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CIMMYT 新引进合成小麦株高性状全基因组关联分析

张红杰[1,2]，邓中印[2]，陶　姝[2]，孙国梁[2]，贾美玲[2]，王振玉[2]，廖如意[2]，
郑兴卫[1,3]，李爱丽[2]，毛　龙[2]，郑　军[1,3]，耿帅锋[2]
（[1] 山西大学生物工程学院，太原 030006；[2] 中国农业科学院作物科学研究所，北京 100081；[3] 山西农业大学小麦研究所，临汾 041000）

摘要：株高是影响小麦产量的重要农艺性状。本研究对从国际玉米小麦改良中心（CIMMYT）新引进的 152 份合成小麦在 3 个环境下的株高进行了观察和统计，并利用 55 K 单核苷酸多态性（SNP，single nucleotide polymorphism）芯片进行全基因组关联分析（GWAS，genome-wide association study），以挖掘与株高相关的新的遗传位点。结果表明：合成小麦株高呈正态分布，变异丰富。不同环境下的平均株高为 97.9 cm，显著高于栽培小麦（70.5 cm），但低于黄淮麦区农家小麦（114.8 cm）。方差分析显示 3 个环境下，株高在基因型之间都表现出极显著的差异。3 个环境下联合方差分析发现株高表型在基因型、环境以及基因型环境互作方面表现出极显著的差异。对获得的 55K SNP 标记经最大杂合率、最小等位基因频率及最大等位基因频率过滤，在合成小麦群体中发现 37916 个有效 SNP，其中 A、B 和 D 3 个亚基因组上各有 14404 个、14566 个和 8946 个。群体结构分析结果表明，152 份合成小麦可分为 3 个类群。利用混合线性模型（MLM，mixed liner model）对不同环境下平均株高和最佳线性无偏预测值（BLUP，best linear unbiased prediction）进行 GWAS 分析，筛选到 24 个显著标记（$P \leqslant 0.0001$），分别位于 1A、3B、4A、4B、4D、5A、5B、6A、6D 和 7B 染色体上，单个标记可解释 12.33%~20.10% 的表型变异。BLUP 值分析共获得 10 个显著标记，对标记物理位置 3 Mb 左右距离内的 669 个基因进行转录组数据筛查，得到 131 个在茎或叶中高表达（TPM ⩾ 5）。通过与水稻同源基因的比较，明确其中 5 个基因可能与小麦株高发育有关。鉴于这些位点与以往已定位的株高数量性状位点并不重叠，本研究的工作可为小麦株高改良提供新的种质和分子标记。

关键词：合成小麦；株高；55K SNP 芯片；全基因组关联分析

Genome-wide Association Study（GWAS）for Plant Height Traits in Synthetic Wheat Lines Introduced in CIMMYT

ZHANG Hong-jie[1,2], DENG Zhong-yin[2], TAO Shu[2], SUN Guo-liang[2], JIA Mei-ling[2], WANG Zhen-yu[2], LIAO Ru-yi[2], ZHENG Xing-wei[1,3], LI Ai-li[2], MAO Long[2], ZHENG Jun[1,3], GENG Shuai-feng[2]
（[1]*College of Bioengineering*, *Shanxi University*, *Taiyuan 030006*; [2]*Institute of Crop Sciences*, *Chinese Academy of Agricultural Sciences*, *Beijing 100081*; [3] *Shanxi Agricultural University*, *Institute of Wheat Research*, *Lifen 041000*）

Abstract: Plant height is an important agronomic trait that affects wheat yield. To identify new genetic loci that are significantly associated to plant height, the genome-wide association study（GWAS）was conducted using 152 newly introduced synthetic wheat lines from International Maize and Wheat Improvement Center（CIMMYT）. This population was subjected for measuring plant height at three environments and genotyping using 55 K single nucleotide polymorphism（SNP）chip. The plant height was observed with a normal distribution in synthetic genotypes, with the mean value of 97.9 cm, which was higher than that of modern cultivars（70.5 cm）but lower than that of local landraces（114.8 cm）in Huanghuai zone. Analysis of variance showed that there

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第一作者研究方向为作物分子遗传，E-mail：2553379140@qq.com；邓中印为共同第一作者
通信作者：郑军，研究方向为小麦遗传育种，E-mail：sxnkyzj@126.com
耿帅锋，研究方向为小麦分子生物学，E-mail：gengshuaifeng@caas.cn
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were significant differences in plant height among genotypes in three environments. Joint variance analysis in three environments found that the phenotype of plant height showed significant differences in genotype, environment and genotype-environment interaction. 37916 markers were qualified using filtering parameters to be polymorphic including 14404, 14566 and 8946 SNPs on the A, B and D sub-genome respectively. Population structure analysis of 152 synthetic wheat lines suggested three groups. GWAS using the mixed liner model (MLM) on the best linear unbiased prediction values (BLUP) revealed 24 significant SNPs ($P \leqslant 0.0001$), which were found on chromosomes 1A, 3B, 4A, 4B, 4D, 5A, 5B, 6A, 6D and 7B, each explaining12.33%-20.10% of the phenotypic variation. A total of 10 significant markers were obtained by BLUP value analysis, and the transcriptome data of 669 genes within 3 Mb of the physical location of the markers were screened, among which 131 genes were found highly expressed in wheat stems or leaves (TPM ⩾ 5) in public transcriptome data. According to the functional annotation of wheat gene models and rice gene homologs, we speculated that five genes were possibly involved in plant height development. Since these significant loci did not overlap with previously reported QTLs, they may represent new genetic loci in controlling plant height. Collectively, these study provided new germplasm and selection markers in order to improve plant height in wheat.

Key words: synthetic wheat; plant height; 55K SNP chip; Genome-wide association study

小麦是世界上主要的粮食作物之一，是全世界45亿以上人口的主食[1]。随着我国耕地面积日趋减少、人口增长，粮食安全问题日益凸显[2]，提高小麦产量对保障我国粮食安全和人民福祉具有重要意义。通过远缘杂交，发掘、创新和利用关键种质资源，采用与传统常规育种技术密切结合新技术，谋求产量突破已成为小麦育种领域新的发展趋势。然而，现有小麦的遗传多样性基础限制了小麦的产量育种，亟待解决遗传基础狭窄的严重问题。近年来，通过重塑小麦进化过程，利用栽培四倍体小麦与节节麦杂交、加倍，创制了大量的合成小麦[3-5]。新合成的六倍体小麦结合了四倍体小麦和节节麦的丰富遗传变异，是小麦遗传改良的宝贵基因资源。

株高是影响小麦产量的重要因素之一。适宜的株高能减少倒伏发生，增加每穗粒数，提高地上生物量，实现增产[6-7]。小麦株高属于多基因控制的复杂数量性状，受加性、上位性及环境互作效应共同调控，具有较高的遗传力。目前已有很多关于小麦株高 QTL 的研究，分别定位于 2B、3A、4A、4B、4D、5A、5B、6B、7A、7B 染色体上[8-9]，并已鉴定出25 个可降低小麦株高的基因（*Rht*）[10-11]，这些基因和遗传位点的应用使六倍体小麦的株高由原来的100 cm 以上降到 70.5 cm[12]。与我国黄淮麦区农家种平均株高 114.8 cm 相比[13]，矮秆、半矮秆基因的引入降低了现代品种的株高。但目前只有 *Rht-D1b*、*Rht-B1b*、*Rht8* 等少数基因应用于生产。其中，*Rht8* 在我国品种中分布频率达 56%，高于 *Rht-D1b*（44%）和 *Rht-B1b*（29%），该遗传位点在世界其他小麦生产区分布也较广[14]。具有 *Rht-D1c* 与太谷核不育基因 *Ms2* 紧密连锁的矮败小麦已成为育种的重要材料。*Rht12* 降秆效应较强，但表现为晚熟、粒小[15]。所以，目前生产上应用的矮秆基因仍然较少，不能满足当前小麦遗传改良的需要。进一步发掘、评价、利用新的矮秆和半矮秆基因具有重要的意义。

