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干湿交替灌溉对水稻产量、水氮利用效率和稻米品质影响的研究进展

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摘要　干湿交替灌溉作为一项重要的节水灌溉技术,对水稻产量、水氮利用效率和稻米品质都具有重要影响,且这种影响的正负效应主要由土壤落干的程度决定。本文从稻田土壤理化与生物学性状、水稻根系形态生理特性以及地上部农艺性状与生理特性等方面综述了干湿交替灌溉对水稻产量、水氮利用效率和稻米品质的作用机制,同时简述了干湿交替灌溉与氮肥互作对水稻产量、水氮利用效率和稻米品质的影响;提出了研究存在土壤落干程度监测标准不统一、调控机制阐明不深入等问题,建议今后利用多组学技术解析干湿交替灌溉对水稻茎蘖成穗率的调控机制并基于籽粒淀粉、蛋白质和脂肪代谢开展干湿交替灌溉、氮肥施用等栽培措施对稻米品质形成的调控机制研究。

关键词　水稻;干湿交替灌溉;产量;水/氮利用效率;稻米品质

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水稻是世界上最重要的粮食作物之一,也是我国一半以上人口的主粮。而水稻生产又是农业用水第一大户,稻田灌水量约为玉米和小麦等其他作物的2.5倍,且其灌溉水利用效率仅达1 kg/m^{3}左右[1-2]。随着时代发展和人们消费观念改变,单纯追求产量的提高已不再是唯一目标,水稻生产已向着“高产、高效、优质”的目标发展[3-4]。因此,如何“高产、高效、优质”地开展水稻生产已成为水稻育种学和栽培学的重要课题。

干湿交替灌溉(alternating wet and dry irrigation,AWD)作为水稻生产上最为行之有效的节水灌溉技术之一,已在亚洲主要水稻生产国(如中国、孟加拉国、印度和越南等)推广应用[5-7]。研究表明,干湿交替灌溉对水稻产量[8-9]、水氮利用效率[10-11]和稻米品质[12]均具有重要的调控作用,是目前实现水稻高产高效优质生产的最具潜力的栽培措施之一。本文在简述干湿交替灌溉概念的基础上,重点综述干湿交替灌溉及其与氮肥互作对水稻产量、水氮利用效率和稻米品质的影响及其机制的研究进展,旨在为水稻高产高效优质的遗传改良和栽培调控提供理论依据。

1　干湿交替灌溉

水稻生产上的干湿交替灌溉指在一段时间里保持土壤浅水层(常规灌溉),随后自然落干一段时间后复水、再落干、再复水,如此循环[11,13]。通常以土壤水势为复水指标,干湿交替灌溉模式主要分为2种类型[14-15]:(1)自浅水层(1～2 cm)自然落干到土壤水势达(−15±5) kPa(15～20 cm深)时再灌水至浅水层,如此循环,称为轻-干湿交替灌溉(alternating wet and moderately dry irrigation,AWMD);(2)自浅水层(1～2 cm)自然落干到土壤水势达(−35±5) kPa(15～20 cm深)时再灌水至浅水层,如此循环,称为重-干湿交替灌溉(alternating wet and severely dry irrigation,AWSD)。根据该灌溉方式采用时期的不同,又有全生育期干湿交替灌溉(自移栽后10 d至收

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获前1周)和结实期干湿交替灌溉(自抽穗后6 d至收获前1周)之分[9,12,16]。此外,也有不少研究者以土壤饱和含水量或田间持水量为复水标准。比如,陈宾宾等[17]将土壤含水量自然落干至饱和含水量的100%、80%和60%后复水分别称为轻-、中-和重-干湿交替灌溉,而丁紫娟等[18]设置的干湿交替灌溉则以土壤质量含水率为田间持水量的80%左右作为复水界值。据此,干湿交替灌溉技术的应用方法各有不同,但技术核心是一致的,都是以水稻生育过程中土壤保持水层和自然落干的相互交替为特征。

