得不能补偿物质生产减少和灌浆期缩短之失而造成粒重和产量降低^[20-22]。Yang等人^[23,24]假设,如果采用适度土壤干旱(moderate soil-drying)的方法,即叶片光合作用不受到严重抑制,植株的水分状况在夜间得到恢复,则可以使茎中NSC向籽粒转运增加之得超过光合作用减少和灌浆期缩短之失,从而促进籽粒灌浆充实。为了验证这一假设,Yang课题组^[22-25]设置了不同时段和不同土壤干旱程度的试验。他们发现,在水稻和小麦开花受精水分敏感期后控制水分供应,使耕层15~20 cm处的土壤水势控制在

水稻不低于-25 kPa、小麦不低于-70 kPa,或中午旗(剑)叶的叶片水势控制在灌浆前、中、后期,水稻分别不低于-0.95, -1.05和-1.15 MPa,小麦分别不低于-1.35, -1.55和-1.75 MPa(表1),可以使叶片光合作用不受到明显抑制,植株的水分状况在夜间得到恢复。这一方法不仅可以增加茎中储存的NSC向籽粒转运,而且可以促进籽粒灌浆;不会明显降低叶片光合速率,可以适时(花后12~15 d)、适度(与供水充足的植株相比,灌浆期叶片平均叶绿素含量降低的幅度小于10%)启动植株的衰老过程,促进同化物向籽粒转运^[22-27]。他们将这一方法称之为适度土壤干旱(moderate soil-drying)或有控制的土壤干旱(controlled soil-drying)。

采用适度干旱的方法,可以显著促进籽粒灌浆,提高灌浆期平均灌浆速率(表2);可显著提高物质运转率低、籽粒灌浆慢的品种(如部分亚种间杂交稻组合)或物质运转率较高、籽粒灌浆较快的高产品种在高施氮量情况下的产量(表2)。对于在正常供氮量下物质运转率较高、籽粒灌浆较快的高产品种,采用适度土壤干旱的方法,可显著减少灌溉水量,对粒重和产量无明显不利影响(表2)。

适度土壤干旱可以协调植株衰老、光合作用与同化物向籽粒转运的关系,促进籽粒灌浆,这一发现为解决谷类作物植株衰老与光合作用的矛盾以及既高产又节水的难题提供了新的途径和方法^[28-30]。对于促进我国稻麦生产的指导意义主要表现在以下4个方面:

(i) 光合同化物向籽粒转运率低、籽粒灌浆慢是一些稻麦品种、特别是部分籼/粳亚种间杂交稻品种(组合)的严重问题,其后果是不能将物质生产优势转化为经济产量优势,导致籽粒充实不良^[15,17,31,32]。采用适度土壤干旱的方法,有助于解决部分亚种间杂交稻和部分超级稻品种营养生长势过强、光合同化物向籽粒转运率低、籽粒灌浆慢和籽粒充实不良的问题。

(ii) 为了追求高产,我国稻麦生产上氮肥施用量普遍偏多。施用多量氮肥往往造成籽粒灌浆缓慢、

表1 适度土壤干旱的低限水势指标^{a)}

Table 1 Water potential indexes of moderate soil-drying^{a)}

作物	离地表15~20 cm 土壤水势(kPa)	灌浆期中午叶片水势(MPa)		
		前期	中期	后期
水稻	-25	-0.95	-1.05	-1.15
小麦	-70	-1.35	-1.55	-1.75

a) 表中数据根据文献[22~27]的数据整理

表 2 适度土壤干旱对稻麦物质转运、籽粒灌浆、产量和灌溉用水的影响^{a)}Table 2 Effect of moderate soil-drying on assimilate remobilization, grain-filling rate, grain yield, and the amount of irrigation water^{a)}

