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基因从普通小麦向山羊草属植物漂移可能性研究

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摘要:分别以山羊草属4个不同的种为母本,以普通小麦为父本杂交,将获得的杂种再进行回交和自交。结果表明,不同种与普通小麦的可交配性存在较大差异,在人工多次授粉并有激素处理的条件下,粗山羊草与普通小麦的杂交结实率最高,2个基因型Ae42和Y92的杂交结实率分别为46.49%和22.58%;其次为卵穗山羊草,2个基因型Ae23和Y100的杂交结实率分别为12.11%和14.76%;柱穗山羊草位列第3,2个基因型Ae7和Y145的杂交结实率分别为2.23%和8.50%;拟斯卑尔脱山羊草最低,基因型Ae48的杂交结实率只有0.19%。不同种的杂种胚产生愈伤组织率不同,柱穗山羊草/小麦表现较高的水平,卵穗山羊草/小麦次之,粗山羊草/小麦第3,拟斯卑尔脱山羊草/小麦最低。卵穗山羊草/小麦的杂种幼胚直接成苗率最高,其次为粗山羊草/小麦,柱穗山羊草/小麦居第3位。山羊草与普通小麦杂种的育性较低,在自然状态下,只有卵穗山羊草/小麦能够自交结实,但自交结实率仅为0.044%,其他杂种自交不能结实。在人工多次授粉并激素处理条件下,用父、母本回交的结实率:卵穗山羊草/普通小麦组合分别为4.36%和3.71%,柱穗山羊草/普通小麦组合分别为0.33%和0,粗山羊草/普通小麦组合分别为0和0.33%。总体而言,在自然条件下,基因从普通小麦向山羊草属植物漂移的可能性比较小,但对个别种如卵穗山羊草和柱穗山羊草成为基因漂移对象的可能性不可忽视。

关键词:山羊草属;普通小麦;基因渐渗;可交配性;结实率

Possibility and Probability of Gene Introgression from Common Wheat into *Aegilops* L.

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Abstract: In order to provide scietific information on the possibility and probability of gene introgression from common wheat(*Triticum astivum*) into *Aegilops* species artificial hybridization was conducted using 7 genotypes from 4 wheat relative species as female parents, and common wheat as male parent. The result indicated that different Aegilops species had variable cross ability. Among the 4 *Aegilops* species, the highest hybridization rate was observed in the combination of *Ae. tauschii* × *T. aestivum*(46.49% for genotype Ae42 and 22.58% for Y92), the second in *Ae. ovata* × *T. astivum*(14.76% for Y100 and 12.11% for Ae23), the third in *Ae. cylindrica* × *T. astivum* (2.23% for Ae7, 8.50% for Y145), and the lowest in *Ae. speltoides* × *T. astivum*(0.19%). Hybrid embryos from different combinations had different ability of callus initiation and germination. The hybrid embryos from *A. ovata* / *T. eastivum* and *Ae. tauschii* / *T. eastivum* had higher level of callus initiation and germination, *Ae. cylindrica* / *T. eastivum* had medium level, while the *Ae. speltoides* had lower level. The interspecific hybrids between *Aegilops* and common wheat had very low fertility. In backcrosses, the seed-set rates of *Ae. ovata* / *T. aestivum* was 3.71% and 4.36%, respec-

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tively when backcrossed with male and female parents, while for the hybrids of *A. cylindrica* / *T. aestivum*, they were 0 and 0.33%, respectively, and for *A. tauschii* / *T. aestivum*, 0.33% and 0, respectively. On selfing of the hybrids, the seed-set rates were 0 (no seed set from 9750 florets) for the combination of *Ae. cylindrica* / *T. aestivum*, 0.044% (3 selfed seeds out of 6870 florets) for *A. ovata* / *T. aestivum*, and 0 (no seed set from 7253 florets) for *A. tauschii* / *T. aestivum*. These results suggested that the probability of gene introgression from *T. aestivum* into *Aegilops* species was very low in nature.

