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植物异三聚体 G 蛋白调控系统研究进展

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摘要 动物异三聚体G蛋白由α, β和γ 3个亚基组成, 通过G蛋白偶联受体(GPCR)感受外部刺激将信号转化为离子通道、酶和其他作用蛋白进而影响一系列的细胞行为. 近10年对模式植物水稻(*Oryza sativa*)和拟南芥(*Arabidopsis thaliana*)G蛋白的研究发现了植物有别于动物G蛋白信号传导途径的新机理. 植物G蛋白与动物一样也含有α, β和γ 3个亚基, 但是植物Gα亚基能自发地进行GTP与GDP的交换, 使得G蛋白能够自我激活, 这也使得植物不需要所以也就不存在GPCR. 此外, 植物还有不同于动物的大型Gα亚基和非典型Gγ亚基. 水稻非典型Gγ亚基表现出C端抑制N端的自我抑制机制, 并显著影响产量性状. 本文着重介绍模式植物拟南芥和水稻G蛋白信号调控、效应和功能的相关研究进展, 总结植物与动物G蛋白信号传导的异同, 讨论通过G蛋白提高农作物产量的可能性.

关键词 动物 G 蛋白, 植物 G 蛋白, 作物增产

1971年的诺贝尔医学奖颁给了E. Surtherland博士, 以表彰其在有第二信使之称的cAMP(cyclic adenosine monophosphate)方面的研究. 随后的研究聚焦在激素如何经由细胞膜表面受体来活化腺苷酸环化酶(adenylate cyclase, AC), 进而将ATP转化成cAMP. 20世纪70年代初, M. Rodbell博士发现AC的产生需要GTP和另外一种活化因子, 这种因子就是GTP相关的蛋白. A. Gilman博士从这个发现中获得启示, 并在1980年成功纯化到了这种激活AC的细胞组分——G蛋白. 因此, Gilman博士和Rodbell博士分享了1994年诺贝尔医学奖. G蛋白的上游是一类具有7个跨膜区域的细胞膜受体蛋白, 它们就是G蛋白偶联受体(G protein-coupled receptor, GPCR). 这些蛋白质横跨在细胞膜之上, 接触外面世界的刺激信号, 与细胞内部的物质发生作用, 是细胞外刺激信号进入细胞内的桥梁. R. Lefkowitz博士与B. Kobika因为在GPCR领域的卓越研究获得了2012年的诺贝尔奖. 很多人类疾病与G蛋白偶联受体相关, 因此它是制药行业重点研究的对象, 在所有现代药物中, 有40%以上是以G蛋白偶联受体作为靶点的[1]. 过去40年5位G蛋白研究者分享了3次诺贝尔奖, G蛋白信号已成为研究最广泛最深入的信号传导途径之一, G蛋白信号也作为最重要的分子生物学基础法则被编入生物学教材[2,3]. 然而这些研究都是以人类健康和医疗为出发点从动物研究上得到的结论, 科学家们开始设想是否能从植物中得到更多的G蛋白信息. 在过去的10年里, 通过对模式植物水稻(*Oryza sativa*)和拟南芥(*Arabidopsis thaliana*)G蛋白的研究, 发现了植物Gα亚基能自发地进行GTP与GDP交换的特性, 从而开辟了植物不同于动物G蛋白传导途径的新机理, 自我

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激活的特性使得植物不需要GPCR来激活G蛋白，而植物中也确实不存在典型的GPCR. 此外植物还有动物中不存在的大型Gα亚基和非典型Gγ亚基，大型Gα在N端有一端较长的包含半胱氨酸富集区域，而非典型Gγ在C端有一段半胱氨酸富集区域，水稻中非典型Gγ亚基C端的半胱氨酸富集区域表现出抑制N端典型Gγ区域的自我抑制机制，并显著影响产量性状. 这些从植物中得到的G蛋白信号传导机制可能有助于更深入了解G蛋白. 本文聚焦植物G蛋白体系，比较动植物G蛋白的差异，评述植物G蛋白调控机理，同时也关注G蛋白在农作物增产方面的应用前景.

1 动植物G蛋白信号的异同

1.1 动物G蛋白信号循环

动物异三聚体G蛋白(heterotrimeric GTP-binding proteins)由Gα，Gβ和Gγ组成，在失活状态时Gα，Gβ和Gγ形成异三聚体G蛋白，此时Gα与GDP嵌合. 在细胞膜上有7次跨膜结构的细胞表面感受子GPCR，GPCR与外部同源配体嵌合后发生跨膜跨度结构改变，使得Gα释放GDP核苷酸，并与GTP相嵌合. Gα与GTP嵌合使后发生结构改变，从Gβγ二聚体中游离出来. 此时自由态的Gβγ二聚体和GαGTP亚基处于激活状态，能够与其各自的靶蛋白相互作用，进而影响下游一系列的生物学过程. 这种靶蛋白在G蛋白体系中称作效应物，动物中两个典型的效应物是能够产生第二信使cAMP的腺苷酸环化酶和可以产生肌醇三磷酸肌醇、甘油二酯的磷脂C[4]. 随后GTP水解成GDP，Gα与GDP嵌合后重新与Gβγ二聚体嵌合，恢复稳定的失活形态(图1). G蛋白处于激活或失活状态取决于与GPCR嵌合的外部同源配体量和GTP水解速度. GTP水解受GTPase加速蛋白(GAPs)调控，特别是被称为G蛋白信号调控者的RGS蛋白，加速GTP水解使G蛋白失活[5]. 人类有至少37种RGS蛋白，分为10种基础结构，尽管其中一些含有膜定位的功能域，但是都没有跨膜结构域[6].

