



# 遗传育种与粮食增产\*

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## 一、作物育种在粮食增产中的作用

增产粮食的途径很多,毛主席概括为土、肥、水、种、密、保、工、管八个字,称为农业八字宪法。种是其中投资最少而效益相当高的一项措施,而且是其他增产措施赖以发挥作用的基础,其他七个字都是围绕着种这个核心(内因)的要求来做贡献的。所以建国以来,党和政府十分重视优良品种的推广应用和种子建设。“六五”以来国家把主要粮食、棉花、油料、蔬菜的育种研究做为重点科技项目组织攻关,取得了显著的经济、社会效益。根据1996年1月国家科委对“八五”期间主要粮食作物新品种选育技术研究项目执行情况组织验收的汇报资料,该项目(包括水稻、小麦、玉米、大麦、谷子、高粱六大粮食作物)共育成审(认)定品种301个,其中达标的207个,占68.8%;这些新品种连同“七五”后期审定品种在“八五”期间扩大种植的面积在内,累计推广15.8亿亩;按平均增产8%计,可增产粮食393亿公斤,再以70%的缩值系数折算,估计实际增产粮食275亿公斤,获得经济效益427亿元。而五年投入2775万元,投入产出比为1:1538,这个比例是很可观的。

关于品种改良在农业科技进步中占有多大比重,其说不一,一般约占30%。据1984年美国农艺学会和美国作物学会联合发行的一份题为“五大作物增产中的遗传贡献”小册子所载(表1),高粱、玉米、大豆、棉花、小麦五大作物由于推广种植优良品种,每亩每年增产0.47-6.13公斤不等,占各自作物单产的0.70-1.78%,以高粱、玉米的年增产率较高,在1.5%上下;大豆、小麦、棉花较低,为0.7%左右。粗略地说,各类作物通过品种改良每年可提高产量1%上下,如果栽培管理进一步改善,其贡献还会增大。

表1. 美国五大作物品种改良对产量的贡献

作物	年 限	年增产率	
		公斤/亩	%
高粱	1950-1980	3.66	1.30
玉米	1930-1980	4.86-6.13	1.42-1.78

\* 参阅《百名院士科技系列报告集(上)》,新华出版社,北京,1996。

大豆	1902-1977	1.25	0.70
棉花	1910-1980	0.47-0.69	0.74
小麦	1958-1980	0.83	0.74

优良品种除能提高产量潜力外还可抗御自然灾害,改善产品质量和增进生产效率,即高产、稳产、优质、低耗四个方面兼而有之。譬如:种植抗寒或早熟品种可使作物分布逐渐向高纬度和高海拔地区扩展;选用耐旱品种是半干旱地区稳产的重要途径,也是发展节水农业的内在因素或基础。利用品种抵抗病虫害为害,既经济有效又不污染环境,是各国作物育种研究最活跃的领域。同一作物不同品种之间,其产品的营养成分、加工性能等品质性状有着很大的差异。选育株矮秆壮,抗倒伏,穗层整齐,成熟一致,不易落粒的谷类作物品种,便于机械化收获;种植有限生长习性和短果枝的棉花,使大部分棉铃能同期吐絮,可减少机械收获的损失等。遗憾的是,这些优点往往分散在不同的品种材料中,而且时常和一些不良性状联系在一起。育种家的任务就是根据生产和生活的需要,按照各类性状的遗传规律,通过育种手段将以上四方面的优越性有重点地逐步集中在一个优良品种上,使其尽可能臻于完善,以满足农业生产不断发展的要求。

## 二、常用的育种方案、途径和做法

从育种学的观点,作物基本上可分为两大类:即自花授粉(自交)作物和异花授粉(异交)作物。一般说来,天然异交率小于4%的为自交作物,如水稻、小麦、大麦、谷子、花生、大豆、烟草、亚麻、豌豆、菜豆、番茄等;天然异交率在50%以上的是异交作物,如向日葵、黑麦、甜菜、大白菜、甘蓝、萝卜(以上雌雄同花)、玉米、西瓜、草莓(以上雌雄异花)、大麻、菠菜(以上雌雄异株)等。天然异交率介于二者之间的叫常异交作物,如棉花、高粱、蚕豆等。自交作物的自然群体是单一的基因型或一些纯合基因型的混合物,其个体在遗传上是高度纯合的。自交后代生育正常,没有衰退现象。异交作物的自然群体是异质的,含有很多不同的基因型,在遗传上是高度杂合的,自交后呈现不同程度的衰退,再杂交时又恢育正常的健壮状态。

自交作物最主要的育种方法是品种间杂交,包括单交、三交、四交、回交等,其目的是将来自不同亲本品种的优良性状组装在一起,形成新的纯系。

现在也在积极利用杂种第一代的优势挖掘增产潜力,已在水稻、烟草、番茄、小麦等作物上应用。异交作物最主要的育种方法是自交系间杂交,包括单交、三交、双交和顶交,都是以利用杂种第一代优势为归宿的,其中以单交种的优势最强,整齐度最好,在生产上应用最广。同时,还常采用轮回选择的方法来改良育种群体。它是高一级的混合选择,即从原始群体中选择优良单株,一方面进行自交,同时与测验种测交以测定其一般配合力,然后根据测交结果选择最优的一些自家系进行互相杂交,组成新的育种群体。这样轮复一轮地自交——测交——互交加上选择,可以把原始群体内的优良基因逐步聚集在一起,形成改良群体,以便从中选育出更好的自交系或合成综合杂交种。所谓综合杂交种就是选择一般配合力好的一些优良自交系(5—10个)混合种植,任其随机互交,以产生异质性大、杂合度高而又相对整齐一致的品种群体。这样的群体可以连续使用多代。常异交作物对自交没有不良影响,其育种原理和方法与自交作物基本相同。此外,还有无性繁殖作物如马铃薯、甘薯、甘蔗、草莓等,其表现型虽然整齐一致,而基因型则高度杂全。它们在自然情况下常会发生芽变,可以进行个体选择;也可在特定条件下进行有性杂交加以改良,其杂种第一代异质性大,可选择优株进行无性繁殖,成为整齐一致的无性系或品种。表2概括说明现用生产品种的类型和基本特点。图1表示四种基本群体的育种方法要点。