作物/ 品种类型	水分处理 ^{b)}	施氮量 ^{c)}	茎中NSC 转运率(%)	平均灌浆速率 (mg 粒 ⁻¹ d ⁻¹)	千粒重(g)	产量(g m ⁻²)	开花至成熟灌溉 水量(L m ⁻²)
水稻常规 高产品种	供水充足	正常量	46±3.2c ^{d)}	0.67±0.01c	26.3±0.32b	834±21b	156±14a
	供水充足	高氮量	23±2.1d	0.55±0.02d	25.2±0.27c	746±15c	162±13a
	适度干旱	正常量	71±4.8a	0.76±0.02a	26.1±0.30b	821±19b	112±11b
	适度干旱	高氮量	57±3.5b	0.71±0.01b	27.4±0.35a	888±25a	116±12b
小麦常规 高产品种	供水充足	正常量	52±3.6c	1.37±0.04c	41.8±0.53b	712±24b	55±3.6a
	供水充足	高氮量	31±2.4d	0.71±0.02d	36.3±0.42c	637±18c	58±3.8a
	适度干旱	正常量	74±5.2a	1.69±0.05a	41.3±0.49b	704±23b	31±2.5b
	适度干旱	高氮量	63±4.6b	1.58±0.03b	44.7±0.68a	783±27a	35±2.7b
亚种间	供水充足	正常量	15±1.3b	0.51±0.01b	25.4±0.31b	940±32b	165±16a
杂交稻	适度干旱	正常量	60±5.2a	0.60±0.03a	26.6±0.43a	1018±43a	120±10b

a) 表中数据根据文献[22~27]的数据整理; b) 离地表15~20 cm 处的土壤水势, 供水充足: 水稻为0~-5 kPa, 小麦为-30~-40 kPa; 适度干旱: 水稻为-20~-25 kPa, 小麦为-60~-70 kPa; c) 正常施氮量: 水稻为150~180 kg ha⁻¹, 小麦为180~210 kg ha⁻¹; 高施氮量: 水稻为240~270 kg ha⁻¹, 小麦为270~300 kg ha⁻¹; d) 不同字母者表示在P=0.05水平上差异显著, 同栏、同作物(同类型品种)内比较

贪青迟熟, 收获指数降低, 甚至发生倒伏^[33~35]. 采用适度土壤干旱的方法, 可以克服由于氮肥施用过量而造成的贪青, 促进同化物向籽粒转运, 加速籽粒灌浆, 提高收获指数, 进而提高产量和肥水利用效率.

(iii) 我国许多地方在稻麦生长季节受到不利气候条件的影响, 如小麦生长后期的干热风或梅雨、水稻生长后期的低温寒潮等. 这些不利的气候条件往往造成减产等严重后果^[23,36]. 实施花后适度土壤干旱, 可以促进稻麦适当早熟, 从而使小麦在干热风或梅雨、水稻在寒潮来临之前可以收获, 避开不利气候的影响. 特别是近年来随着我国机械化插秧和直播稻面积的扩大, 稻麦轮作区水稻和小麦迟播迟收已成为限制产量的一个重要因素^[37,38]. 采用适度土壤干旱的方法, 可以加速籽粒灌浆, 尤其是促进弱势粒灌浆, 适时收获, 提早让茬(可提早3~5 d).

(iv) 水资源短缺始终是制约我国农业生产的瓶颈问题^[39~41]. 采用适度土壤干旱方法, 可以节约水资源, 提高水的利用效率, 有利于农业的可持续发展.

有研究表明, 适度土壤干旱促进同化物转运和籽粒灌浆的方法, 不仅适用于稻、麦等谷类作物, 而且可应用于番茄(*Lycopersicon*)、大豆(*Glycine max*)、棉花(*Gossypium hirsutum*)等多种作物, 提高这些植物的产量和品质^[42~44].

