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植物 SNP 的开发研究进展

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摘 要 植物单核苷酸多态性(SNP)研究正日益受到重视。然而，尽管在遗传变异、连锁作图、群体结构分析、关联分析、图位克隆和植物育种研究上需要大量 SNP，对多数植物而言，当前可用的 SNP 数量仍少之又少。本文概述了当前植物的 SNP 标记开发现状，并对将来植物 SNP 开发进行了展望。

关键词 单核苷酸多态性; 植物; 开发

Advance on Developing SNP Marker in Plants

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Abstract In many plants, single nucleotide polymorphism (SNP) markers are becoming more and more important among marker systems. However, although studies regarding genetic variation, linkage mapping, population structure analysis, association genetics, map-based gene isolation, and plant breeding need a large number of SNP, for many plants the number of currently available SNP is very low. This review summarizes the current status of SNP marker development technologies for plants and provide an outlook into the future regarding possible SNP identification approaches in plants.

Keywords SNP; Plant; Development

1 前言

分子标记广泛应用于植物遗传育种研究，对基因或染色体片段的标记辅助选择有利于提高品种选育效率(Francia et al., 2005)。根据质量性状基因在遗传图谱中的位置，利用分子标记能对其进行分离(Jander et al., 2002)，而对于受多因子控制的性状，通过分子标记可鉴定每个因子，包括遗传因子和环境因子(Cooper et al., 2009)。此外，在植物遗传研究中，分子标记也常用于分析群体结构、进化关系以及模式植物全基因组水平的个体遗传结构(Bomblies and Weigel, 2007)。

近年来，单核苷酸多态性(single nucleotide polymorphism, SNP)研究备受关注(Shi et al., 2009)。由于个体间核苷酸序列存在很大差异，SNP 的数量几乎是无限的，且每个 SNP 也可能是潜在的有用标记。SNP 标记的潜力已在人类基因分型中得到很好展示。随着科研经费的大量投入，目前已从人类基因组序列中开发出几百万个 SNP 标记(International HapMap Consortium et al., 2007)，并发展出能同时检测上百万个 SNP 位点的技术。这使得通过全基因组扫描分析特定性状与标记的关联性成为可能，也就是所谓的全基因组扫描(whole-genome scanning, WGS)、全基因组关联分析(genome-wide association studies, GWAS)、或关联遗传学(association genetics) (McCarthy et al., 2008)。

SNP 标记已广泛应用于人类和动物基因组分析，但在植物上仍处于起步阶段。植物关联分析要求同时检测上千个标记和成百上千个群体单株，除

水稻、拟南芥和玉米外，其他植物尚没有在关联作图群体中大规模检测 SNP 报道(Huang et al., 2010; Li et al., 2010; Poland et al., 2011) 。

2 SNP 开发技术

当前已有几种技术用于大规模植物 SNP 的开发。下面章节将在总结相关 SNP 论文的基础上讨论这些技术在模式植物和模式作物中的应用性、需求性及极限性。

2.1 基于 EST 序列数据开发 SNP

随着测序效率的不断提高，现已在多个作物获得大量 EST 序列。当前 NCBI EST 数据库(URL:http://www.ncbi.nlm.nih.gov/dbEST)收录的作物 EST 序列少的不到 10 000 条，多则达上百万条。截止 2011 年 7 月 15 日，GenBank 收录的模式植物拟南芥 EST 序列达到 1 529 700 条，模式作物水稻 EST 序列 1 252 989 条。EST 序列主要通过国际合作产生，且其供体大多由少数几个品系组成，因此可直接用于 SNP 的开发。基因组纯合的自花授粉作物，如拟南芥(Schmid et al., 2003)、水稻等，可通过比较不同品系间 EST 序列鉴定 SNP 位点。而针对基因组高度杂合的异花授粉作物，利用生物信息学方法则可直接从单个品系的 EST 序列中开发 SNP (Pavy et al., 2006)。尽管利用 EST 序列开发 SNP 优点大，但缺点却比优点多几倍。首先是 EST 序列质量不高(通常 EST 的 Phred 值≈20，意味着平均每 100 bp 序列产生 1 个碱基的错误)。为确保 SNP 的可靠性，用于 SNP 分析的 EST 簇至少包含几个 EST 序列。其次，除均一化文库外，由于基因表达水平不同，每个文库中可用于比对的 EST 序列数量有限。最后，如何区分直系同源序列(来自同一个基因)和旁系同源序列(来自相关基因或基因家族)是个棘手的问题。

