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## 杂交稻与常规稻产量受干旱影响的Meta分析 及干物质分配差异

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**摘要** 为探究干旱对杂交稻和常规稻干物质分配及产量的影响,通过Meta分析整合了1990—2020年中国境内干旱胁迫-水稻产量的文献结果,量化品种、干旱胁迫程度以及胁迫时期对水稻产量的影响,并于湖北省武汉市开展盆栽试验,以籼型杂交稻扬两优6号和汕优63、籼型常规稻黄华占和扬稻6号为试验材料,进一步研究干旱[土壤水势( $-30\pm5$ ) kPa]对抽穗开花期水稻的叶片与根系生理指标、干物质积累与分配的影响。Meta分析结果显示,干旱下水稻产量平均降幅为24.0%;与其他生育期相比,营养生长期干旱胁迫下水稻产量降幅最大,达24.4%;籼型杂交稻和籼型常规稻在干旱下的产量降幅分别为19.3%和13.8%,差异显著,表明常规稻在干旱下的产量相对稳定。武汉盆栽试验结果显示,干旱胁迫下水稻叶片水势和叶绿素含量、根系伤流速度、根系吸收面积与活跃吸收面积均显著下降,其中根系伤流速度的降幅最大,杂交稻与常规稻的降幅分别为94.29%和89.03%,而根系活力显著上升。干旱显著降低了水稻各部位干物质量,其中杂交稻叶片的可溶性糖含量与非结构性碳水化合物(non-structural carbohydrates, NSC)含量显著下降,降幅分别为37.73%和25.35%,常规稻叶片的可溶性糖含量与NSC显著上升,增幅分别为21.89%和10.49%。与杂交稻相比,干旱下常规稻的叶片与根系生理指标变幅更小,其叶、穗、根部的NSC含量积累较多,茎部的光合碳含量较高;常规稻的叶、穗、根在抽穗开花期积累的光合碳中NSC含量占比更大。因此,干旱下常规稻可能是通过积累较多的NSC来保证各器官能量代谢的稳定进行,从而维持较稳定的产量。

**关键词** 杂交稻;常规稻;干旱胁迫;干物质分配;根系活力;产量;非结构性碳水化合物;Meta分析

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水稻(*Oryza sativa* L.)是世界多数人口的主要粮食,同时也是我国第一大口粮作物<sup>[1]</sup>。在传统的淹水灌溉模式下,水稻种植耗水量巨大,约占农业用水的70%<sup>[2]</sup>。基于保障粮食安全和水资源利用最大化的需求,研究人员从水稻节水栽培模式以及水稻品种改良等方面入手,探索水稻高产与水资源利用最优化途径。目前旱直播、间歇性灌溉等模式的推广证明了水稻在稳产基础上的巨大节水潜力。有研究表明,间歇性灌溉下,水稻各部分生物量和产量与传统淹灌条件下相当甚至更佳<sup>[3-4]</sup>。同样地,相较于水直播与传统淹灌结合的模式,旱直播与间歇灌溉相结合在降低灌水量的同时,还维持了水稻产量的稳定性<sup>[5]</sup>。水稻品种在节水抗旱方面的贡献也不容忽视,前人通过探究抗旱型水稻在节水灌溉条件下的产量

和水分利用效率表现优于旱敏感型水稻的机制,发现抗旱型水稻的无效分蘖更少,拥有更好的灌浆能力和更大的根系生物量<sup>[6]</sup>。因此,筛选在干旱胁迫下表现良好的水稻品种也是提高水稻产量的重要途径之一<sup>[7]</sup>。

杂交稻通常被认为具有产量优势,在温光水肥均适宜的条件下更高产<sup>[8]</sup>,而常规稻则因为种子价格相对较低且易于留种而广受农户欢迎<sup>[9]</sup>。目前杂交稻的种植面积约占水稻总种植面积的50%~60%<sup>[10-11]</sup>,说明杂交稻和常规稻均有广大受众。水稻籽粒产量与光合产物的积累、运输、分配息息相关,目前关于杂交稻和常规稻的干物质积累及与产量的关系研究尚无定论,有研究表明,杂交稻较高的生物量积累决定了较高的水稻产量<sup>[12-13]</sup>。与常规稻

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相比,杂交稻生育前期的生物量积累较大,后期的生物量积累较小,成熟期两者生物量无明显差异<sup>[14]</sup>。同时也有人认为杂交稻在各个生育期的生长速率均快于常规稻<sup>[15]</sup>。

Meta分析是一种对同一研究主题下大量独立试验结果综合归纳的统计方法。本研究综合运用Meta分析方法并于武汉市开展盆栽试验,分析不同生育期干旱胁迫、不同干旱程度和不同水稻品种对水稻产量的影响,明确干旱条件下影响水稻产量变化的主要因素。在Meta分析结论的基础上,聚焦于探索杂交稻品种与常规稻品种在干旱条件下的干物质分配及产量差异,以期为水稻的节水栽培与产量稳定提供科学依据。

## 1 材料与方法

### 1.1 Meta分析

通过在“中国知网(CNKI)”“万方数据(WANFANG DATA)”“Web of science”“Google scholar”等数据库进行检索,检索关键词为“干旱”“水分胁迫”“干湿交替”“水稻产量”“rice alternate wetting and drying”“intermittent wetting and drying”“alternate waterlogging”“rice yield”等,筛选出1990—2020年符合以下条件的文章:(1)在中国境内进行;(2)试验条件统一为盆栽试验,避免自然条件下雨水的影响;(3)以常规淹灌为对照,土壤水分状况的衡量值为水势(kPa)或土壤含水量(%);(4)每盆种植穴数和每穴株数明确,指标有实际产量(g/pot或g/plant);(5)试验至少设置3次重复。此外,以图片展示的数据利用WebPlotDigitizer 4.2软件提取,没有SD的情况下,估算SD是平均值的1/10。

经过筛选,有62篇来自19个省份共675个数据符合以上标准,对以上数据进行亚组分类与归纳,将水稻分为杂交稻(hybrid rice, HR)和常规稻(inbred rice, IR),杂交稻又划分为籼型杂交稻和粳型杂交稻,常规稻被划分为籼型常规稻和粳型常规稻,以上水稻类型通过国家水稻数据中心(<https://ricedata.cn/>)查询;土壤水势划分为3个等级:轻度干旱胁迫(mild water stress, 水势值-25~-10 kPa, 土壤含水量80%~100%)、中度干旱胁迫(moderate water stress, 水势值-50~-25 kPa, 土壤含水量50%~80%)、重度干旱胁迫(severe water stress, 水势值-86~-50 kPa, 土壤含水量25%~50%);干旱胁迫时期划分为营养生长期、抽穗开花期(营养生长与生

殖生长并进阶段)、生殖生长期以及全生育期,同时还纳入水稻的产量构成因素等。

使用R程序包metafor生成平均lnR和95%置信区间。进行效应值(effect size)的显著性判断时,以其95%置信区间是否经过坐标零点作为依据。若不经过,说明对照相对于处理组差异显著( $P<0.05$ ),反之则说明差异不显著( $P>0.05$ )。此外,如果不同指标的95%置信区间没有重叠,则认为不同类别变量的效应值间存在显著差异( $P<0.05$ )<sup>[16]</sup>。

### 1.2 武汉盆栽试验

1)试验环境及材料。2022年在湖北省武汉市华中农业大学种子挂藏室( $30^{\circ}28'N, 114^{\circ}20'E$ )网室内进行。试验品种为扬两优6号(YLY6)、汕优63(SY63)、黄华占(HHZ)和扬稻6号(YD6),其中YLY6和SY63为籼型杂交水稻,HHZ和YD6为籼型常规水稻。盆栽试验种植水稻的塑料桶直径28 cm,深31.5 cm。每桶装9 kg土沙混合物,土沙比为5:1。土壤pH 6.71,全磷526.81 mg/kg,速效磷30.18 mg/kg。