表2. 生产品种群体的类型与特点

繁殖 方式	交配 体系	群体 类型	基 本 特 点
有性	自交	纯系	同质,纯合;亲本纯系杂交后在第二至第六代选择超亲后代。
有性	异交	杂交种	同质,高并杂合;选择配合力好的自交系进行杂交,利用第一代优势。
有性	异交	开放授粉群体	异质,杂合;改良群体,增加有利基因频率;或选择优良亲本品系或无性系混合组成综合种。
无性	异交	无性系	同质,杂合;杂合亲本品系杂交的第一代选择超亲的无性系。

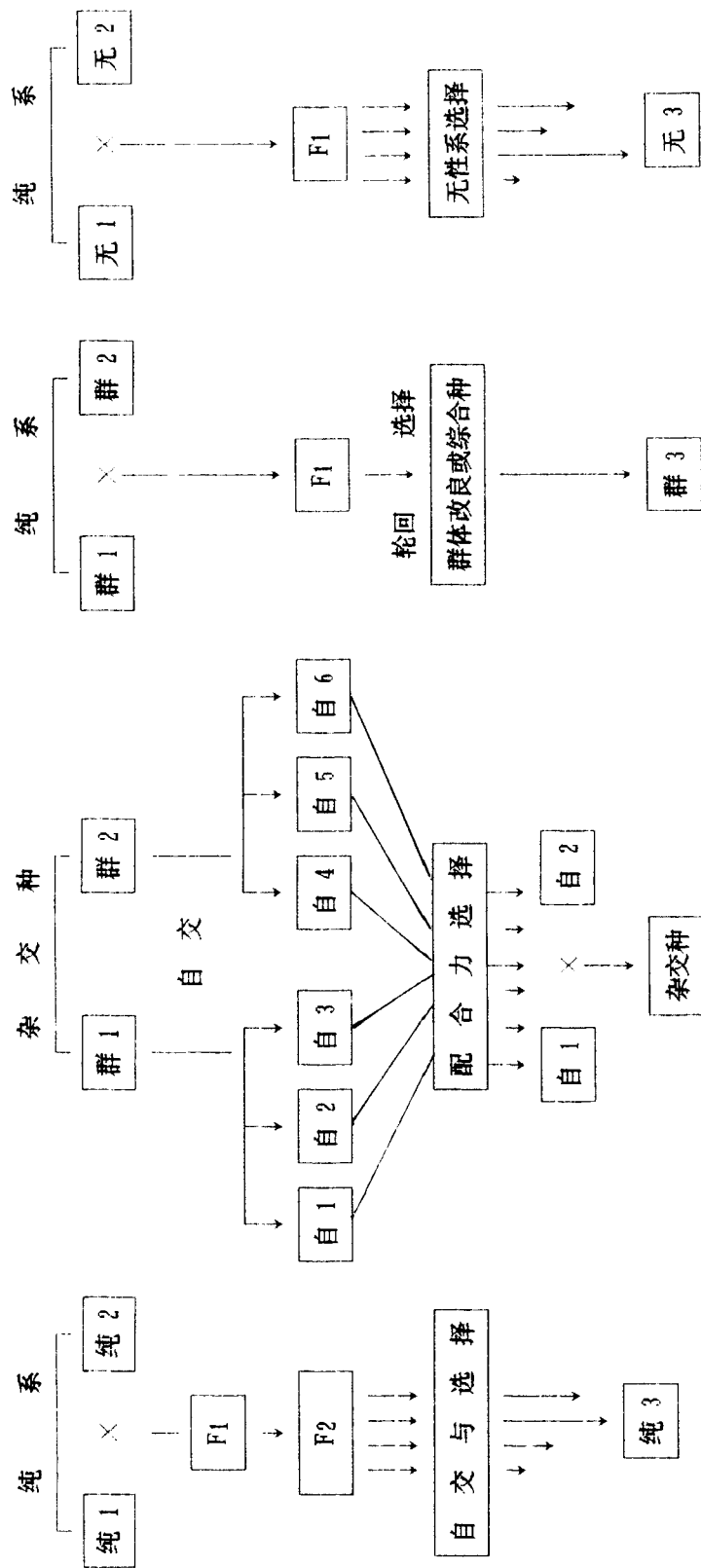


图 1. 四种基本群体的育种方法示意

利用杂交种第一代的优势（表现在产量、品质、抗逆、低耗等方面）是育种工作的发展方向，但需要每年制种、换种。为了节省人工去雄、授粉的麻烦，配制杂交种可采用以下几种途径：(1)核质互作雄性不育系——即不育系、保持系、恢复系“三系”配套法，已在玉米、高粱、水稻、油菜、小麦等作物上应用。(2)光（温）敏核雄性不育系——即一系两用（不育系兼保持系）的“两系法”，已开始在水稻、小麦上应用。(3)自交不亲和系——有配子体型（如烟草）自交不亲和与孢子体型自交不亲和（如白菜、甘蓝等十字花科植物）之分。(4)化学杀雄，已在小麦上应用。其中以核质互作雄性不育系应用最广，但化学杀雄最为简便，如果价格合理又无残毒则更便于推广。

以上是作物育种的“主流”做法，或称常规育种。在实际工作中，配合常规技术进行的还有诱变育种、双单倍体育种和远缘杂交。前者利用理化因素如 $\gamma$ 射线、中子、离子束以及甲基磺酸乙酯（EMS）、硫酸二乙酯（DES）、叠氮化钠（NaN<sub>3</sub>）等化学诱变剂诱发遗传变异，但其变异是随机的，而且有益突变率很低，一般为 $10^{-5} - 10^{-3}$ ，所以多与品种间杂交结合进行。双单倍体育种则通过花药培养或孤雌生殖产生单倍体，继之以染色体加倍形成二倍体，此法可以加速纯化进程，但因诱导频率低（一般不到5%），出现优良基因型的机率小，只能做为辅助措施应用。至于远缘杂交，一般指不同种、属之间的杂交，由于亲缘关系相距稍远，经常会出现杂交不亲和，幼胚不成活，杂种第一代不育，杂种后代育性差和“疯狂”分离等现象。随着科学技术的进展，如利用带有广亲和基因、可交配性基因、部分同源群染色体配对基因、染色体自然加倍基因等的“桥梁”亲本，以及生长激素处理，幼胚、幼穗培养，秋水仙素染色体加倍处理等办法，可在不同程度上克服前述的一系列问题。应该指出，远缘杂交是针对常规育种难以介决的问题或旨在人工创造新类型而制定的，其潜在的遗传变异性很大，但技术难度也较高，不是短时间所能奏效的，一般多是为常规育种培育一些中间材料如双二倍体、附加系、代换系、易位系等，以便进一步育成可供生产利用的新品种。