由于上述缺点，通过 EST 序列开发的 SNP 数量少，且准确率不高(50%~85%)。利用 EST 序列开发 SNP 标记的植物包括拟南芥(Schmid et al., 2003)、玉米(Batley et al., 2003)、大麦(Kota et al., 2003)、番茄(Yamamoto et al., 2005)、豇豆(Muchero et al., 2009)、甜瓜(Deleu et al., 2009) 、鳗草(Ferber et al., 2008)、苹果(Chagné et al., 2008)和松树(Dantec et al., 2004)。

2.2 利用微阵列芯片开发 SNP

开发 SNP 的另一个策略是大量采用来自不同基因的 EST 序列设计寡核苷酸微阵列芯片。微阵列芯片不仅能检测个体基因表达水平，还能与不同个体的 cDNA 或 DNA 杂交，根据结果的差异开发 SNP，即所谓的 SFPs (single feature polymorphisms)。短片段寡核苷酸微阵列芯片能灵敏检测到序列的变异，尤其是寡核苷酸探针中间位置所检测的序列。与利用 EST 序列开发 SNP 比较，微阵列芯片能够在表达水平上无偏差地分析大量基因(10 000~20 000)。利用微阵列芯片已在拟南芥(Borevitz et al., 2003; Borevitz et al., 2007; Singer et al., 2006)、水稻(Kumar et al., 2007)、小麦(Bernardo et al., 2009)、大麦(Cui et al., 2005; Rostoks et al., 2005)、桉树(Neves et al., 2011)、番茄(Sim et al., 2009)、大豆(O'Rourke et al., 2009)和玉米(Krist et al., 2006)上鉴定出大量 SFPs。微阵列芯片除适用于提供核苷酸序列的物种，还可用于基因序列多态性低的近缘物种。现已利用大豆基因组微阵列芯片成功从豇豆中开发出 SFPs (Das et al., 2008)。尽管微阵列芯片开发 SNP 存在诸多优点，但也存在高假阳性率(25%~50%)的缺点，这是由于芯片与大基因组物种核酸杂交容易出错造成。解决途径是采用一系列降低基因组复杂度的方法，如甲基化过滤法(methyl filtration)、c_0t-过滤法(c_0t-filtration)、源自 mRNA 的 cRNA 或 AFLP 法。但经过处理后 SFPs 的假阳性率仍高达 20%，只有部分高度可信(Gore et al., 2007)。

2.3 扩增子重测序开发 SNP

该方法主要用于人类单倍型遗传变异研究(URL: http://www.hapmap.org)。它包括设计引物(用于扩增基因、ESTs 或其他单拷贝基因组序列片段)、全测序 PCR 产物(扩增一系列代表品系)、序列比对三个步骤。此法的优点是扩增子通过双向测序后，SNP 假阳性率通常低于 5%。其他优点还包括：当测序片段足够大时，除开发 SNP 外，还可鉴定单倍型；可准确区分来自直系同源序列和旁系同源序列的 SNP；可估计种质资源中 SNP 位点的等位频率。此法的主要缺点是当分析基因数量多时工作量大，这是由于每个受检测基因均需设计一对特异引物，同时需要扩增和测序大量品系。扩增子重测序在玉米上应用最广，现已从玉米的一套品系中测序几千个基因(Wright et al., 2005; Yamasaki et al., 2005; Yan et al., 2009)，相关数据可从 Panzea 数据库(URL: http://www.panzea.org)获得。国外种子公司已对超过 10 000 个基因和 5 000 个玉米品系进行扩增子重测

序(Beló et al., 2008)。除玉米外，大豆中有关扩增子重测序的研究也较多，目前已从大豆中获得 4240 个扩增子(Choi et al., 2007)。其他采用扩增子重测序方法开发 SNP 且所检测基因数量达几百个的植物包括拟南芥(Nordborg et al., 2005; Schmid et al., 2005)、水稻(Nasu et al., 2002)、番茄(Van et al., 2007)、甜菜(Schneider et al., 2007)、大麦(Kota et al., 2008)、云杉(Pavy et al., 2008)和油菜(Westermeier et al., 2009; Durstewitz et al., 2010)。

2.4 从基因组序列中开发 SNP

目前已公布全基因组序列的植物仅有少数，拟南芥是第一个完成全基因组测序的植物(The Arabidopsis Genome Initiative, 2000)，而水稻则是首个公布全基因组序列的作物(International Rice Genome Sequencing Project, 2005)。毛果杨(Tuskan et al., 2006)、葡萄(Jaillon et al., 2007)、番木瓜(Ming et al., 2008)、玉米(Schnable et al., 2009)、大豆(Schmutz et al., 2010)、 高粱(Paterson et al., 2009)、蒺藜苜蓿(http://www.medicago.org/)的全基因组序列虽已公布，但组装尚不完整。其他全基因组测序即将完成的作物还包括短柄草、木薯、番茄、马铃薯和百脉根。利用已测序的基因组大规模开发 SNP 的方法有几种。对于杂合体如毛果杨，其测序数据包含两套基因组序列，可直接从单个品系的基因组序列中挖掘 SNP。针对水稻(Yu et al., 2005)和葡萄(Velasco et al., 2007)等纯合体，则需要同时测序两个不同品系，根据两者基因组序列差异鉴定 SNP (Shen et al., 2004; Feltus et al., 2004)。利用拟南芥 Col-0 基因组序列，Clark 等开发出拟南芥基因组重测序芯片，并被成功用于拟南芥 SNP 标记开发(Clark et al., 2007; Zeller et al., 2008)，McNally 等也成功利用水稻重测序芯片分析水稻地方种与栽培品种的 SNP 遗传变异(McNally et al., 2009)。