2)试验设计。采用移栽的方式,每盆定植2株,在水稻播种20 d后进行移栽。设置常规淹灌对照(CK)和干旱胁迫处理[drought stress, DS, 土壤水势为(-30±5) kPa]干旱组于水稻移栽20 d后进行全生育期干旱处理,利用土壤张力计(TEN-100, Tuopu Instruments Ltd, 中国浙江)进行土壤水势监测。土壤施肥采用复合肥7.68 g(17-17-17)作为底肥,分蘖盛期和抽穗开花期每盆再追施1 g尿素。

#### 3)测定项目与方法

①叶片水势。用露点水势仪(WP4C, DECA-GON Inc, 美国)进行叶片水势测定。

②叶绿素含量。在抽穗开花期取水稻的剑叶,剪碎(去掉中脉)、混匀。具体测定方法参照文献[17]。

③根系伤流速度。根据伤流液质量,计算伤流速度<sup>[18]</sup>。

④根系活力。用TTC法测定。称取根尖2 cm的样品0.2~0.5 g,用雷根生物植物根系活力检测试剂盒进行测定。

⑤根系吸收面积和活跃吸收面积。取完整根测体积后,参照补红英<sup>[19]</sup>的方法测定根系吸收面积和活跃吸收面积。

⑥植株各部位干物质量。于抽穗开花期取样,

将植株地上部分分成叶、茎、穗,地下部分为根部,于105℃烘箱杀青30 min、80℃条件下烘2~3 d后称质量。

⑦植株各部位可溶性糖、淀粉和非结构性碳水化合物(non-structural carbohydrates, NSC)含量。可溶性糖和淀粉提取与测定参照Yoshida等<sup>[20]</sup>和潘俊峰等<sup>[21]</sup>的方法。

⑧<sup>13</sup>C标记与光合碳含量。在水稻的抽穗开花期进行,标记场所为特制的密闭透明亚克力箱(1.5 m×0.85 m×0.85 m),标记时间为08:00—12:00, $\text{Na}_2^{13}\text{CO}_3$ 由热耳生物科技(上海)有限公司提供(99% <sup>13</sup>C, SODIUM CARBONATE),一次标记试验需要5 g  $\text{Na}_2^{13}\text{CO}_3$ ,在标记过程中,为防止箱内温度过高,需要在箱底部放置冰块来控制箱内温度,脉冲标记的具体方法和计算公式参照尹云锋等<sup>[22]</sup>和刘萍等<sup>[23]</sup>。

表1 Meta分析: 干旱胁迫对水稻产量影响的亚组分析

Table 1 A Meta-analysis of the effects of drought stress on rice yields with a subgroup analysis

项目 Item	K值 K-value	效应值 Effect size (log response ratio)	P值 P-value	产量变化/% Change in yield	95%置信区间 95% CI
总体响应 Overall response	516	-0.274 1	<0.000 1	-24.0	(-26.6~-21.3)
亚组分析 Subgroup analysis					
水势 Water potential	轻度干旱胁迫 Mild water stress	182	-0.007 4	0.009 3	-0.7 (-1.3~-0.2)
Water potential	中度干旱胁迫 Moderate water stress	197	-0.324 9	<0.000 1	-27.7 (-28.2~-27.3)
	重度干旱胁迫 Severe water stress	137	-0.325 1	<0.000 1	-27.8 (-28.5~-27.0)
	营养生长期 Vegetative stage	83	-0.280 0	<0.000 1	-24.4 (-25.3~-23.5)
生育期 Period	抽穗开花期 Heading and flowering period	178	-0.211 5	<0.000 1	-19.1 (-19.7~-18.5)
	生殖生长期 Reproductive stage	182	-0.194 8	<0.000 1	-17.7 (-18.3~-17.1)
	全生育期 Whole growth period	73	-0.121 2	<0.000 1	-11.4 (-11.9~-10.9)
水稻类型 Rice type	杂交稻 Hybrid rice	221	-0.172 0	<0.000 1	-15.8 (-16.3~-15.3)
	常规稻 Inbred rice	295	-0.1815	<0.000 1	-16.6 (-17.0~-16.2)

水稻类型对干旱下水稻产量也有影响,当水稻类型分组为杂交稻品种和常规稻品种时,杂交稻降幅为15.8%,常规稻降幅为16.6%。

根据遗传背景,对杂交稻和常规稻再次进行亚组分析,分组为籼型杂交稻、粳型杂交稻、籼型杂交稻和粳型常规稻。籼型杂交稻和籼型常规稻在干旱下分别减产19.3%和13.8%,粳型杂交稻在干旱下产量增加2.1%,粳型常规稻在干旱下减产18.9%(表2)。

干旱对水稻产量构成因素的影响如图1所示,水稻的有效穗数、每穗粒数、结实率、千粒重在干旱胁迫下均显著下降,千粒重降幅相对较小。其中有效

## 2 结果与分析

### 2.1 干旱胁迫-水稻产量的Meta分析

共收集到符合条件的675条数据,其中243条发表于1990—2010年,432条发表于2010—2020年。采集到的数据试验点主要分布在中国东北部和长江流域及以南地区,基本覆盖了中国所有水稻产区。

如表1所示,水稻产量受水稻品种类型、干旱胁迫程度和胁迫时期的影响。随着干旱胁迫程度的加深,水稻产量下降越明显,轻度干旱胁迫下水稻产量降幅只有0.7%,而重度干旱胁迫则会使水稻减产27.8%。水稻在不同的生育期遭受干旱胁迫时,产量下降幅度不同,当水稻在整个生育期均受到干旱胁迫时,水稻产量的降幅约为11.4%,营养生长期的水稻在遭受干旱胁迫后水稻的降幅为24.4%,比生殖生长期高6.7%。水稻在营养生长和生殖生长并进的抽穗开花期遭遇干旱胁迫时水稻产量的降幅(19.1%)接近生殖生长期(17.7%)。

表1 Meta分析: 干旱胁迫对水稻产量影响的亚组分析

Table 1 A Meta-analysis of the effects of drought stress on rice yields with a subgroup analysis

穗数平均下降7.4%,每穗粒数平均下降8.5%,千粒重平均下降2.5%,结实率平均下降8.4%。

干旱对水稻每穗粒数、有效穗数、结实率影响的亚组分析如图2所示,杂交稻和常规稻的每穗粒数在干旱下的平均降幅分别为7.8%和10.4%(图2A),有效穗数在干旱胁迫下的平均降幅分别为1.8%和0.1%(图2B),结实率在干旱胁迫下的平均降幅分别为4.4%和2.9%(图2C)。可见,相较于常规稻,干旱下杂交稻的每穗粒数平均降幅较小,结实率和有效穗数降幅较大。常规稻在干旱胁迫下的有效穗数较稳定。进一步进行亚组分析发现,干旱胁迫下籼型杂交稻的每穗粒数和结实率分别降低8.0%和

表2 Meta分析:干旱胁迫对水稻产量影响的品种方向的亚组分析

Table 2 Meta-analysis of the effects of drought stress on rice yields with a subgroup analysis of rice variety

亚种 Subspecies	类型 Type	K值 K-value	效应值 Effect size (log response ratio)	P值 P-value	产量变化 Change in yield%	95%置信区间 95% CI
籼型 Indica	杂交稻 Hybrid rice	209	-0.2147	<0.0001	-19.3	-19.9~-18.8
	常规稻 Inbred rice	104	-0.1483	<0.0001	-13.8	-14.4~-13.2
	籼粳杂交稻 Japonica×Indica	5	-0.0737	0.0170	-7.1	-12.5~-1.3
粳型 Japonica	杂交稻 Hybrid rice	7	0.0209	0.0066	2.1	0.6~3.7
	常规稻 Inbred rice	189	-0.2099	<0.0001	-18.9	-19.5~-18.4

