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根茎克隆植物生态学研究进展

汤俊兵，肖　燕，安树青*
（南京大学生命科学学院,湿地生态研究所,南京　210093）

摘要:根茎在植物的无性繁殖、克隆分株间信息交流和物质交换、预测资源斑块的质量等方面具有重要意义,并且根茎克隆植物的研究涉及生物入侵、全球变化等诸多生态学前沿领域。作为一种重要的克隆植物类型,根茎克隆植物在资源异质性生境中表现出特有的适应方式,这种方式可以通过形态可塑性、觅食行为、生理整合以及适合度来具体表征。着眼于根茎克隆植物,总结和分析了国内外近年来的研究案例,并对形态可塑性起源与多样性的限制假说和适应假说、觅食行为中的强度觅食和广度觅食策略、克隆分株间间隔子保持和断裂的利益权衡等热点内容进行了讨论。最后联系生态学学科前沿,提出了本领域在未来需要重视的研究方向。

关键词:形态可塑性;觅食行为;生理整合;适合度

Advance of studies on rhizomatous clonal plants ecology

TANG Junbing, XIAO Yan, AN Shuqing*
School of Life Sciences, Institute of Wetland Ecology, Nanjing University, Nanjing 210093, *China*

Abstract: The rhizomes of plants play an important role in many aspects, including asexual reproduction, communication and resource sharing between ramets, and foraging in heterogeneous environments. Rhizomatous clonal plants are popular research subjects in fields such as invasion ecology and global change biology. Rhizomatous clonal plants show a special adaptation to heterogeneous habitats through morphological plasticity, foraging behavior, physiological integration, as well as fitness. This paper summarizes and analyzes domestic and international case studies of rhizomatous clonal plants from recent years. Some current issues are discussed, such as the limit hypothesis and the adaptation hypothesis on the origin of morphological plasticity and diversity, intensive foraging and extensive foraging in foraging behavior, and the benefit of ramet spacer's maintain or break. Finally, research priorities for this domain are presented.

Key Words: morphological plasticity; foraging behavior; physiological integration; fitness

克隆植物又称无性系植物,是当前生态学研究的热点领域之一[1-4]。克隆植物种群的研究引起生态学家、遗传学家、以及生物进化专家的广泛关注[5-6],其主要原因是这些学科的理论体系都是在研究非克隆植物的基础上建立起来的[7],而对于广泛存在的克隆植物就显得力不从心[8]。因此一些科学家认为上述各学科的一些新的理论将在对克隆植物的研究中诞生[9-11]。

在自然条件下有克隆繁殖相伴的营养生长过程称为克隆生长[12]。根据克隆发生器官不同,克隆植物可分为根状茎型克隆植物(如互花米草),匍匐茎型克隆植物(如草莓),球茎型克隆植物(如马铃薯),鳞茎型克隆植物(如大蒜)和根出条型克隆植物(如小叶杨)等类型[13]。作为一种重要的克隆植物类型,根茎克隆植物的研究得到了国内外学者的广泛关注[14-19]。植物的死亡至少有95%发生在种子阶段[20],而根茎克隆植物的根状茎具有很强的储藏能力[21-22],远远超过种子[23],因此根状茎上的芽萌发形成的幼苗比实生苗具有更强的

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* 通讯作者 Corresponding author. E-mail: anshq@ nju. edu. cn

抗逆境能力[24]。并且根茎在植物的无性繁殖、克隆分株间信息交流和物质交换、预测资源斑块的质量等方面起到了重要的作用[25-27]。相对于其它克隆植物类型,大多数根茎植物属于合轴分枝,其克隆分株由一个地上直立枝和基部的不定根构成而被称为枝性克隆分株[7],另外根茎植物可以通过产生长度不同的根茎从而形成从密集型(phalanx)到游击型(guerilla)的连续的克隆构型系列。根茎克隆植物的研究与诸多生态学前沿领域相联系,例如众多的入侵植物种是根茎克隆植物,如互花米草(*Spartina alterniflora*)[28]、紫茎泽兰(*Eupatorium adenophorum*)[29]等;大部分湿地草本具有根茎[30],而湿地的结构和功能又与全球变化有紧密联系[31-32]。因此对根茎克隆植物的深入研究是必需而迫切的。

