

Research
Crop Genetics and Breeding—Review

六倍体合成小麦——过去、现在与未来

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摘要

近年来, 小麦单产产量已经达到了平台期。随着世界人口的增加, 人们对未来粮食安全的担忧与日俱增。六倍体人工合成小麦 (SHW) 能够将野生近缘种的重要农艺性状转移到栽培小麦, 为现代小麦育种提供产量潜力、抗旱性、抗病性和养分高效利用的新资源, 从而在现代小麦育种中越来越受到重视。本文综述了 SHW 产生、研究和利用的现状, 特别介绍了其对小麦育种的贡献。同时, 简要介绍了基于基因组研究合成小麦生长优势分子机制的新进展。对于利用 SHW 改良现代小麦品种的分子机制的了解, 将进一步促进 SHW 的利用, 为满足世界粮食安全发挥重要作用。

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1. 小麦进化与合成小麦

1.1. 小麦进化与驯化

普通小麦 (*Triticum aestivum* L.) 是通过栽培异源四倍体硬粒小麦 (*T. turgidum* ssp. Desf. MacKey, AABB, $2n = 4x = 28$) 与二倍体节节麦 ($2n = 2x = 14$, DD, *Aegilops tauschii* Coss.) 自然杂交和染色体加倍而产生的 [1–4]。普通小麦不仅能够适应不同光周期和温度条件, 而且能够在盐碱、低 pH 值、含铝和霜冻等逆境条件下比其祖先种生长得更强壮。普通小麦还增强了抗病性, 而且其终端产品的用途更为多样化 [5], 从而超

越其四倍体栽培亲本, 成为人类的主要粮食作物之一。

普通小麦是研究异源多倍体基因组结构、功能和表观遗传变化的一个良好的模型。研究小麦异源六倍体的特性, 并与其他异源多倍体植物进行比较, 将了解小麦成功的分子机制研究提供新的思路。不难想象, 两次异源多倍体化致使普通小麦基因组变得极端复杂, 但同时也使普通小麦成为一种研究成功多倍体独特性状和部分同源基因互作规律的不可多得的基因组系统。

六倍体合成小麦 (SHW) 是一种人工再造的六倍体小麦, 由于引进了来自四倍体和二倍体亲本的特异遗传资源, 其遗传基础更为广泛。同时, SHW 与栽培小麦

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间没有生殖障碍，从而可以有效地将四倍体和二倍体近缘种中的优异农艺性状和基因导入到普通小麦中，使之得到有效改良。

1.2. 为什么需要合成小麦？

为了持续养活世界上不断增长的人口，在未来的50年里，人类需要种植比过去10 000年生产的小麦总量更多的小麦。在过去的半个世纪，普通小麦品种的增产潜力不断增加。然而，这种趋势最近正在放缓，从而引起了人们对未来世界粮食安全的担忧。例如，在过去的12年中，英国全国的平均小麦产量一直保持在 $8 \text{ t} \cdot \text{hm}^{-2}$ 左右，没有进一步增加[6]。小麦遗传多样性的流失应当是小麦单产遗传改良减缓的重要原因之一，致使现有种质库中可发掘的遗传多样性十分有限。现在到了转向利用小麦野生近缘种多样性的时代，而这一方面尚未经过系统的开发。通过人工杂交和加倍重现节节麦与二粒小麦或硬粒小麦之间的杂交，可以引入新的遗传资源，重获小麦起源和驯化过程中失去的许多野生近缘种有价值的遗传变异。利用SHW与现代小麦品种的进一步杂交，可以引入人们所需要的新性状，提高普通小麦产量和抗逆性。