随着基因组学、生物信息学等组学技术的发展，芯片技术已成为小麦重要农艺性状 QTL/ 基因定位和克隆的有效方法，如小麦的 660 K 芯片、90 K 芯片、55 K 芯片[16]等。其中 55 K 芯片是在 660 K 芯片基础上精心挑选的一套核心 SNP，21 条小麦染色体上均匀分布，标记平均遗传距离约为 0.1 cM，平均物理距离小于 300 kb[17]，具有较高的应用价值。本研究以国际玉米小麦改良中心（CIMMYT）新引进的 152 份合成小麦为材料，采用小麦 55 K SNP 芯片对株高性状进行全基因组关联分析，挖掘株高显著相关标记。合成小麦的利用增加了供体物种的遗传多样性，为普通小麦株高改良提供新的基因资源。此外，所获得 SNP 及可能的候选基因可作为普通小麦育种亲本材料选用的分子标记。

1　材料与方法

1.1　试验材料

供试材料为 152 份从国际玉米小麦改良中心新引进的合成小麦，由 Masahiro Kishii 博士提供。

1.2 试验方法

1.2.1 田间试验设计及性状调查 供试材料于2018年在四川成都(104.07°E,30.67°N)、2019年在北京海淀(116.40°E,39.90°N)和河南新乡(113.52°E,35.18°N)3个主要小麦生态区随机分块种植。所有田间试验均随机区组设计,4行区(行长2 m,行距20 cm,播种25粒)。四川成都2018年11月2日播种;北京海淀2019年9月28日播种,且通过盖膜的方法使其越冬,河南新乡10月16日播种,待第2年小麦成熟后,从每个株系中选取5株长势一致的小麦,对株高进行测量。

1.2.2 表型数据分析 用Excel 2016进行株高表型数据统计。利用IBM SPSS Statistics 19数据分析软件,计算表型值的均值、中值、方差、偏度、峰度、变异系数及相关性分析,检验表型值的正态分布。SAS 4.0软件对不同环境下株高最佳线性无偏预测值(BLUP)进行计算分析。通过QTL Icimapping软件分析株高单因素多环境下的联合方差。

1.2.3 基因组DNA的提取 苗期剪取约0.2 g小麦叶片,放入加有钢珠的2.0 mL离心管中,迅速置于液氮中,然后利用快速研磨仪进行组织破碎,参照CTAB法提取小麦叶片基因组DNA[18],加200 μL ddH_2O溶解。利用NanoDrop分光光度计对DNA的浓度进行测定,并通过琼脂糖凝胶电泳检测DNA的质量。

1.2.4 基因型检测 采用55 K SNP芯片,对152份合成小麦材料进行基因分型,由中玉金标记生物有限公司完成。在基因分型之前,先计算样品的Dish QC(DQC)和Call Rate(CR)值,参考基因组为IWGSC_RefSeq_v1.0(https://wheat-urgi.versailles.inra.fr/Seq-Repository/Assemblies)。利用DQC ≥ 0.82且CR ≥ 95对样品SNP进行质控,用Affymetrix(Thermo Fisher)Axiom Analysis Suite软件的apt-genotype-axiom、ps-metrics和ps-classification模块进行基因分型分析,将otv标记进行otv-caller分析,得到样品原始数字基因型;利用apt-format-result模块获得原始基因型数据,进一步获得可使用的基因型数据。

1.2.5 群体结构及全基因组关联分析 应用Structure V2.3.2软件对群体进行结构分析。利用Tassel 5.0过滤最小等位基因频率(≤ 0.05)、最大等位基因频率(≥ 0.95)、最大杂合率(≤ 0.05)数据,获得高质量SNP用于全基因组关联分析(GWAS)分析。关联分析使用Tassel 5.0软件的混合线性模型(MLM),并以主成分分析(PCA)和亲缘关系(K)作为协变量,将$P \leq 0.0001$的标记列为显著的SNP标记。

1.2.6 候选基因的确定 对株高BLUP值关联分析筛选到的10个显著标记位点,利用EnsemblePlants网站(https://plants.ensembl.org/)筛选位点物理位置3 Mb左右距离内基因。并根据已有转录组数据(http://wheatdb.agrinome.org/)统计基因在茎或叶中的表达量,将每千个碱基的转录每百万映射读取的Transcripts数大于且等于5(TPM ≥ 5)的定义为高表达的基因。对高表达基因进行水稻同源基因功能查询(http://www.ricedata.cn/),推测与株高性状相关的为候选基因。

2 结果与分析

2.1 合成小麦株高性状变异分析

对合成小麦株高分析发现,种植于北京海淀的合成小麦平均株高最高,为105.31 cm,其变幅为50.20~134.53 cm;而河南新乡合成小麦平均株高为97.22 cm,其变幅为62.00~136.00 cm;四川成都合成小麦的株高均值最低,为91.39 cm,比在北京海淀种植的平均株高矮近14 cm,其变幅为49.50~132.20 cm,且株高在不同环境下的变异系数均大于10%。相关性分析表明不同环境下株高呈极显著正相关,其中新乡和成都之间株高的相关性最高,达0.642(表1)。对合成小麦不同环境下的株高进行正态分布检验,发现其符合正态分布(图1)。以上结果说明,合成小麦株高在材料间存在较大的遗传变异,适于进行全基因组关联分析。

表1 3个环境株高基本统计描述

Table 1 Basic statistical description of plant height in three environments

环境 Enviroment	范围(cm) Range	均值(cm) Average	中值(cm) Median	方差 Variance	偏度 Skewness	峰度 Kurtosis	变异系数(%) *CV*	新乡 Xinxiang	成都 Chengdu	海淀 Haidian
新乡 Xinxiang	62.00~136.00	97.22	94.70	222.52	0.16	−0.42	15.34	1		
成都 Chengdu	49.50~132.20	91.39	88.13	282.95	0.31	−0.28	18.41	0.642**	1	
海淀 Haidian	50.20~134.53	105.31	106.13	230.55	−0.41	0.13	14.42	0.456**	0.497**	1

** 表示0.01差异显著水平

** indicated a significant level of 0.01 difference

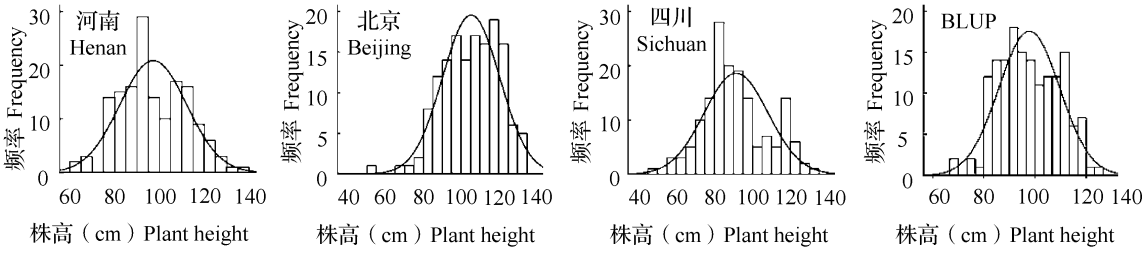


图 1　人工合成小麦 3 个环境株高及 BLUP 值频率分布

Fig.1　Frequency distribution of three environments plant height and BLUP value in the CIMMYT synthetic wheat population

2.2　合成小麦株高方差分析

为检测基因型、环境、基因型环境互作对合成小麦株高的影响，对不同环境下株高进行方差分析。从表 2 可以看出，3 个环境下株高在基因型之间都表现出极显著的差异。3 个环境下联合方差分析发现株高表型在基因型、环境以及基因型环境互作方面表现出极显著的差异，说明株高受基因型、环境、基因型与环境的互作影响较大。株高广义遗传力在河南、北京和四川分别为 0.99、0.98 和 0.98，联合遗传力为 0.87（表 2），说明株高受遗传影响较大。

表 2　合成小麦 3 个环境下株高数据方差分析

Table 2　Variance analysis of plant height of synthetic wheat in three environments

环境 Environment	来源 Source	自由度 Degrees of freedom	总方差 Total variance	平均方差 Mean variance	*F* 值 *F* value	*P* 值 *P* value
新乡	区组	4	94.36	23.59	1.70	0.15
Xinxiang	基因型	151	159134.09	1053.87	75.97	0
	广义遗传力	0.99				
海淀	区组	4	48.64	12.16	0.62	0.65
Haidian	基因型	151	173340.84	1147.95	58.36	0
	广义遗传力	0.98				
成都	区组	4	192.04	48.01	2.14	0.07
Chengdu	基因型	151	206043.28	1364.53	60.84	0
	广义遗传力	0.98				
联合	区组 / 环境	12	334.87	27.91	1.50	0.12
Unite	基因型	151	412913.81	2734.53	146.53	0
	环境	2	69991.44	34995.72	1875.20	0
	基因型环境互作	302	125640.59	416.03	22.29	0
	广义遗传力	0.87				

