土壤水分亏缺对水稻茎秆贮藏碳水化合物向籽粒运转的调节

王 维^{1,2} 蔡一霞¹ 蔡昆争¹ 张建华³ 杨建昌² 朱庆森^{2*}

(1 华南农业大学农学院, 广州 510642) (2 扬州大学, 江苏省作物栽培生理重点实验室, 江苏扬州 225009)

(3 香港浸会大学生物系, 香港九龙塘)

摘 要 以两个茎秆贮藏物质利用效率不同的水稻 (*Oryza sativa*) 杂交组合 (‘汕优 63’和‘Pc311/早猷党’) 为材料, 进行土壤水分亏缺处理 (Water-deficit), 以水层灌溉为对照 (Well-watered), 研究水分亏缺对水稻茎秆贮藏性碳水化合物运转及其关键酶活性的调节作用。结果表明, 水分亏缺促进了水稻茎秆贮藏物质的运转和对籽粒产量的贡献, 开花前茎秆贮藏的碳水化合物对产量贡献率分别提高了 1.9~3.0 倍 (与水层灌溉相比)。土壤水分亏缺诱导了水稻茎节间 α -淀粉酶、 β -淀粉酶、 α -葡萄糖苷酶、D-酶活性上升, 但淀粉磷酸化酶受到了抑制, 说明土壤水分亏缺加强水稻茎秆贮藏淀粉水解途径, 而不是磷酸解途径。就蔗糖代谢而言, 土壤水分亏缺提高了蔗糖磷酸合成酶的活性和活化状态, 抑制蔗糖转化酶活性, 促进蔗糖合成, 加速贮藏物质快速降解和转移, 从而调节稻株贮藏碳水化合物向籽粒的分配。

关键词 水分亏缺 非结构性糖 淀粉水解酶 蔗糖磷酸合成酶 水稻

REGULATION OF SOIL WATER DEFICITS ON STEM-STORED CARBOHYDRATE REMOBILIZATION TO GRAINS OF RICE

WANG Wei^{1,2} CAI Yi-Xia¹ CAI Kun-Zheng¹ ZHANG Jian-Hua³

YANG Jian-Chang² and ZHU Qing-Sen^{2*}

(1 College of Agronomy, South China Agricultural University, Guangzhou 510642, China)

(2 Key Lab of Crop Cultivation & Physiology, Yangzhou University, Yangzhou, Jiangsu 225009, China)

(3 Department of Biology, Hong Kong Baptist University, Kowloon Tong, Hong Kong, China)

Abstract Grain yields of rice in China are often low and vary substantially due to the shortages of available water. Assimilates stored prior to grain filling have been identified as important contributors to grain yield in drought environments, but evaluating their benefit has been hampered by an inadequate understanding of the physiological mechanism of remobilization to grains of stored carbon reserves during grain filling. A moderate soil drying applied at grain filling period can enhance plant senescence and may improve the yield through remobilizing more pre-stored food to grains. The study was designed to test the following hypothesis: if soil drying is controlled properly at the mid-late stage of grain filling, an early senescence induced by drought stress would accelerate the rate of grain filling by enhanced relocation of carbon stored reserves, and improved use of pre-stored carbon reserves may increase yields where photosynthetic assimilation is decreased by soil drying. Further evaluation of enzyme regulation in the remobilization process will help to understand the physiological mechanisms.

In the current study, two rice combinations (cvs ‘Shanyou63’ and ‘Pc311/Zao’) were grown in cement containers and pots at Yangzhou University. Controlled soil water deficit were imposed at 9 d after anthesis in consideration that the division of endosperm cell is sensitive to water deficit.

We found that, compared to well-watered treatments, the remobilization of stored carbohydrates in the rice stem was significantly enhanced under water-deficit conditions, and the increased contribution to grain yields was 1.9–3.0 times as that of rice grown under well-watered conditions. Pronounced effects of water-deficit treatment on carbohydrate metabolism were observed in rice stems. Sugar concentrations and carbon distribution among sugar components were altered under water-deficit conditions. Starch breakdown in rice stems under soil water deficit occurred through action via the hydrolytic pathway: α -amylase, β -amylase, α -glucosi-

dase and D-enzyme were induced and enhanced by soil drying. Starch phosphorylase activity was decreased under water-deficit conditions, indicating that phosphorylase was not involved in the processes of starch remobilization. Water deficit markedly altered the pattern of sucrose metabolism by shutting down the bypass of carbon flow through the sucrose synthase (SuSy) catalyzed system and enhanced the unidirectional flow through the irreversible sucrose-phosphate synthase (SPS) and acid invertase (AINV) catalyzed pathway. SPS was induced and activated by water deficit, and played a pivotal role in enhancing synthesis of sucrose through the conversion of stored carbon into sucrose. During rapid remobilization of stored sugar, the sucrose content was increased by 10.3% in ‘Shanyou63’ and 20.45% in ‘Pc/Zao’ as compared to the well-watered treatments. It is concluded that the enhanced remobilization of stored non-structural carbohydrates (NSC) in rice stems under soil water deficit was due to induced hydrolytic enzyme activities, increased SPS activity and activation state, but decreased invertase activity.

