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# 作物种子萌发生理与遗传研究进展

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**摘要:** 种子萌发是一个多基因控制的数量性状,受环境条件和种子处理等多种因素的影响。本文综述了外界环境和种子引发处理对作物种子发芽的影响,与作物种子萌发相关 QTL 定位以及与种子萌发相关基因的克隆等研究,并对今后作物种子萌发生理和遗传研究进行了展望。

**关键词:** 种子萌发; 种子生理; QTL 定位; 基因克隆
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# Advances in research on physiological and genetic mechanism of seed germination

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**Abstract:** Seed germination, a quantitative trait controlled by multiple genes, is influenced by many factors, including environmental conditions and seed treatments. In this paper, the effects of external environment and seed priming treatment on seed germination, the quantitative trait loci (QTL) mapping of seed germination, and the cloning of genes related to seed germination in crops were reviewed. Furthermore, the future physiological and genetic researches of seed germination were prospected.

**Key words:** seed germination; seed physiology; QTL mapping; gene cloning

种子萌发(Seed germination)是指具有生活力的种子通过休眠或解除休眠后,在适当的发芽条件下,形成具有正常根、茎、叶的幼苗的过程,是植物为适应环境以保持自身繁殖而形成的一种生物特性。在生理上,表现为种子通过休眠或解除休眠吸水后,开始进行物质代谢和能量代谢,经过一定时期种胚突破种皮露出胚根;在分子生物学水平上,表现为种子某些基因的表达、酶活化和诱导,引发一系列与种胚生长相关的反应[1]。在农业生产上,作物种子萌发直接关系到农业生产丰收和国家粮食安全,对深入研究作物种子萌发的生理机制、遗传机理和基因克隆等具有重要的理论意义和生产实践意义。

## 1 环境条件和种子引发处理对种子发芽的影响

种子萌发吸胀(Seed imbibition)过程可以分为3个阶段:开始阶段、滞缓阶段、重新大量吸水阶段[2]。如图1显示,在开始阶段,种子吸水是一个快速吸水期(阶段1),吸水后种子立即开始修复和活化生理生化过程,如细胞器、酶活性等动员。当种子吸水超过60%后,种子吸水进入滞缓阶段(阶段2),种子内部代谢活动开始活跃,转入一个新的生理状态,种胚细

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胞迅速生长,渗透活性物质如糖、氨基酸、钾离子的大量累积,细胞壁酸化促进细胞壁聚合物松动。同时,伴随着 $H^+$-ATP 酶活性增强,进一步促进种子吸水,弱化胚周围组织(如胚乳)限制,最终引起胚轴伸长,胚突破种皮,发芽完成。此后,种子重新进入大量吸水阶段。在种子发芽过程中,种子内部丰富的营养物质(脂质、蛋白质、淀粉)被分解和利用,维持幼苗早期生长直至幼苗能自养(图 1)。