Key words: *Aegilops* L.; *Triticum aestivum* L.; Gene introgression; Cross-ability; Seed-set rate

目标基因由普通小麦(*Triticum aestivum*)向相关近缘野生种漂移的可能性是转基因小麦田间释放时需要考虑的主要问题。根据目前对普通小麦起源的研究,山羊草属(*Aegilops* L.)是普通小麦染色体组的重要来源,与小麦亲缘关系很近。由于山羊草属植物蕴涵着许多抗病、抗虫、抗逆、高蛋白质含量及其他丰富的基因资源,在研究上侧重于其基因库的开拓挖掘、有益基因向小麦遗传背景的导入利用等遗传改良以及遗传进化等方面[1-5]。近年来,随着转基因小麦的问世[6],小麦基因向山羊草属植物转移,以及这些基因能否在杂种后代中稳定传递成为转基因小麦的环境安全性评估的重要内容。小麦基因向山羊草属植物漂移在西班牙、瑞士等国已有发现[7],国内还未见相关报道。

杂交率因亲本的基因型及其生长发育的环境条件的不同而存在差异。属间杂交需要考虑的因素更多,比如亲本间花期相遇与否、开花特性、温度和湿度等。本研究分别以山羊草属中的4个主要种,拟斯卑尔脱山羊草(*Aegilops speltoides*, 2n = 2X = BB = 14)、粗山羊草(*Ae. tauschii*, 2n = 2X = DD = 14)、柱穗山羊草(*Ae. cylindrica*, 2n = 4X = CCDD ≈ 28)和卵穗山羊草(*Ae. ovata* 2n = 2X = $C^uC^uM^oM^o$ ≈ 28)为母本与小麦杂交,并进行杂种自交和回交研究,旨在探究基因由小麦向山羊草转移的最大可能性,为转基因小麦的生态安全性评价提供理论依据。

1 材料与方法

1.1 材料

母本材料为拟斯卑尔脱山羊草Ae48、粗山羊草2个变异类型Ae42和Y92、柱穗山羊草2个变异类型Ae7和Y145、卵穗山羊草的2个变异类型Ae23和Y100。上述这些材料均由中国农科院作物科学研究所提供。父本材料为3个普通小麦品种石4185、石9306和J1361,由石家庄农业科学院提供。

1.2 杂交授粉与激素处理

在温室内分期种植上述母本和父本材料,以保证花期相遇。小麦野生近缘种开花前去雄,1~2d后授以上述3个普通小麦品种的混合花粉,次日重复授粉一次。在授粉后的第2天和第3天,用10 μl 100mg/ml 2,4-D溶液每天滴柱头一次。授粉12~16d后取下杂种穗,统计结实情况。

1.3 幼胚培养及杂种回交

剥取授粉12~16d幼嫩种子,置0.1%的升汞中灭菌8min,无菌水冲洗3次后剖出幼胚,一部分置于愈伤诱导培养基(MS附加2mg/L 2,4-D),先诱导出愈伤,再将杂种愈伤在不附加任何激素的MS培养基上诱导成苗;将另一部分幼胚置于幼苗萌发培养基(MS_0)直接长苗,或者进行活体-离体胚培养(即将幼胚放于同时挖去幼胚的小麦种子胚的部位,并将该杂合种子放置在MS_0培养基上,在人工气候室中培养)的方法直接成苗。再将杂种苗移栽于温室。开花时一部分杂种用原母本或父本回交(继续实施重复授粉、激素处理等方法),12~16d调查回交结实数,并对回交中实行胚拯救。另一部分杂种自然自交,一个月后调查自交结实数。

回交结实率 = 结实数/去雄小花数

自交结实率 = 结实数/调查小花数

2 结果与分析

2.1 小麦与山羊草的可交配性

遗传因素决定父母本的可交配性。山羊草与普通小麦的可交配性因母本的不同而不同。总的来说,粗山羊草与普通小麦间具有较高的可交配性,2个基因型Ae42和Y92与小麦的杂交结实率分别达46.49%和22.58%;卵穗山羊草与小麦的可交配性次之,2个基因型Ae23和Y100与普通小麦的杂交结实率分别为12.11%和14.76%;柱穗山羊草与小麦的可交配性较前两者低,2个基因型Ae7和Y145与普通小麦的杂交结实率分别为2.23%和8.50%;拟斯卑尔脱山羊草与小麦的可交配性最低,基因型Ae48与普通小麦的杂交结实率只有0.19%(表1)。上述普通小麦与山羊草各个种的杂交结实率是相对

表 1　普通小麦与山羊草杂交结实率

Table 1　Hybridization between *T. aestivum* and *Aegilops* L.