2 干湿交替灌溉对水稻产量和水氮利用效率的影响

干湿交替灌溉技术可通过减少灌溉用水量大幅度提高水分利用效率,这是该技术被公认的显著效应[9,19]。但是,干湿交替灌溉技术对水稻产量和氮肥利用效率的影响仍存在争议[20]。与常规灌溉相比,干湿交替灌溉能够保持甚至可以提高水稻产量和氮肥利用效率[21-22],但也有其降低产量和氮肥利用效率的报道[5,23]。这可能与品种自身特性差异或者稻田土壤质地和落干程度、大气温度及降雨量等外界环境的不同有关[13,24]。研究显示,干湿交替灌溉对水稻产量和氮肥利用效率的正负效应主要取决于土壤落干的程度,其中AWMD不仅节约用水,还明显提高了水稻产量和水氮利用效率,而AWSD虽然减少了灌溉用水量,但显著降低了产量和氮肥利用效率[25]。关于干湿交替灌溉对水稻产量和水氮利用效率的作用机制一直受到农业科研人员的高度重视,已有的研究主要集中在稻田土壤理化性状与生物学性状[26-28]、根系形态生理特性[29-31]以及地上部农艺性状与生理特性[24,32]等方面。

2.1 对稻田土壤理化与生物学性状的影响

稻田土壤作为水稻根系活动的主要场所,对水稻根系形态生理、氮素吸收和利用及产量与稻米品质形成具有重要影响。干湿交替灌溉会引起稻田土壤理化特性[33-34]和生物学性状[35]的改变,从而直接或间接地影响水稻的生长发育。

与常规灌溉相比,AWMD(轻-干湿交替灌溉)可提高水稻土壤孔隙度,增加土壤中硝态氮、有机质、速效氮、速效磷和速效钾等含量,降低土壤容重,而AWSD(重-干湿交替灌溉)下土壤铵态氮和有机质含量减少[27,33-34]。而且,干湿交替灌溉会使水稻土壤氧化还原电位(Eh)升高,pH(酸碱度)和EC(电导率)发生变化,土壤通气性提高[26,28,36]。研究者发现玉米隔沟交替灌溉下的土壤呼吸速率高于常规灌溉(沟沟灌溉),而土壤呼吸速率昼夜变化的幅度小于常规灌溉[37]。在大田研究中,水稻灌浆期AWMD方式下土壤水分和氧气含量存在一定的此消彼长关系,而且适度的干湿交替灌溉能在一定程度上调节水稻根系周围水分与氧气的平衡[38]。同样的,周期性干湿交替处理盐碱地的湿地土壤能明显激发土壤的呼吸作用,而长期的水分过饱和或干旱均会抑制土壤呼吸[39]。在生物学性状方面,很多学者提出稻田土壤的蔗糖酶、脲酶和酸性磷酸酶活性与水稻产量呈显著或极显著正相关,细菌、真菌和放线菌数量与水稻结实率和千粒重关系密切[27,33-34]。在水稻盆栽试验中,干湿交替灌溉使土壤细菌、放线菌活性和数量都呈增加趋势,进而促进水稻根系生长和产量形成[36]。简言之,AWMD可通过适度调控土壤水分,一方面改善水稻根际环境,提高土壤相关酶的活性,影响土壤中与营养循环相关的好氧/厌氧细菌的比例,从而增强土壤养分的有效性[26,28];另一方面通过改善土壤通气性,提高根系吸收能力,从而有助于维持植株地上部较高的生理活性,促进籽粒灌浆[40]。

2.2 对水稻根系形态生理的影响

根系作为水稻植株的重要组成部分,既是水分和养分吸收的主要器官,又是合成多种氨基酸、有机酸和激素等物质的重要场所[41-42],其形态生理特征对稻株地上部的生长发育和水氮利用效率至关重要[43]。