1.2 植物G蛋白信号循环

(ⅰ) 植物G蛋白的自我激活. 动植物G蛋白信号的主要差异是植物Gα能自发地进行GTP与GDP的交换，使得G蛋白能够自我激活(图1)[7]. Gα由两个功能域构成，分别是与GTP嵌合蛋白Ras有相似结构的功能域和拥有螺旋结构的功能域. Ras功能域包含能够与GPCR, RGS蛋白, Gβ, GTP等多种位点相关联的motif，而螺旋结构则将鸟嘌呤核苷酸嵌合位点环绕[8]. 动物Gα与GPCR嵌合后结构发生巨大改变，鸟嘌呤核苷酸嵌合位点张开进而进行核酸交换. 拟南芥Gα (*GPA1*)也有RAS功能域和螺旋区域[9,10]，但是*GPA1*结构的分子动态模拟发现，*GPA1*能够在没有GPCR的条件下自发地进行结构改变，这种植物特有的螺旋结构赋予了*GPA1*自发地与GDP分离并与GTP嵌合的能力，而动物这一过程需要GPCR的参与[7,11]. 动植物螺旋结构的动态差异使得三维结构相似的两个蛋白生化功能发生了明显改变，这使研究者们对螺旋结构的功能有了更深的认知.

(ⅱ) 植物没有典型的GPCR. 动植物G蛋白的另一个主要差异是植物没有典型的GPCR. GPCR具有保守的7次跨膜拓扑结构，但是即使在同一物种内GPCR也不具有保守序列，这使得用生物信息学手段很难构建出进化树来确定不同物种的GPCR[12]. 植物确实存在类似动物拥有7次跨膜拓扑结构的蛋白，但是还没有序列上的证据证明这些蛋白就是植物的GPCR. 动物GDP与GTP的交换需要GPCR，而植物G蛋白能自发地释放GDP后与GTP嵌合自我激活，因此植物不需要所以也就不存在GPCR. 但是因为植物确实有7次跨膜结构的蛋白，所以植物不存在GPCR的理论也受到质疑. 七螺旋蛋白heptahelical 1-5 (HHP1-5)与黄体激素和adipoQ受体(PAQRs)序列相似[13,14]，曾被认为是植物GPCR，但是人类PAQRs不是GPCR的同源物，而其与溶血素Ⅲ更加相似，溶血素Ⅲ并不含有7次跨膜结构[15]. GCR2 (G-coupled receptor 2), GTG (GPCR-type G protein), CAND2 (candidate 2), CAND6和CAND7也曾被认为是植物的GPCR，而后来的研究又将其逐一否定[13,14,16~23]. 在众多植物GPCR候选基因当中，GCR1成为最有潜力的候选者. GCR1有7次跨膜结构，与黏菌cAMP受体cAR1具有较弱的序列相似性，具备成为植物GPCR的条件. 但是G蛋白并不参与cAR1的一些功能[24]，而且植物GCR1功能缺失突变体的表型并不符合G蛋白功能缺失突变体的特征，GCR1是否与拟南芥Gα (GPA1)相互作用仍存在疑问[25]. 大多数植物中GAP (GTPase-accelerating protein)扮演着GPCR的角色，GAPs能够加速GTP的固有水解速率，从而加快G蛋白进入失活状态. 拟南芥中AtRGS1是典型的GAP,