Key words Water deficit, Non-structural carbohydrate, Starch-hydrolytic enzymes, Sucrose-phosphate synthase, Rice

水稻抽穗前茎秆储存同化物对产量的贡献取决于品种特性和生态条件,其贡献率的变幅范围为 0~40%(李木英等, 1999; Yang *et al.*, 2001; 王维等, 2004)。水稻灌浆期遭受干旱,稻茎中贮藏的同化物对减轻产量损失显得尤为重要,能够对干旱导致光合作用下降引起的同化物短缺起到一定的补偿作用(陆建飞等, 1998; 王维等, 2004)。禾谷类作物茎秆贮藏碳水化合物的再运转和利用存在基因型差异,并受到环境条件的调节(Austin *et al.*, 1980; Schnyder, 1993)。基因型差异与茎秆容积以及库需求有关,也与代谢调节机制有关(酶、蔗糖浓度),而酶活性对合成与转运均起中枢调节作用(Wardlaw & Willenbrink, 1994)。植物组织中贮藏淀粉的降解可以通过水解和磷酸解来完成(Blennow *et al.*, 2002; Smith *et al.*, 2003)。已有研究表明,在水稻、小麦种子萌发过程中,并不涉及到淀粉的磷酸解过程(Beck & Ziegler, 1989; Gallagher *et al.*, 1997),但最近 Blennow 等(2002)在他们的研究综述中指出,在植物叶片淀粉的降解过程需要淀粉磷酸化作用的积极参与,但有关水稻茎中贮藏淀粉的降解是通过何种途径还未有报道。

土壤水分亏缺对水稻等谷类作物同化物的积累和运转的影响已有较多报道(Austin *et al.*, 1980; Yang *et al.*, 2001; 王维等, 2004)。然而干旱条件下水稻茎秆暂时性贮藏物质的运转和控制机制却缺少系统深入的研究。本研究选用节间贮藏物质输出效率不同的两个水稻材料,以水层灌溉为对照,探讨土壤水分亏缺对水稻茎节间贮藏碳水化合物代谢和蔗糖输出的调节机制,旨在为水稻旱种或节水栽培获得高产、稳产调控途径提供理论依据。

1 材料和方法

1.1 试验设计

试验于 2002 年,扬州大学作物栽培生理重点实验室盆栽试验场进行。供试品种种植于土培池内(深 0.5 m、宽 2 m、长 4 m)。土壤质地为沙壤土,有机质含量为 24.5 g·kg⁻¹,速效 N、P、K 含量分别为 105.0、33.5 和 66.0 mg·kg⁻¹。供试材料为两个杂交稻组合:‘汕优 63’(籼型三系杂交稻)、“Pc311/早献党”(粳粳杂交稻,简称‘Pc/早’),5 月 7 日播种,6 月 5 日移栽,单本栽插,株距为 16.63 cm,行距为 20 cm。移栽前施尿素、磷酸氢二钾各 10 g·m⁻²作基肥,于分蘖期追施氮肥为 5 g·m⁻²的尿素。

于花后 9 天,各处理设置两种土壤水分处理:保持浅水层或湿润(Ψ_{soil} : 0 kPa)和水分亏缺处理(Ψ_{soil} : -30~-40 kPa)。安装真空表式负压计(中国科学院南京土壤研究所制造)监测土壤水分,陶土头底部置于 20 cm 土层处。每天 6:00~7:00、11:00~12:00、16:00~17:00 时记录负压计读数,当读数低于设计值时,手工浇水使土壤水势维持在设计值范围内,用活动塑料大棚挡雨。

1.2 标穗与取样

在抽穗期除去无效分蘖和小茎蘖,选取同日开花生长均一的单茎进行挂牌,开花期、花后 9 天各取样 1 次,以后每隔 2~5 d 取样 1 次,每次取 20 个单茎,用液氮速冻,-80℃贮藏,用于碳水化合物和酶活性的分析。