干湿交替灌溉对水稻根系形态生理特征具有重要调控作用。据报道,免耕抛秧水稻于分蘖高峰期、抽穗期和灌浆盛期干湿交替灌溉处理(土壤落干至田间持水量的70%复水)下单株根干质量、根半径、根表面积和总根数均显著高于常规灌溉[29]。然而,全生育期的AWSD会显著降低水稻主要生育期的根长[30-31]。全生育期的AWMD可显著提高水稻灌浆期根系氧化力、伤流量及其分泌物中有机酸总量和细胞分裂素(玉米素和玉米素核苷)含量,但是AWSD却明显降低了根系伤流量及其分泌物中有机酸总量和细胞分裂素含量[30-31]。而且,适度干湿交替灌溉方式下的免耕抛秧水稻根系活力及其超氧化物歧化酶活性也显著高于常规淹灌[29]。近来有学者指出,结实期AWMD处理下复水后水稻根系形态和根系活力也均明显高于常规灌溉[27]。然而,不同水稻品种根系形态生理特性对干湿交替灌溉的响应特

点存在不同[24]。比如,AWMD可显著提高抗旱性较强品种(扬稻6号和旱优8号)复水后根系氧化力及根系中玉米素和玉米素核苷含量,而对抗旱性较弱品种(两优培九和镇稻88)根系的上述指标无显著影响[24]。综上,干湿交替灌溉对水稻根系形态生理的影响效应会因品种和土壤落干程度的差异而不同。

2.3 对水稻地上部农艺性状与生理特性的影响

干湿交替灌溉对水稻地上部农艺性状与生理特性的影响主要表现在对茎蘖成穗率、叶面积指数、叶片光合生产能力、茎秆(含鞘)物质运转及籽粒灌浆能力的调控方面。

与常规灌溉相比,AWMD减少了无效分蘖数,提高了水稻茎蘖成穗率和叶面积,增加了叶长、粒叶比、透光率、抽穗期-成熟期的干物质积累量和叶片光合速率[14],还促进了茎秆中非结构性碳水化合物(nonstructural carbohydrate,NSC)的积累,并显著提高了花后茎秆中NSC向籽粒的运转量[32]。徐云姬等[15]研究发现AWMD和AWSD可通过增强茎秆α-淀粉酶和β-淀粉酶活性促进同化物质的再运转与分配,进而提高茎秆储藏物质对千粒重的贡献。研究表明,AWMD提高水稻叶片光合速率的原因可能在于叶片硝酸还原酶、谷氨酰胺合成酶和谷氨酸合成酶等氮代谢相关酶活性的增强[44],以及叶绿体生物合成通路、光合作用-天线蛋白通路、光合作用过程和脱落酸信号转导通路中的相关基因的表达上调[45]。而干湿交替灌溉提高水稻茎秆同化物转运的重要原因可能包括:(1)茎秆淀粉和蔗糖代谢通路、植物激素信号转导通路、丝裂原活化蛋白激酶信号通路的相关基因差异表达[46];(2)茎秆中叶绿素a/b结合蛋白、1,5-二磷酸核酮糖羧化酶(RuBisCO)和放氧蛋白(oxygen evolving protein)等光合作用相关蛋白的差异表达[47-48]。目前,关于干湿交替灌溉影响水稻茎蘖成穗率的内在机制还不清楚,需要进一步探究。