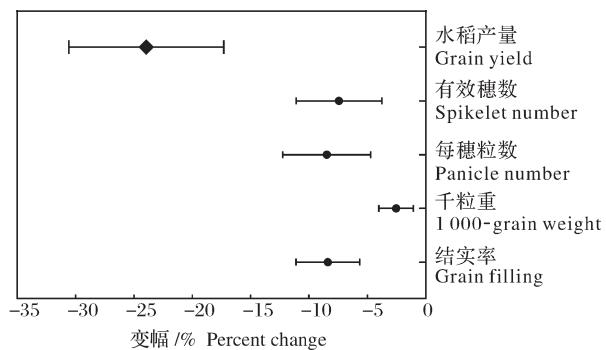


图1 干旱胁迫对水稻产量构成影响的Meta分析  
Fig. 1 A Meta-analysis of the effects of drought stress on rice yield components

4.7%, 粳型常规稻的每穗粒数分别降低 5.7% 和 2.8%。而干旱下籼型常规稻的有效穗数因干旱胁迫而增加, 增幅为 5.1%, 粳型杂交稻的有效穗数因干旱下降 1.9%。粳型杂交稻在干旱下的每穗粒数和结实率呈上升趋势, 有效穗数呈下降趋势, 但均无显著性变化。粳型常规稻的每穗粒数、有效穗数和结实率在干旱下显著下降, 降幅分别为 12.9%、6.0% 和 3.1%。

除品种的亚组分析外, 对水稻产量构成进行干旱胁迫程度和胁迫时期的亚组分析, 结果显示, 轻度、中度、重度干旱胁迫下每穗粒数的降幅分别为 6.5%、13.9% 和 6.5%, 水稻的平均结实率在不同程度干旱胁迫下表现不一致, 其中轻度干旱胁迫下, 水稻的结实率上升, 增幅为 0.6%, 中度和重度干旱胁迫下, 水稻的结实率下降, 降幅分别为 6.1% 和 7.7%。轻度干旱胁迫下水稻的有效穗数无明显变化, 而重度干旱胁迫下水稻的有效穗数显著下降。

水稻平均每穗粒数在生殖生长期遭遇干旱时降幅最小, 为 4.4%, 在全生育期时降幅最大, 达到 15.4%。水稻的有效穗数在营养生长期遭受干旱胁迫时降幅最大, 为 10.7%, 在生殖生长期遭受干旱胁迫时, 水稻的有效穗数增加, 增幅为 13.2%。在营养

生长期遭受干旱时, 水稻的平均结实率上升, 增幅为 2.0%, 结实率在营养生长与生殖生长并进阶段降幅最大, 为 8.5% (图 2)。

## 2.2 干旱胁迫对杂交稻与常规稻叶片生理性状的影响

1) 水稻叶片水势。由图 3 可知, 干旱胁迫下, 除 HHZ 外, 其他水稻品种在抽穗开花期的叶片水势均显著下降, 其中, YLY6 的降幅高达 29.34%, 杂交稻品种的叶片水势显著下降, 平均降幅为 20.55%。

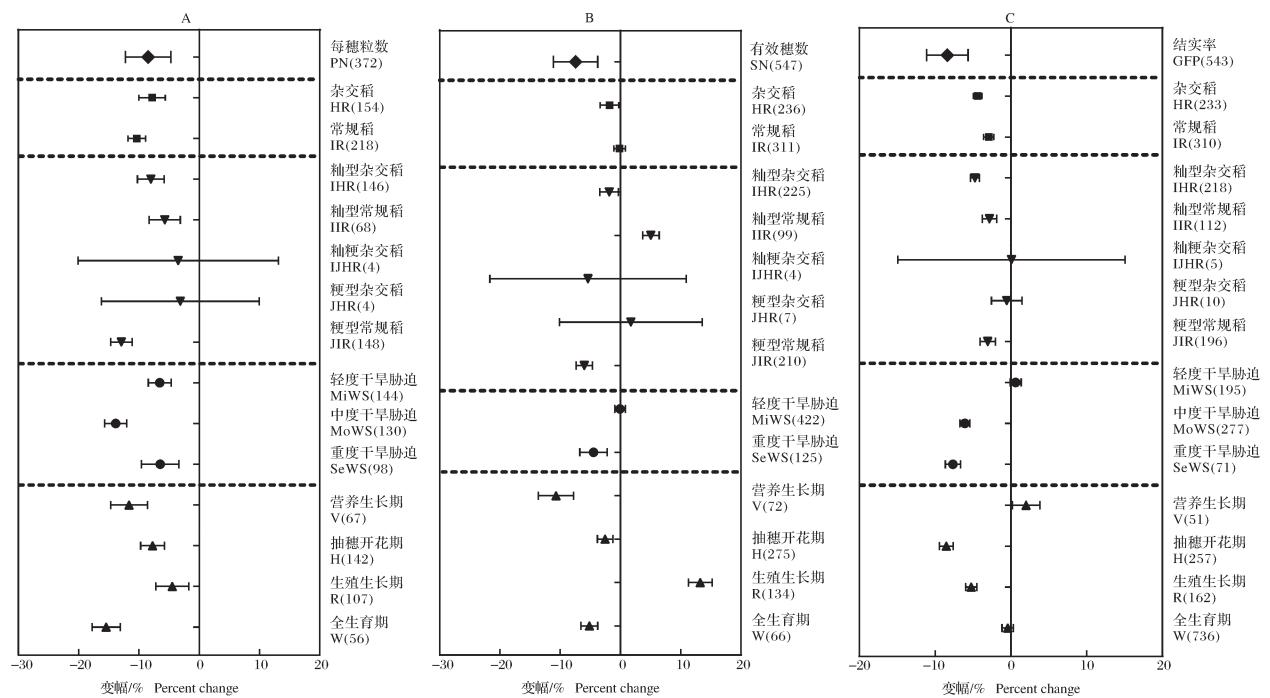
2) 叶片叶绿素含量。如图 4 所示, 干旱胁迫下杂交稻和常规稻的叶绿素 a 含量分别下降了 19.16% 和 3.54%, 其中杂交稻的叶绿素 a 含量显著下降, 从 1.83 mg/g 降至 1.48 mg/g。干旱胁迫下杂交稻和常规稻的叶绿素 b 含量均显著下降, 降幅分别为 26.47% 和 19.86%。干旱降低了抽穗开花期杂交稻和常规稻的叶绿素总含量, 其中杂交稻品种的叶绿素总含量显著下降, 降幅达 21.00%, 常规稻降幅为 7.62%。

## 2.3 干旱胁迫对杂交稻与常规稻根系生理性状的影响

1) 根系伤流速度。如图 5 所示, 干旱显著降低了各生育期的水稻根系伤流速度, 杂交稻和常规稻在抽穗开花期根系伤流速度分别下降了 94.29% 和 89.03%, 杂交稻根系伤流速度的降幅大于常规稻。

2) 根系脱氢酶活力。由图 6 可知, 干旱胁迫显著增加了水稻的根系活力, 杂交稻和常规稻的增幅分别高达 96.34% 和 80.14%, 杂交稻的增幅大于常规稻。

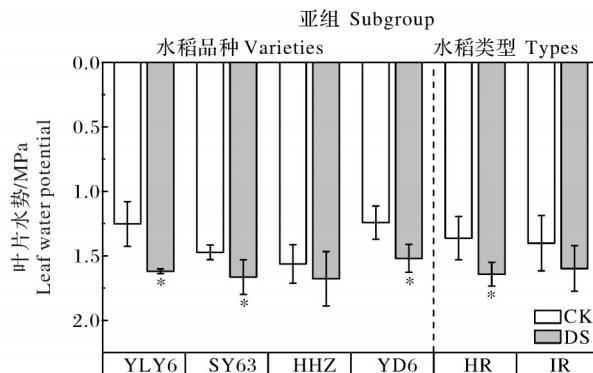
3) 根系吸收面积与活跃吸收面积。干旱显著降低了杂交稻和常规稻的根系吸收面积, 其中杂交稻和常规稻在抽穗开花期的根系吸收面积降幅分别为 51.93% 和 49.33%, 干旱下杂交稻和常规稻在抽穗开花期的根系吸收面积分别为 0.86 和 0.65 m<sup>2</sup>, 由此可知杂交稻在干旱下的根系吸收面积大于常规稻。干



SN: Spikelet number; PN: Panicle number; GFP: Grain filling percent; HR: Hybrid rice; IR: Inbred rice; IHR: Indica hybrid rice; IIR: Indica inbred rice; IIJHR: Indica×Japonica hybrid rice; JHR: Japonica hybrid rice; JIR: Japonica inbred rice; MiWS: Mild water stress; MoWS: Moderate water stress; SeWS: Severe water stress; V: Vegetative stage; H: Heading and flowering period; R: Reproductive stage; W: whole growth period.