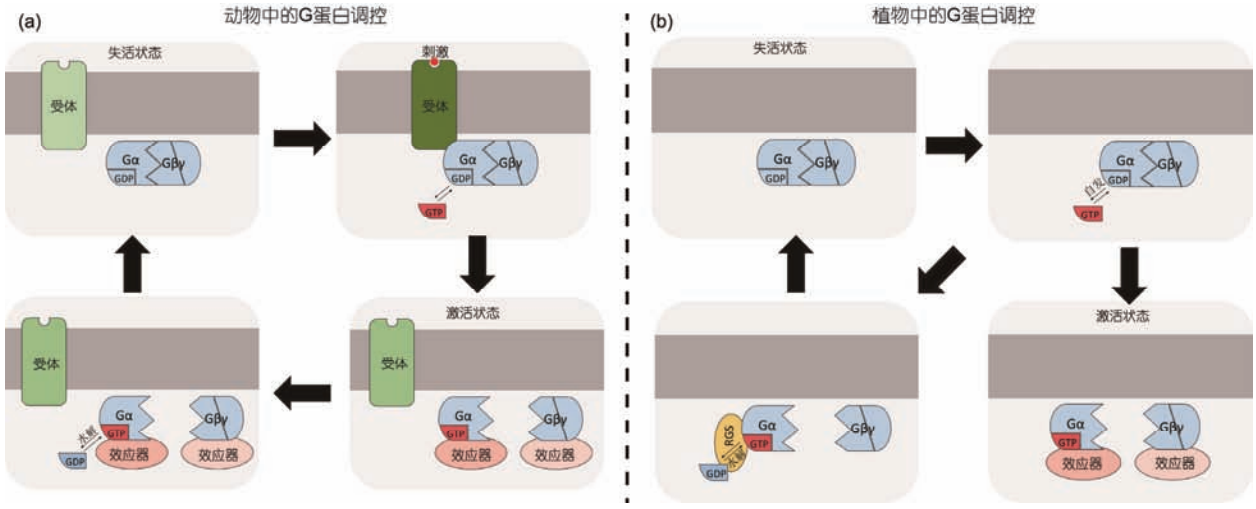

图 1 动植物G蛋白调控比较. 动物中(a)失活状态时Gα, Gβ和Gγ形成异三聚体G蛋白, 此时Gα与GDP嵌合. GPCR与外部同源配体嵌合后Gα释放GDP核苷酸并与GTP相嵌合. Gα与GTP嵌合使后发生结构改变, 从Gβγ二聚体中游离出来, Gβγ二聚体和GαGTP亚基与其各自的靶蛋白相互作用. GTP水解后Gα, Gβ和Gγ重新嵌合形成失活状态的异三聚体G蛋白. 植物中(b)Gα能自发地进行GTP与GDP的交换, 使得G蛋白能够自我激活, Gβγ二聚体和GαGTP亚基与其各自的靶蛋白相互作用. RGS调控GTP水解恢复异三聚体失活状态

Figure 1 Signal transduction mechanism of G proteins in animals and plants. In animals(a), when the absence of ligand, G protein forms an inactive heterotrimer, Ligand-bound GPCR promotes GDP dissociation and GTP binding on G protein, GTP-bound Gα dissociates from Gβγ dimer, and both activated Gα and freely released Gβγ modulate activity of the effectors. Gα hydrolyses GTP to GDP, and re-binds to Gβγ to return to its inactive state. In plants (b), Gα can spontaneously dissociate GDP and activate itself, RGS protein promotes the GTP hydrolysis of Gα

在N端含有一个7次跨膜结构的功能域, C端含有一个细胞质RGS区域, AtRGS1在直接或间接地与外源刺激配体嵌合后, C端发生磷酸化进而影响GTP水解(图1)[26]. 有趣的是, 水稻等谷类作物中并没有发现*AtRGS1*的同源基因, 因此水稻是发现植物G蛋白新的激活与失活调控机理的理想模式作物. 最近, 含有9次跨膜结构的水稻COLD1蛋白被证明与Gα在细胞表面相互作用[27,28]. *COLD1*是水稻籼粳亚种分化的耐冷性QTL, 粳稻*COLD1*型基因明显提高水稻的耐寒性. *COLD1*编码G蛋白信号调节因子, 冷处理时COLD1蛋白与Gα亚基RGA互作, 激活Ca^{2+}通道和G蛋白的GTP活性, 触发下游耐寒防御反应机制[27]. 这表明一些并非GPCR但是与G蛋白相连的候选蛋白可以调节GTP的水解速率, 或者通过调控Gβγ二聚体触发下游的效应子.

2 植物G蛋白研究

2.1 植物G蛋白具有更高的结构多态性

与哺乳动物一样, 植物中的异三聚体G蛋白也是由Gα, Gβ和Gγ构成, 但是每个亚基的成员比动物少[29]. 拟南芥只有1个典型的Gα(*GPA1*)和1个典型的Gβ (*AGB1*)[30,31], 2个典型的Gγ (*AGG1*, *AGG2*)[32,33]和1个G蛋白信号调控因子蛋白(RGS)[26]. 水稻的基因组同样只有一个的典型Gα (*RGA1*)和Gβ (*RGB1*)[34,35]和2个典型的Gγ (*RGG1*和*RGG2*)[36]. 最新的大豆(*Glycine max* (Linn.) Merr.)基因组分析发现了植物中最大的G蛋白家族, 含有4个Gα, 4个Gβ和7个典型的Gγ[37,38]. 除典型的Gγ外植物还有非典型的Gγ, 拟南芥有一个非典型的Gγ(*AGG3*)[39], 水稻有3个非典型Gγ (*GS3* (grain size 3), *DEP1* (dense and erect panicle 1)和*OsGGC2*(G protein g-subunit type C 2))[40], 大豆同样含有3个非典型Gγ (*GmGγ8*, *GmGγ9*和*GmGγ10*)[29,37]. 这些非典型Gγ都在N端含有Gγ相似区域(GGL功能域)[41], GGL功能域能够与Gβ相互作用形成二聚体[42]. 与典型Gγ具有保守的基因长度相比, 非典型Gγ在C端含有半胱氨酸富集区域, 而这段区域长度体现出丰富的多态性[37,43,44]. 拟南芥还有大型Gα同源基因(*XLG*) *XLG1*, *XLG2*和*XLG3*[45], 这3个XLG都有GTP结合性和GTP酶活性[46,47], XLG蛋白可以与Gβγ二聚体物理互作[48]. XLG在N端有一端较长的包含半胱氨酸富集区域和推测的核定位信号(nuclear localization sequence, NIL)区域[45]. 双分子荧光互补实验表明, XLG可以在质膜上和全部3个Gβγ二聚体相互作用[48,49]. *GPA1*只

