

数量遗传学简介

王建康

中国农业科学院作物科学研究所

wangjiankang@caas.cn

<http://www.isbreeding.net>

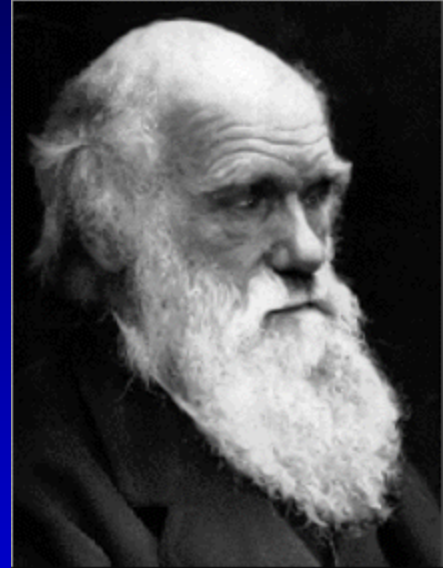
主要内容

- 一、数量遗传学的发展简史
- 二、植物育种与数量遗传
- 三、经典数量遗传的研究内容
- 四、数量遗传在植物育种中的应用
- 五、数量遗传基因定位, 即QTL作图
- 六、利用已知基因信息的育种设计
- 七、CIMMYT小麦育种方法和成就简介
- 八、观看纪录片《The Norman Borlaug Story》

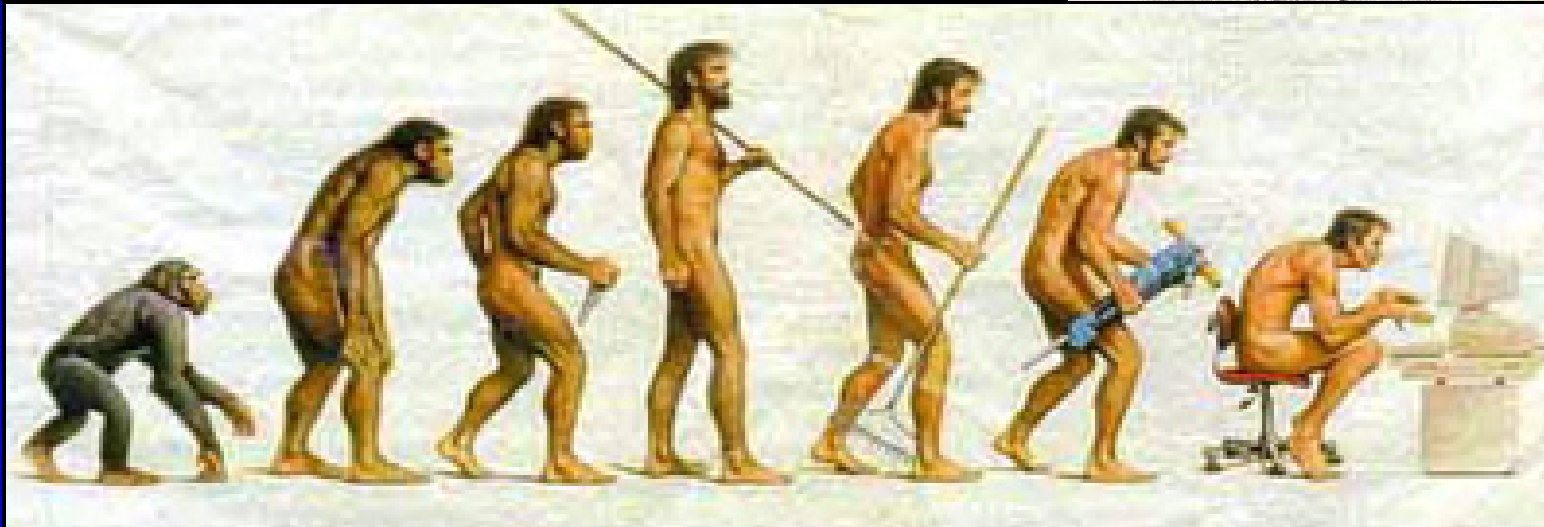
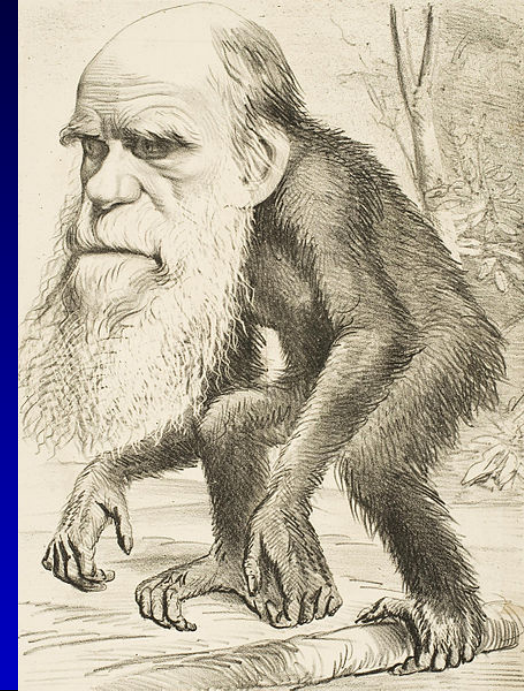
一、数量遗传学的发展简史

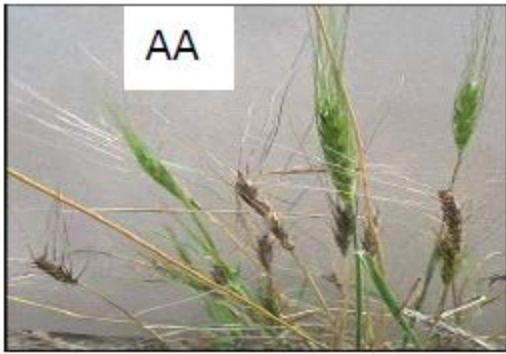
达尔文 (1809–1882) 与进化论

- 《物种起源》 (The Origin of Species) (1859)
 - On the Origin of Species by Means of Natural Selection
 - The Preservation of Favoured Races in the Struggle for Life
- “I have called this principle, by which each slight variation, if useful, is preserved, by the term Natural Selection.”



达尔文主义：物竞天择，适者生存





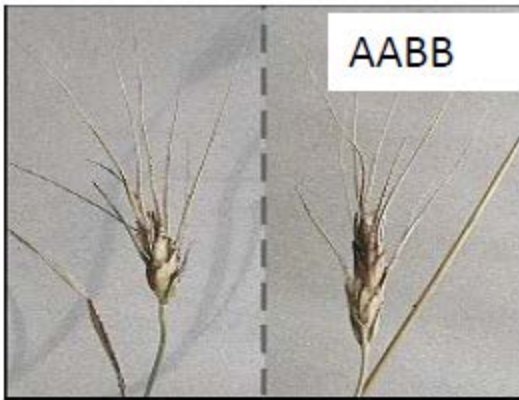
AA



BB



AABBDD



AABB



DD

Thank You



AABB



AABB



AABBDD

孟德尔杂交试验

➤ 孟德尔（1822-1884）遗传试验（1866年）：
豌豆（garden pea），*Experiments with Plant Hybrids*



- Seed shape: 5474 round vs 1850 wrinkled
- Cotyledon color: 6022 yellow vs 2001 green
- Seed coat color: 705 grey-brown vs 224 white
- Pod shape: 882 inflated vs 299 constricted
- Unripe pod color: 428 green vs 152 yellow
- Flower position: 651 axial vs 207 terminal
- Stem length: 787 long (185-230cm) vs 277 short (20-50cm)
- 作业1：对上述分离数据做3:1分离的适合性检验



孟德尔研究的性状

单基因控制的质量性状，不同基因间不存在连锁

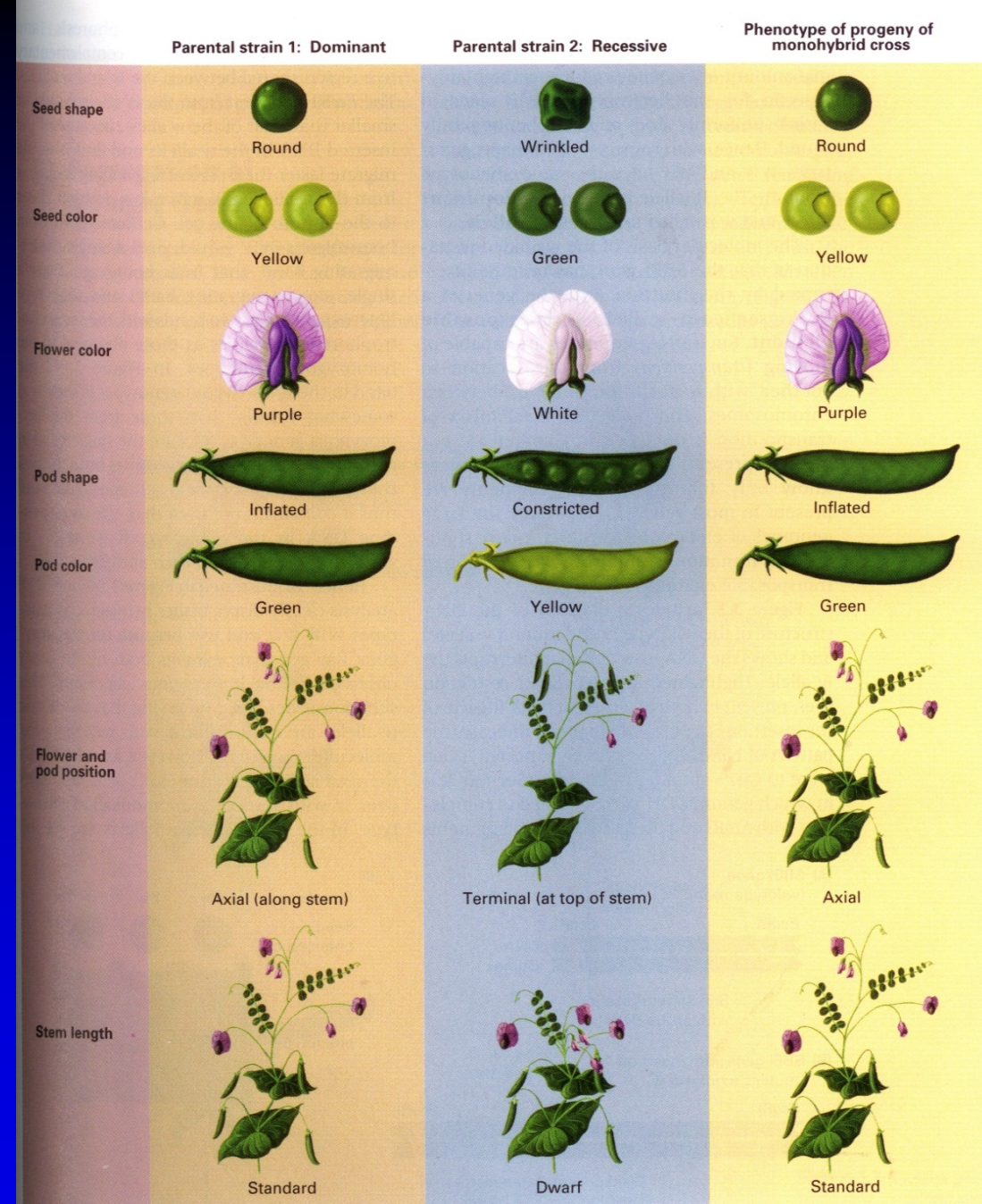


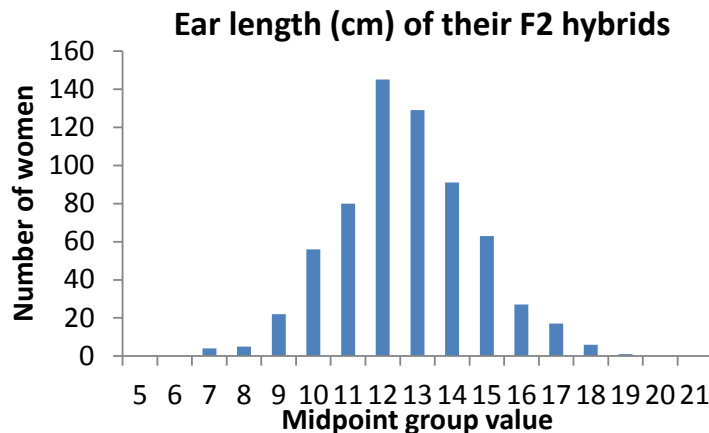
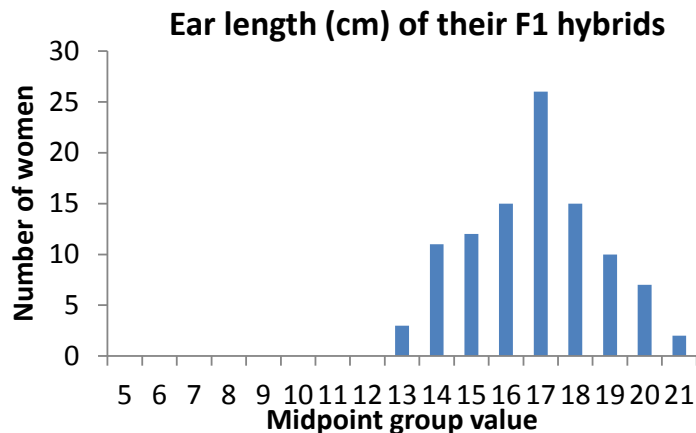
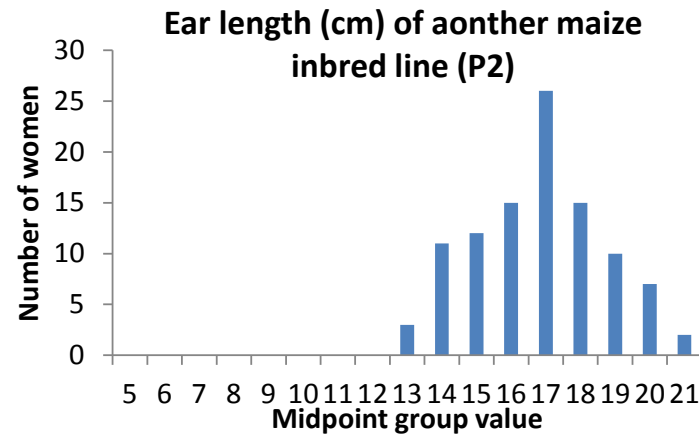
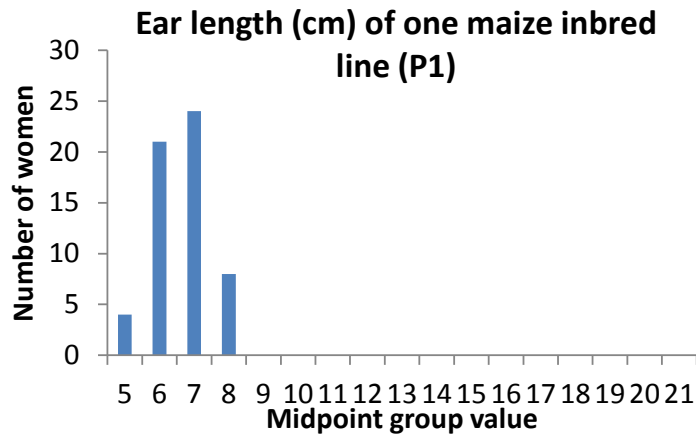
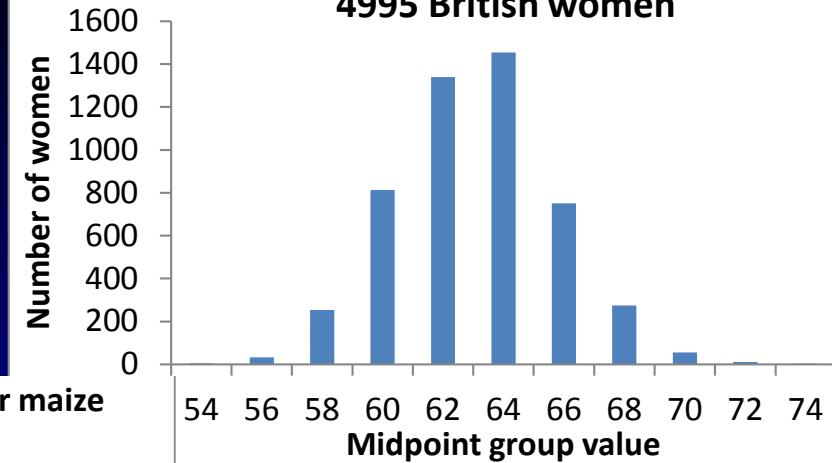
Figure 3.1 The seven different traits in peas studied by Mendel. The phenotype shown at the far right is the dominant trait, which appears in the hybrid produced by crossing.