图2 Meta分析: 干旱胁迫对水稻每穗粒数(A)、有效穗数(B)、结实率(C)影响的亚组分析

Fig.2 A Meta-analysis of drought stress on rice spikelet number(A), panicle number(B) and grain filling percent(C) with a subgroup analysis



杂交稻为扬两优6号(YLY6)和汕优63(SY63),常规稻为黄华占(HHZ)和扬稻6号(YD6),“\*”表示处理间差异达到显著水平( $P<0.05$ )。下同。The value for hybrid rice are the average value of YLY6 and SY63, and the value for inbred rice are the average value of HHZ and YD6. An “\*\*” indicates a significant level of difference between treatments ( $P<0.05$ ). The same as below.

图3 淹灌对照(CK)和干旱胁迫(DS)下杂交稻和常规稻在抽穗开花期的叶片水势比较

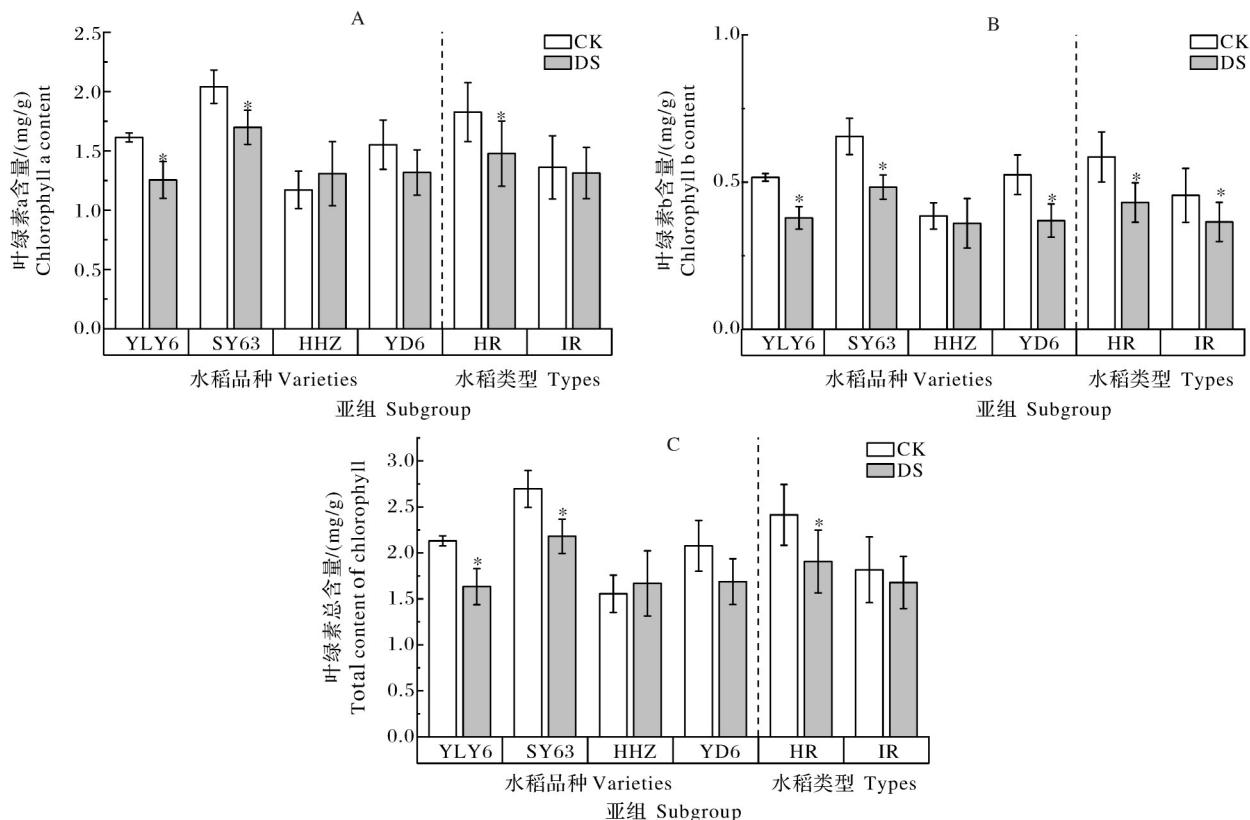
Fig.3 Comparison of leaf water potential of hybrid rice and inbred rice at flowering stage under flood irrigation (CK) and drought stress (DS)

旱显著降低了杂交稻和常规稻的根系活跃吸收面积,其中杂交稻和常规稻降幅分别为51.44%和45.05%(图7)。

#### 2.4 干旱胁迫对杂交稻与常规稻干物质积累和分配的影响

1)水稻单株干物质量。由图8可知,干旱胁迫下,杂交稻和常规稻单株平均干物质量分别为38.84和32.91 g/plant。干旱胁迫显著降低了水稻的单株干物质量,杂交稻和常规稻的单株降幅分别为48.57%和57.16%。表明杂交稻在生育后期的单株干物质量降幅小于常规稻品种。

2)水稻各器官干物质量。干旱胁迫下,抽穗开花期杂交稻的叶、穗、根分别为6.95、2.42、3.33 g/plant,常规稻的分别为6.70、1.46、3.33 g/plant。干旱显著降低了水稻的叶和根干物质量,其中杂交稻的叶和根干物质量降幅分别为52.37%和42.90%,常规稻的降幅分别为50.39%和35.78%。杂交稻的叶片和根系干物质量降幅均大于常规稻品种。干旱显著降低了水稻的穗干物质量,杂交稻和常规稻的



A:叶绿素a含量;B:叶绿素b含量;C:叶绿素总含量。A:Content of chlorophyll a ;B:Content of chlorophyll b ;C:Total content of chlorophyll .

图4 淹灌对照(CK)和干旱胁迫(DS)下杂交稻和常规稻在抽穗开花期的叶绿素含量比较

Fig. 4 Comparison of chlorophyll content of hybrid rice and inbred rice at flowering stage under flood irrigation (CK) and drought stress (DS)

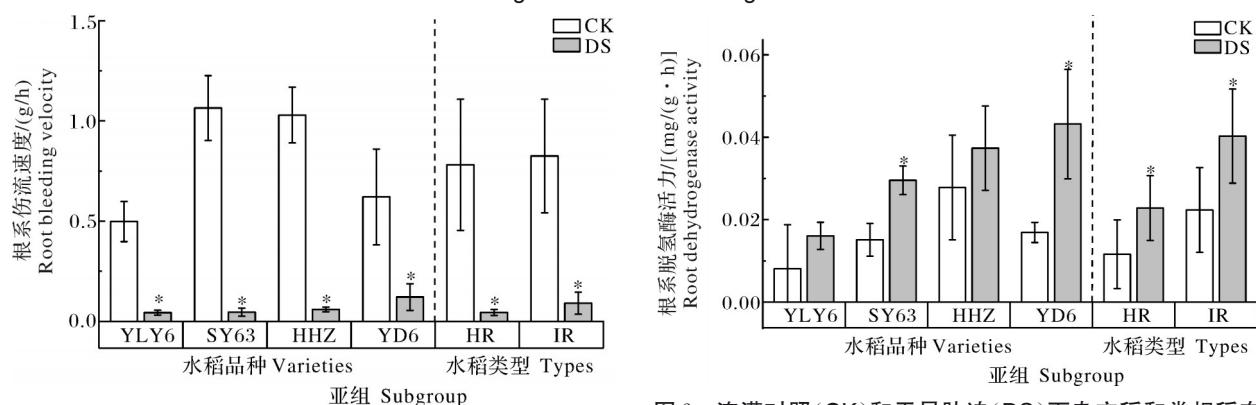


图5 淹灌对照(CK)和干旱胁迫(DS)下杂交稻和常规稻在抽穗开花期的根系伤流速度比较

Fig. 5 Comparison of root bleeding velocity of hybrid rice and inbred rice at flowering stage under flood irrigation (CK) and drought stress (DS)