在籽粒灌浆方面,水稻弱势粒的灌浆速率和粒重显著低于强势粒[49-50]。AWMD较常规灌溉显著提高了水稻弱势粒的平均灌浆速率、最大灌浆速率和粒重,而AWSD的作用相反[18]。这主要归功于AWMD显著增强了弱势粒中蔗糖合酶、腺苷二磷酸葡萄糖焦磷酸化酶、淀粉合酶和淀粉分支酶等淀粉合成关键酶活性[49]。而且,AWMD可明显提高水稻弱势粒蔗糖合酶基因(*SuS2*和*SuS4*)、腺苷二磷酸葡萄糖焦磷酸化酶基因(*AGPL1*、*AGPL2*、*AGPL3*和*AGPS2*)、淀粉合酶基因(*SSI*、*SSIIa*、*SSIIc*和*SSIIIa*)和淀粉分支酶基因(*SBEI*和*SBEIIb*)的相对表达量,而AWSD则降低了弱势粒中上述基因的相对表达量[49]。此外,AWMD上调了水稻弱势粒中光合作用相关蛋白(丙酮酸磷酸双激酶)、糖代谢和能量代谢相关蛋白(甘油醛-3-磷酸脱氢酶)、蛋白质和氨基酸代谢相关蛋白(5-甲基四氢叶酸-同型高半胱氨酸甲基转移酶)、激素及信号转导相关蛋白(S-腺苷甲硫氨酸合酶和乙二醛酶I)以及抗逆相关蛋白(锰超氧化物歧化酶)等的表达,而AWSD不仅下调了弱势粒中上述蛋白质的表达,还上调了抑制信号传导和能量代谢等有关蛋白的表达[50-51]。这些研究进一步表明,AWMD方式下水稻弱势粒中淀粉和蛋白质等物质合成相关酶活性的增强是其粒重提高的重要原因。

3 干湿交替灌溉对稻米品质的影响

干湿交替灌溉对稻米品质形成具有重要调控作用。研究表明,AWMD可显著提高稻米糙米率、精米率、整精米率以及米粉(淀粉)的峰值黏度和崩解值,降低稻米垩白粒率、垩白度以及淀粉的热浆黏度、最终黏度和消减值[16,52],而AWSD的作用与之相反[12,14]。Xu等[52]研究结果显示,AWMD降低了精米蛋白质、总氨基酸和重金属(砷)含量,表明AWMD有利于稻米加工、外观、蒸煮与食味及卫生品质的改善,但对营养品质具有一些负面影响。近年,张耗等[53]提出,AWMD可增加精米支链淀粉和总淀粉含量、中淀粉粒(1.5~20 μm)数量和体积百分比,降低淀粉相对结晶度及大淀粉粒(> 20 μm)数量和体积百分比。Xiong等[54]也发现,AWMD降低了精米淀粉粒尤其是大淀粉粒(> 10 μm)的大小和支链淀粉短链分布比例,但增加了支链淀粉中链和长链分布比例。上述研究结果表明,AWMD具有改善稻米淀粉品质的作用。然而,AWMD对稻米品质的影响也有不同的结果。王肖凤等[55]发现,AWMD较常规灌溉显著降低了再生季稻米的糙米率、精米率和整精米率,增加了垩白度。还有研究提出,AWMD增加了精米氨基酸和酚酸含量,降低了脂类和生物碱含量,从而提高了精米营养品质[56]。关于稻米加工、外观和营养品质对干湿交替灌溉响应差异的原因可能还是在于品种、落干程度及生长环境的不同,需要进一步研究。目前,干湿交替灌溉调控稻米品质形成的作用机制仍集中在根系活性[14]、叶片光合作