孟德尔规律的重新发现

- 孟德尔规律的重新发现（1900年）
- 孟德尔遗传规律有那些？(作业2)
 - The Principle of Segregation
 - The Principle of Independent Assortment
- 什么是新达尔文主义？(作业3)
 - Neo-Darwinism is a term used to describe the 'modern synthesis' of Darwinian evolution through natural selection with Mendelian genetics

Quantitative traits in genetics

Distribution of height (inches) among 4995 British women



Quantitative trait does not have to be “continuous”

- Categorical traits: traits in which the phenotype corresponds to any one of a number of discrete categories
 - Number of skin ridges forming the fingerprints
 - Number of kernels on an ear of corn
 - Number of puppies in a litter
- Threshold traits: traits that have only two, or a few, phenotypic classes, but their inheritance is determined by the effects of multiple genes acting together with the environment
 - Liability to express the trait, which is not directly observable.
 - When liability is high enough (above a “threshold”), the trait will be expressed; Otherwise, the trait is not expressed.

数量性状遗传的生物统计学派

- F. Galton 19世纪末在英国建立研究小组主要研究人类群体中数量性状的遗传，1889年出版《Natural inheritance》
 - 发现了子代回归于亲代的遗传规律: Taller individuals had taller offspring, on the average, than shorter individuals, and, hence, metrical characters were partly heritable
 - Blending inheritance
 - 创建了回归和相关研究的方法
- K. Pearson用数学方法研究生物遗传和进化问题，撰写了《Mathematical contribution to the theory of evolution XII》（1904）一书，并创办了《Biometrika》杂志。

孟德尔学派和生物统计学派之争

- 生物统计学派 (K. Pearson) : 认为连续变异是进化的重要原因, 孟德尔规律不适用于连续变异。
- 孟德尔学派 (W. Bateson) : 不连续变异是进化的重要因素, 连续变异是不能遗传的。
- Yule (1906): There need be no conflict between Mendel's particulate inheritance and the inheritance of continuously varying traits, provided many genes having similar small effects were responsible for continuously varying traits.

孟德尔学派和生物统计学派的统一

- W. L. Johannsen (1903) 的纯系学说将变异区分为遗传的变异与非遗传的变异，提出了基因型和表现型的概念，这为理解连续性变异也是遗传性状提供了依据。
- Nilsson-Ehle (1909) 根据小麦粒色的遗传提出了数量性状的多因子假设，这一假设为E. M. East (1911) 玉米穗长和E. M. East (1913) 烟草花冠长度的遗传试验所证实。
- 通过多因子假设将数量性状的遗传纳入到孟德尔遗传的轨道，从而使两个学派的观点得到统一。

Johannsen (1903, 1909)的菜豆粒重试验

- Landrace: Princess variety of the common bean (*Phaseolus vulgaris*) , consisted of a mixture of pure lines
- Trait: seed size measured by centigram (cg)
- 19 lines with different sizes
 - Line 1 (the heaviest line): 64.2 cg
 - Line 19 (the lightest line): 35.1 cg
- 试验结果 (next slide)

纯系理论（或纯系学说）

➤ 试验结果

- 家系间的变异是部分遗传的
- 家系内的变异是不遗传的
 - Line13: 粒重为20、30、40、50的后代的平均粒重为47.5、45.0、45.1、45.8
 - Line1: 连续6个世代选择最轻和最重的籽粒，后代粒重分别为69和68，选择无效
- 利用亲子间的相关系数估计遗传力
 - 19个家系间: $r = 0.336 \pm 0.08$
 - Line13: $r = 0.018 \pm 0.038$

- ## ➤ W. L. Johannsen (1903) 的纯系学说将变异区分为遗传的变异与非遗传的变异，提出了基因型和表现型的概念，这为理解连续性变异也是遗传性状提供了依据。

Nilsson-Ehle (1906)的小麦粒色试验

- Three Mendelian loci govern red versus white kernel color in bread wheat and cultivated oats
- Any one gave 3 red to 1 white when segregating alone
- Two loci segregating: 15 red to 1 white
- Three loci segregating: 63 red to 1 white
- A cross between white and deep-red parents
- 1:6:15:20:15:6:1 for F₂ individuals carrying 0, 1, 2, 3, 4, 5, and 6 red alleles (identified through progeny test)
- Significance: effects of different alleles of different loci could be cumulative

East (1911) 的玉米穗长(cm)试验

穗长	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	平均
P1	4	21	24	8														7
F1					1	12	12	14	17	9	4							12
P2									3	11	12	15	26	15	10	7	2	17
F2			4	5	22	56	80	145	129	91	63	27	17	6	1			13

➤ P1: 7cm; P2: 17cm

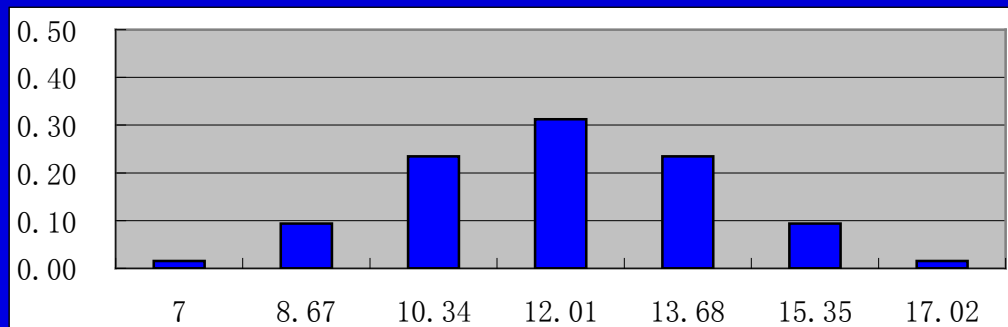
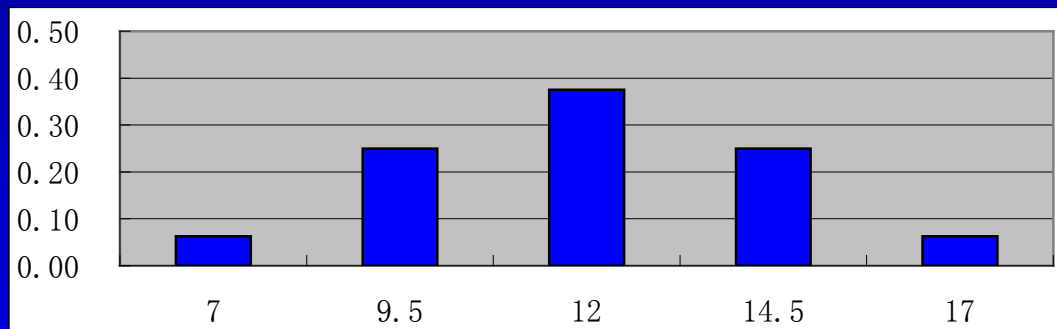
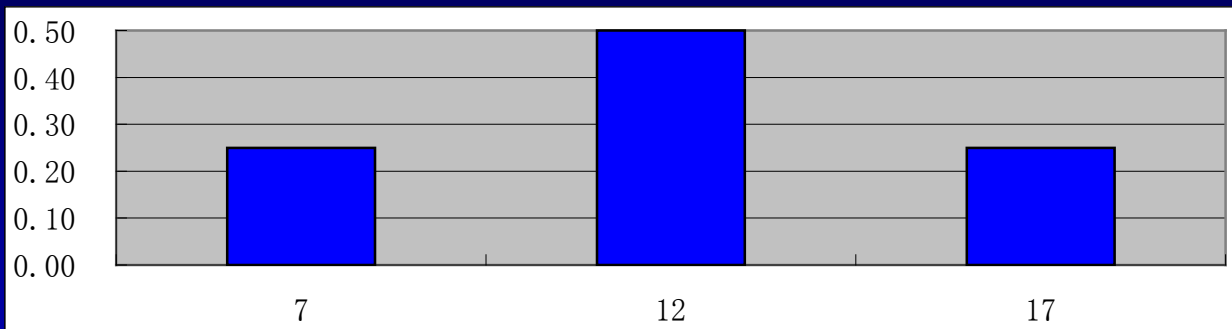
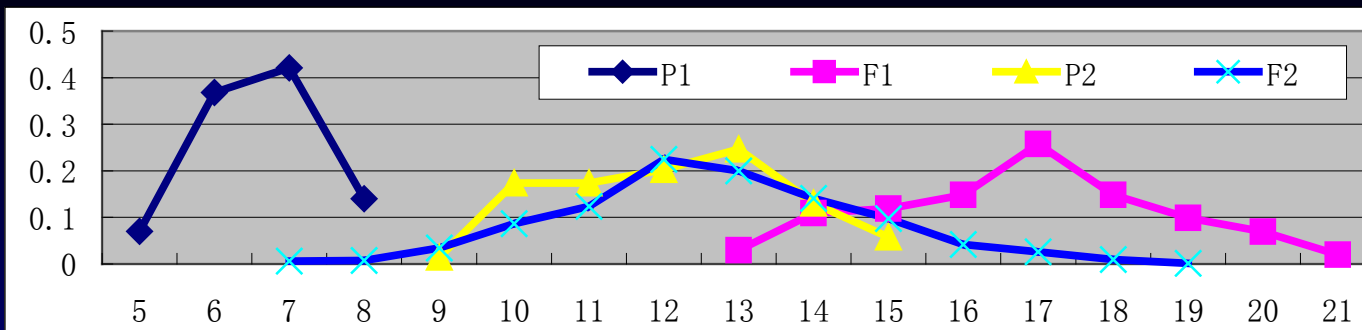
➤ One locus

■ $a=(17-7)/2=5$; F2: $1/4$ aa (7) + $2/4$ Aa (12) + $1/4$ AA (17)

➤ Two locus

■ $a=(17-7)/4=2.5$

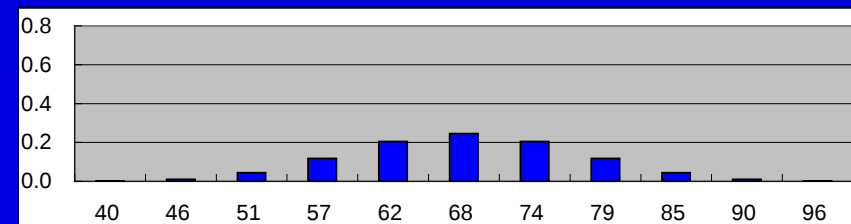
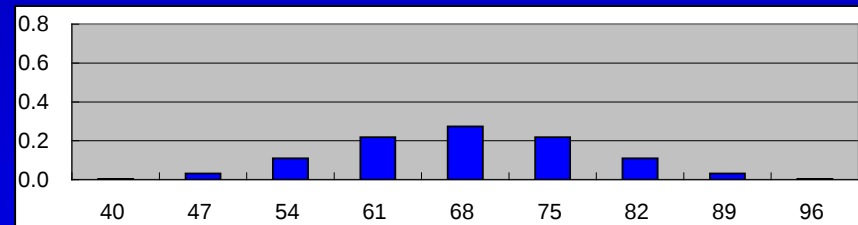
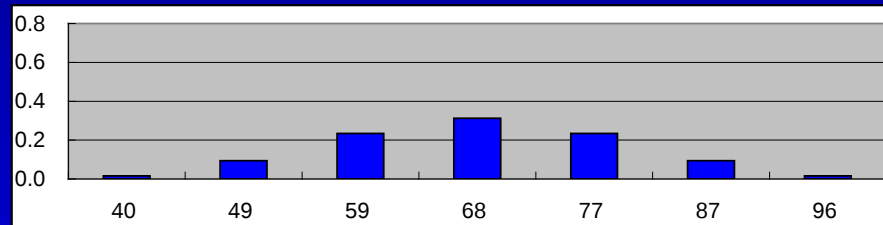
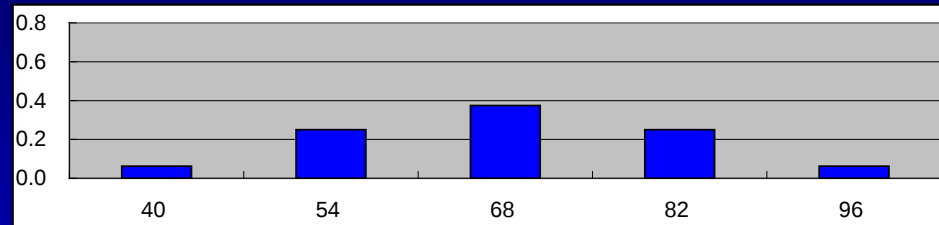
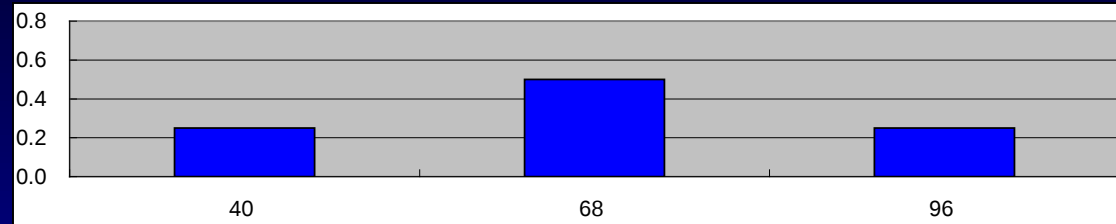
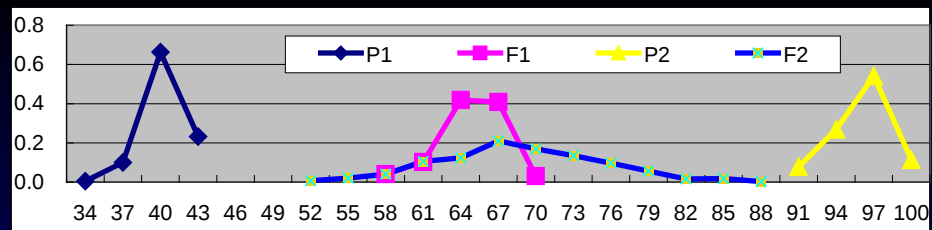
■ F2: $1/16$ (7) + $4/16$ (9.5) + $6/16$ (12) + $4/16$ (14.5) + $1/16$ (17)



East (1913) 的烟草花冠长度 (mm) 试验

		34	37	40	43	46	49	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	97	100
P1		1	21	140	49																			
F1										4	10	41	40	3										
P2																					13	45	91	19
F2								3	9	18	47	55	93	75	60	43	25	7	8	1				
F3	46				1	4	26	44	38	22	7	1												
F3	50				6	20	53	49	15	4														
F3	50					7	25	55	55	18														
F3	60				2	3	9	25	37	70	19	10												
F3	72										4	20	25	59	41	19	2							
F3	77						1	0	1	1	1	2	16	33	43	34	20	6	1					
F3	80										2	8	14	21	39	39	32	10	1					
F3	81										1	1	8	16	20	32	41	17	3	3	1			
F3	82												3	5	12	20	40	41	30	9	2			