母本 Female parent	基因型 Genotype	去雄穗数 No. of castrated spikes	授粉小花数 No. of pollinated florets	结实数 No. of seedsetting	结实率(%) Rate of seed setting
拟斯卑尔脱山羊草 *Ae. speltoides*	Ae48	100	1578	3	0.19
粗山羊草 *Ae. tauschii*	Ae42	82	998	464	46.49
	Y92	103	1262	285	22.58
柱穗山羊草 *Ae. cylindrica*	Ae7	98	628	14	2.23
	Y145	67	741	63	8.50
卵穗山羊草 *Ae. ovata*	Ae23	47	809	98	12.11
	Y100	50	956	141	14.76

稳定的,不会因去雄穗数的相对减少而有太大差异。

山羊草与普通小麦杂种幼胚的出愈率和直接成苗率因母本的不同而不同。虽然粗山羊草与小麦的杂交结实率最高,但杂种胚的出愈率较低约 10%。卵穗山羊草与普通小麦的杂种幼胚的出愈率(66.7% ~72.1%)居第 2 位。柱穗山羊草与普通小麦杂种幼胚的出愈率(80% ~100%)最高(表 2)。卵穗山羊草与普通小麦杂种幼胚的直接成苗率(75% ~84.2%)最高,其次为粗山羊草与小麦的杂种幼胚,直接成苗率为 28.6% ~33.3%,柱穗山羊草与普通小麦的杂种幼胚的直接成苗率为 15.4% ~25%。拟斯卑尔脱山羊草与普通小麦只获得 3 个杂种幼胚,出愈率和直接成苗率均为 0(分别为 0/2 和 0/1)。

表 2　杂种幼胚培养情况

Table 2　Culture results of immature hybrid embryos

杂交组合 Cross combination	诱导愈伤接种胚数 No. of embryos cultured for calli	形成愈伤率(%) Percentage of embryos inducing calli	直接成苗接种胚数 No. of embryos cultured for seedings	直接成苗率(%) Percentage of seedlings produce directly
Ae. speltoides Ae48/ *T. aestivum*	2	0	1	0
Ae. tauschii Ae42/ *T. aestivum*	197	10.2	14	28.6
Ae. tauschii Y92/ *T. aestivum*	39	10.3	6	33.3
Ae. cylindrica Ae7/ *T. aestivum*	10	100	4	25.0
Ae. cylindrica Y145/ *T. aestivum*	40	80.0	13	15.4
Ae. ovata Ae23/ *T. aestivum*	46	72.1	14	75.0
Ae. ovata Y100/ *T. aestivum*	78	66.7	19	84.2

2.2　远缘杂种的育性

山羊草×普通小麦杂种植株生长旺盛,在形态上介于双亲之间。杂种的育性因山羊草种的不同表现差异,但总体来讲育性较差。在自然授粉状态下,粗山羊草/普通小麦和柱穗山羊草/普通小麦的杂种自交结实率均为 0,卵穗山羊草/小麦杂种的自交结实率也仅为 0.044%(表 3)。

表 3　杂种自交结实情况

Table 3　Selfing of interspecific hybrids

杂种 F_1 Hybrid F_1	穗数 No. of spikes	小花数 No. of florets	结实数 No. of seed setting	结实率(%) Percentage of seed setting
粗山羊草/小麦 *Ae. Tauschii /T. aestivum*	225	7253	0	0
柱穗山羊草/小麦 *Ae. cylindrica /T. aestivum*	468	9750	0	0
卵穗山羊草/小麦 *Ae. ovata /T. aestivum*	539	6870	3	0.044

在多次授粉并有激素处理的回交中,粗山羊草/普通小麦杂种用粗山羊草回交不结实,用普通小麦回交可结实,结实率为 0.33%;柱穗山羊草/普通小麦杂种用柱穗山羊草回交可结实,结实率为 0.33%,用普通小麦回交没有产生后代;卵穗山羊草/普通小麦杂种的回交结实率相对较高,用卵穗山羊草作父