平均穗干物质质量降幅分别高达77.95%和88.14%。

干旱胁迫下,杂交稻在干旱胁迫下的根占比和叶占比分别为8.56%和17.88%,常规稻则为10.13%和20.34%,表明干旱胁迫下杂交稻生育后期的根系占比和叶占比均小于常规稻(图9)。

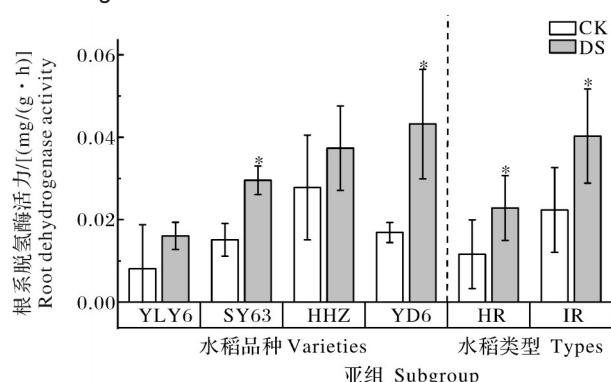


图6 淹灌对照(CK)和干旱胁迫(DS)下杂交稻和常规稻在抽穗开花期的根系脱氢酶活力比较

Fig. 6 Comparison of root dehydrogenase activity of hybrid rice and inbred rice at flowering stage under flood irrigation (CK) and drought stress (DS)

3)可溶性糖、淀粉和非结构性碳水化合物含量。如图10所示,干旱胁迫增加了可溶性糖在穗部和根系的分配,降低了在茎部的分配。杂交稻叶片可溶性糖含量在干旱胁迫下降低显著,降幅高达37.73%,而常规稻叶片可溶性糖含量在干旱胁迫下显著增加,增幅为21.89%。干旱胁迫下杂交稻

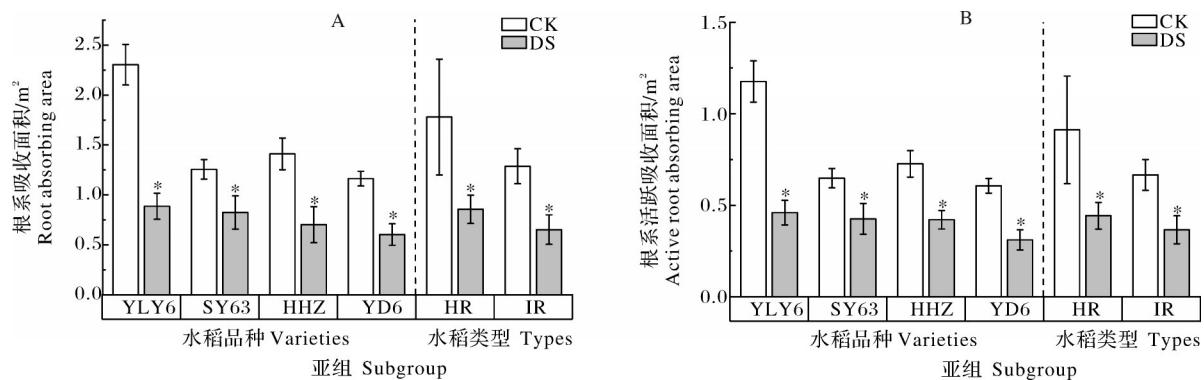


图7 淹灌对照(CK)和干旱胁迫(DS)下杂交稻和常规稻在抽穗开花期的根系吸收面积(A)与活跃吸收面积(B)比较

Fig. 7 Comparison of root absorbing area(A) and active root absorbing area(B) of hybrid rice and inbred rice at flowering stage under flood irrigation (CK) and drought stress (DS)

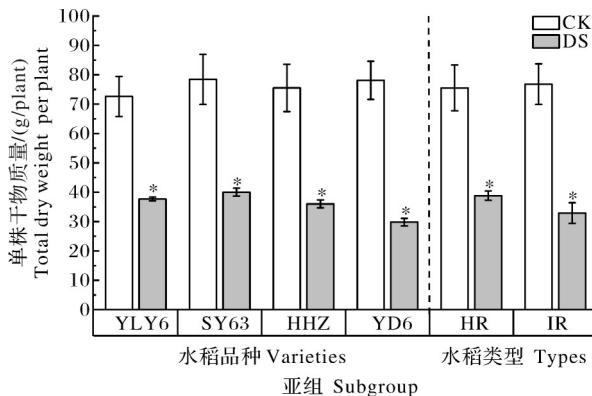


图8 淹灌对照(CK)和干旱胁迫(DS)下杂交稻和常规稻在抽穗开花期的单株干物质量比较

Fig. 8 Comparison of total dry weight per plant of hybrid rice and inbred rice at flowering stage under flood irrigation (CK) and drought stress (DS)

品种茎鞘可溶性糖含量显著下降,降幅达20.14%,常规稻降幅为4.67%。常规稻品种在穗部和根部的可溶性糖含量因干旱胁迫显著增加,增幅分别为33.28%和13.25%,而杂交稻品种的穗部和根部可溶性糖含量略有上升,上升幅度分别为7.68%和6.38%。

干旱条件下,杂交稻的叶片淀粉含量上升至18.60 mg/g,而常规稻的叶片淀粉含量下降至15.32 mg/g。干旱降低了水稻茎部、穗部和根部的淀粉含量,其中,杂交稻根部淀粉含量显著下降,降幅为14.69%,常规稻根部淀粉含量降幅为5.08%。杂交稻和常规稻的茎部淀粉含量降幅分别为7.90%和16.82%,穗部淀粉含量降幅分别为2.38%和5.70%(图11)。

如图12所示,干旱条件下,杂交稻叶片的NSC含量显著下降,降幅高达25.35%;常规稻叶片的NSC含量显著上升,达10.49%。干旱胁迫下,杂交

稻和常规稻的茎鞘NSC含量均显著下降,降幅分别为13.57%和10.83%。杂交稻和常规稻在穗部和根部的NSC含量在干旱胁迫下的变化趋势不一致,干旱下杂交稻的穗部NSC含量上升,增幅为3.41%,根部NSC含量显著下降,降幅为8.48%;常规稻的穗部NSC含量因干旱胁迫而下降,降幅为8.48%,根部NSC含量因干旱胁迫而上升,增幅为2.07%。