定位在膜上，XLG还定位在细胞核上和细胞质上[48,49]. 在水稻中也发现了至少2个*XLG*同源基因，但是其功能仍然未知. 另外，*agb1*突变体所展现出来的表型并没有在*gpa1*突变体上观测到，但是却在*xlg*突变体上得到了重现[49]. 这些结果表明，XLG-Gβγ异三聚体可能是另外的G蛋白传导通路，扩展了对植物异三聚体G蛋白信号的认知. 对比基因组序列发现，Gα, XLG, Gβ和Gγ存在于绝大部分陆生植物[50].

2.2 植物G蛋白参与调控生物学进程

种子发芽受赤霉素(GA)、脱落酸(abscisic acid, ABA)、油菜素内酯(brassinolide, BR)、乙烯、光和糖分等复杂的信号调控，其中GA促进种子发芽，而BR作用于GA的下游，ABA和糖分都抑制种子发芽，乙烯能负向调控ABA的抑制作用[51]. 拟南芥Gα突变体种子表现出休眠时间延长，而且对外源的GA并不敏感[52,53]. 突变体和野生型ABA的浓度相似，说明Gα突变体对如GA等刺激信号钝感，导致推迟发芽[17]. 与*gpa1*突变体相似，*gcr1*突变体也表现出对GA和BR钝感，而*GCR1*过表达突变体会缩短种子休眠[54]. 值得注意的是，在一些条件下*gcr1gpa1*和*gcr1agb1*双突变体表现出加性效应，这与*GCR1*作用于G蛋白上游的预测不符，也进一步说明*GCR1*并不是典型的GPCR[17]. 水稻Gα (*RGA1*)的功能缺失突变体*dwarf1* (*d1*)表现出矮秆、圆粒等表型[36,55,56]. *D1*突变体中由GA诱导的α-淀粉酶基因表达和酶活性降低，而且Gα同样参与了BR途径(图2)[57~59].

根的生长和形态取决于细胞在横向和纵向分裂伸长之间的平衡. 拟南芥*gpa1*和*gcr1*突变体主根变短，与之相反*rgs1*突变体主根因为分生组织活性增加而增长[17,26,60,61]. ABA和Auxin抑制主根的伸长，*gpa1*, *agb1*和*gcr1*突变体以及由这些突变体所构建的三突变都表现为对ABA抑制更为敏感，突变体与野生型对Auxin的响应相似，这说明在主根的抑制与促进调控中，随着响应信号的改变G蛋白的作用也有所不同[60]. *agb1*突变体侧根增加，*gpa1*突变体侧根减少，