本回交的结实率为4.36%,用普通小麦作父本回交时结实率为3.71%(表4)。

表4 杂种回交结实情况

Table 4 Backcrosses of interspecific hybrids

杂种 F_1 Hybrid F_1	轮回亲本 Recurrent parent	去雄穗数 No. of castrated spikes	去雄小花数 No. of castrated florets	结实数 No. of seed setting	结实率(%) Percentage of seed setting
粗山羊草/小麦	普通小麦	30	916	3	0.33
Ae. tauschii /T. aestivum	粗山羊草	86	2432	0	0
柱穗山羊草/小麦	普通小麦	70	1358	0	0
Ae. cylindrica /T. aestivum	柱穗山羊草	70	1204	4	0.33
卵穗山羊草/小麦	普通小麦	154	1886	70	3.71
Ae. ovata /T. aestivum	卵穗山羊草	65	871	38	4.36

3 讨论

山羊草属具有5个基本基因组C、D、M、S和U,其中D和S(也称为B)基因组在小麦的起源和进化中起着非常重要的作用[8-10]。本研究的试验材料涉及了山羊草属中的4个种,包含了上述5个染色体组。山羊草属为一年生自花或常异花授粉植物,也存在天然异交的可能性。拟斯卑尔脱山羊草、粗山羊草、柱穗山羊草和卵穗山羊草与小麦属间人工杂交均有报道[11-14],但多限于远缘杂交在遗传育种中的应用。本研究同时选取上述4个不同种山羊草与普通小麦人工杂交。在实施胚拯救的情况下,与普通小麦最容易杂交的是粗山羊草,最高获得46.49%的属间杂种;其次,获得普通小麦和卵穗山羊草间杂种最高为14.76%;获得普通小麦和柱穗山羊草间杂种最高为12.11%;杂交结实率最低的是拟斯卑尔脱山羊草。不同山羊草种以及同一山羊草种的不同基因型与普通小麦杂交表现不同的可交配性,说明它们与小麦杂交的潜在能力不同。Guadagnuolo等[7]用普通小麦与柱穗山羊草进行大田授粉试验,获得了1%和7%的属间杂交种子。Loureiro等[15]在大田环境下,获得了0.39%的普通小麦和卵穗山羊草间的属间杂种。本试验表明普通小麦和柱穗山羊草间潜在杂交结实率能达到10%以上。本试验实施胚拯救提高了杂交结实率,克服了大田环境下各种自然因素导致的不确定性,更能揭示普通小麦与山羊草间杂交结实潜力。

小麦基因能否在山羊草中稳定传递,取决于回交和自交的结实情况。本研究以山羊草作母本获得的杂种,再用两亲本分别回交。相比而言,杂种回交表现各有不同。用卵穗山羊草回交其与小麦的杂种,结实率较高,为4.36%。用柱穗山羊草回交其与小麦的杂种也能结实,结实率为0.33%。卵穗山羊草/小麦杂种自交也能结实,结实率为0.044%。Loureiro等[15]也证实普通小麦和卵穗山羊草属间杂交能够产生回交后代(达到8%)。普通小麦-卵穗山羊草属间杂种的育性高于普通小麦-柱穗山羊草属间杂种的育性。普通小麦与卵穗山羊草、柱穗山羊草属间杂种的育性很低。

普通小麦基因能否转移到山羊草属中,与很多因素有关。比如花期是否相遇,杂种花粉能否与原母本回交并结实、回交过程能否持续多代等。任何一个环节都可能影响属间基因的转移。试验结果表明,尽管采取重复授粉和激素处理等措施,山羊草与普通小麦杂交和回交结实率仍很低,自然杂交和回交的结实率更低。从这方面讲,在自然条件下,基因从普通小麦转移到山羊草属,并在后者群体中稳定传递比较困难。但对个别种如卵穗山羊草和柱穗山羊草成为基因漂移对象的可能性不可忽视。

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(下转第270页)

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基因从普通小麦向山羊草属植物漂移可能性研究

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