1.3 测定项目与方法

1.3.1 叶片水势测定

水稻从开花到收获每隔 5 d 于上午 10:00~11:00 时,各处理分别取 5 片顶叶,用压力室法测定叶片水势。

1.3.2 水稻茎非结构性糖的提取与测定

0.1~0.2 g 磨碎的冷冻抽干样品,加 20 ml 去离子水于 95 ℃ 水浴中振荡抽提两次,残渣用 5 ml 沸水洗两次,合并所有提取液,60 ℃ 旋转蒸发,定容至 10 ml。将上述的水溶性糖(WSC)提取液用离子交换柱去离子,过 0.45 μm 的滤膜。WSC 组分在 HPLC (HP1100, Hewlett-Packard Inc., USA)上用特定的糖分析柱(Aminex HPX 87C, Bio-Rad, USA)来分离,柱温 85 ℃,流动相为脱气的超纯水,流速 0.5 ml·min⁻¹,20 μl 分析液自动进样,使用折射示差检测器(RI)检测糖峰。标准样品为葡萄糖、果糖、蔗糖、麦芽三糖。不溶部分加入 1 ml 0.2 mol·L⁻¹ NaOH,100 ℃ 水浴 60 min,冷却后加 0.1 mmol Tris,用醋酸调整 pH 值至 6.6~7.5,加 360 EU α -淀粉酶于 85 ℃ 水浴 30 min,再用醋酸调整 pH 值至 5.0,加 122 EU α -葡萄糖苷酶于 55 ℃ 水浴反应 30 min,取出于沸水中 1 min 终止酶的反应,冷却,2 500 $\times g$ 离心,去除沉淀部分,酶解液旋转蒸干,加水定容至 10 ml,用葡萄糖氧化酶法测定淀粉含量(Hendrix, 1993)。

1.3.3 ¹⁴C 的标记与测定

在相同地点和时间,进行水稻盆栽试验。盆钵直径 25 cm,高 30 cm,盆内装 18 kg 过筛田间土。每盆插 3 穴,施肥处理和水分控制同土培试验。于始穗期,选择晴天 9:00~15:00 时进行¹⁴C 标记,同化室每次标记 2 盆(同化室放射活性在 3.3 MBq·L⁻¹左右),标记持续 1 h。标记结束后,每隔 3~5 d 取样 1 次。样品植株分叶、茎、鞘、穗轴枝梗(包括颖壳)、籽粒 5 个部分,于 70 ℃ 烘干至恒重,水溶性糖的提取和淀粉的水解同上述方法。水溶性糖和淀粉水解液中¹⁴C 放射活度于液闪仪(Beckman Instruments Inc., Fullerton, CA, USA)上测定。

1.3.4 水稻茎组织酶的提取与活性测定

在液氮磨碎的茎节间组织中加入 2 ml·g⁻¹的 100 mmol·L⁻¹ Hepes-KOH 缓冲液(pH 7.5,包含 1 mmol·L⁻¹ EDTA,5 mmol·L⁻¹ MgCl₂,5 mmol·L⁻¹ DTT)提取,20 000 $\times g$ 离心 15 min,取部分提取液经 Sephadex G-25 柱脱盐,用于淀粉磷酸化酶、 α -葡萄糖苷酶、脱枝酶和 D-酶的分析。 α 、 β -淀粉酶(Bhatia & Singh, 2002), α -葡萄糖苷酶(Guglielminett *et al.*, 1995),淀粉磷酸化酶(da Silva *et al.*, 1997),脱枝酶(Egger *et al.*, 1996),D-酶(Guglielminett *et al.*, 1995)活性测定分别参照文献所述的方法。

蔗糖磷酸合成酶(SPS)、蔗糖合成酶(SuSy,合成方向)和酸性蔗糖转化酶(AINV)的提取和酶活性测

定:茎节间组织液氮磨碎,用 4 ml·g⁻¹ 100 mmol·L⁻¹ Tris-HCl 缓冲液,pH 7.5(包含 2 mmol·L⁻¹ MgCl₂,2 mmol·L⁻¹ DTT,10 mmol·L⁻¹ β -巯基乙醇,2 mmol·L⁻¹ PMSF)提取。抽提液经 60 μm 尼龙膜过滤,20 000 $\times g$ 离心 5 min 去除粗物质。粗酶液用 30%~60% 饱和硫酸铵沉淀,复溶于 2.5 ml 100 mmol·L⁻¹ (pH 7.5) Tris-HCl,于 4 ℃ 冰箱中透析过夜,然后过 100 mmol·L⁻¹ Tris-HCl (pH 7.5)预平衡的 Sephadex G-25 柱脱盐。SPS、SuSy 和 AINV 活性测定根据 Wang 等(2000)方法,SPS 活化状态(%)=(限制活性/最大活性) $\times$ 100。

