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植物细胞遗传学
基因组结构与染色体功能

Plant Cytogenetics
Genome Structure and Chromosome Function

Hank. W. Bass and James. A. Birchler

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北京

图字：01-2012-6961 号

This is an annotated version of
Plant Cytogenetics: Genome Structure and Chromosome Function
Edited by Hank. W. Bass and James. A. Birchler.

ISBN：978-0-387-70868-3

图书在版编目(CIP)数据

植物细胞遗传学：基因组结构与染色体功能=Plant Cytogenetics: Genome Structure and Chromosome Function：英文 /（美）斯基（Bass, H. W.）等主编．—北京：科学出版社，2013.1
（实验室解决方案）
ISBN 978-7-03-035927-8

Ⅰ.①植… Ⅱ.①斯… Ⅲ.①植物学－细胞遗传学－研究－英文②植物－基因组－结构－研究－英文③植物－染色体－功能－研究－英文
Ⅳ.①Q943

中国版本图书馆 CIP 数据核字（2012）第 258898 号

责任编辑：李小汀 田慎鹏 / 责任印制：钱玉芬
封面设计：耕者设计工作室

科学出版社 出版
北京东黄城根北街 16 号
邮政编码：100717
http://www.sciencep.com
北京佳信达欣艺术印刷有限公司 印刷
科学出版社发行 各地新华书店经销
*
2013 年 1 月第 一 版 开本：787×1092 1/16
2013 年 1 月第一次印刷 印张：22 1/2
字数：530 000
定价：138.00 元
（如有印装质量问题，我社负责调换）

前　言

本参考书旨在为学生、教师和研究人员提供一系列植物细胞遗传学的课题，包括从植物基因组和染色体的结构与功能进行研究的经典细胞遗传学、二十一世纪新兴的分子细胞学和细胞遗传学、现行的研究方法以及适合本科和研究生教学的实验室练习。本书共分为三部分，每一章节均由该研究领域的国际知名学者所撰写。我们的初衷是在本书的章节中能够补充近十年植物细胞遗传学领域发表的优秀综述，也希望本书在这些重要的研究课题中作为参考书发挥持久的贡献。

第一部分，“植物细胞遗传学的结构、变异和图谱”，涵盖了经典的细胞学、染色体畸变、植物 B 型染色体，以及传统或现代 DNA 或染色质纤维技术为基础的细胞遗传学图谱。植物染色体的重排，如缺失、插入和重排的作用在本书中得到了很好的阐述，相关的研究工具也得到了很好的研发。植物非整倍体的产生、检测和影响则是通过与基因渗入繁殖相关的基因剂量和孵育进行概述的。此外，部分章节对多余的 B 型染色体进行了总结，对其潜在的研究应用进行了检测。第一部分的最后两章通过在染色体分散中结合嘌呤碱基 G 的传统细胞学方法和荧光原位杂交技术阐明了细胞遗传学在植物基因组图谱中的应用。利用 DNA 或染色质纤维进行基于荧光原位杂交的高分辨率绘图体现了植物细胞遗传学图谱构建中的最新水平。

第二部分，“植物细胞遗传学的功能、组织和动力学”，涵盖了染色体基本元素的组成，染色体在减数分裂时期的行为以及通过 DNA 甲基化和组蛋白的修饰研究分析对表观遗传学的探究。在植物着丝粒与端粒两个章节后，接下来的一章着重描述了减数分裂期，尤其是减数分裂前期 I 的染色体变化。本部分的最后一章总结了植物中的表观遗传代码，并对其在植物与非植物真核生物中进行了比较。

第三部分，“植物细胞遗传学的方法、信息和指导教学”，本参考书为有理想抱负的年轻导师广泛拓展思路，提供了包括信息学和实验室指导训练等当前先进实验室使用的几种主要研究方法。本部分的前四个章节主要阐述了染色体显微切割技术及其在植物遗传研究中的应用。下一章，详细描述了抗体在植物细胞遗传学中的应用，包括免疫组化和染色质免疫共沉淀技术。接下来的两章，涵盖了荧光原位杂交的先进方法，包括延伸 DNA 纤维荧光原位杂交和荧光原位 PCR 技术。关于植物细胞学基因组数据库的一章，对于我们通过网络资源和数据库访问并理解经典遗传学与现代基因组资源的相关的植物细胞生物遗传学发挥了重要的作用。本书最后一章专为指导教师而写，鼓励他们发展和延续植物细胞遗传学的实验课程，旨在为将来培训出更多的植物细胞遗传学家。本章主要包括若干模块化练习，为指导教师现有的或即将开展的课程提供了一份教学资源。