### 三、扩大遗传变异和灵活运用遗传规律是搞好作物育种工作的关键

上述四个基本育种方案的实施，包括以下三个基本环节，即遗传变异的发现与创制、优良遗传变异的选择与固定（或配合力及杂种优势检测）和育成品种（组合、群体）的产量和适应性评价。其中遗传变异的发现与创制是

最基本的,也是带有战略性的环节,因为没有优良的遗传变异就不可能育成优良品种。育种家要在注意发现与利用已有变异的同时,千方百计扩大育种群体的遗传变异,创造符合育种和生产需要的新的优良变异。异花授粉作物如玉米的轮回选择或群体改育就寓有这个意思。对于自花授粉作物如小麦来说,除了参照运用轮回选择的原理进行群体的性状改良外,还可采用以下两种做法扩大育种群体的遗传变异:

1. 利用雄性不育基因组建综合杂交混合群体——搜集在育种上各具特点的一些亲本材料取样混合做为一方,以具有推广品种遗传背景的若干雄性核不育材料的混合群体为另一方,间行种植,通过自然和人工辅助授粉收取雄性不育株上的种子混合,组成遗传基础广泛复杂的杂种群。这种群体经过年复一年的自然杂交、自然选择和人工辅助授粉、定向选择,使优良基因不断重组,遗传基础日趋丰富和优化,可供各类目标的育种方案随时从中进行选择,从而育成新的优良品种。国际上已用此法于大麦育种并收到一定成效。在小麦方面,我国70年代后期以来利用太谷显性核不育基因开展各类性状的轮回选择,以丰富亲本材料的遗传基础和选育新品种,也取得良好效果。

2. 双列杂交选择交配——选择一些各具特点的优良亲本进行双列杂交,这是第一轮亲本;下年在 $F_1$ 间有选择地进行第二次双列杂交,这是第二轮亲本;第四年在第二轮亲本经过混合选择的 $F_2$ 中选择优良单株互相交配,即第一次选择交配,组成第三轮亲本;第五年又在第三轮亲本的 $F_1$ 代植株之间进行第二次选择交配,组成第四轮亲本,……如此类推;而对每轮亲本的 $F_1$ 代杂种,都进行混合选择以繁殖 $F_2$ 代,然后按常规程序继续选育。这样就把亲本创新与丰富杂种后代遗传基础融为一体,已在燕麦、棉花上取得成效。

从遗传学上说,性状大体上可分质量性状和数量性状两大类;控制性状的基因其作用有大有小,大的叫主效基因,小的称微效基因。质量性状是受一至少数几对主效基因控制的,其表现型差异明显,容易区分,受环境的影响较小,如花、果实、种子颜色、茸毛有无、麦芒有无、抗病感病等。数量性状是由许多微效基因控制的,每个基因的效应(贡献)很小,且容易受环境条件的影响,所以呈现连续变异,没有明显界限,如产量高低、品质好坏、分蘖多少、穗子大小、抗逆性强弱等。还有一些性状是介于二者之间,既有主效基因起主导作用,又有为数不等的微效基因起修饰作用,如植株高矮、

抽穗早晚等。作物育种方案中所考虑的目标性状大多是数量性状。

基因在染色体上占有特定的位置（位点）。同一位点上的基因称等位基因，其作用有显、隐性之分，显性基因能掩盖或抑制隐性基因的表达。不同位点上的基因称非等位基因，它们之间也有不同的相互作用，有相加的，也有非相加的（如互相排斥、相辅相成、互为消长等）。不在一条染色体上的基因，它们在性细胞减数分裂时的分离与组合是独立的，互不干扰。位于同一条染色体上的基因，则彼此联合在一起传递到下一代的机率较大，这种连锁遗传的程度取决于这两个位点的距离。如果相距很近，那就难分难介，紧密连锁遗传；如果相距较远，则可自由组合。正因为控制性状的基因在数目多少、效应大小、作用性质、位点分布以及它们与环境条件的互作等方面各不相同，各种性状在上下代的遗传传递关系就显得错综复杂，常因亲本材料、交配对手和杂种后代所处的环境条件而异。对这些遗传变异规律的认识，需要通过有关实验和育种实践逐渐积累并加以总结和深化。这样，育种家才能灵活运用这些遗传学知识来掌握如何正确选择亲本、配置组合，确定杂种群规模与种植方式，创造有利于暴露和培育目标性状的环境条件，以及对不同目标性状分别进行恰如其分的选择，逐步把所需要的优良性状集中到一个个体上发展成为品系，再通过多年多点的鉴定与评价，尽快决选出最有生产利用价值的优良品种。一般而论，从开始杂交到育成品种投入生产应用，假定一年只种植一代，需要 8—10 年的时间。如果这个育种“车间”能够正常运转，则十年之后应该可以源源不断地育出优良品种。不过，农业研究受气候条件等的影响很大，就目前科学技术水平而言，还难以做到这样理想的境界。正因为如此，作物育种工作要相对稳定。

#### 四、我国作物育种工作现状和前景

1949 年以来，我国作物育种事业虽然取得了很大成绩，主要粮食、经济作物经历了 4—6 次品种更换，每次品种更换都能增产 10% 上下，但也存在一些不可忽视的问题。如果说作物育种工作可以分割成育种前、育种中和育种后三个阶段，我国的育种前和育种后工作相对说来是薄弱环节。我们对育种前的基础工作和理论研究（包括材料和方法）做得较少，还不能对育种实践起到应有的指导作用，也就是说，我们的育种实践在相当程度上还停留在以经验为主的状态。育种后这一领域虽然“技术含量”不高，却关系到如何