➤ 作业4：计算各群体的均值和方差；F2亲代和F3后代间的协方差和相关系数



数量性状遗传的多基因假说

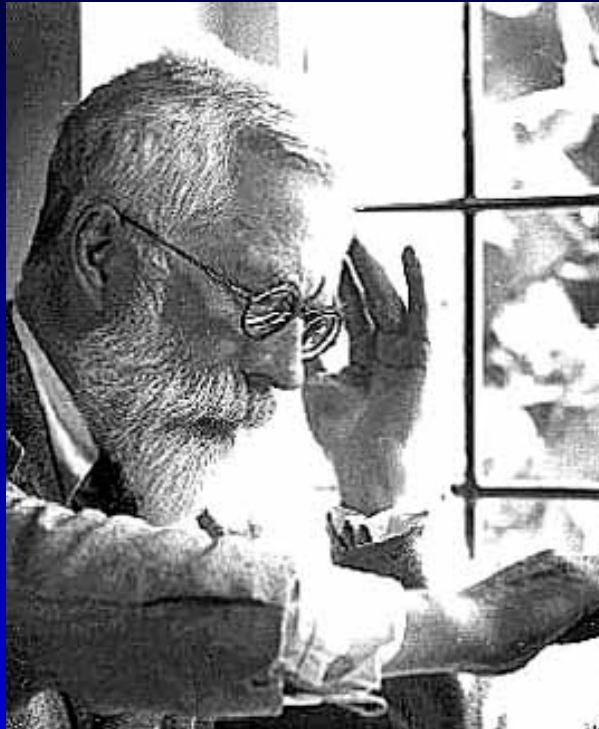
- Multiple-factor hypothesis (polygene system)
 - A hypothesis to explain quantitative variation by assuming the interaction of a large number of genes (polygenes) each with a small additive effect on the character.
 - Number of genes, gene effects, environment

数量遗传基本理论体系的建立（1920s-1940s）

- R.A. Fisher（1918）发表了“The correlation between relatives on the supposition of Mendelian inheritance”。
- J.B.S. Haldane（1924-1927）连续发表了“A mathematical theory of natural and artificial selection I-V”系列文章，用数学方法说明了数量性状在自然和人工选择下的遗传改变。
- S. Wright（1921）的“Systems of mating”概括了群体的交配制度，并提出了近交系数的概念，将不同交配制度的群体通过近交系数相比较，并用其通径系数研究交配制度的遗传效果。
- J.L. Lush（1940）在其“Animal Breeding Plan”一书中提出了遗传力以及广义遗传力和狭义遗传力的概念，用于研究选择效率和遗传进度。
- G. Malecot提出了亲本系数的概念，用来测量双亲的一对等位基因后裔同样的概率，并度量双亲间的亲缘程度以及该个体的近交程度，从而给出了亲属间协方差的通用表达式。
- G.F. Sprague和L.A. Tatum（1942）提出了杂种优势利用中亲本配合力的概念。

R.A. Fisher's contribution to Genetics and Statistics

- Much of Fisher's contributions to statistics were based on biological data from Rothamsted (largest agricultural research centre in the United Kingdom). His work on the theory of population genetics also made him one of the three great figures of that field, together with Sewall Wright and J. B. S. Haldane, and as such was one of the founders of the neo-Darwinian modern evolutionary synthesis. His 1918 paper *The Correlation Between Relatives on the Supposition of Mendelian Inheritance* was the start of the modern evolutionary synthesis — a synthesis which he would later contribute much to in his 1930 book *The Genetical Theory of Natural Selection*.
- Fisher invented the techniques of maximum likelihood and analysis of variance, was a pioneer in the design of experiments, and originated the concepts of sufficiency, ancillarity, and Fisher information, making him a major figure in 20th century statistics. His article "On a distribution yielding the error functions of several well known statistics" presented Karl Pearson's chi-squared and Student's t in the same framework as the normal distribution and his own analysis of variance distribution z . Fisher's book *Statistical methods for research workers* showed how to use these distributions. See also Fisher's linear discriminator.



**Sir Ronald Fisher
(1890-1962)**

**Statistical Methods
Experimental Design
and
Scientific Inference**

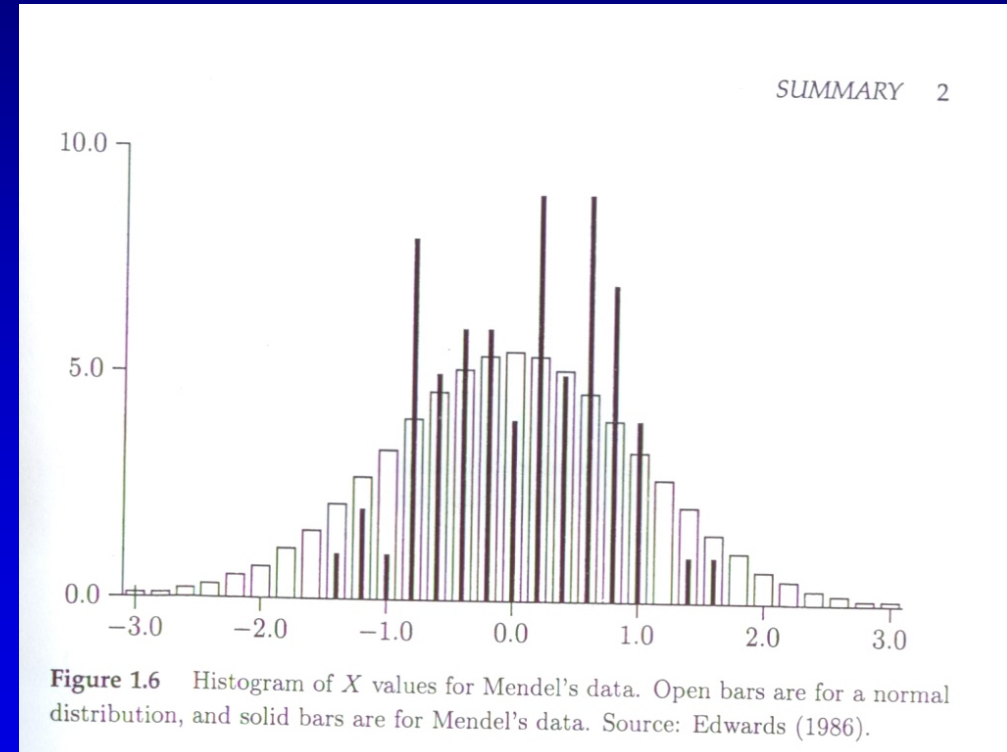
R. A. FISHER



OXFORD SCIENCE PUBLICATIONS

Mendel and Fisher

- Fisher(1936). Has Mendel's work been rediscovered? Annals of Science 1:115-137. Mendel's data was so close to the values that Mendel expected under his theory that there must have been some manipulation, or omission, of data
- Dominant trait: $1/3 AA + 2/3 Aa$
 - Family size: 10
 - Non-segregating (AA) :
Segregating (Aa) = 1:2 (Mendel)
 - Fisher: $\text{Pro} \{Aa \text{ family classified as } AA\} = 0.75^{10} = 0.0563$
 - $\text{Pro} \{\text{Non-segregating (AA)}\} = 2/3 * (1 - 0.0563) = 0.6291$
 - Non-segregating (AA) :
Segregating (Aa) = 0.3709 : 0.6291
= 1 : 1.6961



数量遗传研究的学派之争

➤ Birmingham学派

- 着重研究自交群体亲本间产生的杂种后代中的遗传变异，主要从世代平均数的分析来检测遗传模型和基因效应

➤ Edingburgh学派

- 着重研究随机交配群体的遗传变异，从遗传方差的分析来检测遗传模型及各种基因效应的相对重要性，不考虑基因效应值的估计

➤ 1976年在美国依阿华州立大学召开的第一届国际数量遗传学大会和1978年在英国剑桥大学召开的生统遗传学大会分庭抗礼的形式说明了两个学派的争论达到了高潮

➤ 1987年在北卡州立大学召开了第二届国际数量遗传学大会，不同学派的学者共同交流了数量遗传研究的进展，特别是基因型 and 环境的互作成为两方面共同有兴趣的问题，以往存在的分歧和争论在这次大会上趋于统一

数量遗传研究主线

- $P = G + E + e$
- $G = A + D + I$
- $G = \text{major gene} + \text{polygenes}$
- $G = \text{Summation (QTL effect)}$
- 遗传效应的分解
- 遗传方差的分解

二、植物育种与数量遗传

植物育种的定义

- 植物育种的主要任务是寻找控制目标性状的基因、研究这些基因在不同环境下的表型效应、挑选适当的亲本材料、设计杂交方案和分离群体种植方案、通过基因型/表型选择聚合存在于不同亲本材料中的有利基因、培育符合育种目标的基因型，为农业生产提供适宜的品种
- 植物育种中的科学
- 植物育种中的艺术
- 植物育种中的商业行为
- “机遇”或“运气”

植物育种的一般过程

- **配：** 选择亲本、配制杂交组合
- **选：** 繁殖产生育种群体，根据育种目标选择理想基因型
- **比：** 多环境表型鉴定，通过比较确定适合特定环境的作物新品种

育种家关心的一些问题

- **配**：选择谁做亲本进行杂交？采用什么杂交方式组合？如，
 - 单交： $A \times B$
 - 回交： $(A \times B) \times B$ 或 $(A \times B) \times A$
 - 三交： $(A \times B) \times C$
 - 双交： $(A \times B) \times (C \times D)$
- **选**：种植多大规模的群体？什么时候、选择什么性状、选择多少？如何提高育种效率？
- **比**：如何评价和排除（或利用）基因型和环境互作？如何选择试验地点？田间如何布置基因型？

孟德尔遗传对现代育种的贡献

➤ 杂交育种：重组可以产生新的表型/基因型

杂交育种

假定有2个抗性基因R1和R2，其等位基因为r1和r2；3个高产基因Y1、Y2和Y3，其等位基因y1、y2和y3；一对未来病害基因R和r；不考虑连锁

➤ 亲本基因型（2种）

- P1: **R1R1** r2r2 y1y1 **Y2Y2 Y3Y3** rr: 中抗、产量较高
- P2: r1r1 **R2R2 Y1Y1** y2y2 y3y3 RR: 中抗、产量较低

➤ 目标基因型: R1R1 R2R2 Y1Y1 Y2Y2 Y3Y3 ??

➤ 后代基因型（ $2^5=32$ 种）

- 不抗病、产量低: r1r1 r2r2 y1y1 y2y2 y3y3 ??
- 抗病、产量低: **R1R1 R2R2** y1y1 y2y2 y3y3 ??
- 等等

➤ 育种的目的是从32种可能的基因型中把理想的目标基因型选择出来

基因与基因型是两个不同的概念

- 当分离位点较多时, $2^{30}=1 \times 10^9$; $2^{50}=1 \times 10^{15}$
- 种质库的目的是保存尽可能多的基因; 保存所有可能的基因是容易实现的; 但是, 保存所有可能的基因型几乎是不可能的
- 但是, 也不是说越少越好, 例如,
 - P1: **R1R1 R2R2 Y1Y1 Y2Y2 Y3Y3 rr**
 - P2: r1r1 r2r2 y1y1 y2y2 y3y3 **RR**
 - P3: **R1R1** r2r2 **Y1Y1** y2y2 **Y3Y3 RR**
 - 目标基因型: **R1R1 R2R2 Y1Y1 Y2Y2 Y3Y3 RR**
 - P1×P2育种群体中, 有64种可能的基因型
 - P1×P3育种群体中, 有8种可能的基因型
 - 因此, 组配P1×P3, 育种更容易取得成功

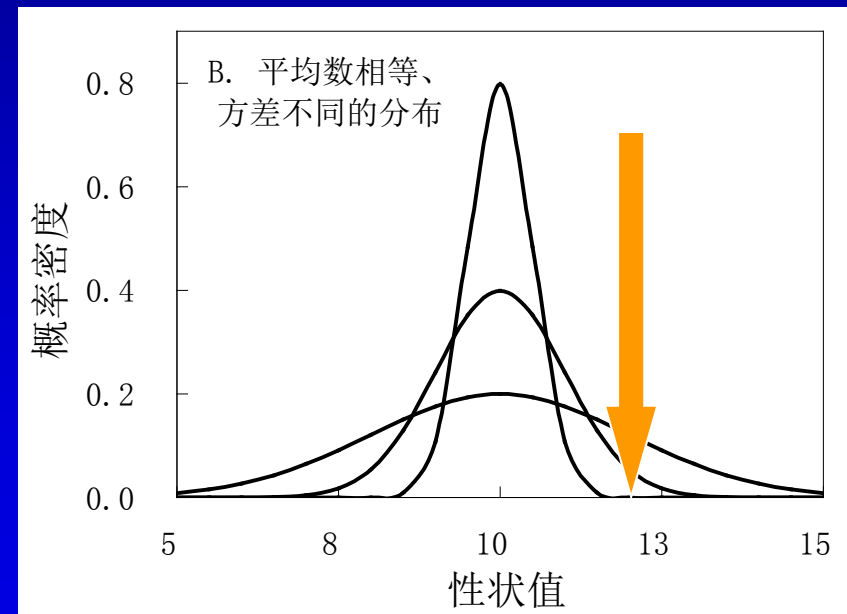
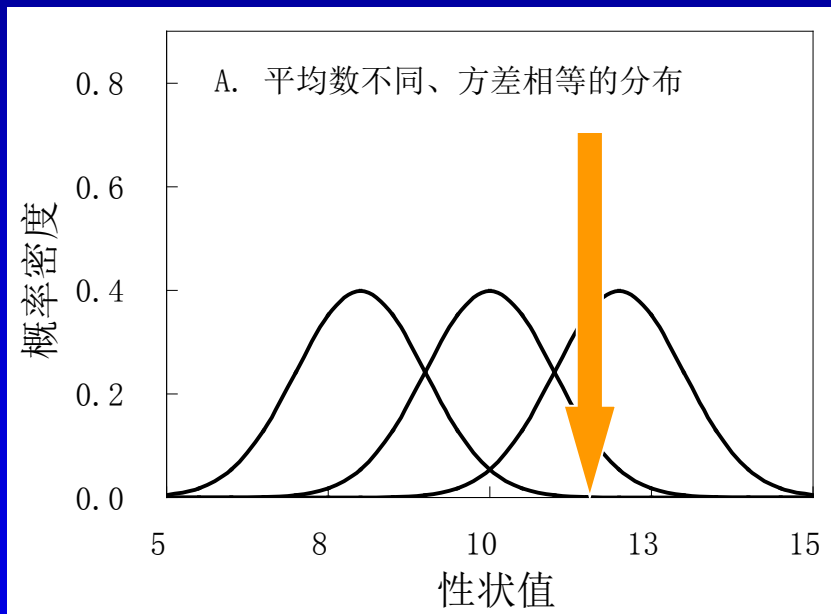
植物繁殖方式与育种目标

- 无性繁殖：香蕉、土豆、甘蔗、木薯（cassava）等
- 有性繁殖
 - 自花授粉
 - 异花授粉
- 育种目标
 - 无性系品种
 - 纯系品种（近交家系品种）
 - 杂种品种
 - 群体品种



理想的育种群体

- 高群体平均数
- 大遗传变异



育种家面临的问题

- 三大问题：周期长、效率低、预见性差（庄巧生）
- 亲本的选择
 - 如何提高优良组合的比例？
 - 如何创造高平均数和大遗传变异育种群体？
- 杂交类型的选择
 - 单交（single cross）
 - 回交（backcross）
 - 顶交（三交, topcross）
 - 复交（double cross）
- 选择方案的制定
- 新技术的应用，如DH，标记辅助选择，转基因等

CIMMYT小麦育种杂交类型

➤ 按亲本来源

- 适应亲本 X 适应亲本（60%）
- 适应亲本 X 半适应亲本（20%）
- 适应亲本 X 不适应亲本（10%）
- 冬性 X 春性（5%）
- 硬粒小麦 X 面包小麦，小黑麦 X 面包小麦，硬粒小麦 X 小黑麦（5%）

➤ 按杂交方式

- 单交
- 简单回交，高代回交，有限回交
- 顶交（三交）

育种性状的遗传

- 有多少？玉米大约有50,000个基因，
 - 控制油分或蛋白质含量的基因有多少？
 - 哪些在物种中已经固定？哪些仍在分离？
- 在哪里？
 - 基因家族？
 - 遍布全基因组？
- 效应有多大？
 - 主基因+多基因？
 - 加性效应？
 - 上位性互作？
 - 环境影响有多大

三、经典数量遗传的研究内容

- 数量遗传学：Quantitative genetics is concerned with the inheritance of those differences between individuals that are of degree rather of kind, quantitative rather qualitative (Falconer)
- 经典数量遗传的多基因假说
 - 孟德尔遗传
 - 数目多
 - 效应相似
 - 效应可加
- 经典数量遗传不区分个别基因的效应