用[53]和灌浆期籽粒蔗糖-淀粉代谢途径关键酶活性[12]等方面。

4　干湿交替灌溉与氮肥互作对水稻产量和水氮利用效率的影响

干湿交替灌溉与氮肥互作对水稻产量和水氮利用效率影响的报道比较多，主要集中在干湿交替灌溉与施氮量或氮肥形态互作效应的研究。研究显示，AWMD 与施氮量为 240 kg/hm^{2}或 360 kg/hm^{2}处理组合的水稻产量及水氮利用效率最高[21,31]。据报道[17]，哈尔滨地区轻-干湿交替灌溉（土壤含水量自然落干至饱和含水量的 100% 后复水）与 150～225 kg/hm^{2}施氮量组合对当地粳稻籽粒灌浆及产量形成最为有利，在中-干湿交替灌溉（土壤含水量自然落干至饱和含水量的 80% 后复水）条件下，氮肥用量可适当降至 75～150 kg/hm^2。在非洲塞内加尔河流域，AWMD 与 150 kg/hm^{2}施氮量组合也是实现水稻产量和水氮利用效率协同提高的最优选择[57]。在浙江富阳地区，AWMD 与 160 kg/hm^{2}施氮量组合也可显著提高三系籼型杂交稻天优华占的产量与水氮利用效率[58]。徐国伟等[44]进一步指出，在 AWMD 方式下水稻氮肥利用效率随施氮量（0～360 kg/hm^2）的增加而增加，而 AWSD 下其氮肥利用效率随施氮量的增加呈先增后降的趋势。在干湿交替灌溉与氮肥形态互作方面，AWMD 与铵态氮、硝态氮耦合施用（1∶1）后产量和氮肥利用效率最高，明显高于单纯与铵态氮或硝态氮配施[59-60]。赵建红等[61]在进行干湿交替灌溉与不同氮肥运筹对免耕厢沟栽培杂交稻氮素利用及产量影响试验时发现，在总施氮量为 150 kg/hm^{2}条件下，干湿交替灌溉与氮肥按基肥∶分蘖肥∶穗肥＝4∶2∶4 比例施用为最佳水氮运筹模式，其产量和水氮利用效率最高。此外，AWMD 与缓控释肥的合理施用也可协同提高水稻产量和水氮利用效率[62-63]。

综上，干湿交替灌溉与氮肥施用存在显著的互作效应，其中 AWMD 与适宜的施氮量或氮肥形态耦合施用对水稻产量和水氮利用效率的提高具有促进作用。究其原因，也主要有 2 个方面：(1) 改善了水稻根际环境，加强了土壤酶活性及微生物数量，进而提高了土壤养分含量[64-65]；(2) 增加了根系生理活性，提高了植株氮吸收量和干物质积累量、叶面积指数和叶片光合性能以及茎秆 NSC 转运率，进而促进了地上部的生长发育以及灌浆中后期弱势粒的充实，最终达到增产增效的目的[59,66-67]。

5　干湿交替灌溉与氮肥互作对稻米品质的影响

干湿交替灌溉与氮肥耦合施用调控稻米品质形成的研究报道虽然较少，但已有研究表明干湿交替灌溉与施氮量可互作调控稻米品质的形成。在前人研究中，中氮（240 kg/hm^2）或高氮（360 kg/hm^2）水平与 AWMD 处理下的稻米加工、外观品质和淀粉品质显著优于常规灌溉，中氮水平与 AWSD 的稻米品质显著劣于常规灌溉[68]。在盆栽试验中，180 kg/hm^{2}和 220 kg/hm^{2}施氮量下，东北粳稻（沈稻 47 和粳优 586）的加工、外观、蒸煮与食味及营养品质均以 AWMD 为佳[68]。在 180 kg/hm^{2}施氮量下，AWSD 方式下稻米的整精米率、胶稠度、峰值黏度和崩解值低于浅水层灌溉，而其垩白粒率、垩白度、直链淀粉含量及消减值高于浅水层灌溉[69]。王春歌等[70]以南粳 9108 为试验材料，研究发现 AWMD 与 276 kg/hm^{2}施氮量耦合模式下，水稻支链淀粉中的短链分布所占比例较大，内部片层的有序性和相对结晶度较高，有利于水稻淀粉的充分糊化，提升口感。因此，AWMD 与适宜施氮量的交互作用对水稻品质形成具有显著的正面效应。关于干湿交替灌溉与氮肥互作对稻米品质的调控机制缺乏研究。