以上所有酶的提取、离心均在 4 ℃ 下进行,可溶性蛋白质的测定采用 Bradford(1976)的方法。

2 结果与分析

2.1 水稻植株顶叶水势动态

两杂交稻组合的顶叶水势变化趋势基本一致(图 1)。从开花到花后 10 天,两处理间顶叶水势差异较小,花后 10 天开始,水分亏缺处理的稻株顶叶水势明显降低,说明土壤水分亏缺对稻株的水分状况有显著的影响。‘Pc/早’的顶叶水势下降幅度要明显低于‘汕优 63’,这可能与亚种间杂交稻比种内杂交稻有更强的根系优势,可从深层土壤吸收较多的水分有关。

2.2 水稻植株茎非结构性糖组分含量

水稻茎中非结构性碳水化合物组分浓度明显受到了土壤水分的影响(图 2)。在茎贮藏物质快速转运期(10~31DAA),水分亏缺促进了节间淀粉的降解,增加了茎中可溶性糖的含量,表现为麦芽糖、蔗糖、葡萄糖的含量显著增加,果糖的含量却明显降低。通过¹⁴C 分析表明,土壤水分亏缺加速了分配进入贮藏淀粉中标记¹⁴C 的输出(图 3A、B),¹⁴C 进入可溶性糖中的比例显著增加(图 3C、D)。说明水分亏缺条件下,稻茎中可溶性糖含量的增加,主要缘于茎中贮藏淀粉的降解。

2.3 水稻茎中淀粉降解酶活性

土壤水分亏缺不同程度诱导了淀粉水解途径中 α -淀粉酶、 β -淀粉酶、 α -葡萄糖苷酶、D-酶活性的上升(图 4A~H),但不影响脱枝酶(数据未列出)的活性;而水分亏缺则对淀粉磷酸化酶表现出一定的抑制作用(淀粉磷酸化酶活性下降)(图 5A、B)。茎贮藏物质运转良好的三系杂交组合‘汕优 63’,在水层灌溉条件下,其茎节间组织中 α -淀粉酶、 β -淀粉酶的活性要明显高于亚种间杂交稻‘Pc/早’,这可能是

图1 水分亏缺对水稻植株顶叶水势变化的影响(池栽试验)
Fig.1 Changes in leaf water potential of rice cultivars cvs ‘Shanyou63’ (A) and ‘Pc/zao’ (B), which were subjected to water deficit from 9 d after anthesis
结果为 5 次重复的平均值 ± SD Values are means ± SD of five replications

‘汕优 63’茎秆贮藏碳水化合物输出量大,收获指数高,籽粒充实较好的一个重要原因。通过以上分析,本研究认为水稻茎贮藏淀粉的降解和向籽粒的调运主要是通过水解途径。

2.4 水稻植株茎中蔗糖代谢酶活性

SPS、SuSy、AINV 是直接参与蔗糖代谢的调节酶,其活性的相对高低决定了茎秆中碳水化合物的流向,对茎中形成有效的蔗糖阈值浓度起着决定性作用,直接影响茎中蔗糖的输出。由图 6 可知,花后 9 天的土壤水分亏缺抑制了水稻茎节间 AINV 的活性(图 6E、F),但 SPS 活性和活化状态的受到显著促进(图 6A~D),并对 SuSy 活性表现出一定的抑制作用(数据未列出)。两个品种间相比较,‘Pc/早’茎节间组织中 SPS、AINV 受土壤水分的诱导效应较大。

对水稻茎中淀粉降解代谢相关酶活性与茎中 ¹⁴C 输出率简单相关分析表明,茎节间 ¹⁴C 的输出率与 α-淀粉酶活性呈极显著正相关(0.897**),与 β-淀粉酶、α-葡萄糖苷酶、D-酶相关性也均达到显著(0.748*、0.805* 和 0.797*);而与脱枝酶、淀粉磷

酸化酶相关性不显著或呈负相关(0.137 和 -0.822*),且 α-淀粉酶的特定活性要显著高于其它几个酶,说明 α-淀粉酶是调节茎节间组织中贮藏淀粉降解的中枢调节酶。蔗糖和可溶性糖的比值与 SPS 活性呈极显著正相关(0.897**),而与 SuSy 活性相关性不显著(-0.443),与 AINV 活性呈显著性负相关(-0.845**),表明在籽粒灌浆期茎秆中 SPS 对茎节间蔗糖的合成和输出具有重要的调节作用,高的 AINV 活性是不利于蔗糖的合成和输出。