更有成效地把科学技术转化为现实生产力的大问题,和先进国家相比则更显得软弱无力,差距很大。中央农业部早在70年代后期就提出种子生产专业化,加工机械化,质量标准化、品种布局区域化和以县为单位统一供种的“四化一供”种子工作方针,但缺乏落实的具体政策和措施,所以长期以来生产上品种“多、杂、乱”现象一直未能得到解决,而且有日益加重的趋势。近几年,有些农民不问品种好坏与适应性争先播种新品种,企图以贩卖新种子做为生财之道,人为地缩短良种寿命并造成混乱,同时在种子经营上也常出现假、冒、伪、劣的坑农行为,严重挫伤了农民的生产积极性。因此一要建立健全良种繁育体系,切实做到种子生产专业化。除要求国营农场和种子部门的良种场承担良种繁育任务外,在一个县的范围内还要选定若干有条件的生产单位做为良种基地,有计划地组织生产各种级别的良种种子。二要认真执行种子检验制度,做到种子质量标准化。政府部门要设立种子检验机构,负责检验繁种单位的种子质量,按标准定级,优级优价。不经检验和检验不合格的种子不能在市场上销售。种子检验机构和种子生产、经营单位是彼此独立的系统,前者对产品质量拥有监督权。三要科学用种,做到因地制宜,合理布局,因种栽培,良种良法配套,使地尽其利,种得其所,充分发挥良种的增产增收性能。过去不少地区在领导生产时习惯采用以“高产”品种带路的做法,主观愿望是好的,但要注意到单产潜力大的品种往往比较“娇气”,对肥水等外界环境条件比较敏感,一旦肥水跟不上或遭受不良气候条件的袭击,容易造成减产。所以应该强调“对口”种植,不搞“一刀切”。

我国从事作物育种的单位不少,但都习惯于单一专业各自为战,而且大多在一个地点进行培育和选拔,不能把早期世代材料有计划地分发给若干有代表性的地点种植,接受不同生态环境和栽培条件的考验。因而育成品种的适应性比较狭窄,难以在生产上发挥更大作用,同时在筛选过程中很有可能丢掉一些不该淘汰的材料,影响育种效率。这是一个严重的缺点,应从体制和政策上加以引导,逐步求得解决。此外,育种规模太小,研究手段落后,田间作业基本上靠人工操作,室内检测设备也十分简陋,影响工作质量和进度。这只能靠增加投入来解决。

作物育种是一门综合性很强的应用科学,需要植物遗传、细胞、生态、病理、昆虫、农业气象、品种资源、作物栽培、生物统计、生物技术等学科的知识做支撑,其中最重要的是遗传学,包括分子遗传学。所以在育种前和

育中围绕育种工作的需要,开展有关性状的组分、形成、发展及其与环境条件的关系,性状本身从群体到分子水平的遗传控制,性状之间的相互关系,高产、优质、多抗的生理生化基础,病虫抗性与病菌、害虫生物型间的相互关系,基因型与环境互作,以及分子生物学、基因工程技术在作物育种中的应用等研究,对提高作物育种水平和工作效率十分重要,应该安排足够的力量,分别轻重缓急予以实施。只有这样才能把作物育种发展为有坚实理论做指导和精确方法武装起来的一门应用科学。

就我国当前和今后一个时期的作物育种工作来看,在育种目标上,应该处理好高产与优质、高产与稳产的关系。我国人多、地少、底子薄,吃饭问题关系重大。选育高产、稳产的优良品种仍是当务之急,也是一个长期的战略任务。从总体上说,高产是优质的前提,离开产量谈品质是行不通的。高产与稳产(抗逆性能)也常有矛盾,高产品种一般产量不够稳定,而抗逆性能强的品种又往往不高产。在育种过程中和利用品种时,都要注意协调好这些方面的关系。在育种途径上,当前要处理好杂种优势利用与常规育种(指品种间杂交)、高新技术与常规技术的关系。从理论上说,杂种优势利用比常规品种增产潜力大,应是努力发展的方向。但不同作物情况不一,玉米、高粱杂种优势较大,小麦、大豆杂种优势较小。在自交作物中,水稻是二倍体作物,杂种优势较大,小麦是六倍体作物,它在进化过程中已经发生过两次自然杂交和染色体加倍,剩余的杂种优势较小。再者单个植株的生育优势是随种植密度增大而降低的,生产上各种作物的种植密度不一,所以其群体优势也各不相同。还应该指出,常规育种是杂种优势利用的基础,用以生产杂种一代优势的亲本品系(自交系、不育系、恢复系等)多来自常规育种,后者的性状水平提高了,杂种优势利用的效果也就更加显著;而杂种优势利用的发展又可进一步推动常规育种水平的提高,二者是互相促进的。

近十多年来,植物基因工程技术有了长足的进步,现在科学家已能人工分离、合成和克隆一些特定基因,采用生物(与根瘤农杆菌共培养)、物理(电穿孔、微射弹、微注射)、化学(聚乙二醇)等方法将目标基因导入植物细胞或胚胎,并通过组织培养或直接转化(花粉管通道)获得转基因植物。它已开始打破生物间亲缘关系的界限,初步实现不同植物间优良基因的交流,既可扩大远缘杂交的范畴,又能缩短育种进程,还有可能将微生物或动物的有益基因向植物中输送。这对提高植物育种水平和效率具有重要的战略

意义。现在已有30多种植物获得了转基因植株,包括不少重要的农作物如烟草、马铃薯、油菜、亚麻、棉花、甜菜、大豆、苜蓿、番茄等。被批准进行田间试验的转基因植物达1400多例,涉及抗虫、抗病毒、抗除草剂、品质改良、雄性不育、延熟保鲜等方面,其中延熟保鲜转基因番茄、抗除草剂转基因烟草等已获准进入市场。我国的抗花叶病毒转基因烟草已在大面积生产上应用,抗棉铃虫转基因棉花也正在扩大示范之中。最近报道,携有抗白叶枯病基因Xa21的转基因水稻和抗黄矮病毒的转基因小麦已获成功。这些都是十分可喜的新进展。不过,总的说来,目前的基因工程技术体系多适用于转化双子叶植物,对于小麦、水稻、玉米等单子叶植物的遗传转化虽有进展,尚未取得明显突破。