目前根茎克隆植物的研究已涉及克隆生长构型与形态可塑性[33-34]、克隆分工与整合[35-36]、克隆种群统计[37]、生境选择[38]、觅食行为[39]及适应对策[40]等诸多领域。本文着眼于根茎克隆植物,对国内外近年来的研究案例进行总结和分析,以明晰该研究领域的发展趋势。

1　根茎植物的形态可塑性

所有的高等植物都是由合子在个体发育过程中产生的一系列构件所构成[41-42],而这些构件通常有自己的生活史和生活周期[42-43]。当克隆植物生长在不同资源水平的生境内,其构件大小和生长结构将会对环境条件发生反应[44-45],从而表现出形态可塑性。通过塑造形态,克隆植物可以在一定范围内突破资源分布的局限,使自己的生长空间得到扩展[44,46]。

在解释克隆可塑性起源与多样性方面,出现了限制假说[12]和适应假说[47]。限制假说认为克隆植物的表型可塑性是由克隆构型决定的,而克隆构型是其在系统进化的过程中形成的。例如 Schmid[48]认为游击型克隆植物的形态可塑性比密集型克隆植物大,Dong 和 de Kroon[22]通过实验证明在资源异质性生境中匍匐茎比根状茎具有更高的反应。适应假说则认为克隆植物的形态可塑性是与生境的资源状况相适应的,并预测来自资源水平高且资源斑块性稳定生境的克隆植物比来自资源水平低且资源斑块性不稳定生境的具有更高的形态可塑性。例如多年生根茎克隆植物黄帚橐吾(*Ligularia virgaurea*)的分枝强度随资源水平增高而上升[49];欧洲落叶林光资源斑块不稳定的林下克隆草本 *Lamiastrum galeobdolon* 比生长在资源稳定环境下的草本 *Hydrocotyle vulgaris* 具有较低的形态可塑性[45];根茎草本结缕草(*Zoysia japonica*)在土壤养分资源总量较高的情况下,同质生境生物量大于异质生境中的生物量[50]。

多年生湿地植物的根茎会由于环境条件的变化而表现出可塑性,如 Weisner 和 Strand[51]的研究表明芦苇(*Phragmites australis*)的根茎长度随水位升高而减小,深水中的芦苇根茎较短,在基质中埋深也浅,可能是为了保持较短的氧气运输距离。而对香蒲(*Typha domingensis*)的研究结果则正好相反[52],在稳定水体中香蒲的根茎长度随水位升高反而增加。克隆植物形态可塑性还可能与海拔高度有关[53-54]。国振杰等[55]对根茎克隆植物羊草(*Leymus chinensis*)的研究表明,其根茎总长度、根茎节间长度随着海拔的升高呈现出递增的趋势,而相邻分株间距没有表现出明显海拔差异。而黄帚橐吾的根茎长度则在海拔处于中等水平时较长,低海拔和高海拔都较短[56]。随着光照强度的增加,华西箭竹(*Fargesia nitida*)的分株高度、基茎、节间长度、隔离者分枝强度、生物量积累和基株的数量等均在大林窗环境中达到最大[57]。因此华西箭竹的可塑性反应可能与林冠层树种的更新有密切关系,并可能为解释同林冠乔木树种间长期稳定共存提供依据。

虽然形态可塑性在异质性资源环境下可以给克隆植物带来较高的适合度利益,但目前大部分研究实例中可塑性反应只是被动的而非适应性的,这说明适应性的可塑性进化可能并不像我们想象的那样常见[58]。Van Kleunen 和 Fischer[59]认为沿着基因表达到表型的过程来研究可塑性及其与适合度的关系将有助于人们更好地理解这种现象,有助于更加实际的预测可塑性反应的进化。