2.3　合成小麦基因型分析

利用 55 K SNP 芯片对 152 份合成小麦材料进行基因型分析，获得 49060 个有染色体位置的 SNP 标记。通过最小等位基因频率（≤ 0.05）、最大等位基因频率（≥ 0.95）、最大杂合率（≤ 0.05）过滤后，获得 37916 个高质量 SNP。37916 个标记绘制 SNP 标记密度图（图 2），发现 A、B 、D 3 个亚基因组分别包含 14404 个、14566 个和 8946 个标记（表 3）。B 亚基因组密度最高（0.355 Mb/ 标记），其次为 A 亚基因组（0.362 Mb/ 标记），而 D 亚基因组标记密度最低（0.441 Mb/ 标记）。密度最大的 6A 染色体包含 2394 个标记，平均为 0.258 Mb/ 标记，密度最小的 4D 染色体包含 787 个标记，平均为 0.647 Mb/ 标记（表 3）。

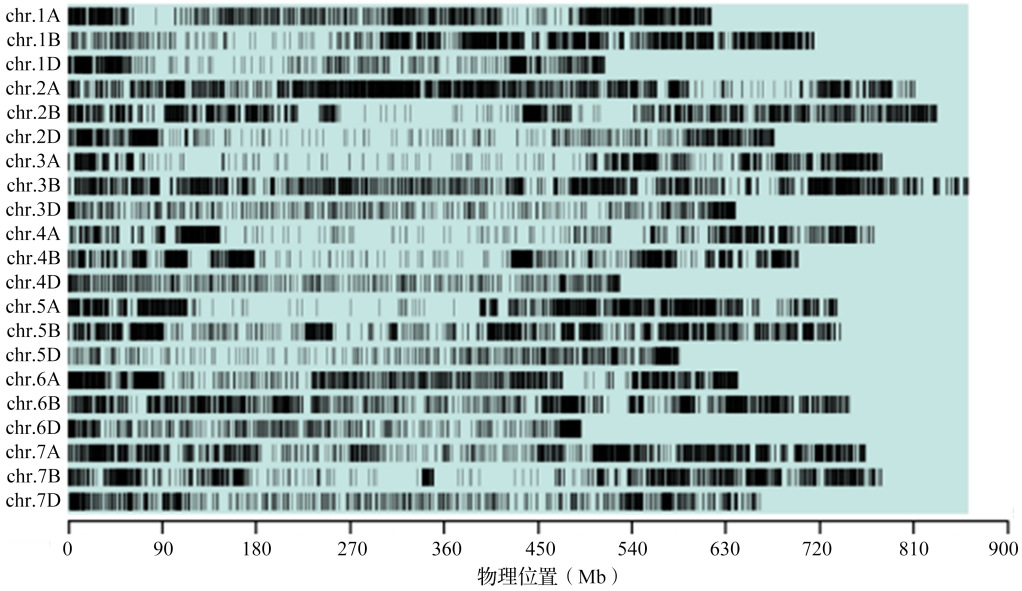


图 2 全基因组关联分析标记密度图

Fig.2 Mark density map of genome-wide association study

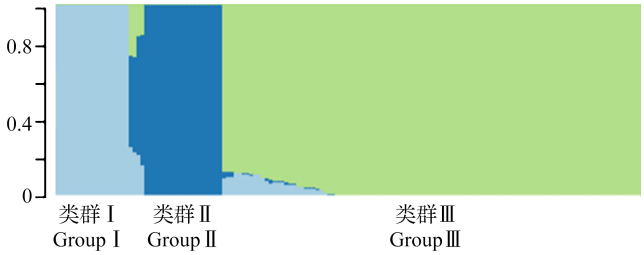
表 3 SNP 标记所在染色体及数目标记密度统计

Table 3 Chromosome and number marker density statistics of SNP markers

染色体 Chromosome	标记数目 No. of markers	长度（Mb） Length	密度（Mb/ 标记） Density（Mb/marker）	染色体 Chromosome	标记数目 No. of markers	长度（Mb） Length	密度（Mb/ 标记） Density（Mb/marker）
Chr.1A	2263	593	0.262	Chr.5A	2203	709	0.322
Chr.1B	2258	688	0.305	Chr.5B	2089	712	0.341
Chr.1D	1589	495	0.312	Chr.5D	1141	565	0.495
Chr.2A	2411	781	0.324	Chr.6A	2394	618	0.258
Chr.2B	2100	801	0.382	Chr.6B	1938	721	0.372
Chr.2D	1365	651	0.477	Chr.6D	1252	473	0.378
Chr.3A	1601	751	0.469	Chr.7A	2170	735	0.339
Chr.3B	2312	830	0.359	Chr.7B	1992	751	0.377
Chr.3D	1269	615	0.485	Chr.7D	1543	639	0.414
Chr.4A	1362	743	0.546	A 亚基因组 A subgenome	14404	5214	0.362
Chr.4B	1877	673	0.359	B 亚基因组 B subgenome	14566	5171	0.355
Chr.4D	787	509	0.647	D 亚基因组 D subgenome	8946	3945	0.441

2.4 合成小麦群体结构及全基因组关联分析

Structure 分析显示，152 份合成小麦材料可分为 3 个类群（图 3），结合合成小麦系谱分析，发现 3 个类群中四倍体小麦和节节麦的亲本组合存在差异。采用 TASSEL 5.0 中的 MLM（PCA+K）模型，以主成分分析（PCA）和亲缘关系（K=3）作为协变量，对 152 份合成小麦株高进行关联分析，在河南新乡检测到 7 个显著的 SNP 位点，四川成都检测到 12 个显著的 SNP 位点，而北京海淀未检测到显著 SNP 位点。其中 AX-110035964、AX-110433692、AX-108729778 在河南新乡和 BLUP 值中共同检测到，AX-109522023 和 AX-110982975 在四川成都和 BLUP 值中共同检测到。其中 BLUP 值检测到 10 个显著的 SNP 位点（$P \leqslant 0.0001$），关联分析曼哈顿图和分位数 - 分位数图见图 4，这些检测到的显著标记分布在 1A、3B、4A、4B、4D、5A、5B、6A、6D 和 7B 染色体上，单个位点可解释表型变异范围为 12.33%~20.10%（表 4），筛选得到的显著标记位点将为株高的改良提供分子标记。



纵坐标表示某个材料属于某个类群的概率，不同的颜色表示不同的类群

The ordinate indicates the probability that a material belongs to a group, and different colors indicate different groups

图 3　152 份人工合成小麦家系关系堆积条形图

Fig.3　Stacked bar plot of ancestry relationships of 152 synthetic wheat

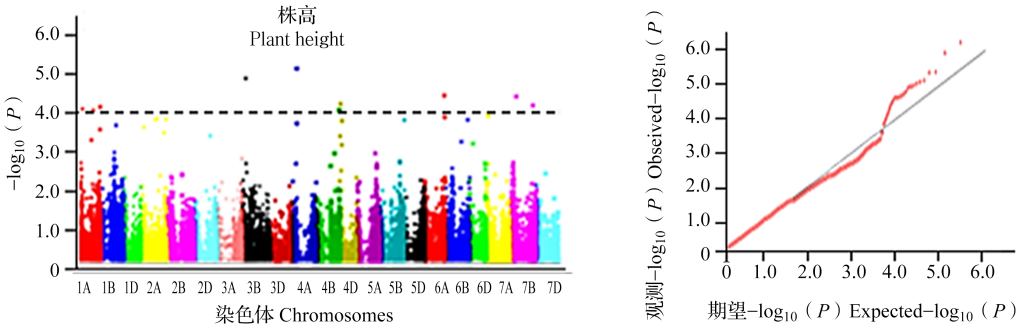


图 4　全基因组关联分析曼哈顿图（左）和分位数 - 分位数图（右）

Fig.4　Manhattan（left）and Quantile-Quantile Plot（right）of genome-wide association study