数量遗传学专著

- Mather (1949) 出版了《Biometrical Genetics》，该书后来在Jinks的参与下出版了第二版（1971）和第三版（1982）
- Kearsey和Pooni 《The Genetical Analysis of Quantitative Traits》（1996）
- Falconer (1960) 出版了《Introduction to Quantitative Genetics》，该书于1981、1989、1996年分别出了第二、三、四版
- Lynch和Walsh 《Genetics and Analysis of Quantitative Traits》（1998）
- 朱军，1997。遗传模型分析方法。中国农业出版社，北京
- 盖钧镒，章元明，王建康，2003。植物数量性状遗传体系(现代遗传学丛书)。科学出版社，北京

数量遗传在植物育种中的应用专著

- Hallauer and Miranda, 1988. Quantitative genetics in maize breeding. Iowa State Univ. Press
- Bernardo, 2002. Breeding for quantitative traits in breeding. Stemma Press, Woodbury, Minnesota
- 马育华, 1982。植物育种的数量遗传学基础。江苏科学技术出版社

研究内容—群体遗传

- 基因和基因型频率
- 不同交配系统下基因和基因型频率的变化
- Hardy-Weinberg平衡的建立和平衡群体的性质
- 连锁对Hardy-Weinberg平衡的影响
- 迁移和突变
- 选择
- 突变和选择的联合效应
- 有限大小的理想群体
- 亲属关联和近交系数

研究内容—加性和显性效应

➤ $P = G + E + GE + \varepsilon$

➤ 单基因模型（等位基因 A_1 和 A_2 ）

■ $p^2: A_1A_1$ 、 $2pq: A_1A_2$ 、 $q^2: A_2A_2$

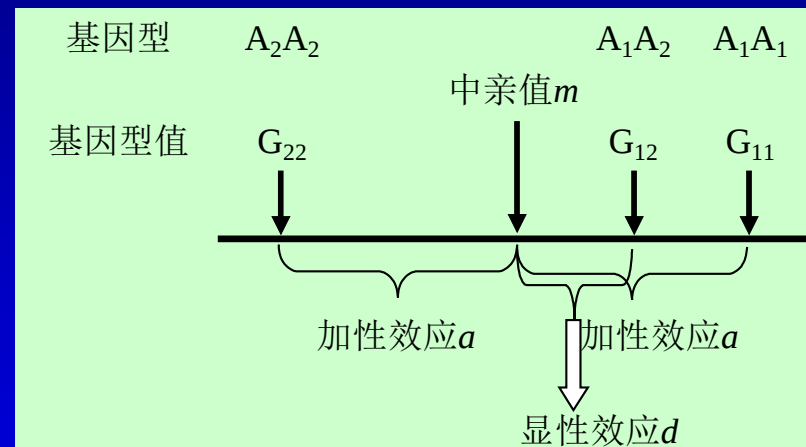
■ 基因型 A_iA_j 的遗传值为 G_{ij}

■ 中亲值： $m = (G_{11} + G_{22}) / 2$

■ 加性效应： $a = G_{11} - m$

■ 显性效应： $d = G_{12} - m$

■ $G_{11} = m + a$; $G_{12} = m + d$; $G_{22} = m - a$



研究内容—育种值和显性离差

➤ 单基因模型（等位基因 A_1 和 A_2 ）

- 群体平均数: $\mu = m + (p-q)a + 2pqd$
- 等位基因效应: $\alpha_1 = q[a + (q-p)d]$; $\alpha_2 = -p[a + (q-p)d]$
- 等位基因的替代效应 $\alpha = \alpha_2 - \alpha_1 = a + (q-p)d$
- $G_{ij} = \mu + \alpha_i + \alpha_j + \delta_{ij}$
- 育种值: $A_{ij} = \alpha_i + \alpha_j$
- 显性离差: $D_{ij} = \delta_{ij}$

➤ 容易推广到复等位基因

研究内容—上位性离差

➤ 2个基因位点模型（ A_i 、 A_j 和 B_k 、 B_l ）

$$G_{ijkl} = \mu + (\alpha_i + \alpha_j + \delta_{ij}) + (\alpha_k + \alpha_l + \delta_{kl}) + I_{ijkl}$$

➤ 育种值： $A = \Sigma \alpha$

➤ 显性离差： $D = \Sigma \delta$

➤ 上位性离差： $I = \Sigma I$

➤ $P = G + \varepsilon = \mu + A + D + I + \varepsilon$

➤ $V_P = V_G + V_\varepsilon = V_A + V_D + V_I + V_\varepsilon$

研究内容--遗传方差的分解

效 应	方 差
表型值 (P)	表型方差 (V_P)
基因型值 (G)	遗传方差(V_G)
育种值 (A)	加性方差 (V_A)
显性离差 (D)	显性方差 (V_D)
上位性离差 (I)	上位性方差 (V_I)
基因型X环境互作效应 (GE)	基因型X环境互作方差 (V_{GE})
随机误差 (ϵ)	随机误差方差 (V_ϵ)

四、数量遗传在植物育种中的应用

- 育种目标的制定
- 遗传力的估计
- 遗传进度的估计
- 不同选择方法的比较
- 多性状选择
- 杂种优势的预测

提高遗传进度的途径分析

$$R = k_p h \sqrt{V_A}$$

$$R = \frac{k_p V_A}{\sqrt{V_P}}$$

- 使用较小的选择比例，即提高选择强度 (k_p)
- 提高加性方差在遗传方差中所占的比例 (h^2)
- 提高加性方差本身 (V_A)
- 降低非遗传方差

玉米轮回选择的遗传进度

轮回选择方法 (V_A 的系数)	每周期年数	产量		穗长	
		每年	每周期	每年	每周期
混合选择, 无花粉控制 (1/2)	1	0.054	0.054	8.9	8.9
混合选择, 花粉控制 (1)	1			17.8	17.8
修饰穗行选择 (1/8)	1	0.175	0.175	5.6	5.6
半同胞家系选择 (1/4)	2	0.175	0.350	5.6	11.3
半同胞家系/S1选择 (1/2)	2	0.350	0.701	11.3	22.5
全同胞家系选择 (1/2)	2	0.225	0.451	7.9	15.8
自交S1家系选择 (1)	2	0.361	0.722	11.3	22.7
自交S1家系选择 (3/2)	3	0.328	0.985	5.2	15.7

杂种优势的定义

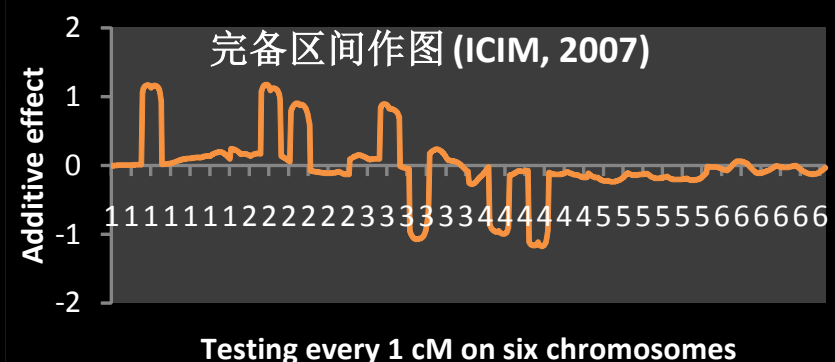
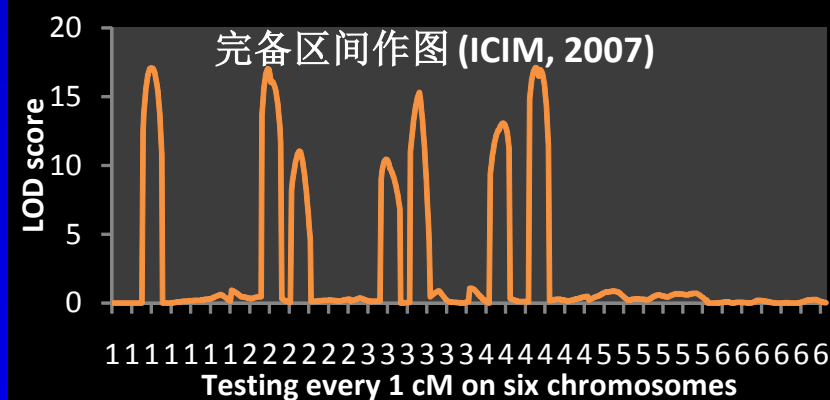
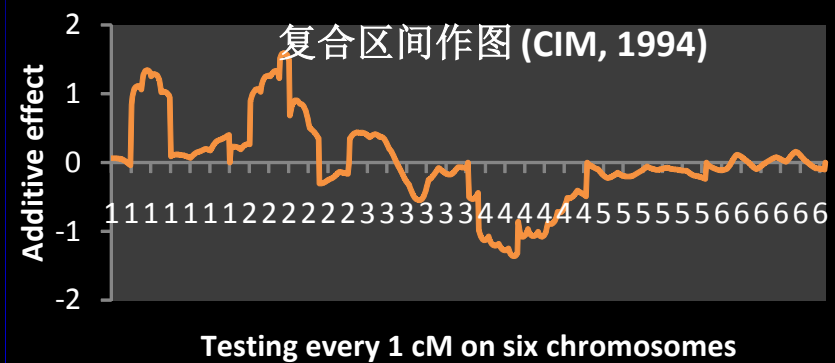
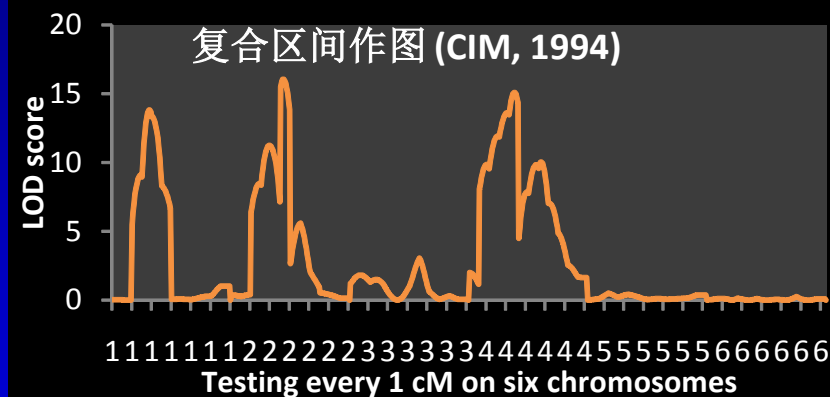
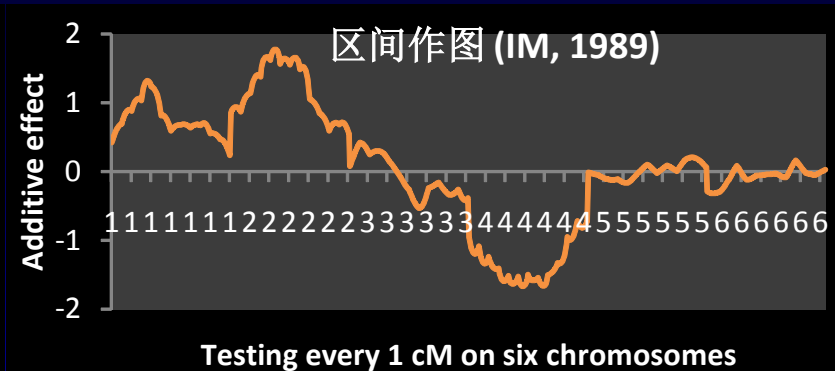
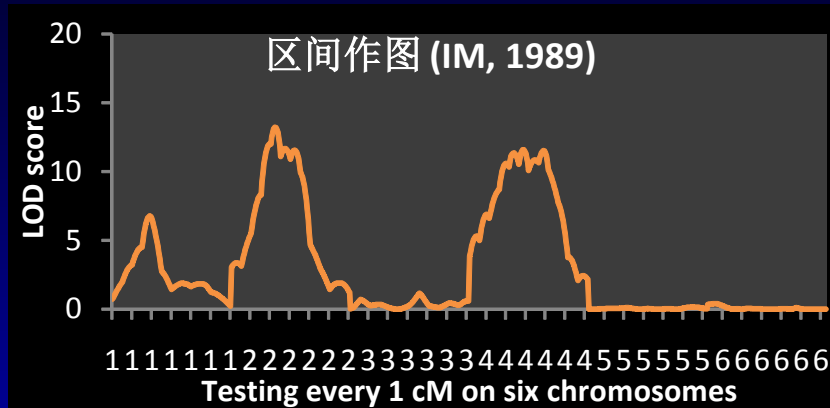
- 认为凡是F1基因型值高于父母的中亲值，均应视为杂种优势（Shull, 1948），这种杂种优势概念与显性有相同的意义
- Powers（1944, 1945, 1952）认为杂种优势和显性是同一生理和遗传现象，只是表现的程度有所不同，他认为只有杂种表现比大值亲本更大，或比小值亲本更小，才认为是杂种优势，因此杂种优势和超显性相同
- 认为应对F1连续自交，F1的表现比表现值最大的近交系还大，或比表现值最小的近交系还小时，认为有杂种优势

上位性对杂种优势的影响

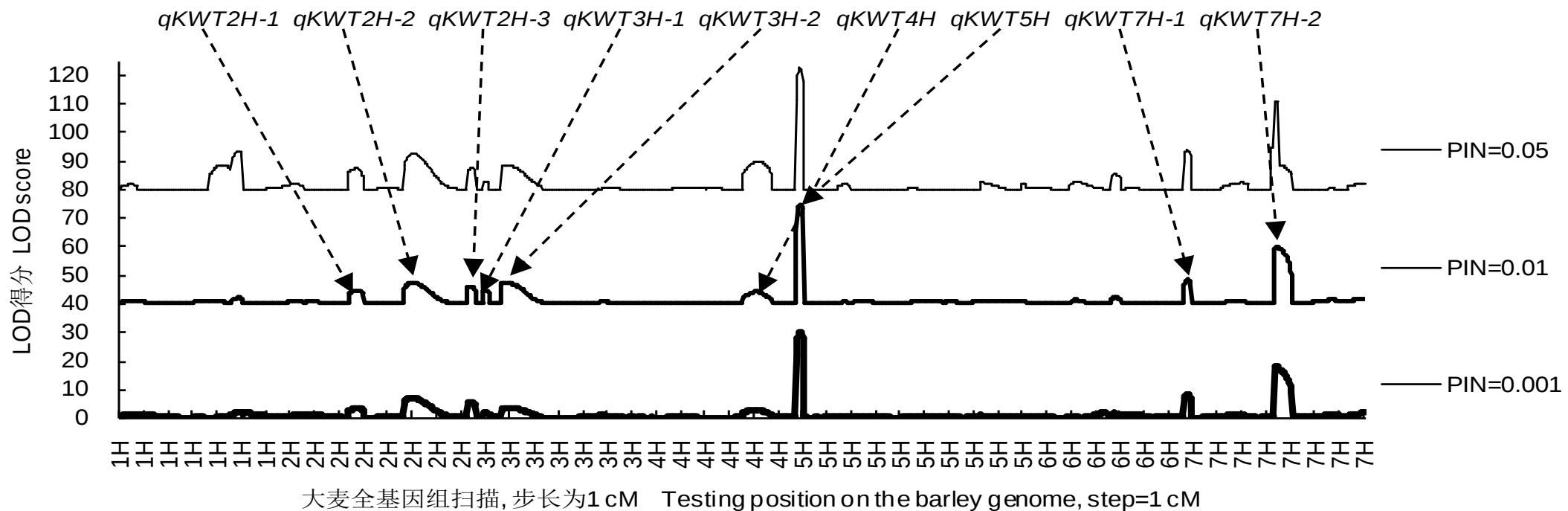
	B1B1	B1B2	B2B2	平均
A1A1	5	3	1	3
A1A2	3	2	1	2
A2A2	1	1	1	1
平均	3	2	1	

加性 × 加性上位

五、数量遗传基因定位, 即QTL作图



145 random DH lines (Harrington × TR306), and 127 markers



六、利用已知基因信息的育种

- 育种模拟
- 设计育种

QuLine在遗传上

- 可以模拟几乎所有的遗传模型，其中包括：
 - 复等位基因
 - 连锁
 - 加性-显性-上位性效应模型
 - 一因多效
 - 基因型和环境互作
 - 分子标记（显性或共显性）