对于多基因控制的数量性状,现已在几种主要农作物上采用RFLP(限制性片段长度多态性)技术绘制出接近饱和的DNA分子标记遗传图,通过分析实验群体中每个个体或株系所携带的分子标记及其与数量性状表现型值间的关系,可将数量性状基因(QTL)逐一定位到染色体的相应位置并估算其遗传效应。有了这样的资料,育种家就可以根据与某些QTL紧密连锁的分子标记进行选择,即分子标记辅助选择,其精确性要比按表现型选择好得多。这是生物技术在作物育种应用上的一个新进展。不过不同作物的DNA多态性不一样,遗传图上分子标记的分布与饱和度各不相同,其辅助选择的效率也就有所差别。为了使这类技术更加简便实用,科学家正在努力探讨一些新的分子标记。

总之,植物基因工程和现代生物技术已不断取得令人瞩目的进展,但它毕竟还在成长之中,不够成熟,而且研究成本很高,距离实际应用还有一段路程。然而,从发展上看,它的应用前景十分诱人。我们必须密切注视,积极支持,促其更快地向实用化发展。即使将来“生物技术育种”或“分子育种”在技术上已臻成熟并达到实用化,也仍然要以常规育种(包括杂种优势利用)为基础,并与之密切结合,才能充分发挥高新技术的作用,把作物育种科学推向更高的水平。

## Present Status of Wheat Genetic Studies in China

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### ABSTRACT

Most genetic studies on wheat in China are oriented by the needs of breeding. This paper gives a briefing under 6 heading: (1) Some studies on wheat genetic resources in which 3 subspecies of common wheat unique to China and the crossability with rye of the landraces are described. (2) Genetic analysis of major breeding objectives, i.e., disease resistance, semidwarfness and bread baking quality, are mentioned. (3) Transfer of alien genes constitutes an active dimension in wheat genetic studies. Intergeneric hybrids between *Triticum* and *Secale*, *Elytrigia*, *Haynaldia* and *Aegilops* are discussed. (4) New materials and methods for chromosome engineering, namely, blue-grained monosomics, self-fertile nullisomics, nullisomic backcrossing for the production of alien substitutions, monosomic addition-disruption-incorporation process for the enhancement of translocations and the use of chromosome autoduplication tetraploid wheats, are suggested. (5) Genetics of anther-derived plants and somaclonal variation are new areas of interest. (6) Molecular aspect of wheat genetics is at its beginning.

China is a big wheat producing country. Extension of improved varieties has long been recognized as one of the most important measures for increasing wheat production. Therefore, most wheat genetic studies in China are oriented by the needs of breeding. This paper gives a briefing on the major progresses in wheat genetic studies in China.

### SOME STUDIES ON WHEAT GENETIC RESOURCES

China has currently owned more than 40,000 accessions of wheat and its wild relatives, 32595 of them being enlisted for long-term preservation in the National Crop Gene Bank. More than 99% of wheats grown in China belong to common wheat, *Triticum aestivum*. Three subspecies of *T. aestivum* indigenous and unique to China are recognized:

a. Yunnan wheat, *T. aestivum* ssp. *yunnanense* King. Distributed along the lower reaches of the Lancang River and the Nu River in Yunnan province, Southwest China. Glume very tough, tightly embracing the spikelet; rachis easily broken below the spikelet when pressed. Double ditelosomic analysis indicated that 8 chromosomes showed some differentiation from those of Chinese Spring (CS) (Chen et al, 1988; Huang et al, 1989).

b. Xinjiang wheat, formerly identified as a distinct hexaploid species, *T. petropavlovskyi* Udacz. et Migush., now recognized as a subspecies by Y.S. Dong. Distributed in the western part of the Tarim Basin, Xinjiang Autonomous District, Northwest China. Spike coarse in texture, lax, having long glume with long beak like *T. orientale*. The majority of PMCs in F<sub>1</sub>s when crossed with hexaploid and tetraploid wheats showed 21" and 14" + 7', respectively. Its genome remained to be ABD with 1 chromosome at least in A/B different from that of common wheat. (Chen et al, 1985).

c. Tibetan weedy wheat, *T. aestivum* ssp. *tibetanum* Shao. Distributed in the upper reaches of the Lancang River and the Nu River and the Yaluzangbu River valley, Tibet Autonomous District. It appears as a weed in wheat and barley fields and no natural community is found. Similar to common wheat in general morphology with a rachis readily broken below the spikelet at maturity, and the spikelets fall to the ground before wheat or barley matures. Double ditelosomic analysis showed its chromosome constitution was essentially the same as CS except that 7BS usually failed to pair (Chen et al, 1991). Its D genome was as primitive as *Aegilops tauschii* (Yen et al, 1988).

Chinese local wheat varieties are noted for their high crossability with rye. Among 864 land races tested, 50, i.e. 5.8%, had a crossability % significantly higher than that of CS. 19 of them showed a

crossability with rye as high as 90% or more. Genetic analysis on a selection, J-11, of a local variety from Sichuan province where CS originated, revealed that it carried a new gene for crossability, *kr4*, located on chromosome 1A. So those local varieties with a crossability % significantly higher than CS might have carried 4 recessive *kr* genes (Luo, 1992; Luo et al, 1992, 1993; Zheng et al, 1992).

## GENETIC ANALYSES ON THE MAJOR BREEDING OBJECTIVES

### 1. Disease resistance

Stripe rust, powdery mildew and scab are the 3 major wheat diseases in China. Stripe rust has essentially been under control in the past 20 and more years through breeding except in some areas where physiological races used to variate from time to time. Powdery mildew has become increasingly important since 1980's as a result from increased application of nitrogen. As 1B/1R translocation lines such as Lovrin 10, Predgornaia 2, Kavkaz, etc. were extensively used as the source of resistance to rusts in 1970's, an overwhelming majority of the varieties released in 1980's were new derivatives of 1B/1R translocations. This would inevitably result in a monotonous spectrum of disease resistance, and loss of disease resistance from these newly released varieties were frequently reported. Thus, second-line sources of resistance were identified and a recommendation list of new resistance genes together with their carriers was provided, i.e., Yr1, Yr2\* (\* high IT in seedling test), Yr3a\*, Yr3b, Yr4a\*, Yr4b, Yr5, Yr8, Yr10, Yr15, YrSu for stripe rust and Pm2, Pm2x, Pm4a, Pm4b and Pm6 for powdery mildew (Yang et al, to be published). 6R from "White Rye" and V6 substitution or translocation lines from *Haynaldia villosa* were even better than the above Pm genes in resistance (Xin, Z. Y., personal communication). Currently these new genes of resistance are being incorporated into the recommended cultivars in North China.