表 4　株高性状显著关联的 SNP 标记

Table 4　SNP markers significantly associated with plant height traits

标记 Marker	染色体 Chromosome	物理位置 Physical position	*P* 值 *P*-value	贡献率 R^2	地点 Location
AX-109522023	1A	579832267	7.06E-05	0.13664	四川成都 /BLUP 值
AX-108917531	1A	53504374	8.02E-05	0.19674	BLUP 值
AX-108729778	1A	367023347	8.74E-05	0.15847	河南新乡 /BLUP 值
AX-110035964	3B	11609645	1.21E-05	0.19192	河南新乡 /BLUP 值
AX-109457007	3B	7297498	9.25E-05	0.12330	四川成都
AX-110982975	4A	136973082	6.55E-06	0.18886	四川成都 /BLUP 值
AX-111657963	4A	704758691	7.90E-05	0.14258	河南新乡
AX-111637187	4B	66322769	8.58E-05	0.14868	BLUP 值
AX-110564408	4B	166350375	5.01E-05	0.15694	河南新乡
AX-110072320	4D	27567795	5.93E-05	0.14511	BLUP 值
AX-111275046	4D	70182149	1.74E-06	0.20103	河南新乡
AX-109382658	5A	450599212	6.49E-05	0.12971	四川成都
AX-108811000	5B	553487684	2.14E-05	0.14735	四川成都
AX-109978576	5B	552482112	2.87E-05	0.14005	四川成都
AX-110403012	5B	552631894	2.92E-05	0.14037	四川成都
AX-111530787	5B	553252460	3.20E-05	0.13891	四川成都
AX-108785621	5B	553510369	3.21E-05	0.13838	四川成都
AX-111215260	5B	552670644	3.22E-05	0.14021	四川成都
AX-110433692	6A	584939203	3.62E-05	0.16586	河南新乡 /BLUP 值
AX-111662632	6A	5901698	3.21E-05	0.18965	四川成都
AX-108891245	6D	472904375	2.05E-05	0.16291	河南新乡
AX-111615856	6D	24230581	3.96E-05	0.14191	四川成都
AX-110660771	7B	13636648	3.74E-05	0.14483	BLUP 值
AX-108838778	7B	627974084	6.42E-05	0.14410	BLUP 值

对BLUP值筛选到的10个显著SNP标记位点叠加效应分析，发现在合成小麦群体中具有正效应位点数目越多的株系，平均株高越低（图5）。其中含有10个正效应位点株系的平均株高约为65 cm，而只含2个位点株系的平均株高则为101.86 cm，筛选正效应位点数目将为降低株高提供帮助。

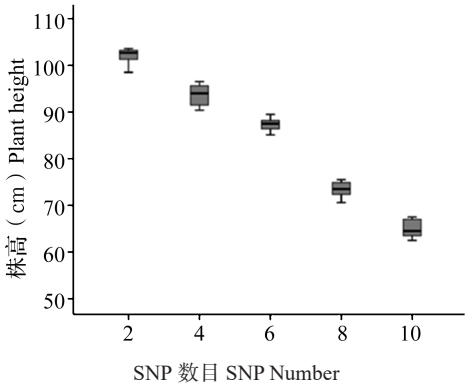


图5 SNP数目对株高的效应

Fig.5 Effect of SNP number on plant height

2.5 候选基因分析和预测

株高BLUP值关联分析筛选到的10个显著标记，对标记物理位置左右3 Mb距离内基因分析，发现这些区间内共包含有669个基因（表5）。利用转录组数据（http://wheatdb.agrinome.org/gene-expression）检索这些基因在茎或叶中的表达量（表6），发现其中131个基因表达较高（TPM ≥ 5），结合注释及水稻同源基因的功能，发现5个可能的候选基因，位于1A染色体上AX-108917531、4A染色体上AX-110982975、4B染色体上AX-111637187、4D染色体上AX-110072320和7B染色体上AX-110660771区间内，对株高表型贡献率分别达19.67%、18.89%、14.87%、14.51%和14.48%（表7）。其中AX-108917531贡献率最高，该标记物理位置左右3Mb区间内共包含36个基因，高表达的11个（图6、图7）。进一步结合水稻同源基因突变体的表型，发现编码*WRKY*类转录因子的*TraesCS1A02G070400*可能是株高的候选基因，因为其水稻正源基因*OsWRKY53*的过表达，可使水稻半矮秆化，株高降低一半[19]。

表5 BLUP值显著位点左右3 Mb区间内的候选基因

Table 5 Candidate genes within 3 Mb interval around significant locus of BLUP value

标记 Marker	区间候选基因 Candidate intervals genes				
AX-108729778	*TraesCS1A02G202800*	*TraesCS1A02G202900*	*TraesCS1A02G203000*	*TraesCS1A02G203100*	*TraesCS1A02G203200*
	TraesCS1A02G203300	*TraesCS1A02G203400*	*TraesCS1A02G203500*	*TraesCS1A02G203600*	*TraesCS1A02G203700*
	TraesCS1A02G203800	*TraesCS1A02G203900*	*TraesCS1A02G204000*	*TraesCS1A02G204100*	*TraesCS1A02G204200*
	TraesCS1A02G204300	*TraesCS1A02G204400*	*TraesCS1A02G204500*	*TraesCS1A02G204600*	*TraesCS1A02G204700*
	TraesCS1A02G204800	*TraesCS1A02G204900*	*TraesCS1A02G205000*	*TraesCS1A02G205100*	*TraesCS1A02G205200*
	TraesCS1A02G205300	*TraesCS1A02G205400*	*TraesCS1A02G205500*	*TraesCS1A02G205600*	*TraesCS1A02G205700*
	TraesCS1A02G205800	*TraesCS1A02G205900*	*TraesCS1A02G206000*	*TraesCS1A02G206100*	*TraesCS1A02G206200*
	TraesCS1A02G206300	*TraesCS1A02G206400*	*TraesCS1A02G206500*	*TraesCS1A02G206600*	*TraesCS1A02G206700*
	TraesCS1A02G206800	*TraesCS1A02G206900*	*TraesCS1A02G207000*	*TraesCS1A02G207100*	*TraesCS1A02G207200*
	TraesCS1A02G207300	*TraesCS1A02G207400*	*TraesCS1A02G207500*	*TraesCS1A02G207600*	*TraesCS1A02G207700*
	TraesCS1A02G207800	*TraesCS1A02G207900*	*TraesCS1A02G208000*	*TraesCS1A02G208100*	*TraesCS1A02G208200*
	TraesCS1A02G208300	*TraesCS1A02G208400*			
AX-108917531	*TraesCS1A02G068800*	*TraesCS1A02G068900*	*TraesCS1A02G069000*	*TraesCS1A02G069100*	*TraesCS1A02G069200*
	TraesCS1A02G069300	*TraesCS1A02G069400*	*TraesCS1A02G069500*	*TraesCS1A02G069600*	*TraesCS1A02G069700*
	TraesCS1A02G069800	*TraesCS1A02G069900*	*TraesCS1A02G070000*	*TraesCS1A02G070100*	*TraesCS1A02G070200*
	TraesCS1A02G070300	*TraesCS1A02G070400*	*TraesCS1A02G070500*	*TraesCS1A02G070600*	*TraesCS1A02G070700*
	TraesCS1A02G070800	*TraesCS1A02G070900*	*TraesCS1A02G071000*	*TraesCS1A02G071100*	*TraesCS1A02G071200*
	TraesCS1A02G071300	*TraesCS1A02G071400*	*TraesCS1A02G071500*	*TraesCS1A02G071600*	*TraesCS1A02G071700*
	TraesCS1A02G071800	*TraesCS1A02G071900*	*TraesCS1A02G072000*	*TraesCS1A02G072100*	*TraesCS1A02G072200*
	TraesCS1A02G072300				