2.5 利用第二代测序技术开发 SNP

如何迅速挖掘大量 SNP，人们对第二代高通量基因组测序技术(454、Solexa、SOLiD)寄予厚望。由于每个 run 能产生几亿到几十亿碱基序列数据，利用第二代测序技术能够以非常低廉的价格开发大量 SNP (Mardis, 2008)。上述方法已应用于拟南芥(Ossowski et al., 2008)、水稻(Arai-Kichise et al., 2011)、大豆(Wu et al., 2011; Hyten et al., 2010)、高粱(Nelson et al., 2011)和毛果杨(Geraldes et al., 2011)等完全测序的物种。而对于其他未完成测序的物种，尽管已取得一些进展(Han et al., 2011; You et al., 2011)，但仍处于起步阶段。为了用足够的冗余序列开发可信 SNP，通常要求在不影响测序通量的前提下，将供测 DNA 序列的复杂度降低到相当水平(占基因组的 1/10 至 1/100)。此法已成功从玉米(Barbazuk et al., 2007)和桉树(Novaes et al., 2008)中开发出数量庞大的 SNP，其假阳性率大概为 20%。另一个减少序列复杂性的方法是利用 AFLP 技术从不同个体中选择特定的限制片段进行扩增(Van et al., 2007)，所得 SNP 假阳性率约 25%。

2.6 多倍体植物 SNP 的开发

遗传研究表明，许多植物并非只拥有单纯的二倍体遗传背景，多倍化现象普通存在，例如四倍体的棉花(*Gossypium hirsutum*)、油菜(*Brassica napus*)、花生(*Arachis hypogea*)和烟草(*Nicotiana tabacum*)，六倍体的小麦(*Triticum aestivum*)。其他植物如甘蔗和马铃薯则是高度杂合的同源多倍体，通常含有 4 个或更多个基因组拷贝。上述介绍用于鉴定二倍体植物 SNP 的方法部分已在多倍体植物中应用，特别是同源多倍体。由于直系同源序列间的差异足以作为真实的 SNP，通过扫描大量同源多倍体 ESTs 序列可从中鉴定 SNP (Cordeiro et al., 2006; Tang et al., 2006)。扩增子重测序方法在不同 DNA 剂量上检测 SNP 均足够灵敏，因此也可用于同源多倍体植物 SNP 的开发(Simko et al., 2006; Li et al., 2008)。微阵列芯片杂交则只能鉴定个体间完全不同的 SNP (例如某一个体全套基因组上某一位点上的碱基序列均为 A，而另一个体对应的位点为 G)，而难于鉴定杂合性多倍体的 SNP。与同源多倍体相比，异源多倍体 SNP 的开发则更加复杂，因为必须区分基因组之间(无用)和基因组之内的 SNP。尽管在某些情况下有办法区分异源多倍体中不同基因组间的 EST 序列(Somers et al., 2003; Trick et al., 2009)，然而这是一个复杂的过程，需要熟练掌握生物信息学知识并分析不同个体间大量的 EST 序列。当前异源多倍体植物 SNP 开发方法主要采用扩增子测序。在异源四倍体植物如油菜(*Brassica napus*)中，由于两套基因组(A 和 C)序列差异小，其 SNP 的开发可效仿同源多倍体植物，同时扩增 A 和 C 基因组并直接测序 PCR 产物(Westermeier et al., 2009)。另一个鉴定油菜 SNP 的途径是利用二倍体祖先种(如 *Brassica rapa* 和 *Brassica oleracea*) (Durstewitz et al., 2010)。

然而，由于多倍化通常与遗传瓶颈关联，祖先二倍体基因组往往比四倍体含有更多的遗传变异，这无疑增加 SNP 开发的难度。而对于其他物种如六倍体小麦，直接对三套基因组的扩增子测序是不够的，因为基因组间存在的插入/缺失使测序结果分析困难，甚至无法分析。对此，变通的方法是采用基因组特异引物进行扩增子测序(序列只来自其中的一套基因组) (Ganal et al., 2007)。此法已在几个小麦 SNP 鉴定的项目中实施，现已设计出几千对基因组特异性引物(URL: http://wheat.pw.usda.gov/SNP)用于扩增子测序和小麦品种间的 SNP 分析(Ravel et al., 2006; Chao et al., 2009)。