2.5 水稻茎秆贮藏性糖向籽粒运转及籽粒充实特征

土壤水分亏缺明显提高了植株叶、茎秆和颖壳中 ¹⁴C 再运转(表 1),但叶片与颖壳中的 ¹⁴C 输出对籽粒中输入 ¹⁴C 的贡献相对较小,籽粒中输入的 ¹⁴C 主要来源于茎秆中贮藏 ¹⁴C 的重新分配。此外,水分亏缺处理显著降低了贮藏同化物运转过程标记 ¹⁴C 的损失,说明水分亏缺对植株的呼吸有明显的抑制作用。本试验水分亏缺处理在花后 9 天实施,因而并不影响到颖花分化、发育,处理间两品种穗数和穗粒数均无显著差异(数据未列出)。土壤水分亏缺显

表 1 水分亏缺对水稻植株各器官中 ¹⁴C 再分配的影响(盆栽试验)
Table 1 Effect of post-anthesis water deficit on the distribution of prefixed ¹⁴C in plants of two rice cultivars (cvs ‘Shanyou63’ and ‘Pc/Zao’)

品种 Cultivars	处理 Treatments	从花后 9 天到成熟期转运的 ¹⁴ C 量 Remobilized ¹⁴ C from 9 d anthesis to harvest			成熟期籽粒中 ¹⁴ C 含量 Recovered ¹⁴ C in grain at harvest stage (kBq)	呼吸损失 ¹⁴ C Loss of respiration (%)
		叶 Leaves (kBq)	茎秆 Stem and sheath (kBq)	颖壳 Glumes (kBq)		
‘汕优 63’ ‘Shanyou63’	水层灌溉 Well-watered	17.7 ^b	136.4 ^b	7.9 ^b	120.7 ^b	25.5 ^b
	水分亏缺 Water-deficit	22.4 ^a	234.9 ^a	9.7 ^a	207.4 ^a	22.3 ^a
‘Pc/早’ ‘Pc/Zao’	水层灌溉 Well-watered	15.5 ^b	122.3 ^b	9.7 ^b	102.54 ^b	30.5 ^b
	水分亏缺 Water-deficit	24.9 ^a	236.3 ^a	13.0 ^a	203.6 ^a	25.7 ^a

图2 水分亏缺对水稻茎非结构性糖含量变化的影响(池栽试验)

Fig.2 Concentration and composition of NSC in the stems of two rice cultivars cvs 'Shanyou63' (A, C, E, G, I) and 'Pc/Zao' (B, D, F, H, J), which were subjected to water deficit from 9 d after anthesis

图例同图1 Legends see Fig.1 结果为3次重复的平均值±SD Values are means ± SD of three replications

图3 水分亏缺对水稻茎中淀粉和可溶性糖分配入的¹⁴C的影响(盆栽试验)
Fig.3 ¹⁴C NSC in the stems of two rice cultivars cvs ‘Shanyou63’ (A, C) and ‘Pc/Zao’ (B, D), which were subjected to water deficit from 9 d after anthesis
图例同图1 Legends see Fig.1 图注同图2 Notes see Fig.2

表2 水分亏缺对水稻茎秆碳贮藏物质的输出及籽粒产量的影响(池栽试验)

Table 2 Effect of post-anthesis water deficit on remobilization of stored reserves and grain yield of two rice cultivars (cvs ‘Shanyou63’ and ‘Pc/Zao’)								
品种 Cultivars	处理 Treatments	茎中滞留糖 Residue NSC (mg·g ⁻¹ DW)	运转率 Remobilized NSC (%)	贡献率 Contribution to grains (%)	收获指数 Harvest index	结实率 (%)	粒重 Kernel weight (mg)	产量 Yield (g·m ⁻²)
‘汕优63’ ‘Shanyou63’	水层灌溉 Well-watered	186.1 ^a	43.4 ^b	12.8 ^b	0.50 ^b	84.5 ^a	26.43 ^a	851.9 ^a
	水分亏缺 Water-deficit	92.7 ^b	71.8 ^a	24.6 ^a	0.56 ^a	79.8 ^b	25.87 ^b	771.3 ^b
‘Pc/早’ ‘Pc/Zao’	水层灌溉 Well-watered	265.1 ^a	16.3 ^b	6.7 ^b	0.40 ^b	77.3 ^a	24.57 ^a	945.6 ^a
	水分亏缺 Water-deficit	130.4 ^b	59.4 ^a	19.8 ^a	0.49 ^a	72.6 ^b	23.64 ^b	859.8 ^b