2　根茎植物的觅食行为

随着 NATURE、SCIENCE、TREE 等期刊上关于植物觅食行为文章的发表[38,60-61],克隆植物觅食行为的研究也越来越受到学者们的关注。较为准确的植物觅食行为的定义是 Hutchings 和 de Kroon[62]给出的:有机体在其生境内进行的促进对必需资源获取的搜寻或分枝过程。当存在资源异质性时,克隆植物可以对高质量的

生境斑块作出反应并通过觅食行为获得最多所需的资源[63-65]。

克隆植物觅食行为理论指出克隆植物觅食行为的表征之一是在资源水平较高或较好的生境条件下克隆分株间的间隔子较短,从而密度较大[7]。单保庆等[49]对根茎克隆植物黄帚橐吾的研究证明了这一结论,随着土壤资源的增多,黄帚橐吾的间隔子迅速缩短,源株表现出主动觅食行为,但随着资源的持续增加,间隔子在短到一定范围之后,又会慢慢变长。对根茎克隆灌木羊柴(*Hedysarum laeve*)的研究也表明,固定沙丘的羊柴分株种群与半固定沙丘比具有较大的密度和较长的根状茎节间,较小的平均株距。这项研究为克隆植物觅食行为的推论提供了又一例证,即在水分和营养条件较好的固定沙丘中羊柴分株种群对根茎的生物量投资高于在条件较差的半固定沙丘中的投资[66]。

种内和种间竞争是塑造植物根茎的重要因素[30],许多克隆植物在异质性资源环境中通过根茎的觅食行为获取更多资源,以获取竞争的胜利[65]。但也有竞争降低根茎扩张能力的案例[67,68]。Xiao 等[11]对匍匐茎克隆植物苦草(*Vallisneria spiralis*)的研究也表明,除了光、水和土壤条件等非生物条件外,竞争是种群结构塑造的重要因素,这可以为根茎植物研究提供参考。

克隆植物的觅食行为主要通过表型可塑性的 3 个因素(即分枝强度、间隔子长度和分枝角度)来起作用[62]。由于分枝强度是植物单纯的对高资源生境的生长反应,因此这一因素通常被看作一个被动的觅食因素。而另外两个因素独立于单纯的生长反应,被看作是积极的觅食因素[39]。

觅食策略可分为强度觅食和广度觅食两种[63]。强度觅食是指克隆植物在环境条件好的地区(或斑块),小范围内通过产生大量的分蘖或由较短间隔物连接的分株来占领所处生境;而广度觅食是指在环境条件不好时通过产生由较长间隔物连接的分株迅速逃离不利生境,从而增加进入条件好的生境的几率。对根茎植物中国沙棘(*Hippophae rhamniodes*)的研究表明,在较高的土壤水分有效性条件下,克隆种群采取强度觅食策略,这有利于种群巩固和利用有利生境斑块,并提高克隆排斥其他植物种类侵入的能力;在较低的土壤水分有效性条件下,克隆种群采取广度觅食策略,即克隆可以在较大的空间内占居并获取必要的资源,避免克隆内部分株之间的竞争,同时促使克隆尽快越过不利生境斑块,并提高分株在有利生境斑块的生长概率[69]。并且随着土壤水分有效性的提高,中国沙棘的资源利用策略将由广度觅食向强度觅食转变,从而形成觅食策略连续体。

3 根茎植物的生理整合性

克隆植物的生理整合性是指植物的光合同化产物、矿质养分和水分等资源通过连接物或间隔子在克隆分株之间进行传输与分享的过程[70-71],它在环境条件不好或存在资源异质性的条件下具有独特的意义[72],因为它使得克隆片段可以通过间隔子从相邻的分株中获得足够的资源,从而减小局部环境不利因素带来的选择压力[73-78]。目前根茎克隆植物生理整合方面的研究主要涉及生理整合的程度[76,79]、生理整合发生的条件[73,80]、生理整合作用的过程与影响因子[3,81]等领域。