表 5（续）

标记 Marker	区间候选基因 Candidate intervals genes				
AX-109522023	*TraesCS1A02G420400*	*TraesCS1A02G420500*	*TraesCS1A02G420600*	*TraesCS1A02G420700*	*TraesCS1A02G420800*
	TraesCS1A02G420900	*TraesCS1A02G421000*	*TraesCS1A02G421100*	*TraesCS1A02G421200*	*TraesCS1A02G421300*
	TraesCS1A02G421400	*TraesCS1A02G421500*	*TraesCS1A02G421600*	*TraesCS1A02G421700*	*TraesCS1A02G421800*
	TraesCS1A02G421900	*TraesCS1A02G422000*	*TraesCS1A02G422100*	*TraesCS1A02G422200*	*TraesCS1A02G422300*
	TraesCS1A02G422400	*TraesCS1A02G422500*	*TraesCS1A02G422600*	*TraesCS1A02G422700*	*TraesCS1A02G422800*
	TraesCS1A02G422900	*TraesCS1A02G423000*	*TraesCS1A02G423100*	*TraesCS1A02G423200*	*TraesCS1A02G423300*
	TraesCS1A02G423400	*TraesCS1A02G423500*	*TraesCS1A02G423600*	*TraesCS1A02G423700*	*TraesCS1A02G423800*
	TraesCS1A02G423900	*TraesCS1A02G424000*	*TraesCS1A02G424100*	*TraesCS1A02G424200*	*TraesCS1A02G424300*
	TraesCS1A02G424400	*TraesCS1A02G424500*	*TraesCS1A02G424600*	*TraesCS1A02G424700*	*TraesCS1A02G424800*
	TraesCS1A02G424900	*TraesCS1A02G425000*	*TraesCS1A02G425100*	*TraesCS1A02G425200*	*TraesCS1A02G425300*
	TraesCS1A02G425400	*TraesCS1A02G425500*	*TraesCS1A02G425600*	*TraesCS1A02G425700*	*TraesCS1A02G425800*
	TraesCS1A02G425900	*TraesCS1A02G426000*	*TraesCS1A02G426100*	*TraesCS1A02G426200*	*TraesCS1A02G426300*
	TraesCS1A02G426400	*TraesCS1A02G426500*	*TraesCS1A02G426600*	*TraesCS1A02G426700*	*TraesCS1A02G426800*
	TraesCS1A02G426900	*TraesCS1A02G427000*	*TraesCS1A02G427100*	*TraesCS1A02G427200*	*TraesCS1A02G427300*
	TraesCS1A02G427400	*TraesCS1A02G427500*	*TraesCS1A02G427600*	*TraesCS1A02G427700*	*TraesCS1A02G427800*
	TraesCS1A02G427900	*TraesCS1A02G428000*	*TraesCS1A02G428100*	*TraesCS1A02G428200*	*TraesCS1A02G428300*
	TraesCS1A02G428400	*TraesCS1A02G428500*	*TraesCS1A02G428600*	*TraesCS1A02G428700*	*TraesCS1A02G428800*
	TraesCS1A02G428900	*TraesCS1A02G429000*	*TraesCS1A02G429100*	*TraesCS1A02G429200*	*TraesCS1A02G429300*
	TraesCS1A02G429400	*TraesCS1A02G429500*	*TraesCS1A02G429600*	*TraesCS1A02G429700*	
AX-110035964	*TraesCS3B02G131000*	*TraesCS3B02G131100*	*TraesCS3B02G131200*	*TraesCS3B02G131300*	*TraesCS3B02G131400*
	TraesCS3B02G131500	*TraesCS3B02G131600*	*TraesCS3B02G131700*	*TraesCS3B02G131800*	*TraesCS3B02G131900*
	TraesCS3B02G132000	*TraesCS3B02G132100*	*TraesCS3B02G132200*	*TraesCS3B02G132300*	*TraesCS3B02G132400*
	TraesCS3B02G132500	*TraesCS3B02G132600*	*TraesCS3B02G132700*	*TraesCS3B02G132800*	*TraesCS3B02G132900*
	TraesCS3B02G133000	*TraesCS3B02G133100*	*TraesCS3B02G133200*	*TraesCS3B02G133300*	*TraesCS3B02G133400*
	TraesCS3B02G133500	*TraesCS3B02G133600*	*TraesCS3B02G133700*	*TraesCS3B02G133800*	*TraesCS3B02G133900*
	TraesCS3B02G134000	*TraesCS3B02G134100*	*TraesCS3B02G134200*	*TraesCS3B02G134300*	*TraesCS3B02G134400*
	TraesCS3B02G134500	*TraesCS3B02G134600*	*TraesCS3B02G134700*	*TraesCS3B02G134800*	*TraesCS3B02G134900*
	TraesCS3B02G135000	*TraesCS3B02G135100*	*TraesCS3B02G135200*	*TraesCS3B02G135300*	*TraesCS3B02G135400*
	TraesCS3B02G135500	*TraesCS3B02G135600*	*TraesCS3B02G135700*	*TraesCS3B02G135800*	*TraesCS3B02G135900*
	TraesCS3B02G136000	*TraesCS3B02G136100*	*TraesCS3B02G136200*	*TraesCS3B02G136300*	
AX-110982975	*TraesCS4A02G110100*	*TraesCS4A02G110200*	*TraesCS4A02G110300*	*TraesCS4A02G110400*	*TraesCS4A02G110500*
	TraesCS4A02G110600	*TraesCS4A02G110700*	*TraesCS4A02G110800*	*TraesCS4A02G110900*	*TraesCS4A02G111000*
	TraesCS4A02G111100	*TraesCS4A02G111200*	*TraesCS4A02G111300*	*TraesCS4A02G111400*	*TraesCS4A02G111500*
	TraesCS4A02G111600	*TraesCS4A02G111700*	*TraesCS4A02G111800*	*TraesCS4A02G111900*	*TraesCS4A02G112000*
	TraesCS4A02G112100	*TraesCS4A02G112200*	*TraesCS4A02G112300*	*TraesCS4A02G112400*	*TraesCS4A02G112500*
	TraesCS4A02G112600	*TraesCS4A02G112700*	*TraesCS4A02G112800*	*TraesCS4A02G112900*	*TraesCS4A02G113000*
	TraesCS4A02G113100	*TraesCS4A02G113200*	*TraesCS4A02G113300*	*TraesCS4A02G113400*	*TraesCS4A02G113500*
	TraesCS4A02G113600	*TraesCS4A02G113700*	*TraesCS4A02G113800*	*TraesCS4A02G113900*	*TraesCS4A02G114000*
	TraesCS4A02G114100	*TraesCS4A02G114200*	*TraesCS4A02G114300*	*TraesCS4A02G114400*	*TraesCS4A02G114500*
	TraesCS4A02G114600	*TraesCS4A02G114700*	*TraesCS4A02G114800*	*TraesCS4A02G114900*	*TraesCS4A02G115000*

表 5(续)