QuLine在育种上

- 可以模拟几乎所有的以选育自（近）交系为目标的育种过程，其中包括：
 - 系谱育种
 - 混合育种
 - 加倍单倍体
 - 标记辅助选择
 - 群体内轮回选择
 - 各种方法的组合

MAS策略的优化

表 2 九个基因在小麦染色体和三个亲本材料中的分布

基因位点	<i>Rht-B1</i>	<i>Rht-D1</i>	<i>Rht8</i>	<i>Sr2</i>	<i>Cre1</i>	<i>VPM</i>	<i>Glu-B1</i>	<i>Glu-A3</i>	<i>tin</i>
染色体	4BS	4DS	2DL	3BS	2BL	7DL	1BL	1AS	1AS
标记类型	共显性	共显性	共显性	共显性	显性	显性	共显性	共显性	共显性
标记与基因的距离 (cM)	0.0	0.0	0.6	1.1	0.0	0.0	0.0	0.0	0.8
HM14BS	<i>Rht-B1a</i>	<i>Rht-D1a</i>	<i>Rht8</i>	<i>sr2</i>	<i>cre1</i>	<i>vpm</i>	<i>Glu-B1a</i>	<i>Glu-A3e</i>	<i>Tin</i>
Sunstate	<i>Rht-B1a</i>	<i>Rht-D1b</i>	<i>rht8</i>	<i>Sr2</i>	<i>cre1</i>	<i>VPM</i>	<i>Glu-B1i</i>	<i>Glu-A3b</i>	<i>Tin</i>
Silverstar+ <i>tin</i>	<i>Rht-B1b</i>	<i>Rht-D1a</i>	<i>rht8</i>	<i>sr2</i>	<i>Cre1</i>	<i>vpm</i>	<i>Glu-B1i</i>	<i>Glu-A3c</i>	<i>tin</i>
目标基因型	<i>Rht-B1a</i>	<i>Rht-D1a</i>	<i>Rht8</i>	<i>Sr2</i>	<i>Cre1</i>	<i>VPM</i>	<i>Glu-B1i</i>	<i>Glu-A3b</i>	<i>tin</i>

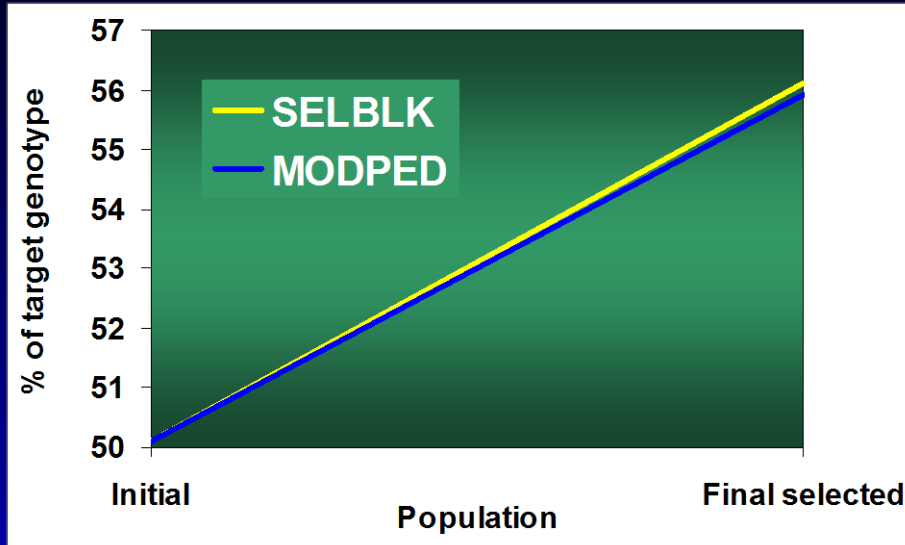
目标基因型：半矮秆（抗倒伏）、长胚芽鞘（根系发达）、抗多种病害、籽粒品质优良、无效分蘖少

Comparison of two breeding strategies: modified pedigree (MODPED) and selected bulk (SELBLK)

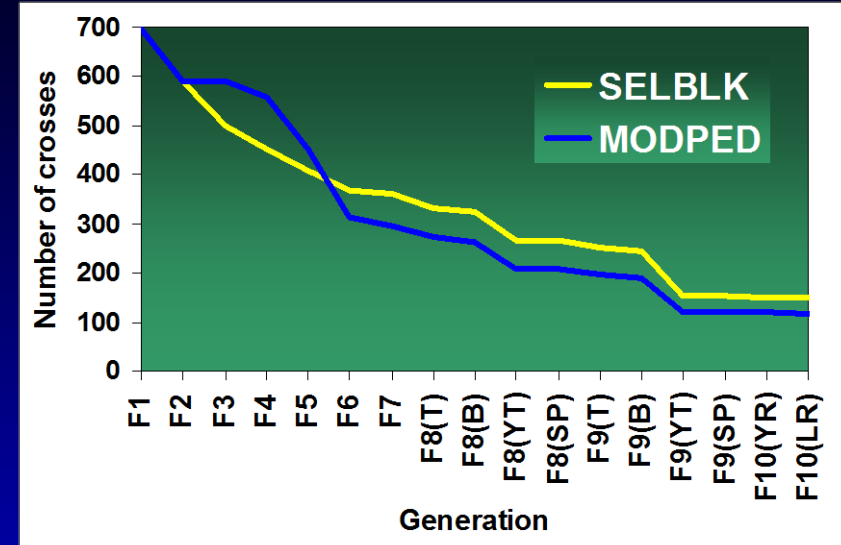
Breeding methods in CIMMYT's Wheat Breeding Program

- Pedigree system: before 1984.
 - “Pedigree selection” is used from F2 to F6.
- Modified pedigree/bulk (MODPED): in 1985-1989/94.
 - “Pedigree selection” is used in F2 and F6, and “bulk selection” is used in other generations.
- Selected bulk (SELBLK): after 1995.
 - “Pedigree selection” is used only in F6, and “bulk selection” is used in other generations.

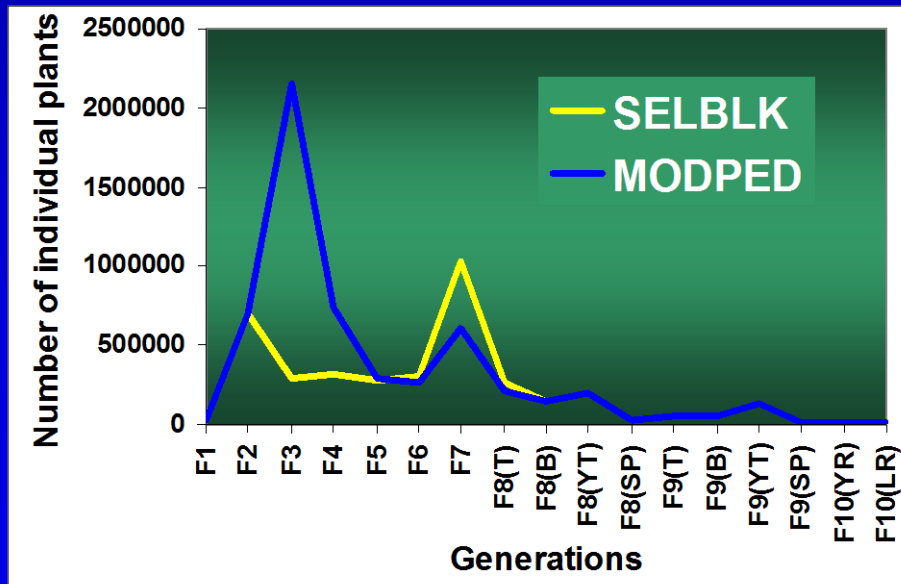
Genetic gain in yield from SELBLK is 3.3% higher than MODPED



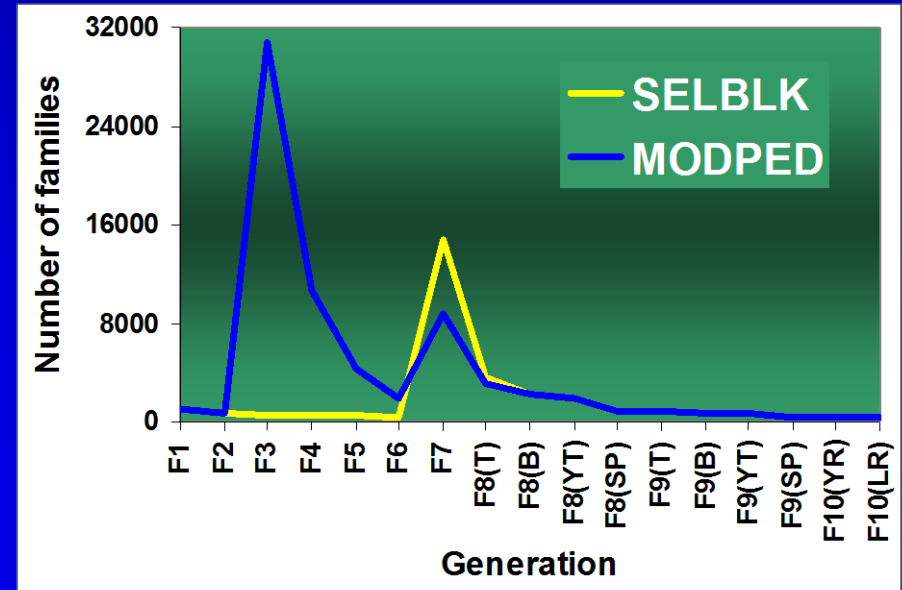
SELBLK retained 25% more crosses in the final selected population