总体而言，本书涵盖了许多植物遗传学领域的基础课题，当今的研究成果和新技术的总结彰显出该研究领域的快速发展和研究动力。包含实验方法和教学指导是本参考书一个独特的优势。我们希望它能刺激新的研究进展，同时有利于指导教师和学生之间植物遗传学知识的亲力传授。

最后，我们对 Anne B. Thistle 博士在本书编写中提供的巨大帮助深表感谢。我们对她无私奉献和事无巨细的精神深表感激。

塔拉哈西，佛罗里达州　　Hank W. Bass
哥伦比亚，密苏里州　　James A. Birchler
（李建勇　译）

Preface

This reference book is intended to provide information for students, instructors, and researchers on a range of topics in plant cytogenetics, including classical cytogenetics of plant genomes and chromosomes from structural or functional perspectives, modern molecular cytology and cytogenetics in the twenty-first century, recent methods, and laboratory exercises suitable for undergraduate or graduate instruction. The book is divided into three sections, each with chapters contributed by leading international scholars in the field. Our hope is that these chapters will supplement the many excellent review articles on plant cytogenetics published in the last 10 years and will provide a lasting contribution as a reference book on this important topic.

The first section, "Structure, Variation, and Mapping in Plant Cytogenetics," covers classical cytology, chromosome aberrations, plant B chromosomes, and cytogenetic mapping by conventional or modern DNA or chromatin-fiber-based techniques. The role of plant chromosomal rearrangements, such as deletions, insertions, and rearrangements, is described, and research tools are explored. The production, detection, and impact of aneuploidy in plants are reviewed in relation to gene dosage and breeding through introgressions. In addition, the supernumerary B chromosomes are reviewed, and their potential research applications examined. This section ends with two chapters on the use of cytogenetics to map plant genomes, from historical cytology with G-banding to fluorescence in situ hybridization (FISH) on chromosome spreads. High-resolution FISH-based mapping using DNA or chromatin fibers highlights the state of the art in plant cytogenetic mapping.

The second section, "Function, Organization, and Dynamics in Plant Cytogenetics," covers the basic elements of chromosomes, their behavior in meiosis, and the epigenetic landscape as surveyed by analysis of DNA methylation and histone modifications. Chapters on plant centromeres and plant telomeres are followed by a chapter on meiotic chromosomes, with emphasis on prophase of meiosis I. The last chapter in this section reviews epigenetic code in plants and a comparison of plants and nonplant eukaryotes.

The third section, "Methods, Informatics, and Instruction in Plant Cytogenetics," provides breadth to the book by covering several major methods used by leading

laboratories as well as including chapters on informatics and laboratory exercises for aspiring or practiced instructors. The techniques for chromosome microdissection and descriptions of their use in several plant genetic applications are covered in the first of four chapters in this section. The next chapter provides detailed methods for the use of antibodies in plant cytogenetics, including immunolocalization and the chromatin immunoprecipitation (ChIP) technique. The next two chapters cover advanced methods in FISH, including extended DNA fiber-FISH and in situ PCR. A chapter on plant cytology in genome databases addresses the growing role of online resources and databases in our access to and comprehension of plant cytogenetics in relation to classic genetic and modern genomic resources. Finally, a chapter for instructors is included to encourage the development or continuation of laboratory courses in plant cytogenetics, an activity deemed important for training future plant cytogeneticists. The chapter includes several modular exercises that can serve as a resource for instructors of new or ongoing courses.

Overall, the book is designed to cover many foundational topics in plant cytogenetics, while reviewing modern research and new techniques that represent the current growth and momentum in the field today. Inclusion of methods and instruction provides a distinct advantage to this reference book. We hope it will stimulate new research and facilitate the hands-on transmission of plant cytogenetic knowledge to students and teachers alike.

Finally, we would like to acknowledge the extraordinary editorial assistance of Dr. Anne B. Thistle. We are deeply appreciative of her dedication and attention to detail.

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（李建勇　译）

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Part I

Structure, Variation, and Mapping in Plant Cytogenetics

Chapter 1
Plant Chromosomal Deletions, Insertions, and Rearrangements

Donald L. Auger and William F. Sheridan

Abstract With the exception of a small subset found within mitochondria and chloroplasts, the genes of plants are arranged along an essential set of chromosomes that are found in the nucleus. Within a species, the placement of genes along the chromosomes is expected to be the same in all individuals. This chapter is a primer on several major aberrations of gene order. These aberrations have consequences not only to the individual that harbors them but also to the population at large in terms of genome evolution. Here, we limit our discussion mainly to the effects on the individual. We are particularly interested in the use of these aberrations as experimental tools and include some discussions to that effect.