为了使促进同化物转运和籽粒灌浆的水分控制方法应用于生产实践, Yang等人^[45]在水稻上建立了比较简单的控水方法, 即在田间安装聚氯乙烯

(polyvinyl chloride, PVC)管. 根据PVC管内离地表的水位, 进行灌溉, 当PVC管内离地表的水位, 砂性土10 cm、壤土12 cm、黏土15 cm时, 田间灌2~3 cm水层, 自然落干至PVC管内离地表水位达10~15 cm时再灌水, 依次循环. 这一方法简单易行, 已在生产上大面积推广应用.

通常, 土壤干旱会加剧高温对作物的伤害^[46,47]. 但Yang等人^[48]和Zhang等人^[49]的研究表明, 在适度土壤干旱条件下的作物冠层温度与正常供水的对照冠层温度没有显著差异, 因此适度土壤干旱不会加剧高温对作物的伤害. 不仅如此, 段骅等人^[50]观察到, 在水稻抽穗开花期高温条件下, 采用轻干湿交替灌溉(土壤落干至土水势为-15 kPa时复水)方法可以显著较水层灌溉降低冠层湿度, 因而减轻了高温对水稻的伤害, 获得较高的产量和较好的稻米品质.

2 植物激素对同化物转运和籽粒灌浆的调控作用

2.1 脱落酸促进同化物向籽粒转运

脱落酸(abscisic acid, ABA)通常被认为与植物的衰老有关^[51,52]. 但Yang等人^[22,26,27,53,54]研究发现, ABA不仅能调控水稻和小麦的衰老, 而且能促进茎中存储的NSC向籽粒转运. 他们的实验数据显示, 花后土壤干旱处理显著增加了水稻和小麦根系伤流液和叶片中ABA的浓度/含量, 促进了茎中NSC及标记

^{14}C 向籽粒的转运。ABA浓度/含量与茎中NSC及标记 ^{14}C 向籽粒的转运率呈极显著正相关,与叶片叶绿素含量呈显著负相关;低浓度($10\times 10^{-6}\sim 20\times 10^{-6}\text{ mol L}^{-1}$)外源ABA处理降低了叶片叶绿素含量,显著增加了茎中NSC及标记 ^{14}C 向籽粒的转运,表明ABA参与调控植株衰老和茎中储存同化物向籽粒转运的过程,花后适度土壤干旱通过增加内源ABA水平,促进茎中存储的NSC向籽粒转运。

2.2 ABA和乙烯的相互作用调控籽粒灌浆

ABA和乙烯是植物应答逆境的两种重要激素^[55,56]。以往研究认为,干旱等逆境条件造成谷类作物籽粒败育或充实不良与内源ABA和乙烯水平的增加密切相关^[45~58]。但Yang等人^[54,59~62]研究表明,ABA对籽粒灌浆的调控作用呈现出剂量效应,即低浓度促进,高浓度抑制;乙烯则可降低籽粒中蔗糖-淀粉代谢途径关键酶活性,抑制籽粒灌浆。在水稻和小麦的活跃灌浆期(籽粒快速增重期),籽粒充实需要较高的ABA浓度和较高的ABA与乙烯的比值^[61,62]。水稻和小麦的弱势粒充实差、粒重低,其较低的ABA含量和较高的乙烯释放速率或较高的1-氨基环丙烷1-羧酸(aminocyclopropane carboxylic acid, ACC, 乙烯合成的前体)含量是一个重要原因^[55,56]。稻麦花后进行适度土壤干旱处理,可以显著增加籽粒特别是弱势粒的ABA含量,降低乙烯释放速率和ACC含量,提高ABA与乙烯(ABA/ACC)的比值,进而促进籽粒特别是弱势粒灌浆,增加粒重;在严重干旱条件下,籽粒乙烯释放速率或ACC含量的增加超过了ABA含量的增加,使得ABA与乙烯(ABA/ACC)的比值降低,导致籽粒灌浆速率减小,粒重降低^[61~63]。对小麦籽粒灌浆速率与ABA及乙烯的相关分析显示,籽粒灌浆速率(G)与ABA含量的相关为多项式关系($G=0.105+0.19X+0.79X^2-0.16X^3$; $X=\text{ABA含量}$);与乙烯释放速率的相关为衰减的指数函数关系($G=0.65+6.41e^{-1.61X}$, $X=\text{乙烯释放速率}$);与ABA/ACC比值的相关为渐近线关系($G=25.54X/(0.23+X)-44.56X$, $X=\text{ABA/ACC}$);经计算得知,当籽粒中ABA=3.41 nmol g⁻¹ DW或ABA/ACC=0.13时,籽粒的灌浆速率最大($G=3.4\sim 3.5\text{ mg kernel}^{-1}\text{ d}^{-1}$)^[62]。以上结果说明,ABA与乙烯的相互作用调控籽粒灌浆。通过适度土壤干旱等方法适当提高ABA水平及ABA与乙烯的比值,可以促进水稻和小麦籽粒灌浆充实。