标记 Marker	区间候选基因 Candidate intervals genes				
AX-111637187	*TraesCS4B02G376900*	*TraesCS4B02G377000*	*TraesCS4B02G377100*	*TraesCS4B02G377200*	*TraesCS4B02G377300*
	TraesCS4B02G377400	*TraesCS4B02G377500*	*TraesCS4B02G377600*	*TraesCS4B02G377700*	*TraesCS4B02G377800*
	TraesCS4B02G377900	*TraesCS4B02G378000*	*TraesCS4B02G378100*	*TraesCS4B02G378200*	*TraesCS4B02G378300*
	TraesCS4B02G378400	*TraesCS4B02G378500*	*TraesCS4B02G378600*	*TraesCS4B02G378700*	*TraesCS4B02G378800*
	TraesCS4B02G378900	*TraesCS4B02G379000*	*TraesCS4B02G379100*	*TraesCS4B02G379200*	*TraesCS4B02G379300*
	TraesCS4B02G379400	*TraesCS4B02G379500*	*TraesCS4B02G379600*	*TraesCS4B02G379700*	*TraesCS4B02G379800*
	TraesCS4B02G379900	*TraesCS4B02G380000*	*TraesCS4B02G380100*	*TraesCS4B02G380200*	*TraesCS4B02G380300*
	TraesCS4B02G380400	*TraesCS4B02G380500*	*TraesCS4B02G380600*	*TraesCS4B02G380700*	*TraesCS4B02G380800*
	TraesCS4B02G380900	*TraesCS4B02G381000*	*TraesCS4B02G381100*	*TraesCS4B02G381200*	*TraesCS4B02G381300*
	TraesCS4B02G381400	*TraesCS4B02G381500*	*TraesCS4B02G381600*	*TraesCS4B02G381700*	*TraesCS4B02G381800*
	TraesCS4B02G381900	*TraesCS4B02G382000*	*TraesCS4B02G382100*	*TraesCS4B02G382200*	*TraesCS4B02G382300*
	TraesCS4B02G382400	*TraesCS4B02G382500*	*TraesCS4B02G382600*	*TraesCS4B02G382700*	*TraesCS4B02G382800*
	TraesCS4B02G382900	*TraesCS4B02G383000*	*TraesCS4B02G383100*	*TraesCS4B02G383200*	*TraesCS4B02G383300*
	TraesCS4B02G383400	*TraesCS4B02G383500*	*TraesCS4B02G383600*	*TraesCS4B02G383700*	*TraesCS4B02G383800*
	TraesCS4B02G383900	*TraesCS4B02G384000*	*TraesCS4B02G384100*	*TraesCS4B02G384200*	*TraesCS4B02G384300*
	TraesCS4B02G384400	*TraesCS4B02G384500*	*TraesCS4B02G384600*	*TraesCS4B02G384700*	*TraesCS4B02G384800*
	TraesCS4B02G384900	*TraesCS4B02G385000*	*TraesCS4B02G385100*	*TraesCS4B02G385200*	*TraesCS4B02G385300*
	TraesCS4B02G385400	*TraesCS4B02G385500*	*TraesCS4B02G385600*	*TraesCS4B02G385700*	*TraesCS4B02G385800*
	TraesCS4B02G385900	*TraesCS4B02G386000*	*TraesCS4B02G386100*	*TraesCS4B02G386200*	*TraesCS4B02G386300*
	TraesCS4B02G386400	*TraesCS4B02G386500*	*TraesCS4B02G386600*	*TraesCS4B02G386700*	*TraesCS4B02G386800*
	TraesCS4B02G386900	*TraesCS4B02G387000*	*TraesCS4B02G387100*	*TraesCS4B02G387200*	*TraesCS4B02G387300*
	TraesCS4B02G387400	*TraesCS4B02G387500*	*TraesCS4B02G387600*	*TraesCS4B02G387700*	*TraesCS4B02G387800*
	TraesCS4B02G387900	*TraesCS4B02G388000*	*TraesCS4B02G388100*	*TraesCS4B02G388200*	*TraesCS4B02G388300*
	TraesCS4B02G388400	*TraesCS4B02G388500*	*TraesCS4B02G388600*	*TraesCS4B02G388700*	*TraesCS4B02G388800*
	TraesCS4B02G388900	*TraesCS4B02G389000*	*TraesCS4B02G389100*	*TraesCS4B02G389200*	*TraesCS4B02G389300*
	TraesCS4B02G389400	*TraesCS4B02G389500*	*TraesCS4B02G389600*	*TraesCS4B02G389700*	
AX-110072320	*TraesCS4D02G048500*	*TraesCS4D02G048600*	*TraesCS4D02G048700*	*TraesCS4D02G048800*	*TraesCS4D02G048900*
	TraesCS4D02G049000	*TraesCS4D02G049100*	*TraesCS4D02G049200*	*TraesCS4D02G049300*	*TraesCS4D02G049400*
	TraesCS4D02G049500	*TraesCS4D02G049600*	*TraesCS4D02G049700*	*TraesCS4D02G049800*	*TraesCS4D02G049900*
	TraesCS4D02G050000	*TraesCS4D02G050100*	*TraesCS4D02G050200*	*TraesCS4D02G050300*	*TraesCS4D02G050400*
	TraesCS4D02G050500	*TraesCS4D02G050600*	*TraesCS4D02G050700*	*TraesCS4D02G050800*	*TraesCS4D02G050900*
	TraesCS4D02G051000	*TraesCS4D02G051100*	*TraesCS4D02G051200*	*TraesCS4D02G051300*	*TraesCS4D02G051400*
	TraesCS4D02G051500	*TraesCS4D02G051600*	*TraesCS4D02G051700*	*TraesCS4D02G051800*	*TraesCS4D02G051900*
	TraesCS4D02G052000	*TraesCS4D02G052100*	*TraesCS4D02G052200*	*TraesCS4D02G052300*	*TraesCS4D02G052400*
	TraesCS4D02G052500	*TraesCS4D02G052600*	*TraesCS4D02G052700*	*TraesCS4D02G052800*	*TraesCS4D02G052900*
	TraesCS4D02G053000	*TraesCS4D02G053100*	*TraesCS4D02G053200*	*TraesCS4D02G053300*	*TraesCS4D02G053400*
	TraesCS4D02G053500	*TraesCS4D02G053600*	*TraesCS4D02G053700*	*TraesCS4D02G053800*	*TraesCS4D02G053900*
	TraesCS4D02G054000	*TraesCS4D02G054100*	*TraesCS4D02G054200*	*TraesCS4D02G054300*	*TraesCS4D02G054400*
	TraesCS4D02G054500	*TraesCS4D02G054600*	*TraesCS4D02G054700*	*TraesCS4D02G054800*	*TraesCS4D02G054900*
	TraesCS4D02G055000	*TraesCS4D02G055100*	*TraesCS4D02G055200*	*TraesCS4D02G055300*	*TraesCS4D02G055400*
	TraesCS4D02G055500	*TraesCS4D02G055600*	*TraesCS4D02G055700*		

表 5（续）

标记 Marker	区间候选基因 Candidate intervals genes				
AX-110433692	*TraesCS6A02G349800*	*TraesCS6A02G349900*	*TraesCS6A02G350000*	*TraesCS6A02G350100*	*TraesCS6A02G350200*
	TraesCS6A02G350300	*TraesCS6A02G350400*	*TraesCS6A02G350500*	*TraesCS6A02G350600*	*TraesCS6A02G350700*
	TraesCS6A02G350800	*TraesCS6A02G350900*	*TraesCS6A02G351000*	*TraesCS6A02G351100*	*TraesCS6A02G351200*
	TraesCS6A02G351300	*TraesCS6A02G351400*	*TraesCS6A02G351500*	*TraesCS6A02G351600*	*TraesCS6A02G351700*
	TraesCS6A02G351800	*TraesCS6A02G351900*	*TraesCS6A02G352000*	*TraesCS6A02G352100*	*TraesCS6A02G352200*
	TraesCS6A02G352300	*TraesCS6A02G352400*	*TraesCS6A02G352500*	*TraesCS6A02G352600*	*TraesCS6A02G352700*
	TraesCS6A02G352800	*TraesCS6A02G352900*	*TraesCS6A02G353000*	*TraesCS6A02G353100*	*TraesCS6A02G353200*
	TraesCS6A02G353300	*TraesCS6A02G353400*	*TraesCS6A02G353500*	*TraesCS6A02G353600*	*TraesCS6A02G353700*
	TraesCS6A02G353800	*TraesCS6A02G353900*	*TraesCS6A02G354000*	*TraesCS6A02G354100*	*TraesCS6A02G354200*
	TraesCS6A02G354300	*TraesCS6A02G354400*	*TraesCS6A02G354500*	*TraesCS6A02G354600*	*TraesCS6A02G354700*
	TraesCS6A02G354800	*TraesCS6A02G354900*	*TraesCS6A02G355000*	*TraesCS6A02G355100*	*TraesCS6A02G355200*
	TraesCS6A02G355300	*TraesCS6A02G355400*	*TraesCS6A02G355500*	*TraesCS6A02G355600*	*TraesCS6A02G355700*
	TraesCS6A02G355800	*TraesCS6A02G355900*	*TraesCS6A02G356000*	*TraesCS6A02G356100*	*TraesCS6A02G356200*
	TraesCS6A02G356300	*TraesCS6A02G356400*	*TraesCS6A02G356500*	*TraesCS6A02G356600*	*TraesCS6A02G356700*
	TraesCS6A02G356800	*TraesCS6A02G356900*	*TraesCS6A02G357000*	*TraesCS6A02G357100*	*TraesCS6A02G357200*
	TraesCS6A02G357300	*TraesCS6A02G357400*	*TraesCS6A02G357500*	*TraesCS6A02G357600*	*TraesCS6A02G357700*
	TraesCS6A02G357800				
AX-110660771	*TraesCS7B02G114700*	*TraesCS7B02G114800*	*TraesCS7B02G114900*	*TraesCS7B02G115000*	*TraesCS7B02G115100*
	TraesCS7B02G115200	*TraesCS7B02G115300*	*TraesCS7B02G115400*	*TraesCS7B02G115500*	*TraesCS7B02G115600*
	TraesCS7B02G115700	*TraesCS7B02G115800*	*TraesCS7B02G115900*	*TraesCS7B02G116000*	*TraesCS7B02G116100*
	TraesCS7B02G116200	*TraesCS7B02G116300*	*TraesCS7B02G116400*	*TraesCS7B02G116500*	*TraesCS7B02G116600*
	TraesCS7B02G116700	*TraesCS7B02G116800*	*TraesCS7B02G116900*	*TraesCS7B02G117000*	*TraesCS7B02G117100*
	TraesCS7B02G117200	*TraesCS7B02G117300*	*TraesCS7B02G117400*	*TraesCS7B02G117500*	*TraesCS7B02G117600*
	TraesCS7B02G117700	*TraesCS7B02G117800*	*TraesCS7B02G117900*	*TraesCS7B02G118000*	*TraesCS7B02G118100*
	TraesCS7B02G118200	*TraesCS7B02G118300*	*TraesCS7B02G118400*	*TraesCS7B02G118500*	*TraesCS7B02G118600*
	TraesCS7B02G118700	*TraesCS7B02G118800*	*TraesCS7B02G118900*	*TraesCS7B02G119000*	*TraesCS7B02G119100*
	TraesCS7B02G119200	*TraesCS7B02G119300*	*TraesCS7B02G119400*	*TraesCS7B02G119500*	*TraesCS7B02G119600*
	TraesCS7B02G119800	*TraesCS7B02G119700*			
AX-108838778	*TraesCS7B02G363100*	*TraesCS7B02G363200*	*TraesCS7B02G363300*	*TraesCS7B02G363400*	*TraesCS7B02G363500*
	TraesCS7B02G363600	*TraesCS7B02G363700*	*TraesCS7B02G363800*	*TraesCS7B02G363900*	*TraesCS7B02G364000*
	TraesCS7B02G364100	*TraesCS7B02G364200*	*TraesCS7B02G364300*	*TraesCS7B02G364400*	*TraesCS7B02G364500*
	TraesCS7B02G364600	*TraesCS7B02G364700*	*TraesCS7B02G364800*	*TraesCS7B02G364900*	*TraesCS7B02G365000*
	TraesCS7B02G365100	*TraesCS7B02G365200*	*TraesCS7B02G365300*	*TraesCS7B02G365400*	*TraesCS7B02G365500*
	TraesCS7B02G365600	*TraesCS7B02G365700*	*TraesCS7B02G365800*	*TraesCS7B02G365900*	*TraesCS7B02G366000*
	TraesCS7B02G366100	*TraesCS7B02G366200*	*TraesCS7B02G366400*	*TraesCS7B02G366300*	*TraesCS7B02G366500*
	TraesCS7B02G366600	*TraesCS7B02G366700*	*TraesCS7B02G366800*	*TraesCS7B02G366900*	*TraesCS7B02G367000*
	TraesCS7B02G367100	*TraesCS7B02G367200*	*TraesCS7B02G367300*		