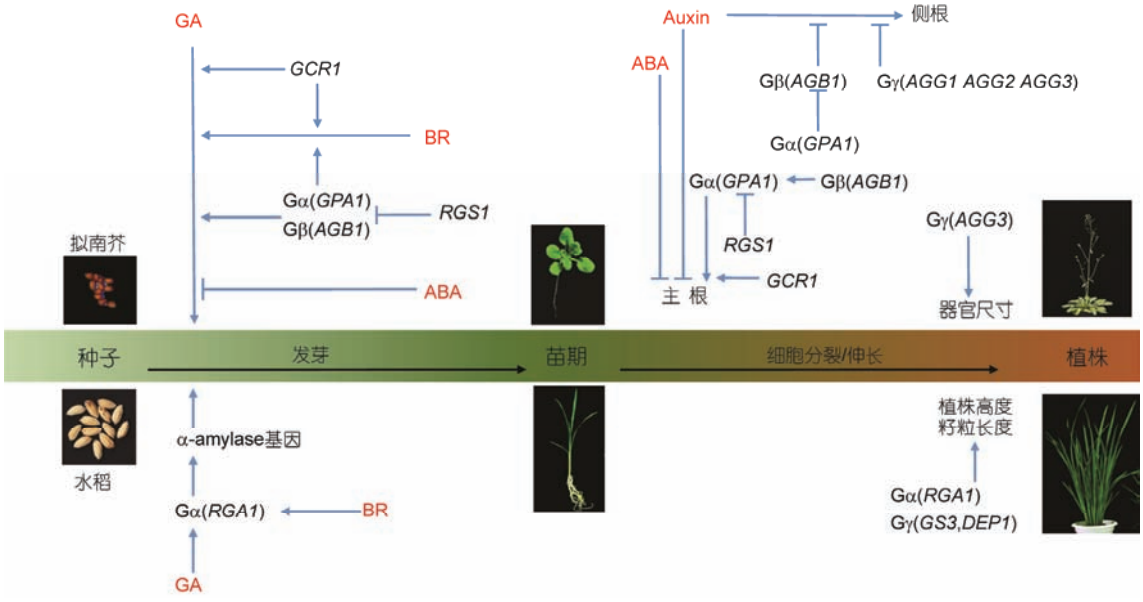

图 2 G蛋白参与调控水稻与拟南芥生长发育进程简图. 拟南芥中, *GCR1* 可能正向调控GA和BR对种子发芽的促进作用. *RGS1* 抑制*GPA1* 的活性. 水稻中, *RGA1* 作用于GA高敏感的信号通路, 并且可能也参与BR信号调控促进种子发芽. 苗期*GPA1*, *AGB1* 和*GCR1* 可能抑制主根的形成, *RGS1* 抑制*GPA1* 在生长点上的活性. 侧根形成中*AGB1* 作用于*GPA1* 下游并且抑制Auxin对细胞分裂的促进, *GPA1* 抑制*AGB1* 的功能. 拟南芥中, *AGG3* 调控叶片大小. 水稻中*RGA1* 调控水稻株高、籽粒大小和剑叶颜色, *DEP1* 和*GS3* 也调控水稻籽粒大小

Figure 2 Simplified model of physiological processes during plant development that involve G proteins based on the phenotypes of *Arabidopsis* and rice G-protein-component mutants. In *Arabidopsis*, *GCR1* may positively regulate seed germination by coupling BR promotion of GA-stimulated germination. *RGS1* antagonizes the activation of *GPA1*. In rice, *RGA1* may work in a high-sensitivity GA pathway that regulates seed germination. *RGA1* may also be a component of BR signaling. During seedling growth, *GPA1*, *AGB1* and *GCR1* may act in the inhibition of primary root development by ABA. *RGS1* antagonizes the activation of *GPA1* in apical root meristems. During lateral root formation, *AGB1* functions downstream of *GPA1* and inhibits auxin-induced cell division, and *GPA1* inhibits *AGB1* function. In *Arabidopsis*, *AGG3* regulates size of leaves. In rice, *RGA1* modulates plant stature by regulating internode and panicle elongation, and also influences the color of leaf blades and sheaths and grain shape, *DEP1* and *GS3* also regulate the size of grain

近期的研究发现，Gγ突变体*agg1*，*agg2*和*agg3*也表现出侧根增加[62,63]. Auxin促进侧根生长，外源Auxin实验发现*agb1*突变体侧根增加而*gpa1*突变体侧根减少，Ullah等人[60]总结Gβ直接参与Auxin诱导的侧根细胞分裂，而Gα在这一过程中起相反的作用(图2).

2.3 植物异三聚体G蛋白突变体的形态学变化

通过对拟南芥Gα突变体*gpa1*和Gβ突变体*agb1*的观察发现G蛋白贯穿整个植物发育过程. *gpa1*和*agb1*突变体表现出短下胚轴和开放顶钩，*agb1*突变体表现出侧根增加而*gpa1*突变体表现出侧根减少[62,64]; *gpa1*，*agb1*，*agg3*和*agg1agg2agg3*突变体表现出叶片变圆，*agb1*和*agg1agg2agg3*突变体表现出花的变异. Gγ (*agg1*)突变体和Gγ (*agg2*)突变体没有显著的表型变化[63]，Gγ (*agg3*)和*agg1agg2agg3*的三突变都表现出与*agb1*相似的突变表型[63~66]. 尽管G蛋白对这些生长和形态表型的调控机理仍然未知，但是这些调控都可能与细胞的分裂与伸长有关. 例如，*gpa1*和*agb1*突变体下胚轴变短是由胚轴表皮细胞轴向分裂减少所引起[60,67]. *gpa1*突变的圆叶片含有更大更少的表皮细胞，可能是因为细胞伸长和细胞分裂减少[67]. *gpa1*突变体侧根减少与*agb1*突变体侧根增加也都是因为侧根原基的活性改变所引起[60]，究其根本都是细胞增殖变化所引起. 拟南芥Gα和Gβ突变体与野生型表型相似，而水稻Gα (*d1*)突变体表现矮秆、叶片变宽且颜色变深等性状[55,56]，水稻Gβ突变体也表现矮秆的性状[68]. 水稻2个非典型Gγ基因*GS3*和*DEP1*都是重要的产量性状QTL，2个基因的突变体都表现出高产的性状[69,70]，拟南芥*gpa1*，*agb1*和*agg3*突变体籽粒均变宽变短[71]. 这些表型上的差异说明G蛋白的信号机制在开花植物上存在差别，拟南芥中重要的G蛋白调控因子RGS蛋白并没有在水稻中发现同源基因[26]，这也许是水稻和拟南芥G蛋白突变体表型存在巨大差异的原因.