6　问题与展望

干湿交替灌溉技术对水稻产量、氮肥利用效率和稻米品质的调控效应虽然存在争议，但是适度的干湿交替灌溉（如：轻-干湿交替灌溉）有利于水稻产量和氮肥利用效率的提高及稻米品质改善。干湿交替灌溉对水稻生长发育、产量与稻米品质形成的调控作用与稻田土壤的落干程度息息相关。在以往的相关研究中，土壤落干程度（如土壤水势、含水量、持水量以及灌水量）的测量标准不一[17,69,71]，有的甚至只是简单地估测落干程度[61]，而这些指标对研究结果或结论具有重要影响。因此，本文提出对土壤落干程度的监测采用统一的方法。鉴于以土壤水势为指标进行干湿交替灌溉的实施不仅具有科学的理论基础，还可避免其他灌溉指标对土壤类型、质地、降雨量和作物蒸腾量及其本身遗传特性等的影响[72]，建议研究者采用土壤水势作为土壤落干程度的测量指标，且对监测的稻田土壤深度作出说明，这样更有利于明确干湿交替灌溉技术对水稻产量、水氮利用

效率和稻米品质的调控效应。

干湿交替灌溉对水稻产量和水氮利用效率的影响及其机制研究相对较多,但还不够全面、不够深入。呼吁更多作物遗传育种学领域的学者关注干湿交替灌溉对水稻产量、水氮利用效率和稻米品质的调控效应研究,从遗传学、分子生物学以及生理学等多角度揭示干湿交替灌溉对水稻产量、稻米品质形成及资源利用效率的调控机制。干湿交替灌溉对水稻茎蘖成穗率的影响机制尚不清楚。茎蘖成穗率是衡量水稻群体质量好坏的重要指标,与水稻产量呈正相关关系[73]。因此,阐明干湿交替灌溉调控水稻茎蘖成穗率的内在机制对高茎蘖成穗率水稻品种的选育具有推动作用。此外,干湿交替灌溉及其与氮肥互作对稻米品质形成的调控机制缺乏研究。水稻籽粒建成期是稻米品质形成的最终决定阶段,籽粒的物质组成及其形成特点对稻米品质必然具有显著影响。稻米中淀粉、蛋白质和脂肪在质和量上的差异决定着稻米品质的优劣[74-75]。然而,水稻籽粒中这三大主要物质代谢的变化特点及其互作机制与稻米品质的关系尚不明确。因此,建议今后重点开展以下研究:(1)利用基因组学、转录组学、蛋白质组学、脂质组学以及代谢组学等技术,深入解析干湿交替灌溉对水稻茎蘖成穗率的调控机制;(2)基于水稻籽粒淀粉、蛋白质和脂肪的合成与分解代谢深入开展干湿交替灌溉、氮肥施用等栽培措施对稻米品质形成的调控机制研究,开发改善稻米品质的新途径。通过上述研究,可为进一步开展水稻"高产、高效、优质"育种和栽培提供理论依据和技术支撑。

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Progress on effects of alternating wet and dry irrigation on use efficiency of water and nitrogen, yield and quality of rice

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Abstract Alternating wet and dry irrigation (AWD), as an important water-saving irrigation technique, has significant impacts on the use efficiency of water and nitrogen, yield and quality of rice. The positive or negative effect of AWD on rice is mainly determined by the degree of soil drying. In this article, the mechanisms underlying effects of AWD on the use efficiency of water and nitrogen, yield and quality of rice were reviewed from the aspects including physicochemical and biological characteristics of soil, morphological and physiological traits of rice root, agronomic and physiological characteristics aboveground. The effects of interaction between AWD and nitrogen fertilizer on the use efficiency of water and nitrogen, yield and quality of rice were briefly introduced. Some problems such as different standards for monitoring soil drying and incomplete regulatory mechanism of AWD were existed, therefore it is recommended that multiple omics techniques should be used to analyze the mechanism of AWD regulating percentage of productive tillers in rice and the mechanism of AWD and nitrogen application regulating rice quality should be studied based on the metabolism of starch, protein and fat in grains. It will provide theoretical basis for cultivating rice with high yield, high efficiency, and good quality.

Keywords rice (*Oryza sativa* L.); alternating wet and dry irrigation; yield; use efficiency of water/nitrogen; rice quality

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