Keywords Cytogenetics · Deletions · Deficiencies · Insertions · Duplications · Inversions · Reciprocal translocations · Maize B-A chromosomes

Abbreviations

Ctr	Centromeres
Df	Deficiency
Dp	Duplication
EMS	Ethyl methanesulfonate
FISH	Fluorescent in situ hybridization

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H.W. Bass and J.A. Birchler (eds.), *Plant Cytogenetics*, Plant Genetics and Genomics: Crops and Models 4, DOI 10.1007/978-0-387-70869-0_1,

In	Inversion
N	Normal
SBE	Starch branching enzymes
TE	Transposable elements

Contents

1.1 Introduction

An analogy useful for explaining genetics to a layperson is to describe the genome as an encyclopedia of instructions necessary to make an organism, in which each gene represents an instruction. Like a traditional encyclopedia, the genome is divided among several volumes or books, which are called chromosomes. Encyclopedias are organized so as to make the data readily available. Chromosomes must be organized as well, so that the cell can access the information correctly and efficiently, when and where needed, but this system of organization is not completely clear. Among members of any given species, the order of genes on a chromosome is generally regarded as canonical – exceptions are considered aberrations. Interestingly, Barbara McClintock, who developed her career and reputation helping to establish this dogma, became one of the earliest dissenters when she described DNA elements capable of being transposed to new sites along the same or even another chromosome. Indeed, extensive sequencing data and other recent techniques are demonstrating that chromosomes are much more labile than was believed even a decade ago. The biological implications of a labile genome affect everything from the individual to the evolution of populations. Here, we offer a primer on some common aberrations from canonical chromosome organization: deficiencies, duplications, and rearrangements.

1.2 Deletions/Deficiencies

Deletion of a chromosomal segment results in a deficiency. When it occurs in a diploid cell, then that cell and its progeny will be hemizygous i.e., it has only one copy of, any gene or locus included in the deficiency. When a whole chromosome is

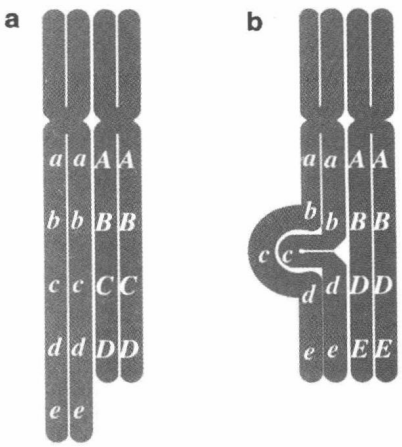

Fig. 1.1 Simple deficiencies. Homologues are lined up as in pachytene with a normal chromosome to the left and deletion chromosome to the right. (**a**) Terminal deficiency. (**b**) Internal deficiency

lost, the resulting cell is said to be monosomic for the remaining homologous chromosome. The word monosomic has also been used to describe larger chromosomal segments that are homologous to large deleted segments. The following discussion focuses on segmental deficiencies rather than losses of whole chromosomes.

A simple case of a chromosomal deficiency is breakage without reunion (Fig. 1.1a). The segment without a centromere is lost quickly in subsequent cell cycles, so the progeny cells are deficient for all loci distal to the breakpoint. In plants with diffuse centromeres, e.g., *Luzula*, a broken piece can be maintained and will not result in a deficiency (Nordenskjold 1961). Internal (interstitial) deficiencies occur when two breaks occur simultaneously in one chromosome, the proximal and distal segments rejoin, and the intervening segment is lost (Fig. 1.1b). McClintock (1931) uses the term "deletion" to describe only this form of deficiency, but the two terms are commonly used interchangeably (see e.g., Burnham 1962, p. 20). Although the deficiency is obvious as shown in Fig. 1.1, small deficiencies are difficult to visualize at pachytene, but larger ones may be visible.

Breaks that occur for unknown reasons are said to occur spontaneously. Breaks can be induced experimentally by means of heat, high-energy radiation, and certain chemicals. Deficiencies seem to be the mode for X-ray-induced mutations. Stadler and Roman (1948), Nuffer (1957), and Mottinger (1970) could not find evidence of base-change mutations when using X-rays; instead these mutations were apparently short deficiencies. Interestingly, the form of induction affects the locations of breaks. Breakages induced by high-energy radiation are more likely to occur in centromeric and heterochromatic regions (Evans and Bigger 1961). X-ray-induced breaks are more likely to be found in heterochromatin both in tomato (Gottschalk 1951; Khush and Rick 1968) and in maize (Longley 1961). In maize exposed to nuclear explosions, the bias toward breaks in heterochromatic regions was not as pronounced (Longley 1961), indicating that fast neutrons are more efficient in producing breaks in euchromatin.