2.3 增大ABA与赤霉素比值可以促进籽粒灌浆

研究表明,一些籽粒灌浆缓慢的稻麦品种,在高施氮量下籽粒灌浆速率小、充实不良,活跃灌浆期内源GAs(GA_1+GA_4)水平过高、ABA与GAs比值低也是一个重要原因^[60]。通过适度土壤干旱等方法增加内源ABA含量和降低籽粒GAs含量,提高ABA与GAs比值,可以促进淀粉在籽粒中累积,增加粒重^[60,64]。在花后9 d连续喷施低浓度外源ABA,所得结果与适度干旱处理的结果十分相似,即籽粒中ABA含量增加,GAs含量减少,灌浆速率增大,茎中储存的NSC向籽粒转运增多^[60,64],表明在适度土壤干旱条件下,籽粒中激素间平衡的改变,特别是乙烯或GAs的减少和ABA的增加,是促进茎中储存同化物向籽粒转运、增加籽粒灌浆速率和粒重的重要生理机制。适度土壤干旱对灌浆前、中期籽粒中细胞分裂素(玉米素+玉米素核苷)和生长素(吲哚-3-乙酸)含量的影响较小,故不会因此影响籽粒灌浆^[53,60,65]。

表3列出了水稻和小麦不同灌浆期籽粒和茎鞘中适宜的ABA含量以及ABA与ACC, ABA与GAs的比值,可作为通过调控激素水平促进稻麦同化物向籽粒转运和籽粒灌浆的参考指标。

2.4 多胺与乙烯相互作用调控水稻籽粒灌浆

多胺是一类新型植物激素,参与细胞分裂、形态建成、胚胎形成、果实形成和生长、衰老以及对逆境响应等生理过程^[66~68]。在多胺合成途径中,S-腺苷-L-甲硫氨酸(S-adenosyl methionine, SAM)是生成亚精胺(三胺)和精胺(四胺)的前体,也是乙烯合成的前体^[67~69]。Chen等人^[70]推测,多胺和乙烯可能在生物合成过程中存在着竞争,他们之间的相互作用对土壤干旱等环境做出响应,进而调控水稻的籽粒灌浆。为了验证这一推测,以水稻为材料,自抽穗后8 d至成熟进行保持浅水层(对照)、轻度土壤落干和重度土壤落干3种土壤水分处理,观察在不同土壤水分条件下水稻强、弱势粒中多胺和乙烯水平的变化特点及其与籽粒灌浆的关系。结果表明,强势粒的胚乳细胞增殖速率、籽粒灌浆速率和粒重在3种土壤水分处理间没有显著差异。与对照相比,轻度土壤落干显著提高了弱势粒细胞增殖速率、籽粒灌浆速率和粒重,而重度土壤落干的结果则相反。轻度土壤落干显著增加了弱势粒中游离精胺和亚精胺含量、SAM脱羧酶和亚精胺合成酶活性、多胺合成相关基因的表达,