表 6 BLUP 值位点候选区间茎 / 叶高表达的基因

Table 6 BLUP value significantly marks the genes highly expressed in stem/leaf of candidate interval

基因名称 Gene name	茎 / 叶表达量 Stem/leaves expression	基因名称 Gene name	茎 / 叶表达量 Stem/leaves expression	基因名称 Gene name	茎 / 叶表达量 Stem/leaves expression
TraesCS1A02G069400	13.99	*TraesCS3B02G132400*	11.57	*TraesCS4D02G052700*	13.77
TraesCS1A02G069600	38.50	*TraesCS3B02G132700*	5.38	*TraesCS4D02G053300*	6.32
TraesCS1A02G069900	15.23	*TraesCS3B02G132900*	8.74	*TraesCS4D02G053400*	17.62
TraesCS1A02G070400	7.30	*TraesCS3B02G133000*	5.64	*TraesCS4D02G053600*	7.31
TraesCS1A02G071400	9.06	*TraesCS3B02G133400*	80.63	*TraesCS4D02G053800*	21.76
TraesCS1A02G071500	19.67	*TraesCS3B02G135400*	30.72	*TraesCS4D02G053900*	13.94
TraesCS1A02G071600	13.43	*TraesCS4A02G110100*	10.77	*TraesCS4D02G054200*	69.40
TraesCS1A02G071700	9.34	*TraesCS4A02G110400*	35.15	*TraesCS4D02G054300*	6.35
TraesCS1A02G071800	11.80	*TraesCS4A02G110600*	6.40	*TraesCS4D02G054500*	17.75
TraesCS1A02G072000	50.90	*TraesCS4A02G110700*	29.57	*TraesCS4D02G055300*	11.60
TraesCS1A02G072200	16.12	*TraesCS4A02G110900*	5.64	*TraesCS6A02G350000*	5.06
TraesCS1A02G203000	22.03	*TraesCS4A02G111100*	11.27	*TraesCS6A02G351300*	20.87
TraesCS1A02G203400	8.76	*TraesCS4A02G111600*	5.37	*TraesCS6A02G353200*	5.67
TraesCS1A02G203600	59.95	*TraesCS4A02G111800*	24.57	*TraesCS6A02G353700*	20.42
TraesCS1A02G203700	19.89	*TraesCS4A02G113200*	5.89	*TraesCS6A02G353800*	51.12
TraesCS1A02G204200	6.83	*TraesCS4A02G113300*	11.50	*TraesCS6A02G354100*	8.79
TraesCS1A02G205300	8.01	*TraesCS4A02G114000*	8.70	*TraesCS6A02G354200*	6.41
TraesCS1A02G205600	16.21	*TraesCS4A02G114100*	133.04	*TraesCS6A02G354400*	38.38
TraesCS1A02G205700	10.39	*TraesCS4A02G114200*	15.87	*TraesCS6A02G354500*	10.74
TraesCS1A02G206700	7.03	*TraesCS4A02G115000*	20.17	*TraesCS6A02G355000*	21.70
TraesCS1A02G206900	26.01	*TraesCS4B02G379500*	41.60	*TraesCS6A02G355300*	40.08
TraesCS1A02G208400	5.53	*TraesCS4B02G380200*	35.22	*TraesCS6A02G357200*	41.34
TraesCS1A02G420500	11.26	*TraesCS4B02G380400*	15.03	*TraesCS7B02G115000*	5.99
TraesCS1A02G420800	18.80	*TraesCS4B02G380800*	15.17	*TraesCS7B02G115300*	24.12
TraesCS1A02G420900	22.29	*TraesCS4B02G381800*	5.13	*TraesCS7B02G115500*	8.70
TraesCS1A02G421000	5.90	*TraesCS4B02G382900*	11.52	*TraesCS7B02G115900*	7.13
TraesCS1A02G422400	5.58	*TraesCS4B02G383100*	18.39	*TraesCS7B02G116800*	67.02
TraesCS1A02G422900	10.24	*TraesCS4B02G384000*	5.54	*TraesCS7B02G117600*	32.88
TraesCS1A02G423100	5.49	*TraesCS4B02G385900*	41.66	*TraesCS7B02G118100*	5.04
TraesCS1A02G423800	51.96	*TraesCS4B02G386000*	18.38	*TraesCS7B02G118400*	12.62
TraesCS1A02G424200	21.40	*TraesCS4B02G387800*	6.71	*TraesCS7B02G119000*	18.18
TraesCS1A02G425000	43.26	*TraesCS4D02G049900*	7.48	*TraesCS7B02G119700*	5.84
TraesCS1A02G425700	5.76	*TraesCS4D02G050100*	33.58	*TraesCS7B02G363100*	10.56
TraesCS1A02G427000	10.59	*TraesCS4D02G050200*	6.34	*TraesCS7B02G363600*	10.95
TraesCS1A02G427100	7.45	*TraesCS4D02G050400*	28.44	*TraesCS7B02G363700*	6.21
TraesCS1A02G427200	8.34	*TraesCS4D02G050600*	12.39	*TraesCS7B02G364100*	5.42
TraesCS1A02G427500	5.30	*TraesCS4D02G050700*	22.07	*TraesCS7B02G364400*	8.42
TraesCS1A02G428400	17.78	*TraesCS4D02G050800*	31.23	*TraesCS7B02G364800*	7.89
TraesCS1A02G428700	18.93	*TraesCS4D02G051000*	6.86	*TraesCS7B02G365100*	5.35
TraesCS1A02G429400	30.43	*TraesCS4D02G051400*	12.27	*TraesCS7B02G365500*	11.56
TraesCS3B02G131400	7.41	*TraesCS4D02G051900*	7.75	*TraesCS7B02G366700*	26.26
TraesCS3B02G131500	34.40	*TraesCS4D02G052100*	6.56	*TraesCS7B02G366900*	5.14
TraesCS3B02G131900	16.71	*TraesCS4D02G052400*	14.13	*TraesCS7B02G367100*	11.27
TraesCS3B02G132300	17.43	*TraesCS4D02G052500*	37.57		