1.3. SHW是怎样产生的？

大多数SHW品系都是通过硬粒小麦（用于制作通心粉的二粒小麦）与节节麦杂交而成。在大多数情况下，二倍体物种作为父本，硬粒小麦作为母本。反交也有可能，但由于胚较小或者有缺陷，成功率较低。在某些情况下，来自节节麦 × 硬粒小麦的杂交胚可以适当发育，但胚乳却不能。因此，须在授粉后2~3周进行胚拯救。也就是将未成熟种子的胚剥离，转移到含有糖、盐、激素等营养成分的琼脂培养基上进行培养，使其发育。不同类型的四倍体亲本，如硬粒小麦的不同品种，可能影响杂交后代胚乳的形成。例如，Langdon是一个众所周知的硬粒小麦品种，用其作四倍体亲本获得的杂交后代胚乳发育相对较好。这个硬粒品种是合成小麦四倍体母本的首选，可以避免胚拯救过程失败。胚拯救再生的植株是三倍体，通常用秋水仙碱处理，使其染色体数目加倍，然后转移到盆栽中，成长为成熟的植株，产生种子。除了使用常规的秋水仙素，还可以通过圆锥小麦-节节麦杂种的未减数配子($2n$)自发实现染色体加倍[7,8]。事实上，自发染色体加倍在新的SHW培育过程中比较常见[7-10]。这些

SHW品系可用于产生部分双二倍体和加倍单倍体，用于现代小麦品种遗传改良[11]。

2. SHW的历史回顾

第一次培育合成小麦的尝试是在20世纪中叶对“合成斯卑尔脱”小麦的研究中进行的，目的在于确定斯卑尔脱小麦(*T. aestivum* subsp. *spelta* L. Thell)的原始性[4]。这些最早的异源多倍体杂种类型被称为“合成六倍体小麦”。20世纪80年代末以来，国际玉米和小麦改良中心(CIMMYT)已经培育了1000多份SHW[12]。随后的研究证实，SHW是提高小麦抗生物胁迫和非生物胁迫性能以及产量潜力（如大穗大粒）等的重要遗传资源[13,14]。当然，由于存在“野生性状”或不良农艺性状（如颖壳坚硬和不易脱粒等），SHW本身不能作为栽培品种，须通过与优良普通小麦品种杂交来去除这些不良性状，培育合成小麦衍生系(SDL)，或将SHW的部分性状转移到普通小麦品种中[6]。2003年，西班牙注册了CIMMYT的合成小麦衍生品种Camona[15]。同期，中国也审定了第一个利用合成小麦培育的品种。从那时起，世界各地至少有62个SDL被注册（表1）。与其亲本相比，合成小麦培育的新品种的遗传多样性显著提高[16]。

世界上四分之一的人口患有由于缺少铁(Fe)元素而引起的健康问题[17]。普通小麦籽粒不能为那些以小麦作为主要微量元素来源的人群提供足够的Fe和锌(Zn)。在这一方面，SHW已被视为培育富含微量元素的“生物强化”小麦的重要材料[18]。一些SHW的微量和大量营养元素含量均较高[19]。CIMMYT已经培育出富锌的高产SDL[20]，有些已经在印度作为小麦新品种被注册，如Zinc Sharkti、WB2和HPBW 01（表1）。可以预见，更多的SDL将在不久的将来得以释放和使用。

中国是利用SHW作为遗传资源获得成功的主要国家之一，尤其是在中国西南部的四川省。自1995年从CIMMYT引进200份SHW以来，四川省小麦育种家已经培育出川麦38、川麦42、川麦43和川麦47等4个高产高抗SDL，并已经通过审定和大规模推广种植[21]。其中，川麦42是四川省连续两年平均产量最高(> $6 \text{ t} \cdot \text{hm}^{-2}$)的品种。川麦42是大粒品种，抗由条锈菌引起的条锈病。这些四川省SDL已经在小麦育种中广泛利用。例如，川麦42和川麦43已经被用来培育和审定了一系列二代合SDL，其中包括川麦51、53、56、58、61、