表 3 促进稻麦同化物转运和籽粒灌浆的内源脱落酸(ABA)含量及其与 1-氨基环丙烷 1-羧酸(ACC)及赤霉素(GAs)的比值^{a)}Table 3 Endogenous abscisic acid (ABA) content and the ratios of ABA to 1-aminocyclopropane-1-carboxylic acid (ACC) and to gibberellins (GAs) for enhancing assimilate remobilization and grain-filling in rice and wheat^{a)}

器官/指标名称	灌浆前期		灌浆中期		灌浆后期	
	水稻	小麦	水稻	小麦	水稻	小麦
籽粒						
ABA ($\mu\text{g g}^{-1}$ DW)	0.30~0.51	0.45~0.63	0.72~0.90	0.85~1.05	0.42~0.62	0.31~0.52
ABA/ACC	1.12~1.33	0.08~0.10	2.52~2.84	0.12~0.14	0.53~0.75	0.09~0.11
ABA/GAs	0.42~0.52	0.54~0.76	1.33~1.52	1.55~1.86	1.76~1.92	1.95~2.15
茎、鞘、叶						
ABA ($\mu\text{g g}^{-1}$ DW)	0.05~0.07	0.07~0.09	0.11~0.32	0.12~0.25	0.03~0.05	0.02~0.04

a) 表中数据根据文献[52~58]的数据整理

显著降低了乙烯释放速率, ACC和过氧化氢含量, ACC合成酶、ACC氧化酶、多胺氧化酶活性及乙烯合成相关基因的表达; 重度土壤落干的结果与土壤轻度落干的结果相反. 对稻穗施用亚精胺、精胺或乙烯合成抑制剂, 显著减少了弱势粒中乙烯释放速率和ACC含量, 但增加了亚精胺和精胺含量、籽粒灌浆速率和粒重. 施用ACC或亚精胺和精胺合成抑制剂的结果则相反. 这些结果证明了多胺(亚精胺和精胺)和乙烯对土壤干旱的响应存在着代谢互作并调控水稻籽粒灌浆.

以上结果说明, 植物激素对籽粒灌浆的调控作用, 在很多情况下是多种激素相互作用的结果. 在何种情形下需要提高ABA与乙烯比值, 或ABA与GAs比值, 或多胺与乙烯比值? 其适用范围因植株内、外部环境或调控对象而不同. 促进稻麦弱势粒灌浆, 主要通过提高ABA与乙烯比值, 或提高ABA水平或降低乙烯合成^[61~63]; 应对贪青品种或在高氮水平下籽粒灌浆慢的问题, 可以提高ABA与赤霉素比值, 或增加ABA或降低GAs水平^[60,64]; 减缓干旱、高温等逆境对籽粒灌浆的不利影响, 可通过提高多胺与乙烯比值, 或提高ABA或降低乙烯水平^[67,70].

3 促进同化物转运和籽粒灌浆的相关酶活性

3.1 花后适度土壤干旱增强稻茎中 α -淀粉酶活性和蔗糖磷酸合成酶活化状态

水稻花前储存在茎中的NSC主要为淀粉^[71]. 淀粉必须降解葡萄糖等己糖, 再合成蔗糖, 然后以蔗糖的形式由茎转运到籽粒^[5,72]. 淀粉的降解在几种酶的

作用下通过淀粉水解和磷酸化作用完成. 这些酶包括 α -淀粉酶(EC 3.2.1.1)、 β -淀粉酶(EC 3.2.1.2)、 α -葡萄糖苷酶(EC 3.2.1.20)和淀粉磷酸化酶(EC 2.4.1.1); 蔗糖磷酸合成酶(SPS, EC 2.4.1.14)在蔗糖的再合成中起关键的作用^[73~75]. Yang等人^[76]研究发现, 花后适度土壤干旱显著增加了水稻灌浆期茎中 α -淀粉酶和 β -淀粉酶活性, 前者活性的增强尤为明显, 并与茎中可溶性糖的含量呈极显著正相关. 其他两种淀粉降解酶活性, α -葡萄糖苷酶和淀粉磷酸化酶, 在适度土壤干旱与对照(供水充足)之间无显著差异, 与茎中可溶性糖含量的相关也不显著. 适度土壤干旱增加了茎中SPS在基质浓度限制(V_{limit})和基质浓度饱和(V_{max})状况下的活性, 以 V_{limit} 的活性增加更多, 即SPS的活化态($V_{\text{limit}}/V_{\text{max}}$)提高. SPS活性与茎中蔗糖含量呈极显著正相关, 说明花后适度土壤干旱通过增强稻茎中 α -淀粉酶活性和SPS活化状态, 促进淀粉快速水解和碳同化物向籽粒的再调运.