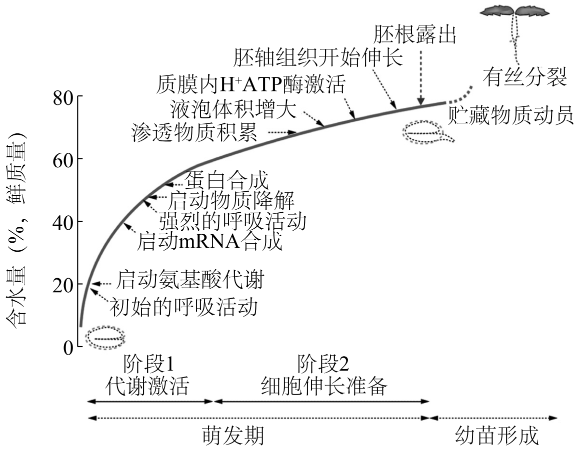

**图 1 种子萌发过程及其生理变化**[2]

**Fig.1 Germination of seed and physiological process**[2]

种子能否正常萌发,萌发后能否发育成正常构造的幼苗,除了种子内部的生理条件外,还需适宜的外部环境条件,如充足的水分、氧气、适宜的温度等。近年来,自然灾害频发,如低温、干旱、土壤盐碱化、土壤中重金属超标等给农业生产带来了巨大的威胁。因此,对低温、干旱、涝害、盐胁迫、重金属污染等非生物逆境条件下种子萌发问题的研究逐渐成为热点[3-10]。对水稻种子萌发期耐盐、耐冷、耐旱、耐重金属等特性的研究,初步阐明了非生物胁迫下水稻种子萌发的生理特点[11-12]。低浓度盐害(50 mmol/L NaCl)对水稻种子萌发影响不大,中度以上盐害(>100 mmol/L NaCl)对种子发芽有明显抑制,种子萌发期盐害主要是渗透效应、离子效应。渗透效应引起溶液渗透势降低而使种子吸水受阻,从而影响种子萌发。离子效应一方面表现为离子抑制种子萌发,另一方面表现为离子渗入种子降低种子渗透势,加速吸水而促进萌发。15 ℃以下的低温对水稻种子发芽率、发芽速度产生较大影响,会引起种子吸胀损伤。在低温下进行吸胀或者在常温下吸胀过程进行得过快,都会造成种子的损伤,以致种子活力下降,影响到田间出苗率和幼苗的健壮生长。种子吸胀冷害和吸胀伤害表现在细胞溶质渗漏、呼吸代谢和细胞结构等方面。

种子引发处理也叫做渗透调控技术,控制种子缓慢吸水使其停留在吸胀的第二阶段,让种子处于准备发芽的代谢状态,防止胚根伸出。种子引发能有效提高种子活力,包括显著提高种子的田间出苗速度、出苗整齐度以及幼苗素质,减少种子休眠,提高其在逆境如低温、高温、干旱、盐渍或淹水胁迫等下的发芽率、出苗率等[13-14]。利用生长素、细胞分裂素、赤霉素、脱落酸和乙烯等激素进行种子引发处理能改善重金属镉胁迫下的豌豆发芽,表明使用激素引发能有效提高种子萌发时耐重金属胁迫的能力[15]。虽然有关引发处理提高种子萌发的机理尚未十分清楚,但在生理水平上,已经发现种子引发处理促进细胞膜修复和提高膜的完整性,减少染色体畸变频率,修复因老化引起的染色体损伤[16]。引发处理也会引起种子内源激素水平变化,促进体内代谢,相关酶类活性的增加[17],促进贮藏物质的分解等[18]。近来有研究结果表明,一定浓度的盐引发处理,激活赤霉素(Gibberellin acid, GA)生物合成相关基因表达,增加种子中 GA 含量,促进种子发芽[19]。种子吸胀的滞缓阶段(图 1,阶段 2)是种子引发的关键过程,利用蛋白组学技术鉴定了多个参与水稻种子引发的基因,从中获得 3 个适合水稻种子引发处理的分子标记[20]。

## 2 种子萌发相关 QTL 的定位

种子萌发是一个由多基因控制的复杂数量性状,随着分子标记和基因组作图技术的发展,有关作物种子萌发相关数量性状位点(Quantitative trait locus, QTL)的研究已有不少报道(表 1)。Miura 等[21]利用 98 个家系组成的水稻回交重组自交系(Backcross recombinant inbred lines, BILs)群体,检测和定位了 *qLG-2*、*qLG-4* 和 *qLG-9* 等 3 个控制种子寿命的 QTLs。Fujino 等[22]利用水稻 BILs 群体定位到 *qLTG-3-1*、*qLTG-3-2* 和 *qLTG-4* 等 3 个控制水稻种子低温发芽的 QTLs。Wang 等[11-12, 23-24]利用水稻重组自交群体(Recombination inbred lines, RILs)于正常条件、高浓度盐胁迫和低温胁迫条件下进行研究,发现了至少 50 个控制水稻种子萌发的 QTLs。其

中,控制发芽速度的 QTLs 与控制种子质量、大小及种子休眠的 QTLs 位置相近,表明种子发芽速率可能与种子质量、大小及种子休眠特性相关[23],水稻种子萌发也受上位性 QTLs 互作的影响[12]。Li 等[25]定位了 1 个低温条件下稳定表达的种子发芽 QTL *qLTG-9*。此外,有关水稻种子休眠 QTL 的研究也有不少报道[26-28]。通过动态分析水稻不同发育时期种子休眠性变化,定位了多个控制水稻种子休眠的加性和上位性 QTLs,定位的种子休眠 QTLs 与抽穗期 QTL 存在共定位现象[27-28]。有关水稻种子萌发期物质利用[29]、低氧条件下水稻种子胚芽鞘伸长[30]等性状 QTL 也有报道。Dias 等[31]在低温条件下检测到 3 个控制苜蓿下胚轴伸长的 QTLs,定位了 1 个控制胚轴宽度的上位性 QTL,且其参与低温条件下胚轴伸长。Basnet 等[32]在正常和盐胁迫下定位了 26 个白菜种子发芽和幼苗活力 QTLs,并检测到 2 个控制种子发芽的 QTL 热点区,发现这 2 个 QTL 热点区存在互作。Hu 等[33]在正常温度下定位了 3 个控制玉米种子发芽率 QTLs,6 个控制种子低温发芽率 QTLs,6 个控制低温条件下主根长度 QTLs,并对 5 个候选基因进行了分析。