表1 用于育种的合成小麦及其衍生品种

| Year | Variety name | Country | Pedigree |
|------|----------------------|--------------|--|
| 2017 | Shumai 830 | China | SHW-L1/Chuannong 16//Pm99915-1/3/Chuannong 24 |
| 2017 | Shumai 580 | China | SHW-L1/Chuanyu 17//Chuanyu 18/3/Chuanmai 107 |
| 2017 | Talaei | Iran | Pastor//Site/MO/3/Chen/ <i>Ae. squarrosa</i> (TAUS)/BCN/4/WBLL1 |
| 2017 | Tirgan | Iran | Pfau/Milan/5/Chen/ <i>Ae. squarrosa</i> (TAUS)/BCN/3/VEE#7/BOW/4/Pastor |
| 2016 | Wane (ETBW 6130) | Ethiopia | Sokoll /Excalibur |
| 2016 | HPBW 01 ^a | India | <i>T. dicoccon</i> C19309/ <i>Ae. squarrosa</i> (409)//Mutus/3/2*Mutus |
| 2016 | PBW 677 | India | Pfau/Milan/5/Chen/ <i>Ae. squarrosa</i> /BCN/3/VEE#7/BOW/4/Pastor |
| 2016 | WB2 ^a | India | <i>T. dicoccon</i> C19309/ <i>Ae. squarrosa</i> (409)//Mutus/3/2*Mutus |
| 2016 | Kenya Falcon | Kenya | KSW/5/2*Altar 84/ <i>Ae. squarrosa</i> (221)//3*BORL95/3/URES/JUN/Kauz/4/WBLL1 |
| 2016 | Kenya Hornbill | Kenya | Pastor//HXL7573/2*BAU/3/ Sokoll /WBLL1 |
| 2016 | Kenya Pelican | Kenya | KSW/5/2*Altar 84/ <i>Ae. squarrosa</i> (221)//3*BORL95/3/URES/JUN/Kauz/4/WBLL1 |
| 2016 | Kenya Songbird | Kenya | KSW/5/2*Altar 84/ <i>Ae. squarrosa</i> (221)//3*BORL95/3/URES/JUN/Kauz/4/WBLL1 |
| 2016 | Kenya Weaverbird | Kenya | Prinia/3/Altar 84/ <i>Ae. squarrosa</i> /2*Opata/4/Chen/ <i>Ae. squarrosa</i> (TAUS)/BCN/3/BAV92 |
| 2016 | Borlaug 2016 | Pakistan | Sokoll /3/Pastor//HXL7573/2*BAU |
| 2016 | Ihsan 16 | Pakistan | Pastor/3/Altar 84/ <i>Ae. squarrosa</i> //Opata |
| 2016 | Sindhu 16 | Pakistan | Flake*2/Bisu/3/Chen/ <i>Ae. squarrosa</i> (TASU) |
| 2015 | WH 1142 | India | Chen/ <i>Ae. squarrosa</i> (TAUS)//FCT/3/2*Weaver |
| 2015 | Bacorehuis F2015 | Mexico | ROLF07*2/5/REH/HARE//2*BCN/3/Croc_1/ <i>Ae. squarrosa</i> (213)//PGO/4/Huites |
| 2015 | Davlatle | Turkmenistan | 135U 6.1/5/CNDO/R143//ENTE/MEX175/3/ <i>Ae. squarrosa</i> /4/2*OCI |
| 2014 | Yakamoz | Turkey | BL 1496/Milan/3/CROC_1/ <i>Ae. squarrosa</i> (205)//Kauz |
| 2014 | Sarvar | Tajikistan | Chen/ <i>Ae. squarrosa</i> (TAUS)/BCN/3/BAV92 |
| 2014 | Bouhouth 10 | Syria | Chen/ <i>Ae. squarrosa</i> (TAUS)/BCN/3/2*Kauz |
| 2014 | WH 1142 | India | Chen/ <i>Ae. squarrosa</i> (TAUS)/FCT/3/2*Weaver |
| 2014 | Zinc Shakti | India | Croc_1/ <i>Ae. squarrosa</i> (210)//Inqalab 91*2/Kukuna/3/PBW 343*2/Kukuna |
| 2013 | Murodi | Tajikistan | Chen/ <i>Ae. squarrosa</i> //Weaver/3/Seri |
| 2013 | Zarnisor | Tajikistan | Croc_1/ <i>Ae. squarrosa</i> (205)//BORL95/3/2*Milan |
| 2013 | Altinbasak | Turkey | Chen/ <i>Ae. squarrosa</i> (TAUS)/BCN/3/2*Kauz |
| 2013 | Chuanmai 64 | China | Chuanmai 42 /Chuannong 16 |
| 2013 | Mianmai-1618 | China | 1275-1/NEI-2938// Chuanmai 43 |
| 2013 | Shumai 969 | China | SHW-L1/SW-8188//Chuanyu 18/3/ Chuanmai 42 |
| 2013 | Pakistan-13 | Pakistan | MEX94.27.1.20/3/Sokoll//Attila/3*BCN |
| 2013 | Nejmah-14 | Ethiopia | Skauz/BAV92/3/Croc_1/ <i>Ae. squarrosa</i> (224)//Opata |
| 2012 | Hidase | Ethiopia | Yanac/3/PRL/SARA//TSI/VEE#5/4/Croc_1/ <i>Ae. squarrosa</i> (224)//Opata |
| 2012 | Conquista-NL-F2012 | Mexico | Elvira/5/CNDO/R143//ENTE/MEX175/3/ <i>Ae. squarrosa</i> /4/2*OCI |
| 2012 | Maravilla-NL-F2012 | Mexico | <i>T. dicoccon</i> PI94625/ <i>Ae. squarrosa</i> (372)//3*Pastor |
| 2012 | Benazir | Pakistan | Chen/ <i>Ae. squarrosa</i> (TAUS)/BCN/3/VEE#7/BOW/4/Pastor |
| 2012 | Nifa-Lalma | Pakistan | Pastor/3/Altar 84/ <i>Ae. squarrosa</i> (TAUS)//Opata (Sokoll) |
| 2012 | Chuanmai 104 | China | Chuanmai 42 /Chuannong 16 |
| 2012 | Mianmai 51 | China | 1275-1/ Chuanmai 43 |
| 2012 | Mianmai 228 | China | 1275-1/NEI-2938// Chuanmai 43 |
| 2012 | Chuanmai 61 | China | Zheng-9023/Jian 3//Jian 3/3/ Chuanmai 43 |
| 2011 | HD 3043 | India | PJN/BOW//Opata*2//3/Croc_1/ <i>Ae. squarrosa</i> (224)//Opata |
| 2010 | Chuanmai 58 | China | Chuanmai 42 /03 Jian 3/ Chuanmai 42 |
| 2010 | Mianmai-367 | China | 1275-1/ Chuanmai 43 |
| 2010 | Kharoba | Morocco | Altar 84/ <i>Ae. squarrosa</i> (221)//Pastor/3/K-134-6/Veery//Bobwhite/Pavon/4/Tilila |
| 2010 | KT 2009 | Pakistan | Altar 84/ <i>Ae. squarrosa</i> (219)//Seri |
| 2010 | Genesis 2354 | Uruguay | — |
| 2010 | Genesis 2359 | Uruguay | — |