为了检验克隆植物是否存在生理整合,Evans[40,82]对多年生根茎克隆植物 *Hydrocotyle bonariensis* 进行了一系列的实验研究。结果表明,水分、光合产物、N 素都能通过间隔子从高质资源斑块分株向低质资源斑块部分转移。对根茎半灌木 *H. laeve* 生理整合性进行同位素示踪研究表明其母株和子株能通过相连的根茎而相互传输光合同化物[18],这与对根茎克隆植物 *Carex bigelowii* 和 *Uncinia meridensis* 的研究结果相同[83-84]。克隆植物的生理整合具有遗传基础,不同植物种间的资源共享程度不同,即使同种克隆植物的不同基因型,其整合表现也不同[85]。如 Alpert 和 Mooney[86]对不同基因型的 *Fragaria chiloensis* 在碳素整合能力方面的研究表明,异质性程度较高的沙丘生境中的基因型比异质性较低的草地生境中的基因型具有更明显的同化物共享现象;Pan 和 Keith[87]对 *Glyceria striata* 的研究也表明生理整合受不同基因型的影响。在异质性环境中,具有整合习性的基因型在环境压力下被选择的可能性更大,从而发生适应性进化。

克隆整合通常对源株影响很小[88-89],但对被整合克隆分株的成活与生长有重大意义。Liu 等[90]的研究表明,根茎克隆植物沙地雀麦(*Bromus ircutensis*)和沙鞭(*Psammochloa villosa*)在重度放牧干扰的情况下能够从未受损分株处获得养分,因此能够占领更多的异质性资源斑块,这种降低损失的策略能够使得克隆种相对

于非克隆种(如 *Artemisia intramongolica* 和 *Astragalus melilotoides*)拥有更高的恢复能力和更强的抗啃食能力。但是当环境胁迫或外界扰动强度过大,超过植物本身的耐受力和调节能力时,使植物所具有的风险分散能力不足以“分散”基株死亡的风险,则基株的绝灭就不可避免[91]。

目前根茎克隆植物生理整合的研究方法主要有同位素示踪法[92-93],去叶试验[70,94],切断试验[95-96],遮光试验[97-98]等。王长爱等[99]对克隆植物生理整合作用的研究方法做了较为详细的论述。

4　根茎植物的适应策略

克隆植物的适合度是生态学家普遍关注的问题[100-102]。大多数学者认为植物的克隆生长习性能增强其在资源异质性生境下的适合度[14,72,76,86,103],即通过构件不同部分的分工,更好的适应资源异质性的环境[80,88],Roiloa[104]等认为克隆片段的分工是克隆植物最显著的潜在利益之一。并且普遍认为克隆植物的种类和数量在环境严酷的地区要多于环境温和的地区[105]、水生要多于陆生[106]、光照和营养不足的地区要多于光照和营养充足的地区[107]。但克隆分株间相连的间隔子以及新的克隆片段的生长和发育都需要初始成本(initial cost)[63],如果用于维持间隔子生长的成本过大,将会导致整株克隆植物的适合度下降[72]。因此从长远的适应性角度来看,克隆植物必须权衡生理整合与间隔子维持所需资源之间的重要性,假如用于间隔子维持的成本过大,克隆植物的适合度将会低于非克隆植物[108]。另外,分株间连接的断裂的早迟也可能取决于利弊的权衡,即取决于克隆生长对环境异质性反应的结果[2]。