随着关联分析方法的发展,全基因组关联方法定位作物种子萌发 QTLs,已在水稻[34-35]、苜蓿[36]、大豆[37]、油菜[38]等作物上得到应用。Yu 等[36]利用全基因关联分析定位到 36 个苜蓿种子萌发期耐盐性位点,确定了 14 个候选基因。Kan 等[37]利用 191 份大豆地方品种,利用不同耐盐指标,定位了 8 个稳定表达的大豆种子耐盐萌发 SNP 位点,并预测了 5 个与种子耐盐萌发相关候选基因。Hatzig 等[38]利用 248 份油菜资源检测到多个控制种子发芽速度、发芽率、胚根伸长等位点,并预测了 18 个候选基因。

**表 1　主要农作物种子萌发 QTL 定位总结**

**Table 1　Summary of the quantiative trait loci (QTLs) controlling seed germination of some crops**

| 作物 | 性状 | 群体 | 参考文献 |
|---|---|---|---|
| 水稻 | 种子寿命 | Nipponbare/Kasalath BILs | [21] |
| 水稻 | 低温发芽 | Italica Livorno/Hayamasari BILs | [22] |
| 水稻 | 种子活力 | IR28/Daguandao RILs | [23] |
| 苜蓿 | 低温、高温发芽 | LR5/LR4 RILs | [31] |
| 水稻 | 低温发芽 | IR28/Daguandao RILs | [11] |
| 水稻 | 耐盐发芽 | IR26/Jiucaiqing RILs | [12] |
| 水稻 | 种子休眠 | Nona Bokra/Koshihikari CSSLs | [26] |
| 水稻 | 低温发芽 | USSR5/N22 RILs | [25] |
| 水稻 | 物质利用 | IR26/Jiucaiqing RILs | [29] |
| 水稻 | 低温发芽 | Hokuriku-142、Yume-Toiro/Nada-Hikari、Gohyaku-Mangoku RILs | [39] |
| 水稻 | 种子活力 | ZS97/ MH63 RILs | [40] |
| 水稻 | 种子休眠 | IR28/Daguandao RILs | [27] |
| 水稻 | 种子休眠 | IR26/Jiucaiqing RILs | [28] |
| 水稻 | 种子耐贮藏 | Nanjing35/N22//Nanjing35 BILs、USSR5/N22 RILs | [41] |
| 白菜 | 种子发芽、种子活力 | DH 群体 | [32] |
| 水稻 | 低氧萌发 | 自然群体、Nipponbare/IR64 RILs | [30] |
| 水稻 | 低温发芽 | 自然群体 | [34] |
| 大豆 | 耐盐发芽 | 自然群体 | [37] |
| 油菜 | 种子发芽 | 自然群体 | [38] |
| 小麦 | 种子休眠 | Yangxiaomai/Zhongyou 9507 RILs | [42] |
| 甜玉米 | 物质利用 | 109/Q267 RILs | [43] |
| 高粱 | 低温发芽 | 自然群体 | [44] |
| 水稻 | 种子休眠 | 自然群体 | [35] |
| 玉米 | 低温发芽 | B73/Mo17 RILs | [33] |
| 苜蓿 | 耐盐发芽 | 自然群体 | [36] |