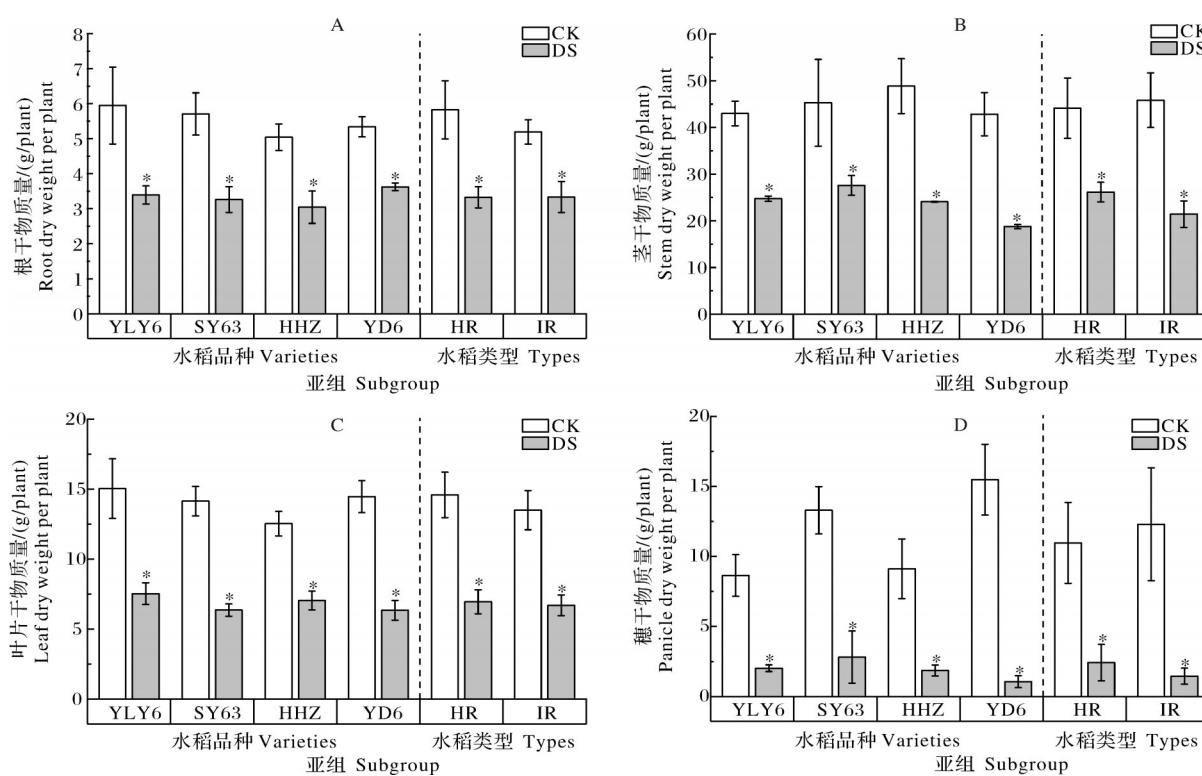
综上,干旱显著降低了杂交稻在叶、茎、根部的可溶性糖含量和NSC含量,显著增加了常规稻在叶、穗、根部的可溶性糖含量,显著降低了常规稻在茎部的NSC含量。干旱条件下,常规稻叶、穗、根的可溶性糖含量和NSC含量均大于杂交稻,穗部的淀粉含量大于杂交稻。

4)光合碳含量及分配比例。如表3所示,干旱显著降低了杂交稻和常规稻的光合碳总含量,降幅分别为63.08%和58.66%。干旱显著降低了水稻在各器官的光合碳含量,增加了光合碳在根系的分配比例,其中杂交稻和常规稻的根系光合碳分配比例分别为15.47%和15.48%,说明干旱胁迫使常规稻分配在根系的光合碳比例增加。干旱条件下,杂交稻在叶片、穗部和根系的光合碳含量大于常规稻,在茎部的光合碳含量小于常规稻。

### 3 讨 论

#### 3.1 干旱胁迫对水稻产量的影响

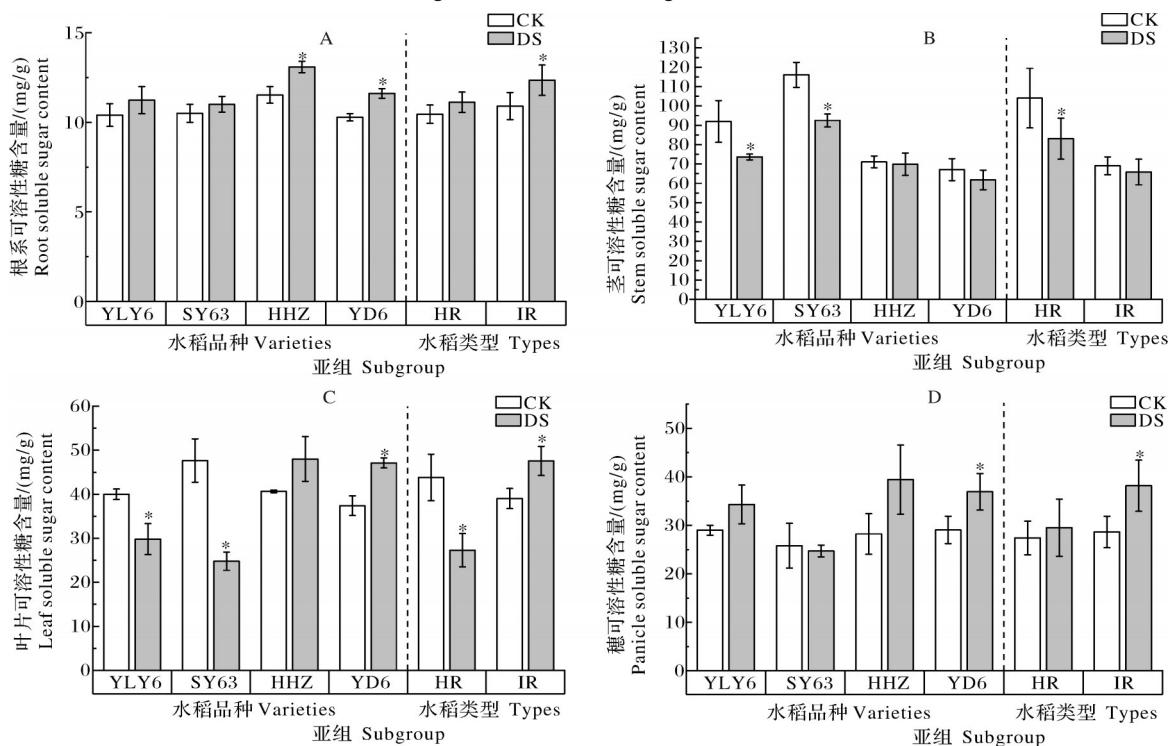
大量研究表明,水稻在遭受干旱胁迫时,胁迫时期、胁迫程度以及水稻种类均会导致最终产量的变化<sup>[24-26]</sup>。本文Meta分析结果显示,随着水分胁迫程度的加深,水稻的产量降幅越大;水稻的营养生长期遭受干旱胁迫后,水稻产量降幅最大;籼型杂交稻在干旱胁迫下的产量降幅大于籼型常规稻。相较于籼



A:根; B:茎; C:叶片; D:穗。A:Root; B:Stem; C:Leaf; D:Panicle.

图9 淹灌对照(CK)和干旱胁迫(DS)下杂交稻和常规稻在抽穗开花期的各部位干物质量比较

Fig. 9 Comparison of different parts of dry weight per plant of hybrid rice and inbred rice at flowering stage under flood irrigation (CK) and drought stress (DS)



A:根系; B:茎; C:叶片; D:穗。A:Root; B:Stem; C:Leaf; D:Panicle.