| Year | Variety name | Country | Pedigree |
|------|---------------|-------------|--|
| 2009 | Chuanmai 56 | China | SW-3243/ Chuanmai 42 |
| 2009 | Chuanmai 53 | China | Chuanmai 43 /Miannong 4//Y-314 |
| 2009 | KRL 213 | India | CNDO/R143/ENTE/MEXI-1-1/3/ <i>Ae. squarrosa</i> (TAUS)/4/Weaver/5/2*Kauz |
| 2009 | Tepahui F2009 | Mexico | BETTU/3/Chen/TR.TA//2*Opata |
| 2008 | CBW 38 | India | CNDO/R143/ENTE/MEXI-1-1/3/ <i>Ae. squarrosa</i> (TAUS)/4/Weaver/5/2*Kauz |
| 2008 | MP 1203 | India | FASN/2*TEPOKA/3/Chen/ <i>Ae. squarrosa</i> /TA |
| 2008 | Drokhshan-08 | Afghanistan | CDNO/R143//ENTE/MEXI-2/3/ <i>Ae. squarrosa</i> (TAUS)/4/Weaver/5/2*Kauz |
| 2008 | Chuanmai 51 | China | 174/183// Chuanmai 42 |
| 2006 | SRM-NOGAL | Argentina | — |
| 2005 | Chuanmai 47 | China | SYN-CD786 /Mianyang 26//Mianyang 26 |
| 2004 | Chuanmai 43 | China | SYN-CD769 /SW89-3243//Chuan 6415 |
| 2003 | Chuanmai 38 | China | SYN-CD769 /SW89-3243//Chuan 6415 |
| 2003 | Chuanmai 42 | China | SYN-CD769 /SW89-3243//Chuan 6415 |
| 2003 | Carmona | Spain | — |