2.4 非典型Gγ的自我抑制

植物G蛋白各亚基的基因数少于动物，但是植物中非典型Gγ却是动物中所不存在的. 因此非典型Gγ是研究植物复杂G蛋白的重点. 水稻含有3个非典型Gγ即*GS3*，*OsGCC2*和*DEP1*. 水稻*GS3*负向调控籽粒长度、宽度和粒重. *GS3*蛋白N端含有调控器官尺寸(organ size regulation, ORS)区域，中部是推定的TM区域，C端是半胱氨酸富集区域，不同的*GS3*等位基因引起不同的粒型，缺失半胱氨酸富集区域的*GS3*蛋白引起超短粒，与之相反带有功能缺失*gs3*突变等位基因的植株籽粒较野生型更长[72,73]. 通过对*GS3*不同变种的转基因实验发现N端的ORS负向调控粒长，而C端的半胱氨酸富集区域能够抑制ORS的功能[74]. 相似的缺失部分半胱氨酸富集区域的显性*dep1-1*等位基因也引起籽粒变短[41,69]. 根据这些结果，提出了非典型Gγ的C端可以抑制N端的典型Gγ蛋白的自我抑制机制[40]. 虽然这种自我抑制的分子机理仍然不清楚，但是C端的半胱氨酸富集区域中含有vWFC功能域，能够与其他蛋白相互作用[41,74]，暗示一种首尾相互作用可以使C端尾巴屏蔽N端头部的功能.

Botella研究团队[43]通过使用分体式泛素酵母双杂合和pH敏感性secGFP汇报子(reporter)验证了拟南芥*AGG3*具有跨膜区域[75]. GFP融合蛋白定位实验表明*AGG3*蛋白既存在膜上也存在于高尔基体和核上[37,76]. 多项关于*dep1*蛋白的研究也证明了dep1蛋白在细胞中无处不在[41,69,77~79]，大豆*GmGγ8*与YFP融合蛋白在类小囊结构中[37]. 因此非典型Gγ的TM和cys-C端富集区域可能会跨过生物膜结构后与其他胞外因子相互作用，屏蔽胞内N端的活性，但是仍没有足够的实验证据证明这个假设. 另外水稻基因组并不编码RGS蛋白，这意味这类似RGS的调控因子存在于水稻基因组中. 更重要的是，野生型*DEP1*蛋白和突变型*dep1*蛋白都通过Cys富集区域与*RGA1*相互作用[41]. 尽管Gγ和Gα之间相互作用的分子机理并不清楚，但是为研究植物中G蛋白的激活与失活提供了新的见解.

3 通过调控G蛋白信号实现作物增产

通过对功能缺失突变体和转基因植株的研究，发现异三聚体G蛋白在多种生长发育进程中都起着重要的生理功能. 其中包括种子萌发、幼苗和根系生长、植株形态、气孔开闭[80]、细胞分裂和伸长[26,67]，对病原体[81]、光[82]、臭氧[83]、糖分[84]和一些植物激素的响应[80]. 玉米(*Zea mays*)中Gα功能缺失突变体*ct2*表现出根生长减少，穗簇生和雄穗变粗，表明玉米中Gα抑制侧生穗的形成和发育[85]. Gγ在作物生产上起着重要的作用，水稻中2个主效QTL(*DEP1*和*GS3*)编码非典型Gγ，并能通过调控水稻每穗粒数和粒型影响产量. *GS3*在多项研究中被定位为影响水稻粒长和粒宽的QTL[72]，功能缺失型*gs3*等位基因引起长粒

型[72,86]，表明*GS3*抑制细胞分裂，负向调控水稻籽粒大小. *DEP1*位点的自然变异调控水稻的穗型和枝梗数进而影响产量[41,69,77~79]. 含有获得功能性等位基因*dep1-1*植株表现出直立穗型，维管束数增加，每穗粒数增加，进而增加产量[69]. 最近的研究证明了*DEP1*参与水稻氮素吸收和积累，不同的*DEP1*等位基因表现出不同的氮素响应. 大田试验表明，中等施氮条件下含有*dep1-1*等位基因的植株表现出更高的氮素吸收，引起经济系数的提高(图3). *DEP1*与*RGA1*和*RGB1*产生物理交互，*RGA1*功能缺失突变体和*RGB1*过表达转基因植株均表现出营养生长期氮素不敏感和氮素含量增加的特性，表明*dep1*等位基因通过与Gα和Gβ相互作用抑制氮素响应，降低Gα的活性或者提高Gβ的活性也抑制氮素响应[41]. 此外，还有研究表明，*DEP1*/*qPE9-1*负向调控水稻对脱落酸反应和抗旱性[87]. 由*dep1-1*等位基因所引起的直立穗型，不仅显著提高水稻单株产量，还通过形态学的优势提高群体产量. 直立穗型减少穗对穗颈的侧向压力，增强水稻抗倒伏性，而且直立的穗型减少穗部对叶片的遮挡，改善群体的受光结构，进而通过加大种