SELBLK required 1/3 less land from F1 to F8 than MODPED

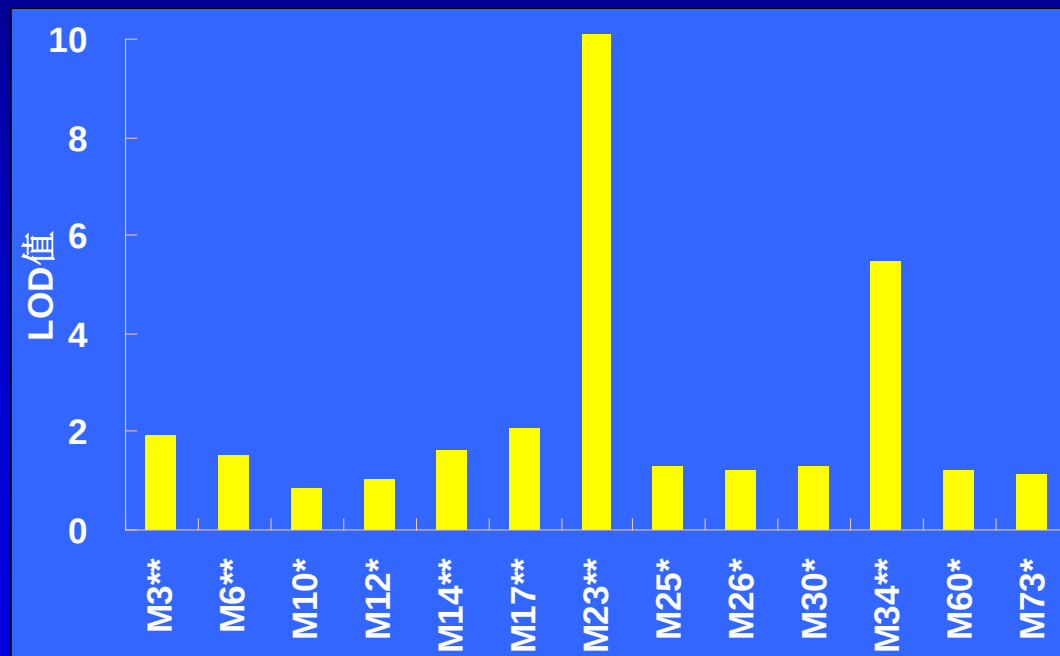


SELBLK produced 40% less families to be planted from F1 to F8

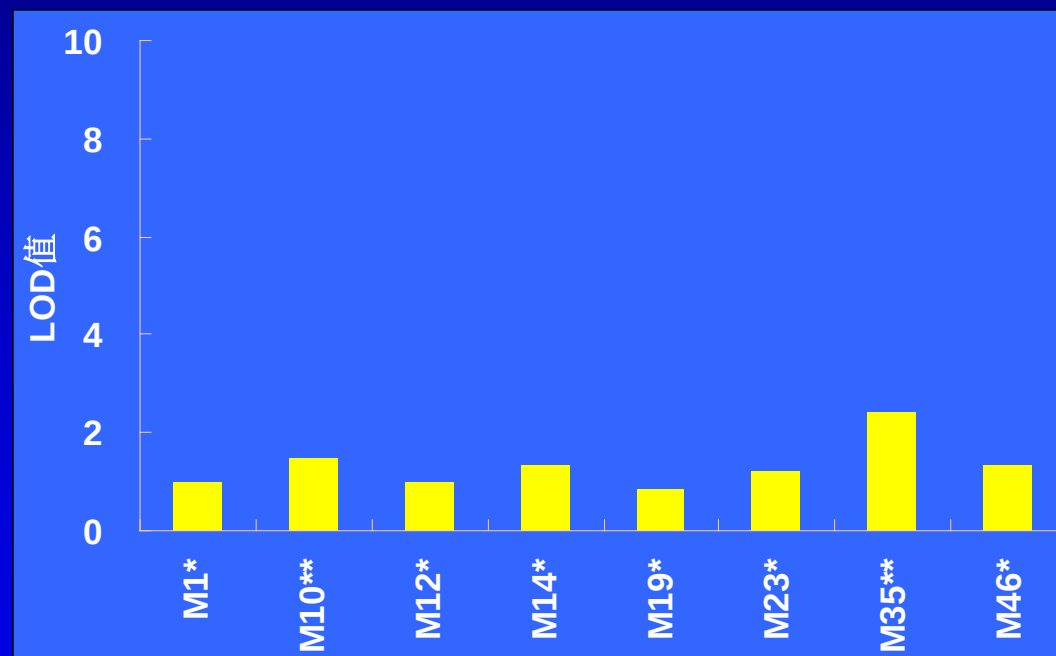


粒长和粒宽QTLs

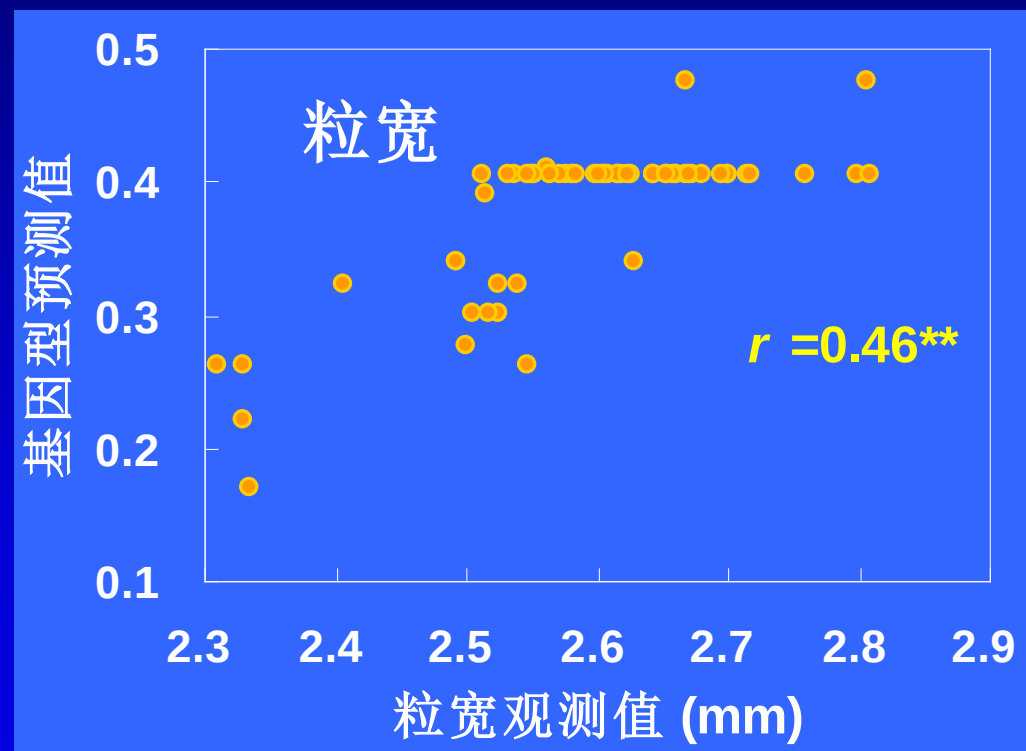
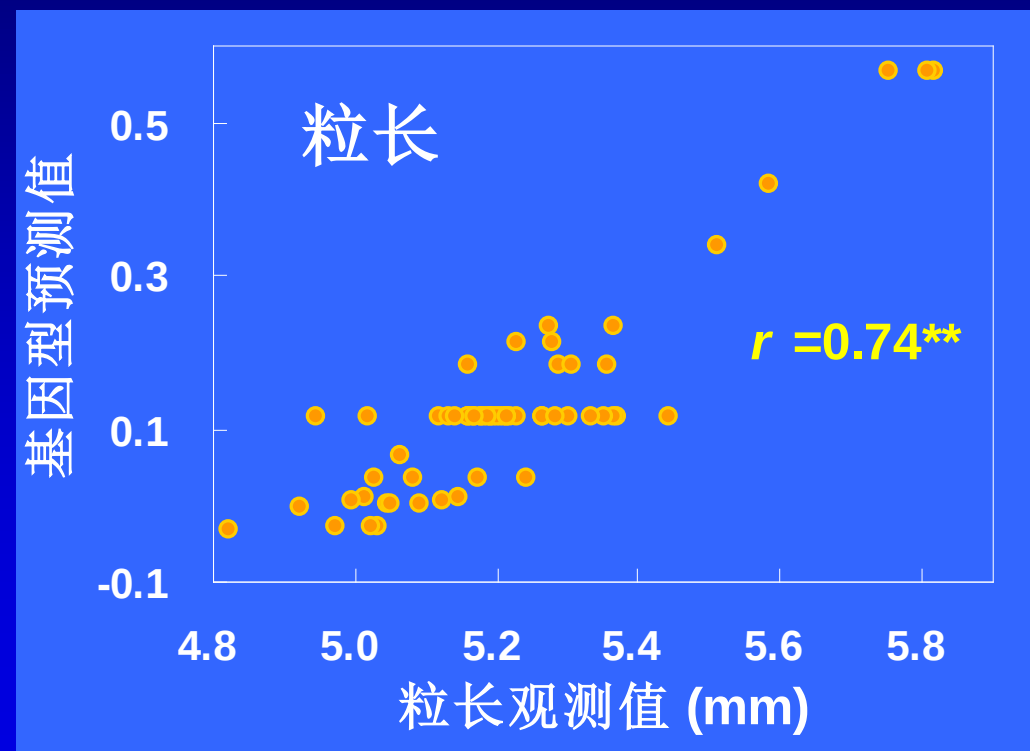
粒 长



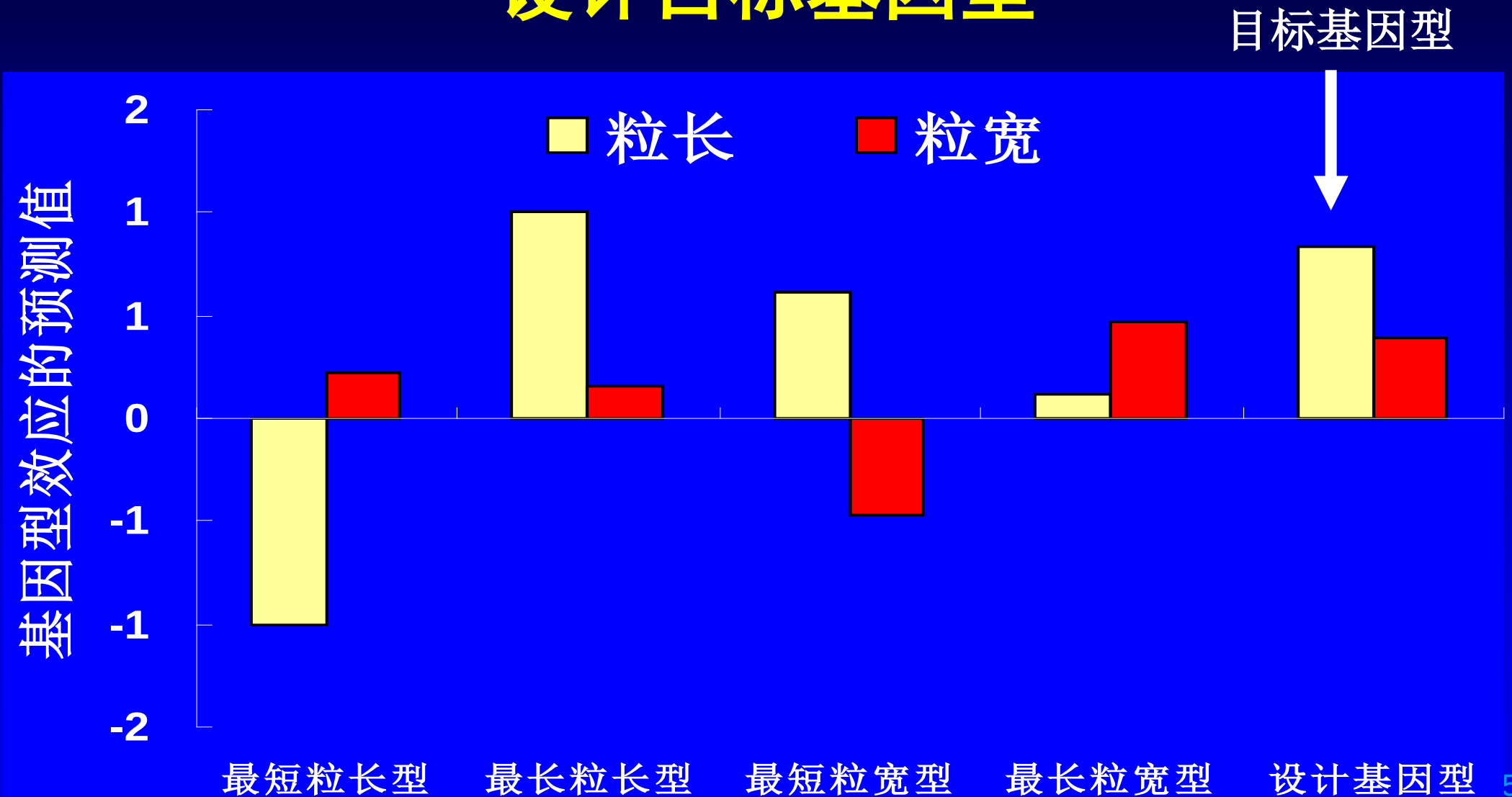
粒 宽



根据定位的QTL预测基因型值



根据育种目标（假定为长粒和宽粒型） 设计目标基因型



选择产生设计基因型的亲本

基因型	M1	M6	M12	M23	M25	基因型预测值	
						粒长(mm)	粒宽(mm)
最长粒基因型	1	2	2	2	2	6.21	2.74
最宽粒基因型	2	1	1	1	1	5.32	3.07
设计基因型	2	2	1	2	2	6.05	2.98
CSSL5	1	2	1	1	1	5.44	3.00
CSSL16	2	1	1	2	1	5.77	2.98
CSSL19	1	1	2	1	2	5.54	2.93

获得目标基因型的途径分析

➤ 3种三交组合

- 组合1: $(\text{CSSL5} \times \text{CSSL16}) \times \text{CSSL19}$
- 组合2: $(\text{CSSL5} \times \text{CSSL19}) \times \text{CSSL16}$
- 组合3: $\text{CSSL5} \times (\text{CSSL16} \times \text{CSSL19})$

➤ 2种标记辅助选择方案

- 方案1: 100个三交F2个体，每个产生30个F8家系，对3000个F8个体作标记辅助选择，以获得目标基因型（1次标记选择）
- 方案2: 100个三交F2个体，施以标记辅助选择，选择每个位点均存在有利等位基因的个体，中选F2个体每个产生30个F4家系，然后再对F4个体作标记辅助选择，以获得目标基因型（2次标记选择）

选择最佳的杂交和选择方案

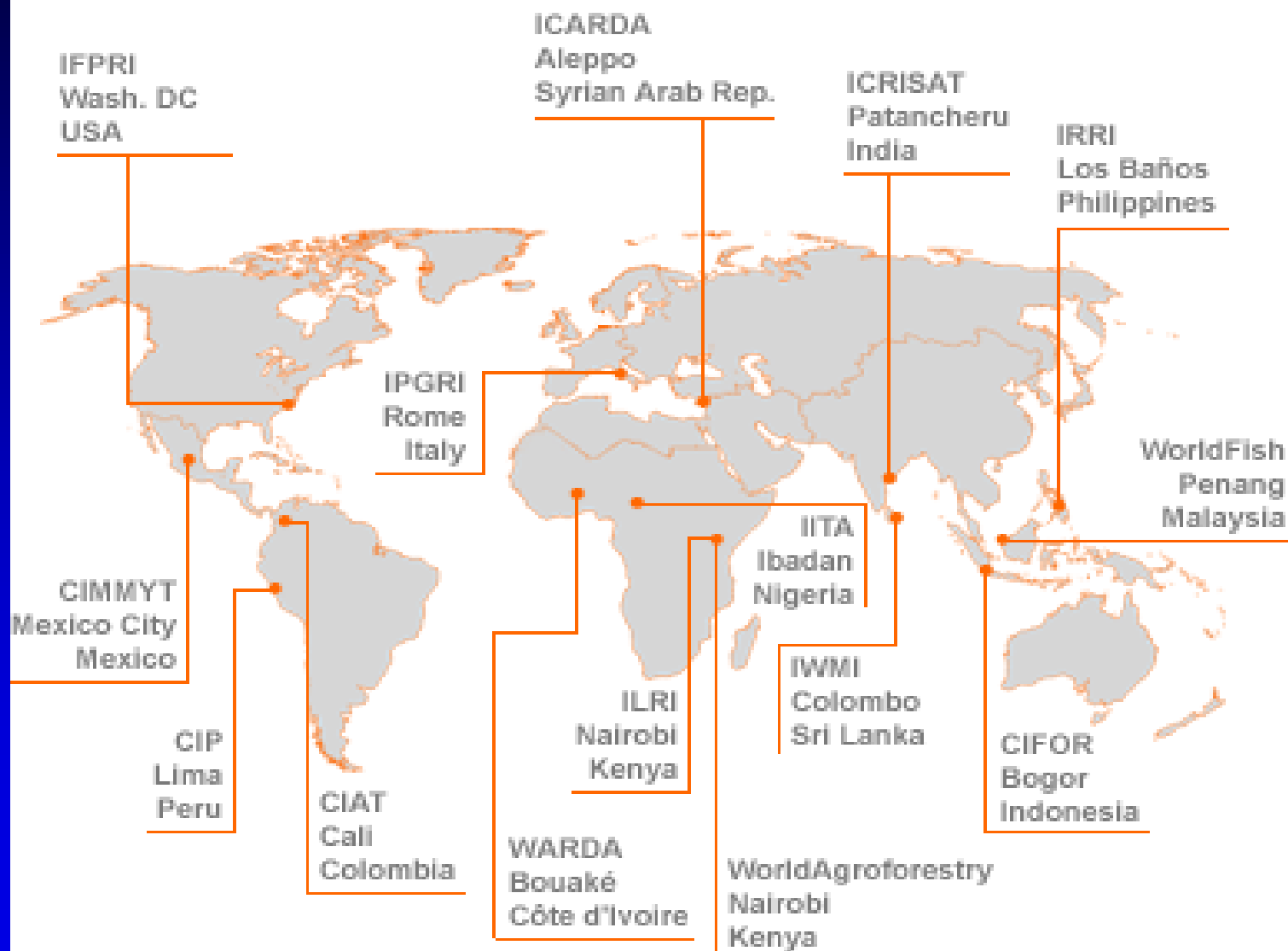
- 组合2获得目标基因型的概率明显高于组合1和3
- 方案2需要测试的DNA样品数明显低于方案1
- **结论：应采用组合2和方案2获取设计基因型**

组合	选择方案	F2中选个体	MAS前F8家系数	中选F8家系数 (S.E.)	DNA样品数	DNA样品数/中选F8家系
组合1	方案1	100	3000	7.6 (3.27)	3000	395
	方案2	12.0	359	7.6 (3.37)	459	60
组合2	方案1	100	3000	24.3 (7.06)	3000	123
	方案2	24.8	745	23.3 (7.16)	845	36
组合3	方案1	100	3000	11.2 (5.45)	3000	268
	方案2	7.5	226	12.3 (5.14)	326	26

七、CIMMYT小麦育种方法和成就简介



Consultative Group on International Agricultural Research CGIAR



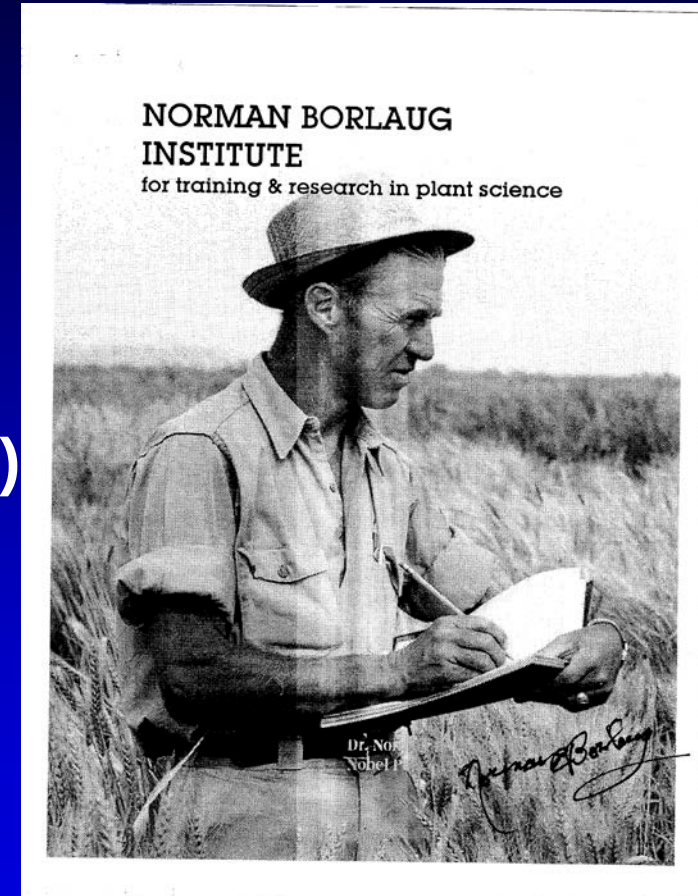
Select the Area
of your interest
on the map