Scab prevails in the middle and lower reaches of the Yangtze River valley, coastal areas in southeastern China and eastern parts of Heilongjiang province. Up to now no wheat variety is found immune or highly resistant to the disease. Only a very few landraces are more or less resistant to the extension of infection, but they possess too poor agronomic characters. Fortunately in 1970, a relatively resistant (to extension of infection) variety known as Sumai 3 was developed from a cross of 2 susceptible varieties (Funo x Taiwan). Since then numerous crosses were made between Sumai 3 and various improved varieties, and a series of new cultivars were developed but rarely their resistance to scab could surpass that of Sumai 3. Recently recurrent selection against scab was adopted in some breeding programs and a slow but steady progress was reported. In regard to the mode of inheritance most authors recognized it was polygenic in nature. Monosomic analysis of scab resistance with Sumai 3 showed that many chromosomes were involved with differential contributions (Li and Yu, 1990; Yu, 1990). But some authors provided evidence that scab resistance was controlled by a few major genes with modifiers since segregation pattern in  $F_2$  usually showed 2 peaks with one high and one low (Zhou et al. 1987, Bai et al., 1990). The discrepancy may be attributed to the ways of expressing the infection indices and related also to the fact that whether infection data are taken at successive stages of disease development or not (Li and Yu, 1990).

### 2. Semidwarfness

Presently about 40% of the total wheat acreage is sown with semidwarfs. In summarizing the representative dwarf-source varieties or dwarfing genes which led to the successful development of semidwarf cultivars in China, 5 categories are recognized: (a) Suwan 86 which carried 2 pairs of GA3 insensitive semidwarf genes, Rht1 and Rht2; (b) St2422/464 (a material of Italian origin) bearing 1 pair of semidwarf genes similar to that of Saitama 27 with weak GA3 insensitivity designated as Rht1S; (c) 2 Chinese varieties Huixian Red and Youbao each carrying a pair of Rht2; (d) Funo, Abbondanza and other derivatives of Akagumughi, each carrying 1 or 2 pairs of GA3 sensitive dwarfing genes designated as Rht8 and Rht9; and (e) Tom Thumb carrying Rht3 and Aibian 1 bearing Rht10 which were used in hybrid wheat development and recurrent selection for semidwarfness, respectively (Gao et al., 1992).

### 3. Bread baking quality

The bread baking quality of the Chinese wheats is, in general, significantly inferior to that of the hard red winter wheats from the US. They are characterized with short dough development time, short dough stability time, less tolerance to mixing, and finally small loaf volume and poor bread score, although with a few exceptions. Consequently, good bread baking quality wheats from the US, Canada, the former USSR, Mexico (CIMMYT) and eastern European countries are widely used as parents in quality breeding programs. In the past few years studies on the composition of HMW glutenin subunits of the Chinese wheats and its relation to bread baking quality were made by several institutes. In a study by Mao, P. (1992, unpublished), the HMW glutenin subunits composition of 5071 common wheats, comprising 936 landraces, 2307 improved varieties and 1828 foreign introductions, were determined by SDS-PAGE and the corresponding quality indices were scored. It was observed that the 3 categories of wheats differed quite significantly in their distribution pattern of HMW subunits as follows (%):

Accession	Glu-A1			Glu-B1			Glu-D1	
	Null	1	2*	7+8	7+9	22	2+12	5+10
Landrace	88.6	6.2	5.2	84.7	4.9	2.7	94.3	3.7
Improved variety	57.4	27.6	15.0	42.0	41.9	2.8	73.7	5.7
Foreign introduction	54.5	27.3	18.3	25.2	37.2	11.7	46.4	45.9

In a subset data from 126 varieties, using sedimentation value, valorimeter, and bread score as criteria of bread baking quality, the magnitude of effect in 3 loci of Glu-1 after standardization was in the order of  $5+10 > 2* > 7 = 20 > 1 = 7+8 = 4+12 > N = 22 = 2+12 > 7+9$ . The smallest effect shown in the subunit 7+9 has to be verified since it is contradictory to some other reports.

### TRANSFER OF ALIEN GENES

Alien genes transfer constitutes an active dimension in wheat genetic studies (Li and Hao, 1992). Production of amphidiploids or partial amphidiploids is the first step in alien genes transfer. Early in 1950's an octoploid triticales program was started in China. After successive improvements on seed setting, kernel plumpness, easiness of threshing, earliness and plant stature, several octoploid triticales varieties were released for production in the mountainous areas of Guizhou province in late 1970's and late 1980's (Bao and Yan, 1993). However, for other intergeneric crosses involving common wheat, amphidiploids or partial amphidiploids obtained are still too wild to be used in cultivation. They must be backcrossed to wheat once or twice followed by selfing and selected for disomic alien addition lines carrying the target gene(s) through cytological and morphological analysis. The alien addition lines are then transformed into alien substitution lines by the aid of aneuploid technic. Furtherly, radiation/tissue culture or the use of nulli-5B wheat/ph mutant is practised to induce translocations between wheat and alien chromosomes forming translocation lines, i. e. homozygous, stable plants with  $2n=42$  possessing the wanted character(s) or gene(s). In China, up to the present, 36 kinds of intergeneric hybrids between wheat (including tetraploids) and 11 genera of *Triticeae* have been successfully made, and 14 kinds of amphidiploids or partial amphidiploids have been obtained, among which 6 are reported for the first time. Alien addition and substitution/translocation lines have been reported in 6 and 5 genera, respectively.