运转率(%)=(开花期茎秆中 NSC - 成熟期茎秆中 NSC)/开花期茎秆中 NSC×100
Remobilized NSC (%)=(NSC of stems and sheaths at anthesis - NSC of stems and sheaths at maturity)/NSC of stems and sheaths at anthesis×100
贡献率(%)=(开花期茎秆中 NSC - 成熟期茎秆中 NSC)/粒重×100
Contribution to grains (%)=(NSC of stems and sheaths at anthesis - NSC of stems and sheaths at maturity)/grain weight×100

著地增加了茎秆中贮藏性糖的输出和对籽粒产量的贡献,收获指数显著提高,两杂交稻组合茎秆贮藏性糖的运转率和贡献率分别是对照(水层灌溉)的1.7~3.6和1.9~3.0倍。与正常灌水处理相比,土壤水分亏缺均显著降低了两杂交稻组合籽粒产量,说明在中度水分亏缺条件下(Ψ_{soil} : -30~-40 kPa),水稻茎秆贮藏同化物向籽粒运转地增加并不能够补偿光合同化下降之所失,从而导致籽粒粒重和产量的下降。值得强调的是,本试验条件下,产量仅降低

不到10%,但与水层灌溉相比,浇水要减少40%~50%,说明在不严重降低产量的前提下,可取得明显的节水效益。

3 讨论

3.1 土壤水分亏缺促进了水稻茎秆贮藏碳水化合物向籽粒的转运,增加对籽粒产量的贡献

水稻植株茎节间碳水化合物的组成,已有相关的报道(李木英等,1999),但有关土壤水分对水稻

图4 水分亏缺对水稻茎贮藏淀粉水解酶活性的影响(池栽试验)

Fig.4 Changes in activities of starch degradation enzymes and in the stems of two rice cultivars 'Shanyou63' (A, C, E, G) and 'Pc/Zao' (B, D, F, H), which were subjected to water deficit from 9 d after anthesis

图例同图1 Legends see Fig.1 图注同图2 Notes see Fig.2

茎碳水化合物代谢,特别是对茎糖组分的影响报道甚少。本研究通过对茎中各组分的分析,表明花后的土壤水分亏缺促进了茎秆内淀粉的水解,增加了蔗糖的含量,蔗糖所占可溶性糖的比例有较大幅度的提高。本研究通过¹⁴C示踪试验,直接证明水分亏缺加强了贮藏淀粉的降解,促进茎中贮藏的¹⁴C向籽粒中的运转。虽然 Schnyder(1993)指出,胁迫环境

往往造成籽粒产量严重下降,可能会夸大茎秆贮藏物质对籽粒产量的贡献,部分结果证实了如此推测(Aggarwal & Sinha, 1984; 陆建飞等, 1998),但 Palta等(1994)在小麦的实验上发现,茎秆贮藏物质的运转明显受到土壤水分亏缺程度和亏缺速率的影响,在严重的土壤水分亏缺下运转量降低主要与贮藏同化物运转的生理代谢或库活性受到限制有关。本研

图 5 水分亏缺对水稻茎淀粉磷酸化酶活性的影响(盆栽试验)
Fig.5 Changes in activities of starch phosphorylase in the stems of two rice cultivars ‘Shanyou63’ (A) and ‘Pc/Zao’ (B), Which were subjected to water deficit from 9 d after anthesis
图例同图 1 Legends see Fig.1

究中,水分亏缺条件下,贮藏同化物向籽粒运转的增加是非常显著的,也证实了 Palta 等(1994)的观点,但土壤水分亏缺导致结实率和粒重均有不同幅度的降低,主要是由于水分亏缺已严重影响到叶片的光合作用(数据未列出),籽粒灌浆物质的总量减少所致。因此在何种土壤水势下光合作用既不明显降低,又能促进茎秆贮藏物质的输出,改善其结实性状,还有待进一步研究。

3.2 土壤水分亏缺增加水稻茎中贮藏碳水化合物运转的生理生化机制

植物器官中贮藏淀粉主要位于细胞内的淀粉体中,通过水解或磷酸解途径产生葡萄糖或葡萄糖-1-磷酸。但有关水稻茎中贮藏淀粉降解机制还不清楚,也没有文献报道脱枝酶和 D-酶在水稻茎秆贮藏碳水化合物代谢过程中的具体生理作用(李木英等, 1999; Yang *et al.*, 2001)。本研究发现,土壤水分亏缺极大地诱导了节间组织中 α-淀粉酶活性的上升,并且此酶活性与淀粉的降解速率成极显著性正相关,说明水分亏缺主要通过调节 α-淀粉酶活性的升高,增加对贮藏淀粉的水解从而促进茎秆碳水化合物的运转;而水亏缺条件下 β-淀粉酶活性的增加,可能与 β-淀粉酶促进麦芽糖的进一步分解有关(Gallagher *et al.*, 1997)。此外,水分亏缺下,α-葡萄糖苷酶、D-酶均受到不同程度的上调,说明这两个酶在淀粉降解产物的进一步分解过程中扮演了重要“角色”,α-葡萄糖苷酶活性的增强直接促进麦芽糖分解,从而提高了茎中葡萄糖的含量,为蔗糖合成提供底物(Guglielminetti *et al.*, 1995);而土壤水分亏缺诱导 D-酶活性的上升,可以促进短链的葡聚糖分子形成长链的葡聚糖分子,为 β-淀粉酶提供充足的底物,