CIMMYT's headquarter in Mexico



Dr. Borlaug and green revolution

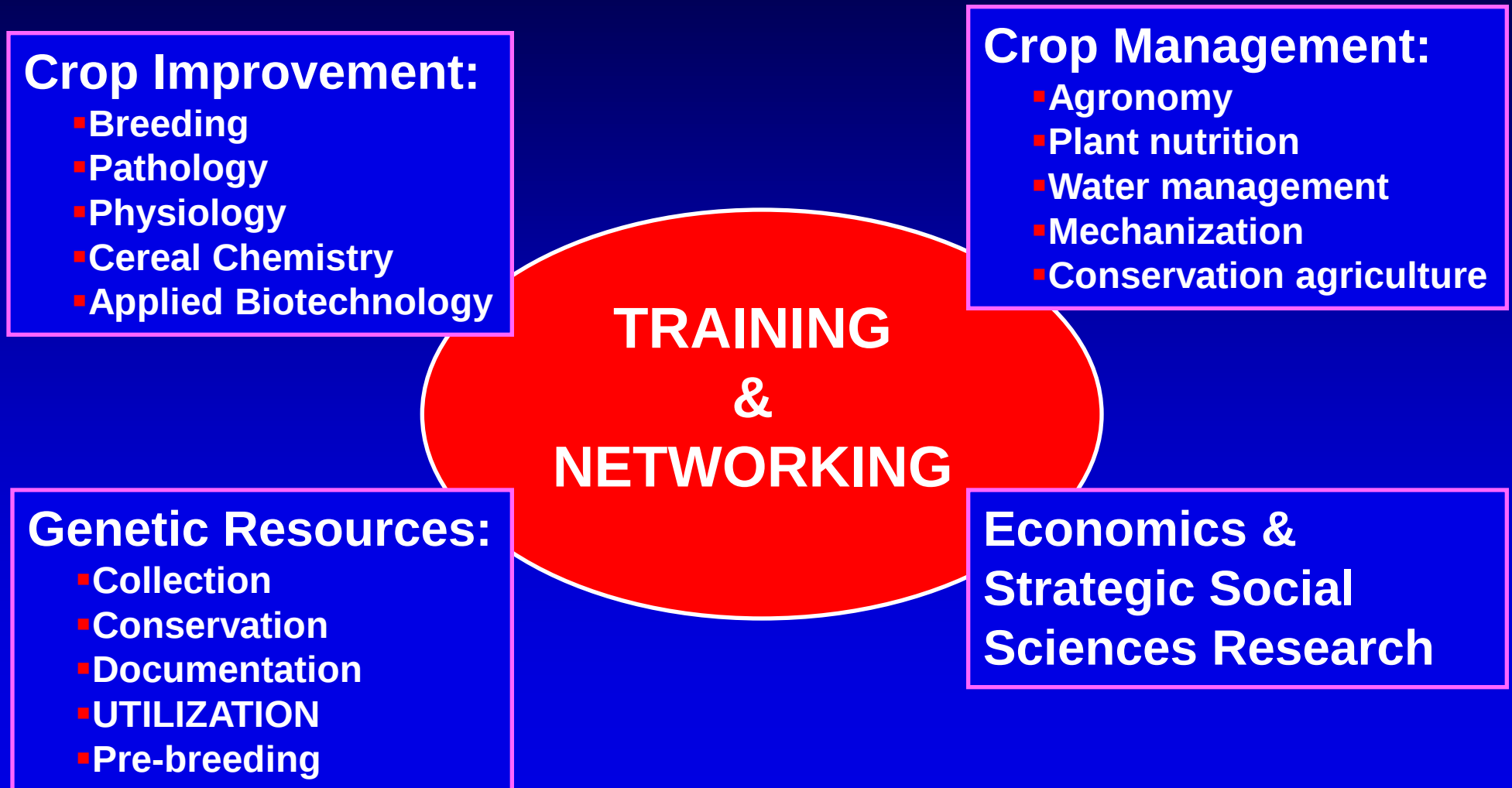
- Mexican-Rockefeller Foundation Agricultural Program, 1944
- Mexico became self-sufficient in most food commodities by the late 1950s
- Young scientists were trained in Mexico
- Semidwarf wheats (*Rht1* gene and Norin 10)
- 1965-1975, wheat and rice production had increased by 50%
- Awarded Nobel Peace Prize in 1970
- Criticism of the Green Revolution
 - The rich got richer, the poor got poorer
 - Environment damage
 - Loss of biodiversity



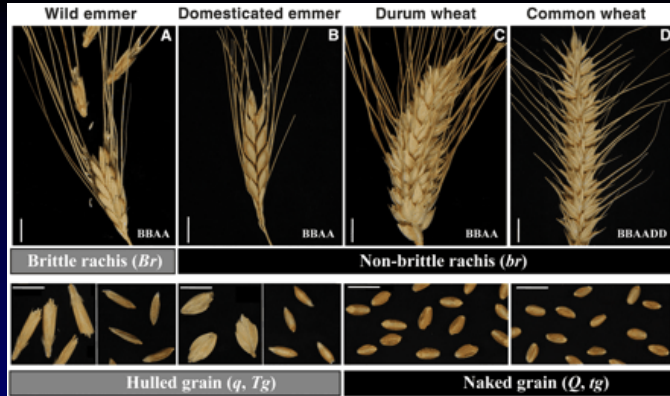
CIMMYT's Shuttle breeding



GLOBAL center for wheat global research



Multi-disciplinary and several crop options



Bread Wheat

Triticale

Durum Wheat

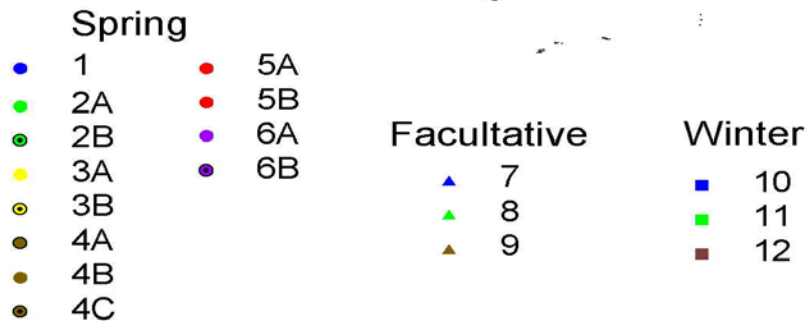
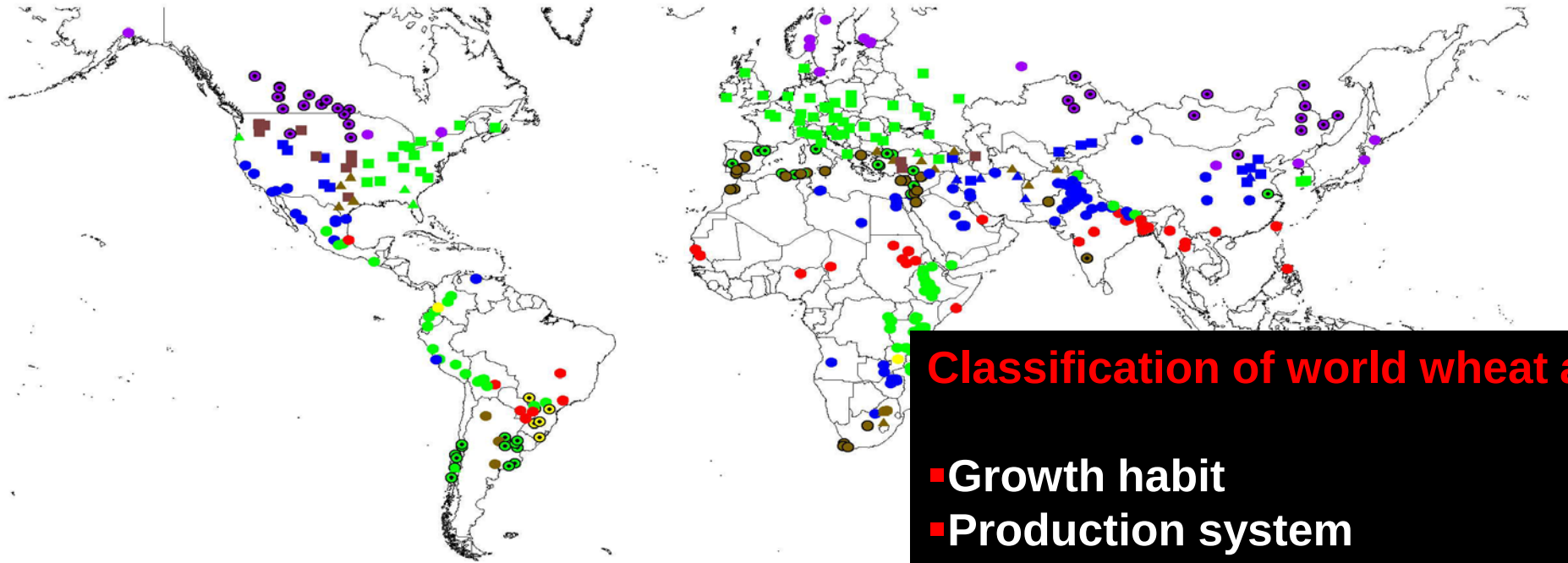
Barley

Shared mandate with ICARDA

Global breeding...

... rational organization of activities

The mega-environment (ME) concept



Classification of world wheat area by:

- Growth habit
- Production system
- Main biotic and abiotic stresses
- Consumer preference

- Not all constraints occur in all environments
- Focus on only few relevant traits at a time
- Truly targeted and relevant breeding objectives

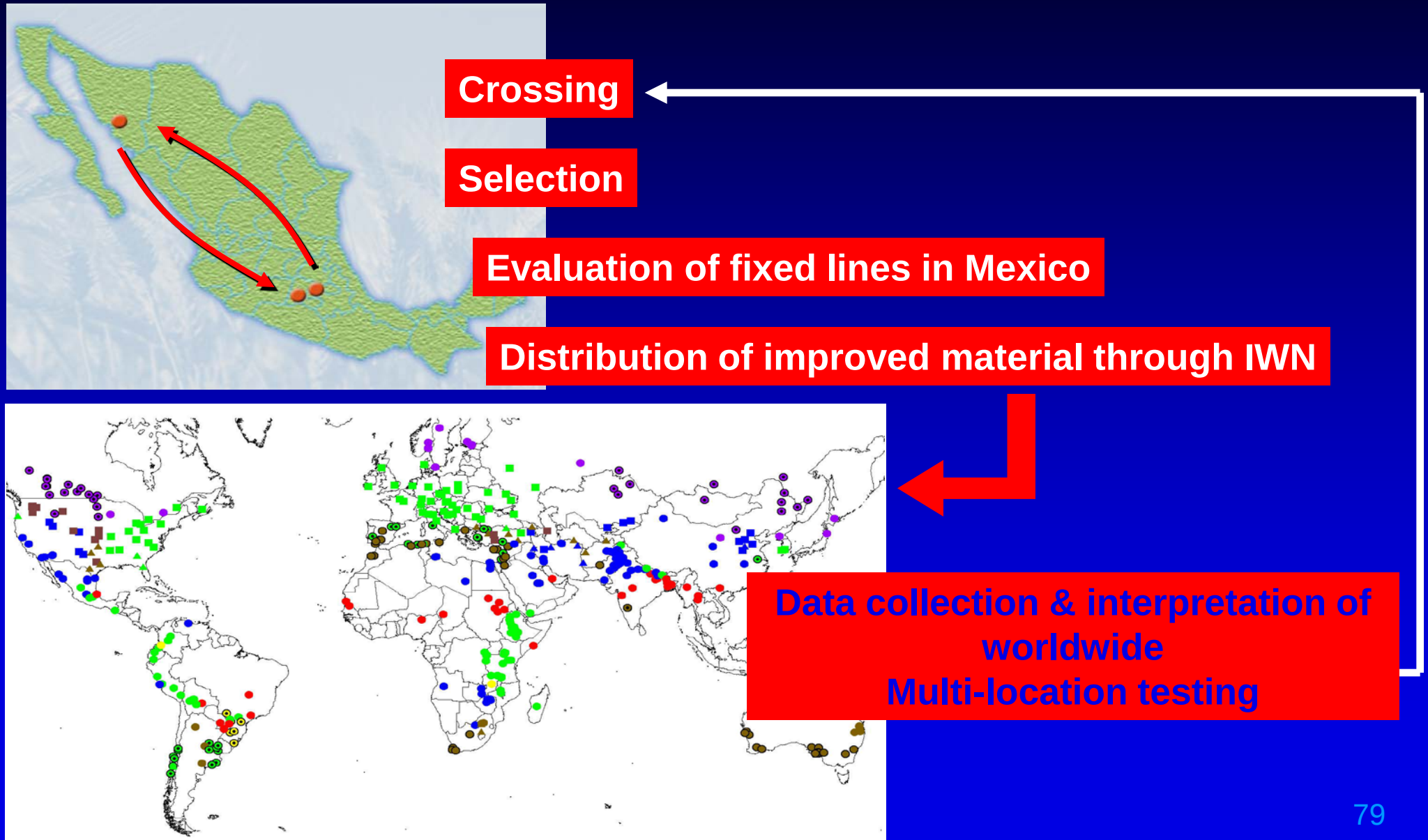
Spring wheat mega-environments

Mega-Environment	Water Supply	Major Diseases	Major Constraints	Grain Color
ME 1 Temperate	Irrigated	LR, YR	Terminal heat Some salinity	White
ME 5 Hot		LR, YR, HLB	Heat permanent Some salinity	White
ME 2 Normal Soils	High Rainfall	LR, YR, ST, FHS	Sprouting	Red
ME 3 Acid Soils		LR, YR, ST, FHS	Acid Soils Sprouting	Red
ME 4 Drought	Low Rainfall	LR, YR, FG, Nem.	Drought Some heat	White/red
ME 6 High Latitude		LR, YR	Photoperiod Sensitivity	red

Facultative/winter wheat mega-environments (breeding out of TURKEY)

Mega-Environment	Water Supply	Growth Habit	Vernalization Requirements	Cold Tolerance
ME 7	Irrigated	FACULTATIVE	Low	Low
ME 8	High Rainfall	FACULTATIVE	Low	Low
ME 9	Drought	FACULTATIVE	Low	Low
ME 10	Irrigated	WINTER	Strong	Strong
ME 11	High Rainfall	WINTER	Strong	Strong
ME 12	Drought	WINTER	Strong	Strong

General breeding scheme



Crossing plan

Choice of Parents

- Widely adapted major variety
- Performance in Mexico under different water regimes
- Global or Regional performance in IN
- Agronomic, Disease and Quality data from Mexico and worldwide
- Collaborator/outreach information
- Donors of important traits/genes
- Use of novel material for enhancing genetic diversity



Crossing

Crop	Crosses/year
Bread Wheat Intensive	3000-5000
Bread Wheat Rainfed drought	2000-2500
Durum Wheat All	2500-3000
Triticale All	800-1300

General selection scheme

Cross

F1

F2

F3

F4

F5

- Disease resistance
- Good agronomic type
- ME-specific adaptation traits

- High yield potential (preliminary)
- Disease resistance
- Good agronomic type
- ME-specific adaptative traits
- Acceptable general quality attributes
- Uniformity