图10 淹灌对照(CK)和干旱胁迫(DS)下杂交稻和常规稻在抽穗开花期的可溶性糖含量比较

Fig. 10 Comparison of soluble sugar content of hybrid rice and inbred rice at flowering stage under flood irrigation (CK) and drought stress (DS)

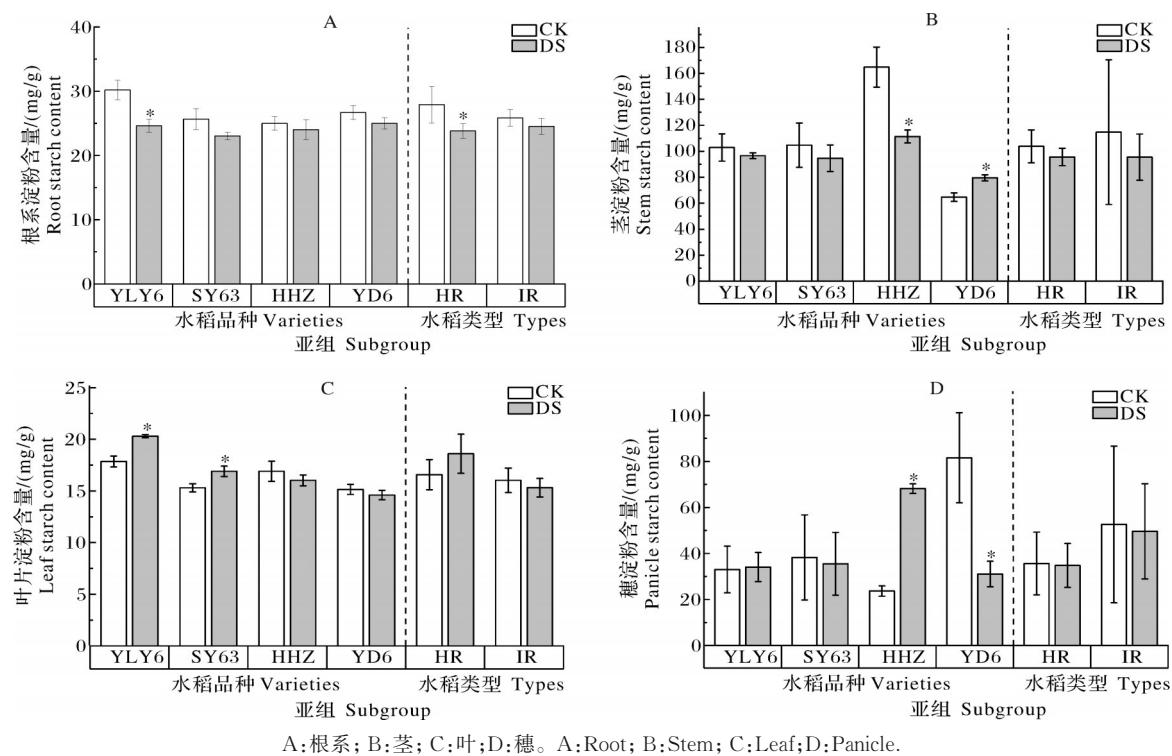


图11 淹灌对照(CK)和干旱胁迫(DS)下杂交稻和常规稻在抽穗开花期的淀粉含量比较  
Fig. 11 Comparison of starch content of hybrid rice and inbred rice at flowering stage under flood irrigation (CK) and drought stress (DS)

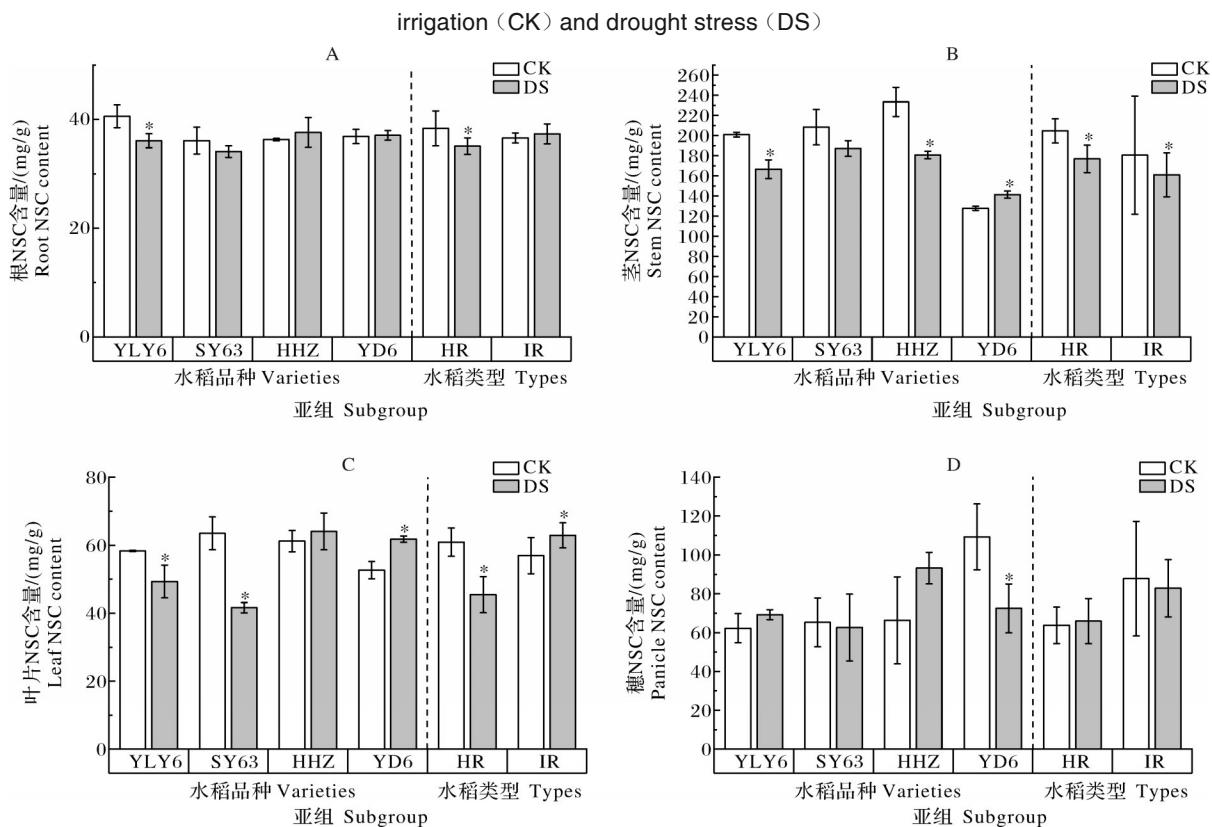


图12 淹灌对照(CK)和干旱胁迫(DS)下杂交稻和常规稻在抽穗开花期的NSC含量比较  
Fig. 12 Comparison of NSC content of hybrid rice and inbred rice at flowering stage under flood irrigation (CK) and drought stress (DS)

表3 淹灌对照(CK)和干旱胁迫(DS)下杂交稻和常规稻在抽穗开花期的<sup>13</sup>C含量比较  
Table 3 Comparison of <sup>13</sup>C content of hybrid rice and inbred rice at flowering stage under flood irrigation (CK) and drought stress (DS)

水稻品种或类型 Rice varieties or types	处理 Treatment	<sup>13</sup> C总含量 Total <sup>13</sup> C content	各器官 <sup>13</sup> C含量 Different parts of <sup>13</sup> C content				mg/plant
			叶 Leaf	茎 Stem	穗 Pannicle	根 Root	
YLY6	CK	40.29	4.31	18.05	14.44	3.49	
	DS	14.71*	3.54*	7.85*	1.58*	1.73*	
SY63	CK	43.51	5.34	25.90	6.46	5.81	
	DS	16.23*	4.40	8.10*	1.34*	2.39*	
HHZ	CK	41.51	5.74	28.11	4.38	3.28	
	DS	14.94*	4.27*	7.95*	0.97*	1.75*	
YD6	CK	36.53	4.27	22.05	7.50	2.71	
	DS	16.04*	2.64*	10.05*	1.13*	2.21*	
杂交稻 HR	CK	41.90	4.83	21.97	10.45	4.65	
	DS	15.47*	3.97*	7.98*	1.46*	2.06*	
常规稻 IR	CK	39.02	5.00	25.08	5.94	3.00	
	DS	16.13*	3.45*	9.00*	1.05*	1.98*	

型杂交稻,籼型常规稻的结实率降幅较小,推测常规稻相对稳定的结实率保证了产量的相对稳定(较小降幅)。

### 3.2 干旱下水稻的叶片与根系生理性状变化

叶片水势常被用于评价水稻的保水抗旱能力。干旱会降低水稻的叶片水势,随着胁迫时间的延长,叶片水势降幅变大<sup>[27]</sup>。叶绿素直接参与光合作用,叶绿素含量与水稻的光合性能有关,能直接影响水稻光合产物的生成。研究表明,水分胁迫会导致水稻叶绿素含量下降,且胁迫越严重,叶绿素含量越低<sup>[28-30]</sup>。武汉盆栽试验结果表明,干旱胁迫下,与杂交稻相比,常规稻的叶片水势、叶绿素含量降幅更小。