Synthetic wheat or their parental combinations are underlined; synthetic wheat derivatives are bolded and underlined.

/: cross with; //: second cross; /3/: third cross; /4/: fourth cross; /5/: fifth cross; *: times.

^aThe primary synthetics were derived from *T. dicoccum* instead of *T. durum*.

64、104、绵麦51、228、367、1618和蜀麦969等[21,22] (表1)。蜀麦969还含有另一个由中国四倍体圆锥小麦 (*T. turgidum* ssp. *turgidum*) 品系AS2255与一个伊朗节节麦品系AS60杂交产生的合成小麦SHW-L1。这个品种的完整系谱是SHW-L1/川麦32//川育16/3/川麦42。在四川培育的另一个SHW-L1 SDL蜀麦580已经通过云南省的预审定,表明这些品种具有较为广泛的适应性。尽管SHW在小麦品种选育方面取得一些成功,但已经利用的SHW总数仍然十分有限,特别是在我国其他小麦主产区(如山东省和河南省等小麦主栽省)。因此,SHW的利用和研究还应大大加强。

3. SHW 是普通小麦遗传改良的优异资源

3.1. 生物胁迫抗性

SHW为寻找多种抗病性提供了一个机会。SHW已经报道具有抗叶锈病、秆锈病和条锈病的新基因,包括抗叶锈病(病原菌为*P. recondite* Erikss.) 基因*Lr32*[23]、抗秆锈病(病原菌为*P. graminis* f. sp. *tritici*) 基因*Sr33*和*Sr45* [24,25]及抗条锈病基因*Yr28* [26]。许多SHW还能抗其他严重病害,包括抗叶斑病(*Septoria tritici*) 基因*Stb5*和*Stb17* [27,28]、抗黄斑叶枯病(病原菌为*Pyrenophora tritici-repentis*) 基因*Tsr3*[29,30]以及抗白粉病(*Blumeria graminis* f. sp. *tritici*) 基因*Pm2*和*Pm18* [31]。此外,还发现了新的抗虫基因,如抗麦二叉蚜基因*GB3*和*GB7* [32,33]、抗麦双尾蚜(*Diuraphis noxia*

Kurdjumov) 基因*DN3* [34]、抗小麦卷叶螨(*Aceria tosichella* Keifer) 基因*Cmc1* [35]和抗黑森麦秆蝇[*Mayetiola destructor* (Say)]基因*H13*和*H26* [36,37]等。