从而提高整个水解途径的催化效率(Todaka *et al.*, 2000)。淀粉磷酸化酶是催化淀粉合成和降解的双向调节酶,土壤水分亏缺对酶活性表现出一定的抑制作用。Stitt 等(1985)认为,淀粉通过磷酸化降解产生的葡萄糖-1-磷酸,形成丙糖磷酸输出并参与细胞的呼吸和生物合成代谢。因此,水稻茎秆中较高的淀粉磷酸化酶活性可能与催化淀粉降解、产生 G1P 进入呼吸代谢途径有关,本研究发现正常灌水情况下茎秆中较高淀粉磷酸化酶活性相应地呼吸代谢 ¹⁴C 损失较多,也间接证实了这一结论,但有关淀粉的磷酸化过程在水稻茎贮藏同化物代谢中的生理意义还有待进一步研究证实。

水分亏缺促进植物叶片中蔗糖的合成和淀粉的降解,造成这种同化物分配的变化主要缘于加强了 SPS 基因表达(Wang *et al.*, 2000),或由于促进了 SPS 蛋白去磷酸化作用(Geigenberger *et al.*, 1997)。本研究发现,水分亏缺明显诱导了 SPS 活性和活化状态的上升,但对 SuSy 活性影响较小。许多研究发现,在植物不同器官 SuSy 的活性和基因表达与淀粉的合成有着密切关系,其活性的高低往往认为是库强的一个生化标志(Egger *et al.*, 1996; Weber *et al.*, 1997)。本研究认为水稻茎中 SuSy 可能主要参与淀粉的贮藏而不是降解。笔者在小麦研究上发现,茎秆中蔗糖转化酶活性过高不利于贮藏碳水化合物向籽粒的运转(王维等, 2005)。本研究再一次证实,通过土壤水分亏缺适当抑制茎秆中 AINV 活性,则有利于形成在源和库之间蔗糖的浓度梯度,增加贮藏同化物向籽粒的分配。

本研究表明在不严重的干旱条件下,可以增加水稻营养器官中贮藏物质向籽粒的分配,从而降低

图6 水分亏缺对水稻茎蔗糖代谢酶活性的影响(池栽试验)
Fig.6 Changes in activities of sucrose-metabolizing enzymes in the stems of two rice cultivars 'Shanyou63' (A, C, E) and 'Pc/Zao' (B, D, F), which were subjected to water deficit from 9 d after anthesis
图例同图1 Legends see Fig.1

由于干旱导致光合速率下降带来的产量损失。这提示我们在节水栽培和育种实践中,注意控制土壤水分亏缺程度和选择水稻茎秆中运转代谢关键酶活性高的品种或组合,协调水分亏缺对光合同化的限制和增加贮藏同化物运转这一对矛盾关系,可以达到

节水、高产的目标。

参 考 文 献

Aggarwal PK, Sinha SK (1984). Effect of water stress on grain growth and assimilate partitioning in two cultivars of wheat contrasting in their yield in a drought environment. *Annals of Botany*,