## 3　种子萌发相关基因的克隆

植物激素通过信号传导对种子内的各种生理变化做出反应，调节种子内部一系列蛋白质、酶的代谢，从而控制种子的萌发。与种子萌发有关的植物激素主要是赤霉素（GA）和脱落酸（ABA）。GA 促进种子萌发是增强胚的生长势，软化胚周围组织（如种皮和胚乳）以利于胚根的突破。ABA 对种子萌发和萌发后的与贮藏物代谢有关的某些酶活性有抑制作用。通过对拟南芥突变体的研究，已经鉴定出一些与 GA 信号转导有关的蛋白组分，如 RGL2、SPY、SLY1、CTS、Gar2-1、G 蛋白偶联受体等[45-47]，克隆了多个与 ABA 合成和信号传导相关的基因，如 *ABI1*、*ABI2*、*ABI3*、*ABI4*、*ABI5*、*LEC1*、*LEC2*、*FUS*、*MARD1*、*CIPK3*。*ABI3* 具有种子专一性，*abi3* 突变体种子贮藏物的积累减少，胚胎晚期丰富蛋白（Late embryogenesis abundant protein，LEA）表达量降低，表明 *ABI3* 表达产物参与调节种子发育基因的表达[48]。*ABI4* 和 *ABI5* 突变体与 *ABI3* 具有相似的表型，但不如 *ABI3* 突变体的表型变化明显，推测 *ABI4* 和 *ABI5* 可能与 *ABI3* 共用相同的 ABA 响应途径[49]。近年来，有关激素对种子萌发影响的研究又有不少相关报道[50-53]。拟南芥 *PYL/RCAR* 同源基因在水稻中能正调节 ABA 信号转导通路[50]，拟南芥 *SKP1* 基因参与 ABA 信号转导，*SKP1* 类基因通过 SCF 介导的蛋白降解正向调控 ABA 信号转导[51]，拟南芥 RAV1 转录因子通过调控 *ABI3*、*ABI4* 和 *ABI5* 表达在 ABA 信号途径中发挥着重要的作用[52]，s-亚硝基化能引起 ABI5 降解，促进种子萌发和幼苗的生长[53]。ABA、GA 以及乙烯等激素互作在种子萌发过程中的作用也是今后研究的热点[54]。

通过图位克隆的方法，已有多个与种子萌发相关的主效 QTL 被克隆。控制水稻低温发芽的 QTL *qLTG-3-1* 具有细胞囊泡化作用，其分子作用机理尚不清楚[55]。控制水稻种子休眠的 *Sdr4* 基因也被成功克隆，*Sdr4* 基因能依次正调控 3 个种子与成熟相关的蛋白基因，从而诱导 ABA 的合成，抑制萌发后基因的表达，增强休眠性并防止穗发芽[56]。Schwember 等[57]利用莴苣 RILs 群体定位到的 1 个控制引发处理能提高高温胁迫下种子发芽率的主效 QTL，通过精细定位与克隆，该基因为 *LsNCED4*，是 1 个编码脱落酸生物合成途径中关键酶（9-cis-epoxy-carotinoid dioxygenase）基因。近年来多个参与作物种子萌发相关基因被克隆与验证。Park 等[58]通过突变体克隆方法鉴定到 1 个 RING 型 E3 连接酶基因 *OsDSG1*，能延迟种子萌发，试验证明该基因是水稻种子萌发中 ABA 信号途径的主要调节因子。Nakamura 等[59]通过同源克隆方法鉴定到 1 个控制小麦种子休眠基因 *MFT*，该基因在较低温度成熟的休眠种子中上调表达。Kretzschmar 等[60]通过 QTL 图位克隆了水稻海藻糖-6-磷酸酶基因 *ostpp7*，该基因参与海藻糖-6-磷酸代谢，通过增加“源库”从而提高种子萌发过程淀粉动员，促进胚芽鞘生长，最终提高水稻种子厌氧萌发能力。Li 等[61]采用同源克隆方法的研究结果表明，上调玉米 ABA 失活基因 *zmaba8ox1b* 能促进种子萌发，该基因通过促进细胞膨胀从而引起种子萌发杂种优势。

## 4　展　望

目前，作物种子萌发的生理与分子遗传研究还主要集中在模式作物水稻、油菜等少数几个作物上，在其他农作物和蔬菜等作物上的研究相对较少。种子萌发过程受种子发育、收获、贮藏和处理等多个因素影响，受环境因素影响较大，研究过程中尤其要考虑逆境胁迫下种子萌发的生理与分子遗传机理。今后，为了准确开展种子萌发遗传研究，应建立高通量、现代化、标准化的种子萌发和种子活力等的鉴定技术，准确开展表型鉴定。在基因定位方法方面，除了采用连锁作图法分析和定位种子萌发 QTL 以外，可以更多地采用关联分析法发掘和定位更多与种子萌发相关的基因。种子萌发是复杂的数量性状，真正探明种子萌发机理还需要从生理、生化、生理生态、分子遗传、系统演化以及模型构建等多个角度，进行多学科交叉研究。要进一步加强 QTL/基因克隆与功能研究，对克隆的与种子萌发相关的关键 QTL/基因，可以通过分子标记辅助选择技术或转基因技术培育高种子活力品种。同时，掌握种子引发处理提高种子萌发的机理，可以建立、优化种子处理技术，进一步提高种子处理效果，实现种子处理的大规模应用，提升种业竞争力。

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