节节麦是多种抗病基因的重要来源,CIMMYT SHW的关联分析工作报道了很多抗病基因位点[38,39]。例如,Kazi等[40]发现37个从CIMMYT Elite-1材料中选择到的大粒合成小麦材料均抗腥黑穗病(病原菌为*Tilletia indica* Mitra),其中62%还兼抗小麦条锈菌流行小种。这些抗性为在这两种生物胁迫为主要限制因素地区提高小麦的产量潜力提供了重要的保障。又如,*YrAS2388*是来源于里海地区的一个节节麦品系的广为利用的抗条锈病基因[41],定位于节节麦4DS染色体上[42,43],可能是与一个SHW品种的*Yr28*相同的基因[44]。有趣的是,许多用于培育SHW的节节麦品系都是感条锈病的。这意味着SHW中的一些抗性基因可能来自硬粒小麦。它们可能是因为被报道的几个抗条锈病和腥黑穗病基因来自合成小麦的硬粒小麦亲本,包括川麦42的关键抗条锈病基因*YrCh42* [45]。值得注意的是,四倍体小麦和节节麦均存在抗性抑制基因,合成小麦杂交后的某些性状可能受到抑制,为性状的转移制造了一定的困难,需要克服[46]。

3.2. 非生物胁迫抗性

节节麦和SHW是小麦改良中抗非生物胁迫的新遗传变异的潜在来源。研究表明,在干旱条件下,SDL与普通小麦亲本相比可使产量增加高达45%[47]。在澳大

利亚的雨养条件下,与亲本和本地对照品种相比,SDL的产量可提高8%~30%[48]。在印度、巴基斯坦、厄瓜多尔和阿根廷也实现了类似的增产幅度。这些合成品种根系发达,可以在更深的土壤中生长,这种特性在干旱环境中尤其重要。据报道,SHW还具有较高的耐盐性[49,50],而普通小麦的耐盐性则非常有限。此外,在灌浆期,合成小麦可耐高达35~40℃的高温[51]。Jafarzadeh等[52]利用33个CIMMYT SHW品系及SDL进行研究发现,在高温胁迫条件下,SHW可以提高SDL的产量,甚至比干旱或灌溉条件下表现更好。

另外,D基因组的不同基因组组合使SHW对脱落酸(ABA)响应机制产生有益变化。鉴于ABA在植物适应环境胁迫中的作用,采用ABA高度敏感的节节麦材料,有可能培育出高耐干旱的抗逆小麦品种[53]。

3.3. 抗穗发芽

穗发芽(籽粒收获前即已发芽,PHS)在东亚是一个特别重要的问题,因为该地区常常在收获期之前和(或)收获期间出现高温高湿天气,导致种子提前发芽,从而降低面粉品质,减少农民收入。节节麦种子休眠期较长,是抗穗发芽(PHSR)性状的良好资源[54,55]。合成小麦回交衍生品系(SBL)是通过一个PHSR SHW品系与一个非PHSR普通小麦品系几次回交产生的,是通过导入和聚合抗穗发芽基因的方法培育优良小麦品种的重要材料。采用这种策略,已获得PHSR的红粒节节麦材料培育的白粒抗穗发芽小麦种质[56]。

3.4. 产量和产量因素

节节麦有许多产量性状或产量因素性状可能被导入到SHW中加以利用。节节麦种质在籽粒大小和形状上表现出较大的变异,而这些性状是现代小麦育种的主要目标之一。为了分析控制这些性状的数量遗传位点(QTL),Okamoto等[57]利用SHW品系配制了4个F₂作图群体,并进一步测定了杂种后代的6个与籽粒大小和形状相关的参数。他们共定位出18个QTL,分布于小麦7条染色体中的5条染色体上。这项工作表明,至少有部分来自节节麦的QTL在SHW中起作用,因此可用于提高普通小麦产量。

虽然SHW的产量潜力似乎比普通小麦要低,但生物量较高,可以将其转化为更高的籽粒产量。这种生物量也可以增加收获指数和粒重[58-60]。例如,大粒、多粒和多分蘖等性状可以被转移到SDL中加以利用[61]。