- 53, 329 – 340.
- Austin RBC, Morgan L, Ford MA, Blackwell RD (1980). Contributions to grain yield from pre-anthesis assimilation in tall and dwarf barley phenotypes in two contrasting seasons. *Annals of Botany*, 45, 309 – 319.
- Beck E, Ziegler P (1989). Biosynthesis and degradation of starch in high plants. *Annual Review of Plant Physiology and Plant Molecular Biology*, 40, 95 – 117.
- Bhatia S, Singh R (2002). Phytohormone-mediated transformation of sugars to starch in relation to the activities of amylases, sucrose-metabolizing enzymes in sorghum grain. *Plant Growth Regulation*, 36, 97 – 104.
- Blennow A, Engelsens SB, Nielson TH, Baunsgaard L, Mikkelsen R (2002). Starch phosphorylation: a new front line in starch research. *Trends in Plant Science*, 7, 445 – 450.
- Bradford MM (1976). A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. *Analytical Biochemistry*, 72, 248 – 254.
- da Silva PMFR, Eastmond PJ, Hill LM, Smith AM, Rawsthorne S (1997). Starch metabolism in developing embryos of oilseed rape. *Planta*, 203, 480 – 487.
- Egger B, Einig W, Schlereth A, Wallenda T, Magel E, Loewe A, Hampp R (1996). Carbohydrate metabolism in one- and two-year-old spruce needles, and stem carbohydrates from three months before until three months after bud break. *Physiologia Plantarum*, 96, 91 – 100.
- Gallagher JA, Volence JJ, Turner LB, Pollock CJ (1997). Starch hydrolytic enzyme activities following defoliation of white clover. *Crop Science*, 37, 1812 – 1818.
- Geigenberger P, Reimholz R, Geiger M, Canale V, Stitt M (1997). Regulation of sucrose and starch metabolism in potato tubers in response to short-term water deficit. *Planta*, 207, 502 – 518.
- Guglielminetti L, Yamaguchi J, Perata P, Alpi A (1995). Amylolytic activities in cereal seeds under aerobic and anaerobic conditions. *Plant Physiology*, 109, 1069 – 1076.
- Hendrix DL (1993). Rapid extraction and analysis of nonstructural carbohydrates in plant tissues. *Crop Science*, 33, 1306 – 1311.
- Li MY (李木英), Shi QH (石庆华), Pan XH (潘晓华) (1999). Studies on the physiological factors affecting the carbohydrate transfer in stem and sheath during filling stage in two-line hybrid rice. *Acta Agriculturae Universitatis Jiangxiensis* (江西农业大学学报), 21, 229 – 332. (in Chinese with English abstract)
- Lu JF (陆建飞), Huang PS (黄丕生), Ding YF (丁艳峰), Zhang WJ (张卫建) (1998). Accumulation and translocation of dry matter in two rice cultivars in relation to sustained soil water stress. *Jiangsu Journal of Agricultural Science* (江苏农业科学), 14, 135 – 140. (in Chinese with English abstract)
- Palta JA, Kobata T, Turner NC, Fillery IR (1994). Remobilization of carbon and nitrogen in wheat as influenced by post-anthesis water deficits. *Crop Science*, 34, 118 – 124.
- Schnyder H (1993). The role of carbohydrate storage and redistribution in the source-sink relations of wheat and barley during grain filling—a review. *New Phytologist*, 123, 233 – 245.
- Smith AM, Zeeman SC, Thorneycroft D, Smith SM (2003). Starch mobilization in leaves. *Journal of Experimental Botany*, 54, 577 – 583.
- Stitt M, Wirtz W, Gerhardt R, Heldt HW, Spencer C, Walker D, Foyer C (1985). A comparative study of metabolite levels in plant leaf material in the dark. *Planta*, 166, 354 – 364.
- Todaka D, Matsushima H, Morohashi Y (2000). Water stress enhances β -amylase activity in cucumber cotyledons. *Journal of Experimental Botany*, 51, 739 – 745.
- Wang H, Lee P, Chen W, Huang D, Su J (2000). Osmotic stress-induced changes of sucrose metabolism in cultured sweet potato cells. *Journal of Experiment Botany*, 51, 1991 – 1999.
- Wang W (王维), Zhang JH (张建华), Yang JC (杨建昌), Zhu QS (朱庆森) (2004). Effect of water stress on metabolism of stored carbohydrate of stem and yield in rice grown under unfavorable-delayed senescence. *Acta Agronomica Sinica* (作物学报), 30, 196 – 204. (in Chinese with English abstract)
- Wang W (王维), Cai YX (蔡一霞), Zhang JH (张建华), Yang JC (杨建昌), Zhu QS (朱庆森) (2005). Regulation of controlled soil drying on remobilization of stem-stored carbohydrate to grain in wheat grown under unfavorably-delayed senescence. *Acta Agronomica Sinica* (作物学报), 31, 289 – 296. (in Chinese with English abstract)
- Wardlaw IF, Willenbrink J (1994). Carbohydrate storage and mobilization by the culm of wheat between heading and grain maturity: the relation to sucrose synthase and sucrose-phosphate synthase. *Australian Journal of Plant Physiology*, 21, 255 – 271.
- Weber H, Borisjuk L, Wobus U (1997). Sugar import and metabolism during seed development. *Trends in Plant Science*, 2, 169 – 174.
- Yang JC, Zhang JH, Wang ZQ, Zhu QS, Liu LJ (2001). Activities of starch hydrolytic enzymes and sucrose-phosphate synthase in the stems of rice subjected to water stress during grain filling. *Journal of Experimental Botany*, 52, 2169 – 2179.