3.2 花后适度土壤干旱提高小麦茎中果聚糖外水解酶和SPS活性

小麦花前储存在茎中的NSC主要为果聚糖和蔗糖^[77,78]. 参与果聚糖合成和水解的关键酶分别为蔗糖: 蔗糖果糖基转移酶(SST, EC 2.4.1.99)和果聚糖外水解酶(FEH, EC 3.2.1. 80). 参与蔗糖代谢的关键酶则为SPS, 蔗糖合酶(SuSase, EC 2.4.1.13)和酸性转化酶(EC 3.2.1.26)^[79~81]. Yang等人^[82]研究表明, 花后适度土壤干旱显著增强了小麦茎中FEH和SPS活性. 该两种酶活性与茎中总的NSC及果聚糖向籽粒的运转量呈极显著相关. 花后适度土壤干旱虽然增强了茎中酸性转化酶活性, 但其活性与茎中NSC及果聚糖

向籽粒运转量的相关不显著。花后适度土壤干旱显著抑制了茎中SST活性。茎中SuSase活性随籽粒灌浆进程显著下降,在供水充足与适度土壤干旱处理间无显著差异,表明花后适度土壤干旱主要通过增强小麦茎中FEH和SPS活性,促进茎中储存的NSC向籽粒转运。根据这一研究结果,Zhang等人^[83,84]用分子生物学手段增强小麦茎中FEH活性及*1-FEH* w3基因的表达,进而促进了小麦茎中NSC向籽粒转运,提高了粒重和产量。

3.3 花后适度土壤干旱增强籽粒蔗糖-淀粉代谢途径关键酶活性

水稻和小麦籽粒的主要成分是淀粉^[71,75]。光合同化物以蔗糖为运输形式从源(叶、茎或鞘)输送到籽粒,经一系列酶的催化反应形成淀粉^[71,75]。在蔗糖-淀粉代谢途径中,SuSase,腺苷二磷酸葡萄糖焦磷酸化酶(ADPase, EC 2.7.7.27)、淀粉合酶(StSase, EC 2.4.1.21)和淀粉分枝酶或Q-酶(SBE, EC 2.4.1.18)在淀粉的合成过程中起重要的作用^[71,72,85,86]。有研究者认为,谷类作物籽粒灌浆期干旱等逆境会降低籽粒蔗糖-淀粉代谢途径酶活性,从而抑制籽粒库生理活性^[87,88]。但Yang等人^[26,27]研究发现,在水稻籽粒灌浆过程中,适度土壤干旱可以增强SuSase, SBE和可溶性StSase活性,进而增加了库强,促进光合同化物向籽粒转运和淀粉在籽粒的合成。适度土壤干旱对水稻籽粒ADPase活性及可溶性和非可溶性转化酶活性的影响很小,在小麦籽粒中,适度土壤干旱则主要

通过增强ADPase, SuSase, SBE和可溶性StSase活性,促进籽粒灌浆。适度土壤干旱对小麦籽粒中颗粒结合StSase活性及可溶性和非可溶性转化酶的活性无显著影响。