根系伤流可以反映根系的水分情况,是鉴定根系活力的重要指标之一,同时与作物产量呈显著正相关<sup>[31-33]</sup>。徐国伟等<sup>[34]</sup>研究表明,水稻的伤流量随着干旱胁迫程度的加深而呈现先上升后下降的趋势。TTC法测定的脱氢酶活性与根系活力正相关,可以通过测定根系脱氢酶活性来反映根系活力<sup>[35]</sup>。而根系吸收面积与根系活跃吸收面积反映了根系吸收水分和养分的能力,前人研究表明,干旱胁迫下根系脱氢酶活性上升<sup>[18]</sup>,干旱会降低水稻的根系吸收面积和活跃吸收面积<sup>[36]</sup>。武汉盆栽试验结果表明,干旱显著降低了水稻的根系伤流速度(根系伤流量)、根系吸收面积与活跃吸收面积,显著提高了根系脱氢酶活性,与杂交稻相比,常规稻在抽穗开花期的根系指标变幅更小。

### 3.3 干旱胁迫下水稻干物质积累与分配变化

水稻产量的形成离不开干物质的积累与分配,高产水稻一般认为需要较高的干物质积累量和较高的穗部分配比例<sup>[37]</sup>。研究表明,干旱胁迫显著影响水稻干物质的积累,同时干旱胁迫下干物质在水稻根、茎、叶、穗各部位的分配也存在差异,杨桦<sup>[38]</sup>通过对不同生育期水稻设置不同程度水分胁迫处理,发现随着水分胁迫程度的加深,水稻的干物质积累量降低越明显。分蘖期干旱处理会降低在拔节前的干物质量,提高在拔节期后的干物质量及其占总干物质量的比值,且幼穗分化期前干物质量积累越多,成穗率越低,在分蘖期进行轻度和中度干旱处理有利于分蘖成穗,提高水稻产量<sup>[39]</sup>。徐一兰等<sup>[40]</sup>认为干旱胁迫降低了水稻的根、茎干物质量,对穗干物质量无显著影响。武汉盆栽试验结果表明,杂交稻在抽穗开花期的茎、穗和单株干物质量均大于常规稻,叶、根干物质量与常规稻无明显差异。

可溶性糖是重要的渗透调节物质,当植物遭受逆境胁迫时,可溶性糖含量的增加有利于维持细胞渗透压。淀粉是植株体内贮藏碳水化合物的主要形式,淀粉代谢也是植物应对干旱胁迫的重要手段,在水分胁迫下,淀粉会降解,转化为糖类和脯氨酸来维持细胞的正常生理活动<sup>[41-42]</sup>。有研究表明水稻在孕穗期遭受干旱胁迫时,其叶片可溶性糖含量上升<sup>[43]</sup>,同时干旱胁迫会增加茎鞘中可溶性糖的含量<sup>[44]</sup>。武汉盆栽试验结果表明,在水稻的抽穗开花期,常规淹灌和干旱处理下,可溶性糖、淀粉和NSC含量均在茎

部分配最多。干旱显著降低了杂交稻在叶、茎、根部的可溶性糖含量和NSC含量,显著增加了常规稻在叶、穗、根部的可溶性糖含量,显著降低了常规稻在茎部的NSC含量。干旱条件下,与杂交稻相比,常规稻在叶片、穗部和根系的可溶性糖含量和NSC含量较大,在茎部的可溶性糖和NSC含量较小,穗部的淀粉含量较大。这与前人的研究<sup>[43-44]</sup>稍有出入,可见水稻各部位的可溶性糖、淀粉含量不仅与干旱胁迫的时期有关,还与水稻类型有关。

脉冲标记可以量化水稻在某生长阶段内的光合碳积累量与分配比例,有研究表明,植株干物质积累量与净输入的<sup>13</sup>C含量及分配率显著正相关<sup>[45]</sup>。因此利用脉冲标记研究干旱胁迫下,水稻抽穗开花期阶段时间的光合碳输入量以及在水稻各部位的分配有重要意义。武汉盆栽试验研究结果表明,常规淹灌条件下,相较于杂交稻,常规稻的光合碳积累总量、穗部和根部的光合碳含量以及分配在根部的光合碳比例较小,叶部和茎部的光合碳含量较大。干旱胁迫显著降低了水稻的总光合碳积累量,增加了光合碳在根系的分配比例,其中常规稻的增幅大于杂交稻。与杂交稻相比,常规稻在叶片、穗部和根系的光合碳含量较小,茎部的光合碳含量较大。

本研究综合Meta分析和盆栽试验,揭示了干旱对杂交稻与常规稻产量及生理机制的影响。Meta分析结果显示,干旱时期、干旱胁迫程度及水稻品种选择均显著影响水稻产量,但常规稻比杂交稻在干旱胁迫下的减产幅度小。在此基础上开展的盆栽试验则进一步表明,干旱降低水稻根系及叶片生理活性,与杂交稻相比,常规稻的叶片水势、叶绿素含量、根系伤流速度在干旱处理下的降幅小。干旱显著降低了水稻植株的干物质量与光合碳积累,相较于杂交稻,常规稻可通过在叶、穗、根部积累较多的非结构性碳水化合物(NSC),保证各器官能量代谢的稳定进行,从而在干旱条件下仍维持较稳定的产量。

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## Meta-analysis of effects of drought on yield and differences in dry matter allocation of hybrid rice and inbred rice

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**Abstract** Literature on drought stress and rice yield in China from 1990 to 2020 were integrated through Meta-analysis and the effects of rice varieties, the degree of drought stress, and the period of stress on yield were quantified to study the effects of drought on the allocation of dry matter and the yield of hybrid rice and inbred rice. The hybrid indica rice varieties including Yangliangyou 6 and Shanyou 63, the conventional indica rice varieties including Huanghuazhan and Yangdao 6 were used to conduct a pot experiment in Wuhan, Hubei Province, to further investigate the effects of drought (soil water potential  $-30 \text{ kPa} \pm 5 \text{ kPa}$ ) on the physiological indexes of leaves and roots, the accumulation and distribution of dry matter at the stages of heading and flowering in rice. The results of Meta-analysis showed that the average decrease in rice yield under drought was 24.0%. Compared with other stages of growth, the yield of rice decreased the most at the stage of vegetative growth under drought stress, reaching 24.4%. The significant difference in the decrease of yield between indica hybrid rice and indica inbred rice under drought stress was 19.3% and 13.8%, respectively, indicating that the yield of indica inbred rice is relatively stable under drought stress. The results of the pot experiment in Wuhan showed that the water potential and the content of chlorophyll in rice leaves, the injury velocity in roots, the absorption area of root, and the active absorption area all significantly decreased under drought stress. Among them, the injury velocity in roots decreased the most, with a decrease of 94.29% and 89.03% for hybrid rice and inbred 1 rice, respectively, while the vigor of root significantly increased. Drought significantly reduced the dry weight of all parts of rice, among which the content of soluble sugar and non-structural carbohydrate (NSC) in leaves of hybrid rice decreased significantly by 37.73% and 25.35%, respectively. The content of soluble sugar and NSC in leaves of inbred rice increased significantly by 21.89% and 10.49%, respectively. The physiological indexes in leaves and roots of inbred rice under drought had smaller variation compared with those of hybrid rice, and its leaves, spikes, and roots accumulated more content of NSC, and its stems had higher content of photosynthetic carbon. The proportion of the content of NSC in the photosynthetic carbon accumulated in the leaves, spikes, and roots of inbred rice at the stages of heading and flowering was higher. It is indicated that the inbred rice may maintain stable yield under drought by accumulating more NSC to ensure stable metabolism of energy in all organs.

**Keywords** hybrid rice; inbred rice; drought stress; dry matter allocation; root activity; yield; non-structural carbohydrate (NSC); Meta-analysis

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