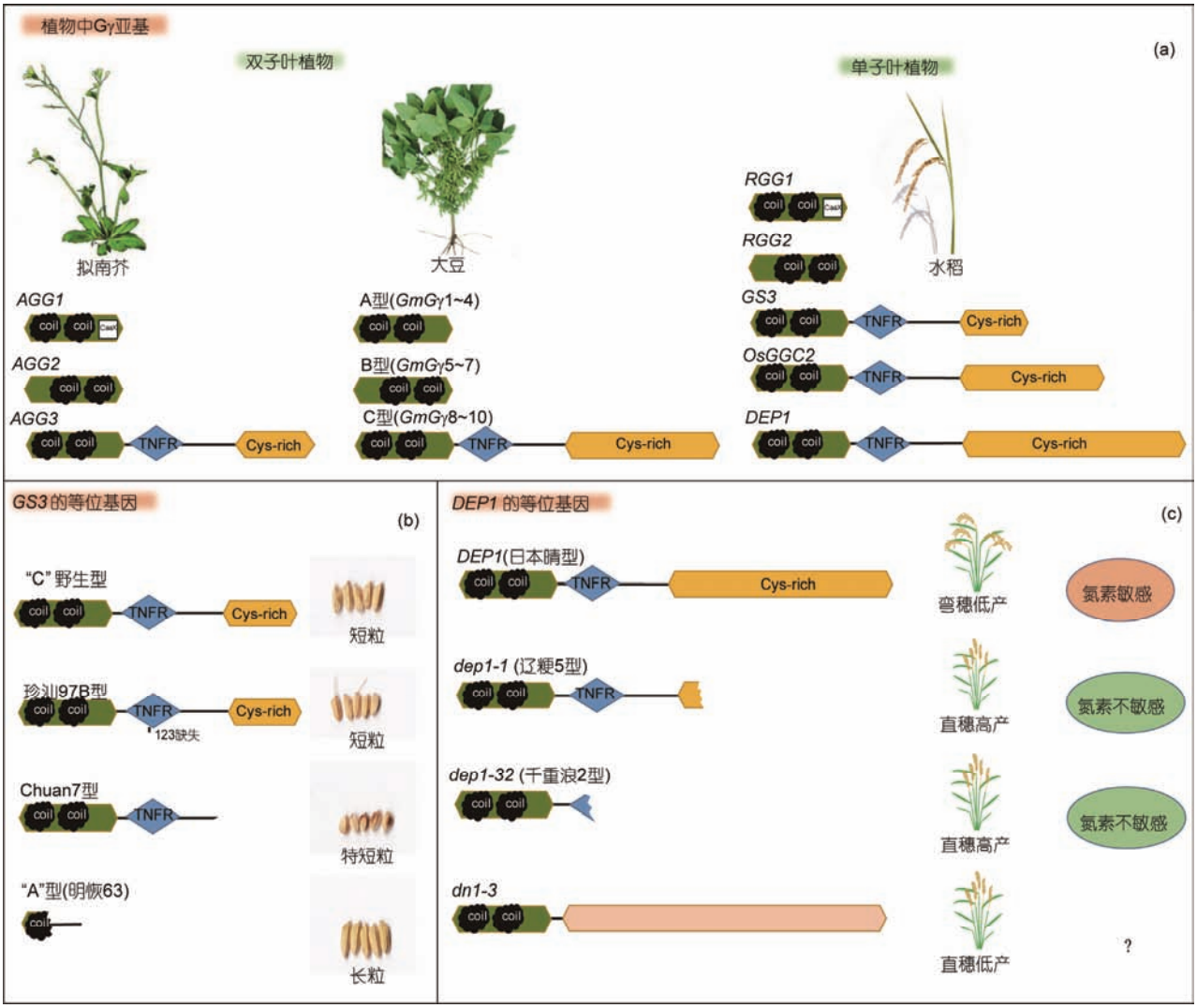

图 3 单子叶植物水稻与双子叶植物拟南芥和大豆中Gγ及其对表型的影响. 双子叶植物拟南芥、大豆和单子叶植物水稻中分别含有 3, 10 和 5 个Gγ亚基. 水稻中不同Gγ亚基(*GS3*)等位基因表现出不同粒型，不同*DEP1* 等位基因表现出不同穗型的氮素敏感性

Figure 3 Non-canonical Gγ subunits in monocots(rice) and dicots (*Arabidopsis* and soybean) and its effects in yield components. There are 3 and 10 Gγ subunits gene in dicots plant *Arabidopsis* and soybean, respectively. Monocots plant rice contains 5 Gγ subunits gene. Among 5 Gγ genes, different alleles of *GS3* result in various grain shape, and *DEP1* regulates the panicle architecture and the sensitivity to nitrogen