3.4 ABA对茎和籽粒中糖代谢相关酶活性起重要调控作用

之前的研究认为,谷类作物籽粒灌浆期遇干旱会增加内源ABA含量,降低籽粒蔗糖-淀粉代谢途径中酶的活性,从而抑制库的活性和同化物在库端的卸载^[88-90]。但近年的研究发现,水稻灌浆期茎中与糖代谢有关的一些酶,如 β -淀粉酶、淀粉磷酸化酶和蔗糖磷酸合成酶等的活性及基因表达与茎中ABA含量及ABA合成相关基因(*NCED1*)的表达密切相关,茎中较高的ABA含量及*NCED1*表达有利于糖代谢相关基因的表达和酶活性的增强,促进茎中同化物向籽粒转运^[91]。在水稻或小麦籽粒中,灌浆期ABA通过调控籽粒中蔗糖-淀粉代谢途径关键酶活性及相关蛋白质表达,调控籽粒淀粉合成,通过花后适度土壤干旱或喷施低浓度ABA适度提高籽粒ABA水平,可以增强籽粒中蔗糖-淀粉代谢途径关键酶活性及相关蛋白质表达,促进籽粒淀粉合成和累积^[26,27,57,86,92]。以上结果说明,ABA对茎和籽粒中糖代谢相关酶活性起重要调控作用,适度提高体内ABA水平有利于茎中同化物向籽粒转运和籽粒灌浆。

综上,促进稻麦同化物转运和籽粒灌浆的调控途径与生理机制总结于图1。

图1 促进稻麦同化物转运和籽粒灌浆的途径与机制

Figure 1 Approach and mechanism in enhancing the remobilization of assimilates and grain-filling in rice and wheat

4 存在的问题和今后研究的重点

4.1 根系信号调控同化物转运和籽粒灌浆的作用

目前对于促进同化物运和籽粒灌浆的机制研究主要局限于地上部分,对地下部分根系研究甚少.植物根系既是水分和养分吸收的主要器官,又是多种激素、有机酸和氨基酸合成的重要场所,其形态和生理特性与地上部的生长发育、产量和品质形成均有着密切的关系^[93~95].有研究表明,ABA通常是由根系产生并传输到地上部分调控植株的生长发育^[96~98].但目前有关ABA等根系信号传导调控同化物转运和籽粒灌浆的分子机理知之甚少.今后需要重点研究:(i)根系信号的种类与传导方式及其对植株衰老、光合作用、同化物转运和籽粒灌浆的调控作用与机理;(ii)冠层结构与功能对根系信号产生与传导的影响及其机制;(iii)调控根系信号产生与传导的途径和技术及其原理.

4.2 氮素向籽粒转运的机理

水稻和小麦籽粒重量的80%~90%是碳水化合物,碳水化合物向籽粒转运状况是决定粒重的关键因素^[71,86].因此,现有研究主要集中在稻麦碳同化物转运的调控途径与生理机制方面,对氮素转运的调控途径与机制研究较少.王维^[99]曾观察到,采用适度土壤干旱的方法不仅可以促进碳同化物向籽粒转运,而且可以促进营养器官中氮素向籽粒转运,进而提高氮素收获指数.今后需重点研究:稻麦等谷类作物

花后营养器官中氮素向籽粒转运的特点与机理;协调植株花后碳氮转运、碳氮代谢关系的途径及其机制.开展上述研究,可以为实现作物高产和氮素高效利用提供理论和实践依据.

4.3 减少颖花/小花退化的调控途径及其机理

水稻等谷类作物的颖花或小花退化是进一步高产的重要限制因素,揭示颖花或小花退化机理、减少颖花或小花退化已成为科学和生产上的一个难题^[100].Yang等人^[101]和Zhang等人^[102]研究表明,在水稻幼穗发育期或减数分裂期采用适度干旱的方法,可以减少颖花退化,提高结实率.今后需要进一步研究谷类作物颖花或小花退化的机理和调控途径,以及适度土壤干旱减少水稻颖花退化的调控机制,以进一步提高谷类作物的增产潜力.