3 问题与展望

在 SNP 开发过程中，为了避免由于资源库遗传背景狭窄所造成的测量偏倚，必须仔细挑选一套具有代表性的材料。只从少数几个感兴趣的品系或带有不同等位基因频率的材料中鉴定出的 SNP 可能在其他与之差异明显的资源中没有多态性或者用处不大。通过大量扩增子测序并结合品系混合基因池测序可在最大程度上避免测量偏倚，后者的目的在于估计等位基因频率。将来，利用第二代测序技术能够在一个特定的资源库中同时分析大量品系，届时等位基因频率能被可靠地估算。

目前，不管从整个基因组或者只针对基因的编码区进行大规模 SNP 开发仍面临很大挑战，因为完成主要作物的全基因组测序还需要一定时间。例如，虽然现在玉米基因组的序列草图已经可用(URL: http://www.maizesequence.org)，但为完成剩余序列的测序，至少仍需要 1~2 年甚至更长时间才能够得到高质量的玉米全基因组序列，而对于像大麦和小麦等基因组大于 5 pg 的作物，将需要花费更多时间。

由于全基因组测序只是大规模 SNP 鉴定的开始，在主要二倍体作物中通过测序几个个体去获得详细的 SNP 数据将需要更长时间。而对尚未完成全基因组测序的植物，大规模鉴定 SNP 的最可靠方法仍是扩增并测序尽可能多的基因。对于已获得完整全基因组序列的植物，利用第二代测序技术对全基因组进行重测序是大规模开发 SNP 并进行全基因组关联分析的不二选择。最近在拟南芥(Atwell et al., 2010)和水稻(Huang et al., 2010)上的两个研究成果已充分展示全基因组重测序结合第二代测序技术的强大能量。Huang 等(2010)采用第二代测序技术 Solexa 对 517 个水稻地方品种进行全基因组重测序，从中鉴定出大约 360 万个 SNP 位点，构建了超高密度的水稻单倍型图谱，并在此基础上对 14 个农艺性状进行全基因组关联分析。该研究标示着水稻全基因组关联作图时代的到来。

除了前面提到的 SNP 开发方法之外，目前人们正对一种涉及序列捕获的 SNP 鉴定新方法颇感兴趣。这种方法已成功用于探测人类基因组外显子区域的 SNP (Hodges et al., 2007)。其原理是利用基因序列(如外显子)合成芯片，并通过与基因组总 DNA 杂交富集目的 DNA，接着用第二代测序技术测序。最后以芯片上的序列为参考序列，快速而有效地鉴定大量 SNP。然而，此法迄今尚未在植物上应用。由于该法同样能捕获旁系同源序列，它在直系同源序列中鉴定 SNP 的成效如何尚不清楚，将其应用于异源多倍体或古多倍体(如玉米)则更具挑战性。

随着基因分型芯片平行分析 SNP 的数量(10 000~60 000)不断增加，精确测序显得格外重要。为开发成千上万个伴随着 25%~50%误差率或者没有单倍型信息的 SNP 而设计芯片是不明智的，因为用于鉴定假阳性 SNP 或者来自同一单倍型的几个 SNP 的费用比利用可靠但不高效的 SNP 鉴定方法多花的费用还高。就此而言，先进的生物信息学筛选算法和高精度测序将和第二代测序技术一样变得非常重要。

4 结语

尽管当前几种大规模 SNP 开发方法被证明行之有效，在第二代测序技术的推动下，多数植物的 SNP 开发速度也将加快，但在 SNP 大规模用于关联分析和育种研究之前，仍存在许多需要解决的难题。由于短期内无法获得主要农作物的完整全基因组序列，SNP 开发应主要通过分析尽可能多的品系和基因。即使缺乏全基因组序列，利用扩增子重测序或者序列捕获技术并结合第二代测序技术，我们仍将能够在几年时间内从一种作物 30 000~60 000 个基因中鉴定出 SNP 或单倍型。此外，我们的重点应该放在能反映育种材料真正遗传变异的 SNP 开发上，经过验证的 SNP 可通过作图群体进行精确定位。

目前，许多作物上大范围的 SNP 分析仍基于个体型 SNP。将来，为了像分析人类基因组一样更有效地进行关联分析，需要转向单倍型特异性 SNP

的开发。一旦作物单倍型特异 SNP 鉴定出来，将能在全基因组水平上详细分析种质资源，高效地进行 SNP 标记与植物性状的关联分析，并最终在育种上有效地利用植物的遗传多样性。

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