植密度进一步提高群体产量[88]. 生物信息学序列分析发现, 大麦(*Hordeum vulgare* L.)和小麦(*Triticum aestivum*)中含有*GS3*和*DEP1*的同源基因, 但是缺失Cys富集的C端[69]. 小麦中下调表达*TaDEP1*的转基因植株表现出较长但是松散的穗, 表明在农作物中非典型Gγ在生长点、花絮结构和籽粒数上功能相对保守[69]. 综上所述, 调控异三聚体G蛋白复合物为作物增产和提高氮素利用率提供新的育种策略. 事实上, *dep1-1*显性等位基因已经广泛应用于中国北方粳稻育种, 并获得了巨大的经济收益[69], 而*gs3*等位基因也广泛应用于籼稻杂交稻[73,89]. 本研究组认为, *dep1*和*gs3*, 以及其他产量相关的优异等位基因的组合可以使水稻产量在现有的基础上进一步提高.

4 总结与展望

尽管植物G蛋白家族要小于动物, 但是异三聚体G蛋白参与调控植物许多重要生长发育过程[29,44,50]. 而且植物不仅含有典型的Gα和Gγ, 还含有非典型的大型Gα和非典型的Gγ. 大型Gα含有半胱氨酸富集的N端, 表现出了不同的亚细胞定位[49], 所以对大型Gα功能的探索将为了解G蛋白体系提供更多的信息. 根据相似的序列和保守的蛋白拓扑结构, 一些具有7次跨膜结构的蛋白被认为是植物GPCR的候选者, 但是现在仍然没有足够的证据证明植物存在GPCR, 而且植物Gα的自我激活特性使得G蛋白体系不再需要GPCR来激活. *COLD1*的发现表明, 植物中一些非GPCR的候选蛋白可以调节GTP水解速率, 进而影响下游的效应子. 尽管G蛋白在调控水稻生长, 抗逆境和产量潜力方面起着重要的作用, 但是调控异三聚体G蛋白激活与失活以及下游效应子循环的分子机理仍然不明. 因此, 为了阐明植物G蛋白如何与多种激素和环境信号相互作用来在多变的环境下维持稳定的生长发育, 今后应该深入开展生物化学和系统生物学等多方面研究.

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Heterotrimeric G protein signaling in plant

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Heterotrimeric guanine nucleotide-binding protein (G protein) signaling is an evolutionarily conserved mechanism in diverse eukaryotic organisms. In the past half century, five Nobel Prizes are awarded to researchers working in the G protein field, these seminal studies make the G protein pathway become the best understood signaling transmit system in the world. In animals, heterotrimeric G proteins contains α, β and γ subunits, perceives extracellular stimuli through G protein-coupled receptors (GPCR), and transmit signals to ion channels, enzymes and other effectors to affect numerous cellular behaviors. In recent years, much has been learned about the diversity of signal transduction through plant G proteins thanks to the identification and mutation of genes in Arabidopsis and rice. Plant cells have most of the core elements found in animal G signaling, such as α, β and γ subunits. However, plant G proteins transmit signals by atypical mechanisms. The plant Gα subunit spontaneously releases GDP and forms a stable GTP bound state *in vitro*, and thus are self-activating. The self-activating characteristic also means that plant G protein paradigm do not need and therefore do not have typical animal GPCR. Indeed, the current evidence supports that no typical GPCR exists in plant. In most plants, the role of GPCR is performed by GTPase-accelerating protein (GAP), such as *Arabidopsis* regulator of G protein signaling 1 (AtRGS1). Interestingly, there is no ortholog of AtRGS1 in rice genome. Recently, an important advance has been proved that up-regulation of *COLD1* is positively correlated with chilling tolerance in rice. *COLD1* has nine-transmembrane domains, and localize to plasma membrane (PM) and endoplasmic reticulum (ER). The COLD1 physically interacts with RGA1 and acts as RGS protein that senses low temperature signals and accelerates G-protein GTPase activity. These results indicate that non-GPCR proteins in plant can topologically and functionally resemble animal GPCRs. In plants, the repertoire of the heterotrimeric G protein is much simpler than that in mammalian, but Gγ subunits exhibit an extraordinary level of structural diversity and show significant differences from their animal counterparts. The non-canonical Gγ subunits in plant kingdom have a large cysteine domain on C terminal, can be four times larger than the average mammalian Gγ subunits size. The non-canonical Gγ subunits present an inhibitory effects of N terminal on C terminal. Recent studies have shown that the manipulation of two non-canonical Gγ subunits, GS3 (grain size 3) and DEP1 (dense and erect panicle 1), represents new strategy to simultaneously increase grain yield and nitrogen use efficiency in rice breeding. In this review, we focus on the recent insights of G protein network derived from the research about the model plant rice and *Arabidopsis*, the difference of G protein signal between plants and animals, and the potential of G protein to improve the crops productivity.

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