4.4 适度土壤干旱对稻麦籽粒品质的影响及其机理

以往有关土壤干旱对稻麦等谷类作物籽粒灌浆和产量的影响及其机理研究较多,有关土壤干旱对籽粒品质的影响机理研究较少.徐云姬^[103]近年的研究表明,采用适度土壤干旱的方法不仅可以促进水稻、小麦和玉米的籽粒灌浆,而且可以改善籽粒品质,但其机理不清楚.今后应重点研究:适度土壤干旱对稻麦等谷类作物籽粒各品质指标的影响;适度土壤干旱改善籽粒品质的机理.通过研究,为作物优质高产的育种与栽培提供理论与实践指导.

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Summary for “促进稻麦同化物转运和籽粒灌浆的途径与机制”

Approach and mechanism in enhancing the remobilization of assimilates and grain-filling in rice and wheat

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Monocarpic plants such as rice and wheat need to initiate the whole plant senescence before their pre-stored assimilates can be remobilized for the grain filling. However, plant senescence and photosynthesis are a pair of trade-off processes. How to coordinate plant senescence, photosynthesis, and remobilization of assimilates is a long-term unsolved problem in cereals. Solving this problem would have great significance in not only understanding the mechanism of the remobilization of assimilates to grain and grain-filling but also effectively coping with the poor remobilization of assimilates from vegetative tissues to grain and slow grain-filling for some cultivars or under the condition of heavy use of nitrogen in the current rice and wheat production systems. This paper reviewed crop management and physiological mechanism in enhancing the remobilization of assimilates to grain and grain-filling in rice and wheat. There are three important findings. (i) Moderate soil-drying (MSD) during post-anthesis can regulate the relationship of plant senescence, photosynthesis, and remobilization of assimilates, and accelerate grain-filling. With post-anthesis MSD, plant can rehydrate overnight but not severely inhibit leaf photosynthesis at day time. More importantly, it can timely and appropriately initiate the process of plant senescence, trigger assimilate remobilization from vegetative tissues to grain, accelerate grain-filling, especially for the late-flowering inferior caryopses, and lead to increases in grain yield, harvest index, and water use efficiency. The MSD therefore provides a new way to coordinate the relationship among plant senescence, photosynthesis, and remobilization of assimilates during grain-filling and to achieve the dual goal of increasing grain yield and saving water in cereals. (ii) Abscissic acid (ABA) and its interaction with ethylene and gibberellins (GAs) regulate assimilate remobilization and grain-filling. During the active grain-filling period, the filling of grain requires a higher level of endogenous ABA and higher ratios of ABA to ethylene and to GAs. Post-anthesis MSD enhances the remobilization of assimilates to grain and grain-filling through increases in ABA levels and the ratios of ABA to ethylene and/or to GAs, which reveals the mechanism in which plant hormones regulate assimilate remobilization and grain-filling, and provides a physiological regulation to improve grain-filling in cereals. (iii) A modest increase in ABA level in plants can enhance activities of the key enzymes involved in carbon metabolism, and thereby increase assimilate loading and unloading capacity. An elevated ABA level through MSD or applying ABA with a low concentration can increase activities of the key enzymes in starch or fructan degradation and sucrose synthesis in vegetative tissues, leading to the enhancement in assimilate loading capacity, and enhance activities of the key enzymes in sucrose-to-starch conversion in the sink organ, and consequently, increase assimilate unloading capacity and starch synthesis in grain, which reveals the mechanism in which ABA regulates assimilate remobilization and grain-filling. Further research is needed to understand the molecular mechanism, such as from the aspect of signal transduction, in which assimilate remobilization and grain filling are regulated in cereals, to investigate the regulatory mechanism underlying nitrogen remobilization from vegetative tissues to grain, and to elucidate the mechanism in which the MSD reduces spikelet degeneration and improves grain quality of cereals.

rice, wheat, moderate soil-drying, assimilate remobilization, grain-filling, physiological mechanism

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