表 7　显著 BLUP 值根据注释确定的候选基因

Table 7　Candidate genes with significant BLUP values determined according to annotations

标记 Marker	水稻基因号 Rice gene number	基因注释 Gene annotation	E- 值 E-value	同源性 Homology	可能候选基因 Possible candidate gene	基因区间 Gene interval
AX-108917531	*LOC_Os05g27730*	*WRKY* 转录因子	2.3E-47	98.4	*TraesCS1A02G070400*	53187274~3189460
AX-110982975	*LOC_Os03g18360*	乙烯合成过量基因	3.0E-171	86.6	*TraesCS4A02G110100*	134208144~134210191
AX-111637187	*LOC_Os03g01910*	碱性转录因子	7.5E-39	98.0	*TraesCS4B02G385900*	664762713~664764452
AX-110072320	*LOC_Os03g45194*	叶绿素 b 还原酶基因	3.2E-53	96.2	*TraesCS4D02G053400*	29405725~29410300
AX-110660771	*LOC_Os06g15990*	乙醛脱氢酶	0	89.5	*TraesCS7B02G116800*	136309835~136315047

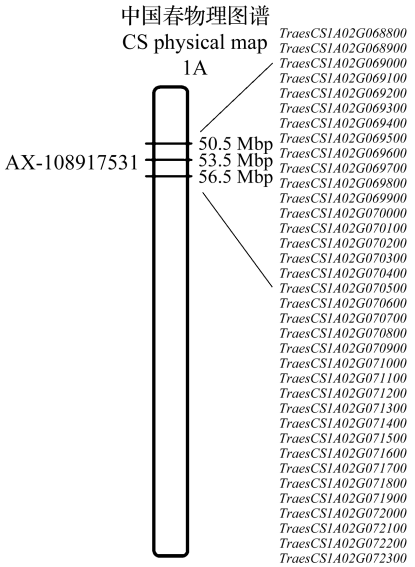


图 6　AX-108917531 物理位置区间内的候选基因

Fig.6　AX-108917531 candidate genes in physical location and interval

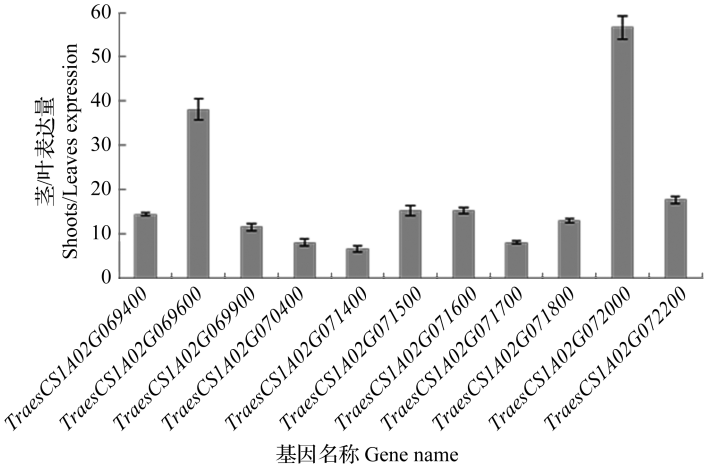


图 7　AX-108917531 标记候选区间茎 / 叶高表达基因

Fig.7　AX-108917531 marks the highly expressed genes in stem/leaf of candidate interval

3　讨论

全基因组关联分析通过基因型与表型数据关联，可直接检测出与表型变异相关的显著 SNP。小麦株高受多基因控制，易受环境条件的影响，适于应用全基因组关联分析研究[20]。Cadalen 等[21]利用 DH 群体定位了 9 个与小麦株高相关的 QTL，其中 2 个 RFLP 标记 *Xfba1-4B* 和 *Xfba211-4D* 分别与矮秆基因 *Rht1* 和 *Rht2* 连锁；Huang 等[22]利用 BC_2F_2 群体，定位了 5 个株高 QTL；Liu 等[23]以普通小麦品系 NongDa3331 和西藏半野生小麦品种 Zang1817 杂交构建的 RIL 群体为试验材料，在 3A、4B 和 4D 上检测到与株高相关的 QTL；Borner 等[24]利用 Opata85 和 W-7984 构建的 114 个家系的 RIL 群体，定位了 4 个与株高相关的主效 QTL；周淼平等[25]利用 RIL 群体在 1D、2B、4A 和 4D 染色体上检测到 4 个控制小麦株高的 QTL；李聪等[26]利用 RIL 进行株高的遗传分析，检测出 17 个控制株高的 QTL；陈广凤等[27]利用 205 份冬麦品种，发现 38 个与株高显著的 SNP。前期研究虽然定位了大量的 QTL，但共定位的 QTL 数量较少，表明株高性状的遗传机制较为复杂。本研究对从 CIMMYT 新引进的合成小麦株高进行全基因组关联分析，在 1A、3B、4A、4B、4D 和 7B 染色体上发现 10 个与株高 BLUP 值显著关联的 SNP。这些标记与前人研究结果染色体分布有一致性，但未发现与之前定位接近的主效 QTL。这一现象可能与合成小麦群体还未受过环境压力的选择，其等位基因频率较低有关。全基因组关联分析采用 MLM，以主成分分析（PCA）和亲缘关系（K=3）作为协变量纳入回归分析，并通过较高的阈值（$P \leqslant 0.0001$），

消除由群体分层和亲缘关系引起的假阳性与假阴性，增加关联结果的可信度。统计SNP在亚基因组中的分布，发现B亚基因组标记数目最多，D亚基因组标记数目最少，与崔德周等[28]基于90K SNP芯片对莱州953×山农辐63组合构建的F_2群体进行遗传图谱绘制发现的标记分布趋势一致。

株高BLUP值关联分析筛选到的10个显著标记，对标记物理位置左右3 Mb距离内基因进行分析，在5个位点区间发现可能候选基因，贡献率最高的AX-108917531，编码*WRKY*类转录因子的*TraesCS1A02G070400*，其水稻正源基因*OsWRKY53*的过表达，会使水稻半矮秆化[19]；4A染色体AX-110982975，编码乙烯生产过量的*TraesCS4A02G110100*，其水稻正源基因*OsETOL1*的等位突变体在穗发育时期表现出干旱胁迫抗性增加[29]，暗示其通过提高小麦根部的吸水能力来影响植物茎的生长，影响株高；4B染色体上AX-111637187，编码*BTF3*碱性转录因子的*TraesCS4B02G385900*，其水稻正源基因*Osj10gBTF3*编码1个基础转录因子，表达受到抑制后会导致水稻株型矮化[30]；4D染色体上AX-110072320，编码叶绿素b还原酶的*TraesCS4D02G053400*，与光捕获复合体和叶绿体基粒的降解密切相关，并通过影响植物的光合作用，最终影响植物的生长发育；7B染色体上的AX-110660771，编码乙醛脱氢酶的*TraesCS7B02G116800*，其水稻正源基因*osaldh2b1*突变体可引起株高降低[31]。本研究鉴定到的候选基因与植物株高发育都有一定的联系，其具体功能需要在小麦中进行进一步研究。本研究发现的合成小麦与株高显著SNP将为后续基因精细定位和分子标记开发奠定一定的基础，为小麦株高的改良提供遗传资源。

4 结论

利用小麦55K SNP芯片，对152份合成小麦的株高性状进行GWAS分析，其中BLUP值筛选到10个显著相关的SNP。对这些标记邻近区间的基因进行注释分析，发现5个可能与株高性状相关的候选基因。这些显著的株高标记及可能的候选基因，不仅可以增加供体物种的遗传多样性，而且为改良普通小麦株高提供基因资源。

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