此外,产量配合力高的合成小麦,其穗数或穗粒数的配合力也较高。而从合成小麦群体中选择穗粒数增加的材料则可以用于提高普通小麦的产量。有研究表明,SDL比普通小麦亲本材料的产量高11%[62]。在一个SHW冬小麦栽培品种(Karl 92)杂交组合中,BC₂衍生群体的产量比Karl 92高30%以上[63]。SDL品种川麦42比对照品种川麦107高22.7%[64]。遗传标记分析表明,SHW亲本的4D染色体对川麦42的增产具有重要作用[65,66]。CIMMYT的第一批SDL出现在20世纪90年代后期的国际育种圃(即供国际发放的优异小麦品系系列),尽管在不同的育种圃和年度间的数量有所不同,但SDL在2010年半干旱条件产量试验(SAWYT)中增产的品种比例达到52%,5年(2010—2015年)平均比例为35%。这些资料表明,SDL在世界范围内都是具有竞争力的资源,具有独特而广泛的适应性和产量改良潜力[67]。

4. SHW 生长势分子机制的认识

六倍体小麦具有比其祖先种更好的品质和适应性。新合成的异源六倍体小麦是研究其祖先种如何通过遗传改良成为现代品种的分子基础的良好模型[68]。新合成SHW粒长通常与圆锥小麦相似。其株高、株型、面粉特性(如胚乳淀粉构成)、生物胁迫抗性(如抗白粉病)以及开花等习性也与其四倍体母本相似。例如,SHW常常表现为春性[68]。SHW的幼苗、穗及籽粒的大小等方面与亲本相比也表现出相当的优势。鉴于SHW的遗传稳定性及其固定的杂合性,它已成为研究多倍体植物生长优势分子机制的理想材料。

4.1. 合成小麦的基因组变化

由于异源四倍体和异源六倍体小麦均可在实验室中合成,因此SHW可用于追踪多倍化引起的基因组遗传、功能和表达遗传变化的研究。异源六倍体可以通过种间杂交后的自发染色体加倍合成[69]。为了成功合成异源四倍体小麦,秋水仙碱处理是染色体加倍的必需条件。早期研究证明,小麦中的异源四倍体和异源六倍体等多倍化事件的发生与基因组快速和广泛的变异有关,如DNA重排[70]。最近人们发现大多数结构变化可能发生在异源四倍化过程中[69,71,72]。与其亲本相比,SHW品系的基因组结构和某些片段的拷贝数发生了变化[73]。尽管如此,具有整倍染色体的SHW品系

在遗传上是稳定的，适合于研究其生长优势的分子机制[69,72,74]。

4.2. SHW 中的基因表达变化

微阵列和RNA-Seq等新技术已应用于SHW、现代品种及其直接亲本的比较研究[75–81]。将SHW中的基因表达水平与中亲值（即两亲本的基因表达水平的平均值，MPV）进行了比较，后者是根据两个亲本的基因表达水平的平均值得到的[82]。六倍体小麦中普遍存在的是基因的加性而不是非加性表达[77,78]。此类研究需要在不同物种间进行基因表达差异的比较。在这方面，Li等[68]采用“表达水平优势”的概念研究异源多倍化过程中的基因表达模式[83]。根据这一概念，SHW中与四倍体亲本表达水平相似的基因富集发育相关基因，而与节节麦表达水平相似的基因则富集适应性调节。这种现象表明，SHW中来自于双亲的基因在一定程度上发生功能分化[68]。