Those intergeneric hybrids involving *Elytrigia*, *Haynaldia*, and *Aegilops* (besides *Secale*) were studied more extensively. Five octoploids of wheat-*Elytrigia intermedia*, namely Zhong 1, Zhong 2, Zhong 3, Zhong 4 and Zhong 5 were developed in the mid-1960's. Zhong 1 and Zhong 2 carried a group of 7

chromosomes from *Et.intermedia* designated as X, and Zhong 3, Zhong 4 and Zhong 5 carried a second group of 7 chromosomes designated as E<sub>1</sub> (He et al, 1989). Thus the genome constitution of *Et.intermedia* was suggested as XE<sub>1</sub>E<sub>2</sub>(He et al, 1989). Two sets of alien addition lines, one from X genome and one from E<sub>1</sub> genome, were developed (He et al, 1989). Similarly, 5 octoploids of wheat-*Et.elongata*, namely, Xiaoyan 7430, Xiaoyan 68, Xiaoyan 693, Xiaoyan 7361 and Xiaoyan 784 were also produced in 1960's which carried genomes E<sub>1</sub>, E<sub>2</sub>, F<sub>1</sub>, F<sub>2</sub> and N respectively, from *Et.elongata*. The genome constitution of *Et. elongata* would be E<sub>1</sub>E<sub>2</sub>F<sub>1</sub>F<sub>2</sub>N, in which E and F genomes bear some homeology (Zhong et al, 1991). Twelve amphidiploids between tetraploid wheats and *Aegilops* species were produced in 1985-1990 by the aid of chromosome autoduplication tetraploid wheats (Dong et al, 1990; Xu and Dong, 1992), and 5 common wheat-*Ae.comosa* addition lines, namely, 1M, 2M, 3M, 4M and 7M were obtained (Weng and Dong, to be published). From durum wheat-*Haynaldia villosa* amphidiploid 6 common wheat-*Haynaldia villosa* addition lines, i.e. V2, V3, V4, V5, V6 and V7 were produced, and the powdery mildew resistance gene(s) from *Haynaldia* was located on V6 chromosome (Chen and Liu, 1986; Liu et al, 1988, 1990).

Among the varieties generated from alien genes transfer, Xiaoyan 6 is the most successful one. It has been widely grown in the western parts of the Yellow River and the Huai River valleys for 13 years. Cytological examination showed that it was a translocation line carrying 2 translocations between 2 small *elongata* chromosome segments and 2 wheat chromosomes(Li et al, 1990).

## MATERIAL AND METHODS FOR CHROMOSOME ENGINEERING

### 1. New monosomic and nullisomic series of wheat

Wheat monosomic series are important tools for gene location and the development of alien substitutions. In China 9 monosomic series have been derived from the standard monosomics of Chinese Spring. However, the enormous labor involved in chromosome counting and the problem such as univalent shift have caused much trouble in its general application. Li et al. (1986) established a blue-grained monosomic wheat in which the wheat chromosome 4D was substituted by an *Elytrigia elongata* chromosome 4Ag (4Ag/4D) carrying the gene responsible for the blue coloration of aleurone layers of seeds. The blue-grained character manifests a distinct xenia effect. When the endosperm cells receive 3, 2, 1 and 0 blue gene doses, the seeds are dark blue, medium blue, light blue and white in color respectively. Later on, the same authors treated the blue-grained disomic wheat with  $\gamma$ -rays and fast neutron radiation to induce the transfer of blue gene to other wheat chromosomes, and as a result, 8 new blue-grained monosomics (1B, 2D, 3D, 3A, 5A, 6A, 7A and 7B) were obtained. The advantage of using such blue-grained monosomic lines in chromosome engineering is that the chromosome number can be deduced from the seed color without cytological examination. Moreover, Li et al. (1990) were successful in obtaining first self-fertile 4D and subsequently self-fertile 2D, 3D, 3A, 5A and 6A nullisomics from the blue-grained monosomics through screening for fertility in large populations. By employing similar procedures Xue et al. (1991) developed self-fertile nullisomics for all but 3 chromosomes (2B, 4B and 7D) from the progenies of Abbondanza monosomics. The use of self-fertile nullisomics would enhance the development of alien substitutions.

### 2. Nullisomic backcrossing method for the production of alien substitutions

Li et al. (1990) initiated the nullisomic backcrossing method as a new approach to the establishment of alien substitution lines. The essential steps are: Crossing wheat nullisomics to alien species or amphidiploids, for the former it is preferable to induce chromosome doubling in F<sub>1</sub>. The F<sub>1</sub> (or selected F<sub>2</sub>) plants are then backcrossed once or twice with nullisomic wheat, and individuals with 20" + 1' or 20" + 2' are selected and selfed to produce alien substitutions. Test-crossing all the selfed products with 21" configuration to common wheat, those plants whose F<sub>1</sub> progeny showing 20" + 2' can be ascertained to be alien substitutions. The apparent advantage of this method is that the choice of a corresponding

homology between the nulli-chromosome in wheat and the alien chromosome in the addition line is not necessary. Moreover, since the missing chromosome in the nullisomic being used is known, it is possible to deduce whether the substituting alien chromosome and the nulli-chromosome in wheat are homologous by observing the compensation effect in the alien substitution line obtained. Thus the process for the development of alien substitutions is shortened.

### 3. Monosomic addition-disruption-incorporation process (MADI)

In genetic studies on the progenies of octoploid triticale x common wheat, Ren (1990) and Ren et al. (1990a, 1990b) observed that the monosomic addition chromosomes of rye in wheat background were eliminated rapidly upon selfing. The added rye chromosomes, in varying number, affected significantly the transmission rate of wheat chromosomes and caused a remarkable high rate of Robertsonian translocations between wheat and rye chromosomes. The small DNA fragments, which were produced by disruption of the added rye chromosomes, can be incorporated in wheat chromosomes to accomplish the transfer of alien genes. Translocations were identified by using the C-banding technic. In one study the frequency of wheat/rye translocation in different generations of backcrossing or selfing, varied between 4.23% and 14.67%. This procedure for genetic transfer is known as monosomic addition-disruption-incorporation process, abbreviated as MADI process. In comparison with the traditional disomic addition line method the process saves more time and is easy to operate if the C-banding technic is mastered. The original authors were successful in transferring the powdery mildew resistance genes from 6R of rye and *Haynaldia villosa* to common wheats.