张称意等[18]对根茎半灌木羊柴的研究表明其根茎在地上分株支持下的连接长期保持,主要是其确保分株建植和存活的途径,而不是其在环境中获得资源的觅食解决方案。尽管羊柴分株间的克隆整合需要一定的资源耗费,基株的适合度却从这一整合中获得了净收益。当光合产物和可用的营养减少时克隆植物开花结实的概率一般也会降低[109],对根茎草本 H*ydrocotyle bonarie*nsis 的研究基本符合上述规律,但在局部低氮时其分株的有性繁殖反而增加[110]。Evans[40]的研究表明,*H. bonariensis* 主要通过生理整合来提高资源的利用率以及整株对环境的适合度。

植物间的竞争或化感作用可能会抑制植物的克隆生长[15,39]。Elisabeth 等[17]对根茎克隆植物 *Elymus lanceolatus* 所做的研究显示,当 *E. lanceolatus* 与 *Pseudoroegneria spicata* 相邻种植时其克隆生物量最高,与 *Bromus tectorum* 相邻种植时次之,而与 *Agropyron desertorum* 相邻种植时克隆生物量最低。所以克隆植物的生长模式不能仅仅用资源竞争的观点来解释,还很大程度上取决于与其相邻植物的种类。即克隆植物与特定植物相邻生长时可以提高其对环境的适合度。

对于去叶干扰,特别是在重度放牧条件下,植物的补偿需要大量资源的投资[111],但克隆植物与非克隆植物的适应策略是不同的:非克隆植物只能通过残留的叶片、茎和根来获取能量[90];而克隆植物除此之外还能通过根茎从其它分株获得能量,或直接获取根状茎储藏的能量[112]。所以在胁迫生境中,植物能通过克隆生长习性提高自身对不稳定环境的适合度。

另外陈玉福和董鸣[113]对毛乌素沙地群落的研究表明,与多年生非克隆植物相比,依靠根茎繁殖的多年生克隆植物有 3 个明显的优势:(1)克隆植物(沙鞭、羊草等)的根茎多分布在地下 10 cm 以下,这一土层水分含量较高,有利于其分株的萌发和生长;(2)克隆植物通过其根茎和分株向裸露流沙斑块扩展,扩展到邻近裸沙斑块的分株可以共享植被斑块内其它分株的水分和养分,有利于其迅速地占据裸沙斑块;(3)根茎型克隆植物的单个基株可以占据很大的空间,形成数个方向上延伸的由多个形体相连的分株构成的植株结构,其防沙固沙效果优于单丛多年生非克隆植物。因此从生态适合度的角度来讲,多年生根茎克隆植物可以大大提高逆境生态系统的自我恢复能力。

5　展望

近年来根茎克隆植物的研究已越来越深入,试验方法也不断趋于精细。由于根茎克隆植物的研究与诸多生态学前沿领域相联系,例如生物入侵、全球变化、物种多样性、生物进化等,因此以下问题的解决有望推动根茎克隆植物研究的进一步发展:

(1)已知众多生物入侵种是根茎克隆植物,根茎的形态适应与生物入侵是否存在某种必然联系,与根茎有关的根际微生物,N、P 等沉降是否影响了入侵的过程。

(2)研究表明,克隆植物的表型可塑性和觅食行为是具有可遗传性的,自然选择压力如何决定其进化方向。

(3)多年生湿地植物大部分是根茎克隆植物,因此湿地的结构与功能必定与根茎克隆植物之间存在某种关联,而湿地与全球变化又是紧密相关的,这种联系的内在机制如何。

(4)目前大部分研究实例中可塑性反应只是被动的而非适应性的,克隆植物对异质性环境资源是否具有主动适应性。

(5)根茎克隆植物是很多生态系统中不可缺少的组成部分,它必然对群落稳定性、物种多样性和养分循环等生态过程具有十分重要的意义,它们之间相互作用的机制如何。

(6)根茎克隆植物与其它类型克隆植物在储存能力、整合速率和强度、觅食行为方式等方面都存在差异,但有关根茎克隆植物和其它类型克隆植物在这些方面的比较研究是欠缺的,如何选择材料和设计实验来进行此方面的对比研究。

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