F6

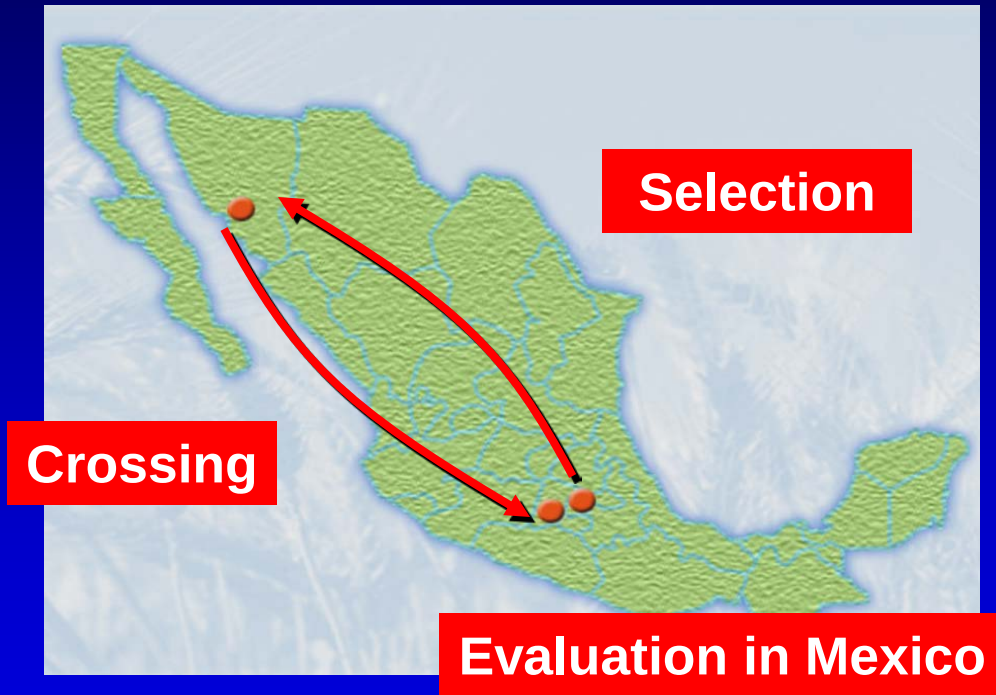
F7

F8

Replicated/Multi-Environment yield testing, Selection of candidates for INs

General breeding scheme

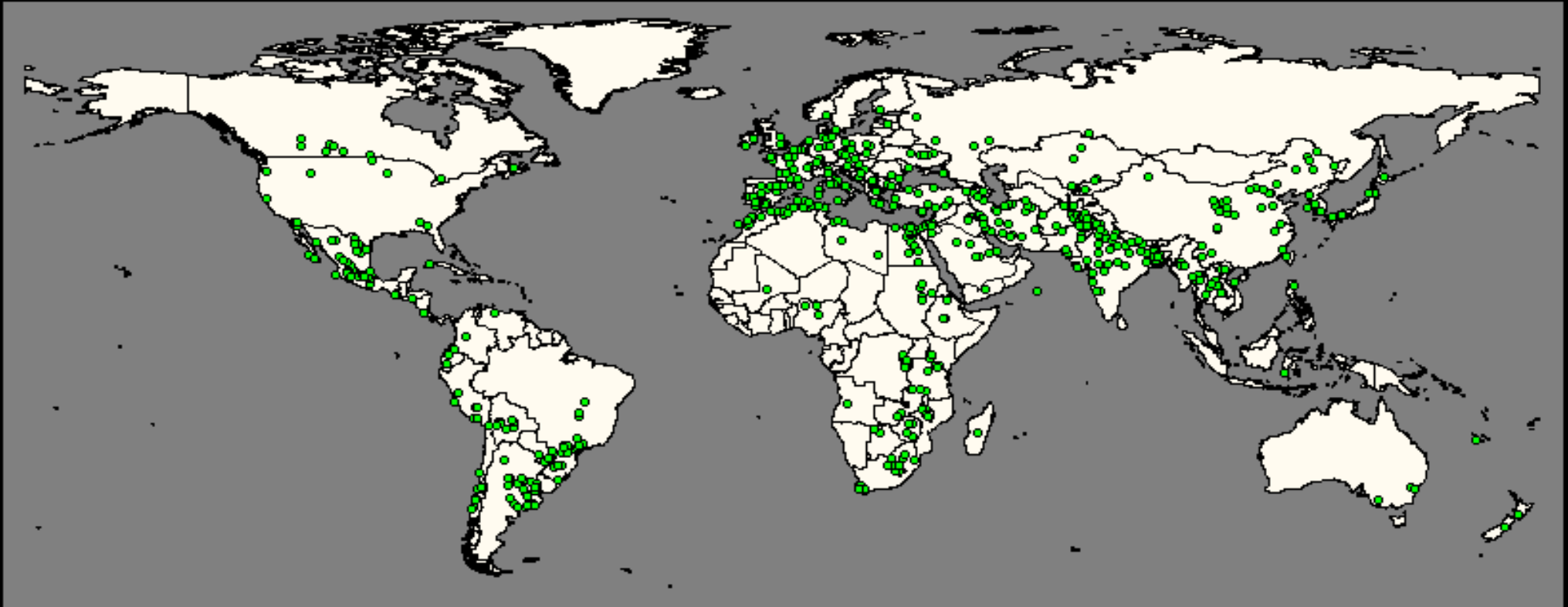
Competitive advantage:



2 crops/year

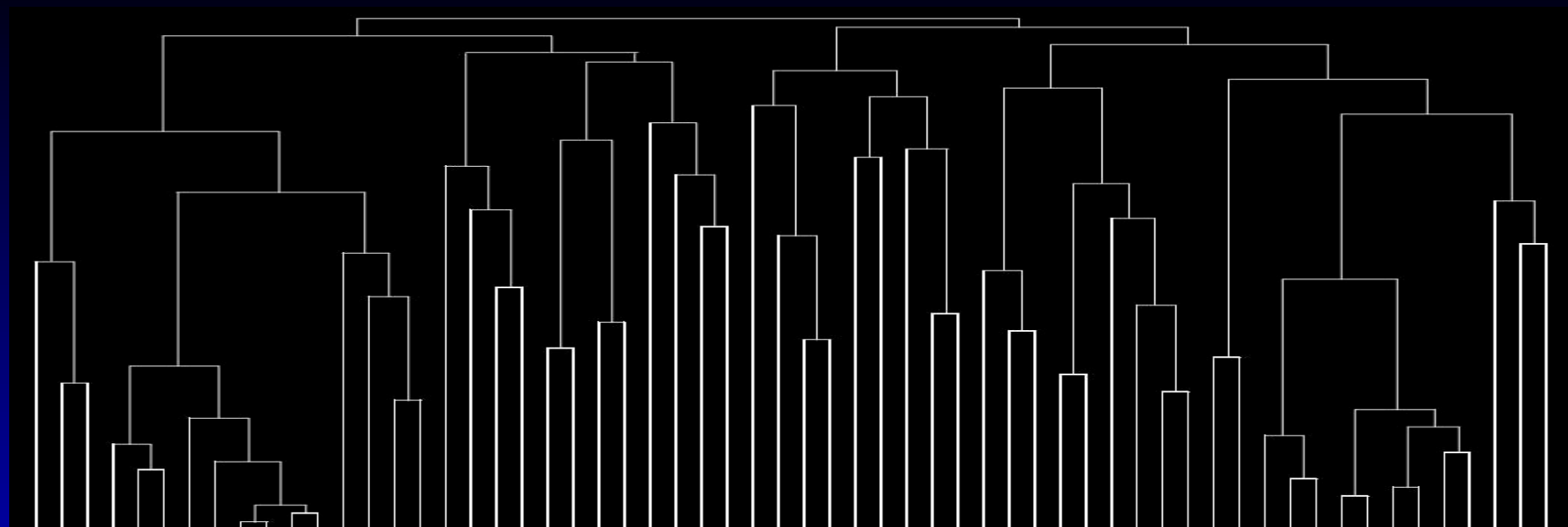
4 years,
from cross....
...to identification of
promising lines

CIMMYT International trial locations





**Drip irrigation to generate
moisture stress in Cd. Obregon**



Group	1		2	3	4	5	6	7
Stress generated in Mexico	Gravity continuous stress		Drip Terminal stress	Gravity No Stress	Drip Continuous stress	Heat and terminal moisture stress	Drip Moisture stress pre-flowering	Gravity terminal stress
International Sites	Brazil Algeria Spain Bolivia Pakistan		No sites	No sites	Saudi Arabia Argentina South Africa Egypt Canada	Zimbabwe Iran Pakistan	Nepal Pakistan Brazil Iran Canada	Iran Bangladesh Saudi Arabia Spain Afghanistan

Associations among stress environments, irrigation systems and international test sites (bread wheat)



Old & new challenges

Breeding for durable rust resistance

- ✓ Monitor worldwide changes in races
- ✓ Identify new genetic variability for resistance
- ✓ Accumulate resistance genes that cannot be defeated by pathogen
- ✓ Prepare for replacement of major varieties

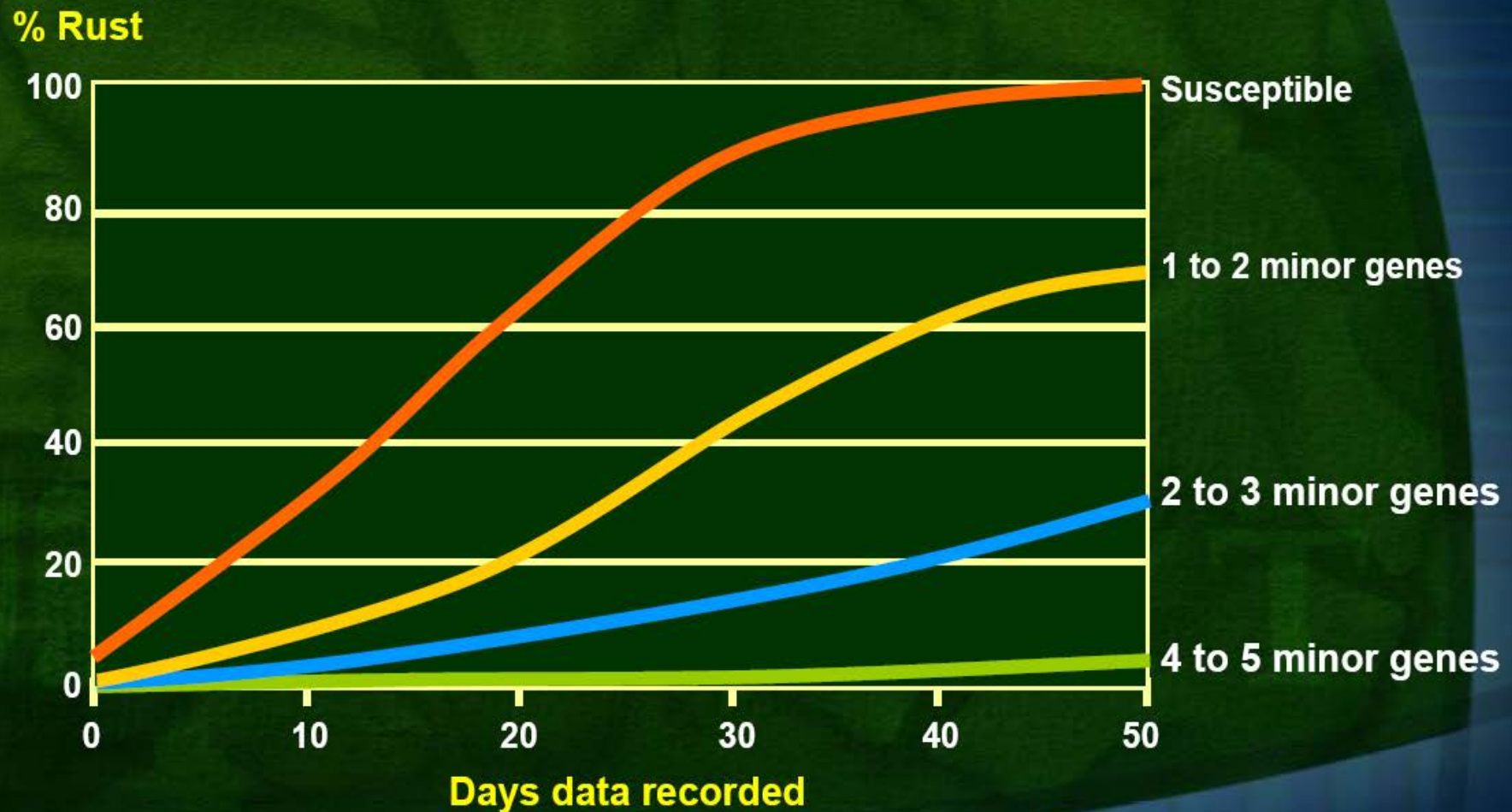


Leaf Rust

Types of Resistance

- Race-specific $\approx$ Monogenic $\approx$ Major genes $\approx$ Hypersensitive (**Boom & Bust**)
- Non race-specific $\approx$ Polygenic $\approx$ Minor genes $\approx$ Slow rusting / Partial (**Durable**)

Race-Nonspecific Resistance to Leaf and Stripe Rusts in Wheat: Genetic-Phenotypic Model



Maintaining Genetic Diversity

- Necessary for a long-term durability
- High in CIMMYT germplasm: over 10 slow rusting genes present
- Characterized genes
 - Leaf rust: *Lr34*, *Lr46* and *LrPrl1*
 - Yellow rust: *Yr18*, *Yr29*, *YrPrl1* and *Yr30*

锈病持久抗性研究: Ravi Singh



- 广适应品种 X 锈病持久抗性材料
- 与广适应品种回交1-2次
- 大分离群体
- 选择与广适应品种类似、同时又具有持久抗性的后代

Old & new challenges

Breeding for drought tolerance
through improving water use efficiency

1. Deep planting

2. Alien resources



Screening for tolerance to moisture stress

New synthetic derivative



Commercial cultivar

抗旱育种: Richard Trethowan



➤ Deep planting

➤ Yield trial

- Full irrigation
- Reduced irrigation
- No irrigation

提高产量潜力 (Yield Potential)

- Yield trial under full irrigation
- Yield trial under reduced irrigation
- Yield trial under no irrigation

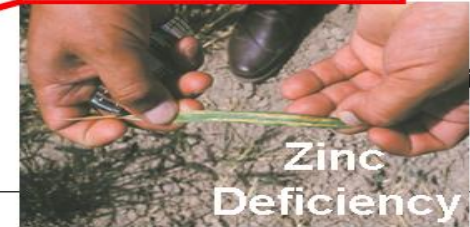
Old & new challenges

Breeding for drought tolerance

Through improving root health + Nutrient use efficiency

Abiotic Stresses

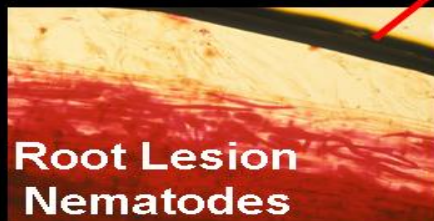
Moisture Stress	Temperature Extremes	Nutrient Stress - Macro/Micro & pH Extremes
• Terminal • Pre-Anthesis • Residual Moisture • Reduced Irrigation • General Low Rainfall • Shallow, Marginal, Infertile, Eroded Lands	• Heat Stress Humid • Heat Stress Dry • Cold Stress • Cold Stress – Late Frost	• P and N Deficiency/ Efficiency • Deficiency (e.g. Zinc) • • • •



Combined Stress



Biotic Stresses



New challenges, new tools

Drought tolerance through better root health

Use of molecular markers

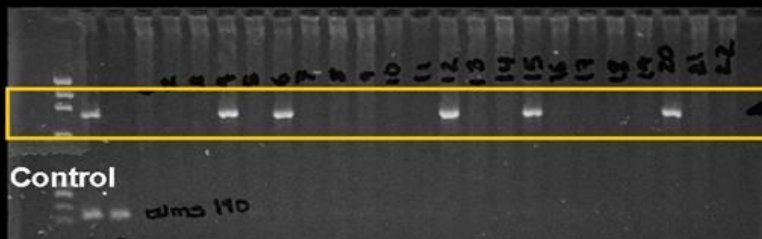
Durum Wheat Assays

Bread Wheat x Durum cross Derivatives

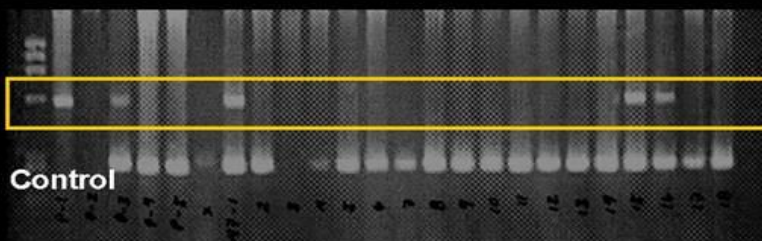
Cre 1



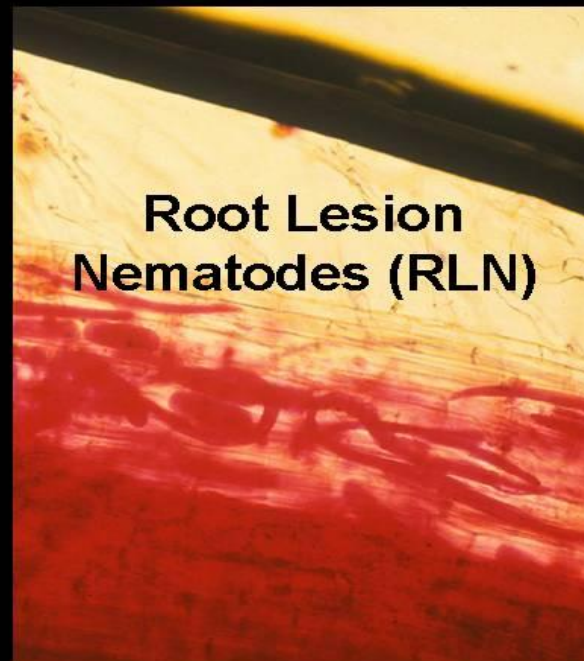
Cre 3



VPM



Root Lesion
Nematodes (RLN)



Molecular markers routinely applied in wheat breeding to incorporate resistance to low heritability traits e.g. CCN and RLN nematodes

Make crosses and conduct selection in Cd. Obregon



Hand planting in Toluca



八、观看纪录片 《The Norman Borlaug Story》