4.3. SHW 中小 RNA 表达水平的动态变化

小RNA是21~24个核苷酸的非编码RNA，通过转录后机制和表观遗传修饰调控基因表达[84,85]。小RNA分为microRNA (miRNA) 和小干扰RNA (siRNA)。miRNA通过直接切割其转录本或翻译抑制来调节靶基因表达。拟南芥等模式植物的研究为小麦等作物提供了良好的经验。在拟南芥中，miRNA靶基因的非加性表达可能是由于miRNA表达水平的变化引起的。miRNA表达水平的变化可能是拟南芥生长优势和适应性的重要因素[86]。另一方面，siRNA可介导DNA甲基化，动态调节在其近旁具有转座元件 (TE) 基因的表达，因此可以抑制在同一种植物中不同基因组的融合所引起的冲击。siRNA可能具有亲本效应，并优先抑制来自一个亲本的同源基因[82,87,88]，导致基因在异源四倍体子代中的偏好性表达。普通小麦及其祖先种以及SHW富含重复序列 (> 80%)，这些重复序列主要来源于各种TE。当多倍化发生时，与TE相应的siRNA数目显著减少，这表明TE在这一过程中具有重要作用[89]。Li等[68]还发现有很大比例的miRNA在多倍体化过程中是非加性表达的。miRNA表达水平的改变可能是由靶基因的非加性表达引起的，而靶基因对SHW的生长势非常重要。Li等[68]还发现在SHW中，D基因组的siRNA密度增加。这些增加的siRNA可能通过介导甲基化来抑制D基因组部分同源基因的表达，并导致SHW中AB基因组部分同

源基因的偏好性表达。这些信息以及在早期异源多倍化事件中建立的那些知识，为普通小麦的成功出现奠定了基础。

5. 展望

异源多倍化包括杂交和加倍。基因组的互作会导致异源多倍体植物在遗传、表观遗传、生化和调控网络水平上的复杂变化，并产生各种生长优势。对遗传框架变化的研究可以揭示这一过程中起作用的生化机制。随着各种技术的不断涌现，多倍化研究应当综合采用全基因组关联分析 (GWAS)、转录组学、表观基因组学、蛋白质组学和代谢组学等手段，为不同发育阶段SHW表现出的优势表型的分子机制提供新的依据，包括更长的麦穗、更大的籽粒和更高的生物量等和栽培小麦农艺性状紧密相关的问题，与这种方法一样，应该对调控网络进行单独剖析，以便评估它们对个体优势性状的贡献，其中的关键基因就可以通过使用诸如转基因工具等附加方法予以验证[90]。

合成小麦是一种有价值的遗传资源，利用它可以把存在于四倍体或二倍体供体（包括野生种）中的重要农艺性状基因转移所需至普通小麦，加以改良。基因组学和功能组学研究可以帮助我们更好地了解其生长优势的分子基础。而各种小麦基因组的完成将从基因组角度大大促进这些研究的进程。几年前，小麦A和D供体种的基因组序列[91,92]被公布，而六倍体小麦的基因组测序也即将完成[93]。2017年，野生二粒小麦 (*T. turgidum* ssp. *dicoccoides*) 的基因组完成，使人们对普通小麦的四倍体供体种的基因含量、基因组结构和遗传多样性有了进一步的了解[94]。金标准的六倍体小麦基因组[95]以及进一步改善的二倍体祖先基因组也将很快完成[96]。这些基因组信息的获得，将进一步加速小麦功能基因组学研究。

现在，世界对小麦需求随着世界人口的增长日益增加，用如绿色革命一样的新技术、新方法、新材料来大幅提升小麦的产量已迫在眉睫。小麦生产却处在一个平台期。更糟糕的是，全球变暖使干旱和高温更加频繁地发生。气候变化也导致新的病原菌菌株（特别是锈菌）和病害更为频繁地出现，为小麦生产带来了更多的问题。2010年，一个能克服Yr27抗病基因的条锈菌小种危害了约三分之一的埃塞俄比亚小麦的生长。2013年，埃塞俄比亚再次受到秆锈病的重创，又导致小麦生产遭受

重大损失[97]。令人吃惊的是侵染水稻的稻瘟病菌 (*Magnaporthe oryzae*) 引起[开始侵染小麦, 在孟加拉出现所谓的麦瘟病, 造成2016年该国16%的小麦绝收[98]。这些严峻形势迫切需要一种高产稳产、抗性强的新型“超级小麦”。合成小麦具有来自野生种的广泛遗传背景, 有望在即将到来的且更为严峻的环境挑战中发挥更大的作用。

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Compliance with ethics guidelines

Aili Li, Dengcai Liu, Wuyun Yang, Masahiro Kishii, and Long Mao declare that they have no conflict of interest or financial conflicts to disclose.

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