### 4. Use of chromosome autoduplication tetraploid wheats in the production of amphidiploids

As mentioned above, Xu and Dong (1989, 1992) found that PS<sub>3</sub> of *Triticum persicum* and DR 147 of *T. durum* were able to generate amphidiploids through spontaneous chromosome doubling when crossed with *Aegilops* species. There were 2 ways by which unreduced gametes could be formed: firstly, some PMCs omitted the first meiotic division, and secondly, first division restitution with premature cytokinesis which resulted in an asymmetrical dyad composed of one anucleate cell and one cell with a restitution nucleus. The use of this knowledge has resulted in the production of many amphidiploids between *T. persicum* and 8 *Aegilops* species. This meiotic mechanism also worked when crossed with *Secale cereale*.

## GENETICS OF POLLEN-DERIVED PLANTS AND SOMACLONAL VARIATION

Pollen-derived plants are good materials for genetic study as there is no interference of dominance/recessiveness on character expression. Hu (1992) and Tao and Hu (1989, 1990) revealed, in a study of pollen-derived plants from a cross (hexaploid triticale x common wheat) F<sub>1</sub>, that distribution of R chromosomes in the gametes was random while that of D chromosomes was not (most of the D chromosomes remained intact), and this was accounted for the predominating occurrence of diploid pollen plants with 2n=46 in the progeny, a phenomenon which was scarcely observed under ordinary condition. They also noticed that different rye chromosomes manifested different rate of transmission, 6R being the highest (64.5%), 1R and 3R the second highest (60.2-55.9%) and 7R the lowest. Recently Zhang et al. (1993) using powdery mildew resistance gene(s) of 6RL as a marker observed that the transmission rates of 6R *in vivo* through male and female gametes was nearly equal, about 10% in magnitude, which was significantly lower than the expected value (50%); while that of microspores *in vitro* was 23.3%, which was significantly higher than that *in vivo*. This indicated that anther culture would enhance the transmission of the alien chromosome 6R in wheat cell generations.

Moreover, Wang and Hu (1993) and Miao et al. (1988) showed evidence of various changes in chromosome number and structure in pollen-derived plants. They noted in the pollen plant progenies from octoploid triticale x common wheat the occurrence of alien addition lines with a frequency as high



as 5% which was many times higher than that produced in the ordinary way. Therefore, Hu and his co-workers (1988-1993) stressed the importance of incorporating anther culture technique with conventional chromosome engineering by which a high and effective system of alien genes transfer in wheat could be established. They had succeeded in developing and identifying 1B/1R, 1D/1R and 6D/6R wheat-rye alien substitutions and some translocations with disease resistance through the combined efforts of aneuploid technic, chromosome banding, isozyme markers and RFLP analysis (Tao et al, 1990a, 1991b).

In the study of somaclonal variation a number of workers were successful in obtaining variants or mutants which acquired higher resistance or tolerance to scab (*Fusarium graminearum*, Ouyang et al, 1990), root rot (*Helminthosporium sativum*, Guo et al, 1990) or salinity (Zheng et al, 1990) than the starting materials by successive tissue culturing in media of increasing concentration for the treatment in question. Usually a small dosage of  $^{60}\text{Co}$  radiation was practiced before screening.

Successful generation of wheat plantlets from protoplast culture was first reported by Wang et al. in 1988 and then followed by some workers in 5 other laboratories from 1989 to 1993. The key to success was: (a) proper choice of embryogenic calli with high regeneration capability from numerous genotypes; and (b) careful regulation of callus type formation through changing the composition of culture medium and cultural procedure in such a manner that cell division capacity of the culture was enhanced before isolation of protoplast and then weakened after regeneration of callus from the protoplast so as to facilitate further differentiation of plantlets.

### MOLECULAR ASPECTS OF WHEAT GENETIC STUDIES

Currently, molecular genetics of wheat in China is just at its beginning. Most studies deal with the use of biochemical and molecular markers for the identification of alien genes or chromosome fragments in wheat background. Gao et al. (1992) analysed the esterase zymogram of some somaclonal variants from common wheat x *Elytrigia intermedia* hybrids and their parents, and found that those isozymes coded by specific chromosomes of *Et.intermedia* were, to a certain degree, homeologous to groups 3, 7 and 6 of wheat. Zhang et al. (1993) analysed the isozyme EST-5 and alpha AMY-1 of a series of addition, substitution and translocation lines from wheat-rye hybrids and found that they all showed rye 6R-specific bands in addition to wheat 3AL-specific bands in the case of EST-5 and wheat groups 6 and 7-specific bands in the case of alpha AMY-1. Furthermore, in some lines like M17-3 there were no wheat 3AL-specific bands in the case of EST-5, and in others like M24 (a substitution line) new bands which were lacking in both parents appeared. These results imply that isozyme analysis not only reveals the existence of alien fragments but also gives some hints on chromosome interactions. Although a few laboratories reported some studies on the storage proteins relevant to wheat quality, using protein pattern assay as biochemical markers for various wheat genetic studies was still meager. Zhang et al (1992) in comparing leaf protein patterns between powdery mildew resistant and susceptible wheat lines found that the former had two additional bands with molecular weights 40 kd to 60 kd.

Molecular markers based on the polymorphism of nucleotide composition and sequence come into use too. Zhang et al. (1993) analysed the RFLPs of a series wheat-rye addition, substitution and translocation lines by using rye-specific dispersed repeat sequence pSc5.3H3 and wheat group 6(short arm)-specific sequence Xpsr167 as probes. They all showed bands from rye chromosome component, while the group 6 substitution lines showed no bands from wheat group 6. The line MO9 showed condensed bands with low copy number when hybridized with pSc5.3H3, and lacked a rye 6R-specific band at 2.8 kb when hybridized with Xpsr167, indicating that it carried an incomplete 6R and was most probably a translocation line. Xin et al. (1991) succeeded in screening two cDNA probes pEleAcc3 and pPJN8(E<sub>1</sub>-T<sub>1</sub>) for detecting *Elytrigia intermedia* DNA in wheat background. A specific band for the DNA of *Et.intermedia* and its derivatives was found in southern hybridization. This specific band could be used as a marker to identify the BYDV resistance in wheat breeding program. *In situ* hybridization is a direct