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抗草甘膦转基因油菜与4个种群野芥菜抗性回交2代(BC2F$_1$)的适合度

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摘　要　转基因技术快速发展的同时，转基因渗入野生近缘杂草的生态安全问题也备受关注。为评估抗除草剂转基因油菜(*Brassica napus*)的抗性基因能否成功渗入不同种群野芥菜(wild *Brassica juncea*)中，本研究测定了抗草甘膦转基因油菜与句容市、南通市、西宁市和西安市4个种群野芥菜的抗草甘膦正向回交2代BC2mF$_1$和反向回交2代BC2pF$_1$ (m表示以野芥菜为母本的回交2代, p表示以野芥菜为父本的回交2代)的适合度。通过测定供试回交2代在温室条件下和田间条件下的营养生长和生殖生长的适合度指标，计算总适合度，并比较供试回交2代的总适合度与野芥菜的差异，评价各回交2代在不同种植条件下的适合度。结果表明，4个种群野芥菜的抗性回交2代的总适合度在温室条件下均与野芥菜相当。在田间条件下，句容市、西宁市和西安市种群的抗性正向回交2代和南通市、西安市种群的抗性反向回交2代的总适合度均与野芥菜无显著差异，句容市、西宁市种群的抗性反向回交2代和南通市种群的抗性正向回交2代的总适合度均显著高于野芥菜($P<0.05$)。综上所述，4个种群抗草甘膦回交2代均具有在野外生存定植的能力，在大面积种植转基因油菜时，务必要防范转基因油菜向不同种群野芥菜的首次基因漂移和通过回交导致的基因渗入。本研究将为抗草甘膦转基因油菜的抗性基因渗入不同种群野芥菜可能导致的生态后果提供数据支持。

关键词　抗草甘膦转基因油菜；野芥菜；回交后代；基因渗入；适合度
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Fitness of the Glyphosate-resistant Second Backcross Generation (BC2F$_1$) Between Glyphosate-resistant Transgenic Oilseed Rape (*Brassica napus*) and Four Populations of Wild *Brassica juncea*

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Abstract　With the rapid development of genetically modified technology, the environmental biosafety of transgene introgression into wild relatives has attracted much attention. To evaluate whether the transgene endowing glyphosate-resistance to *Brassica napus* could successfully introgress to the different populations of wild *Brassica juncea*, the fitness of the glyphosate-resistant second backcross generations BC2mF$_1$ and BC2pF$_1$ (m and p represent wild *B. juncea* as maternal plants and paternal plants, respectively) between 4 populations of wild *B. juncea* (Jurong, Nantong, Xining, Xi'an) and glyphosate-resistant oilseed rape was studied in the greenhouse and field. Vegetative growth indicators and reproductive growth indicators of these 4 second

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backcross generations were measured and used to calculate their composite fitness. Furthermore, the differences of the composite fitness between the second backcross generations and wild *B. juncea* were analyzed. The results showed that the composite fitness of all BC2mF_1 and BC2pF_1 were similar with that of their respective wild *B. juncea* under greenhouse conditions. Similarly, in the field, the BC2mF_1 of Jurong, Xining, and Xi'an and BC2pF_1 of Nantong and Xi'an were equivalent in composite fitness to their respective wild *B. juncea*, However, composite fitness of BC2pF_1 of Jurong, Xining and BC2mF_1 of Nantong surpassed that of their respective wild *B. juncea* progenitor. In conclusion, the glyphosate-resistant BC2mF_1 and BC2pF_1 of transgenic oilseed rape and the 4 wild *B. juncea* had a strong survival ability and potential possibility of establishing populations in the field. It was necessary to prevent initial gene flow and introgression to backcrosses between the herbicide-resistant transgenic oilseed rape and wild *B. juncea* upon commercial release of the transgenic crop. The results will provide data on the possible ecological consequences of the introgress of transgene from glyphosate-resistant transgenic oilseed rape into different populations of wild *B. juncea*.

Keywords Glyphosate-resistant transgenic oilseed rape; Wild *Brassica juncea*; Backcross generations; Introgression; Fitness

转基因油菜(*Brassica napus*)是世界四大转基因作物之一，其种植面积从1996年的10万hm^{2}增长到2018年的1 010万hm^2，占全球转基因作物的5.3% (国际农业生物技术应用服务组织, 2019)。目前转基因油菜在我国还未商业化种植，但经过多年努力，已培育出一批具有商业化价值的抗除草剂转基因油菜(钟蓉, 朱峰, 1997; 金红等, 1997; 沈志成等, 2012; 胡茂龙等, 2013; 李杰华, 2018)。2004年以来我国油菜籽总产量、单产水平仅有小幅提高，油菜生产处于徘徊不前状态，逐渐扩大的供需矛盾导致大量进口油菜籽，且绝大多数都是抗除草剂转基因油菜籽(李想等, 2011; 程泰等, 2019)。这些油菜种子在运输、加工生产等过程中洒落可能会在我国形成自生苗。已有报道表明，在未商业化种植转基因油菜的国家如比利时、日本和阿根廷发现了抗除草剂转基因油菜的自生苗(Aono et al., 2006; Kawata et al., 2009; Devos et al., 2012; Katsuta et al., 2015; Nishizawa et al., 2016; Pandolfo et al., 2016)。一旦形成自生苗，这些植株开花后，花粉就可能漂移到近缘杂草中，产生抗性杂交种，杂交种还有可能与近缘杂草不断回交，导致抗性基因渗入近缘杂草中。因此在我国进行抗除草剂转基因油菜的生态风险评估具有现实意义。

油菜(2n=38=AACC)属于常异花授粉作物，具有花期持续时间长、花粉传播距离远、且花粉活力保持时间长的特点，并且在自然生态环境和农田生态环境中存在分布广泛的野生近缘杂草(宋小玲等, 2007)，因此抗性基因从转基因油菜向近缘杂草渗入(introgression)的问题已经受到广泛关注(Stewart et al., 2003; Tsuda et al., 2012; Cao et al., 2014)。抗性基因渗入的第一步是转基因作物和近缘种能自发杂交产生抗性杂交种，之后杂交种和亲本通过不断回交，产生适合度(fitness)较高的后代，完成抗性基因渗入(Song et al., 2010; Tsuda et al., 2012; 张庆玲等, 2017; 王晓蕾等, 2017)。适合度是指在自然条件下植物的生存竞争能力，与植物的生长势、繁殖力、种子库持久能力等性状的表现密切相关，且由于杂交种染色体的重组以及选择压力，适合度会随着杂交和回交代数的增加呈现提高的趋势(Jenczewski et al., 2003)。

在田间条件下，转基因油菜可以和近缘种芜菁(*B. rapa*) (Jørgensen, Andersen., 1994; Snow et al., 1999)、野萝卜(*Raphanus raphanistrum*) (Eber et al., 1994; Darmency et al., 1998; Gueritaine et al., 2002)自发杂交，能产生抗性杂交后代。且转基因油菜与芜菁的杂交和回交后代随着代数的增加适合度提高 (Jørgensen, Andersen, 1994; Mikkelsen et al., 1996; Hauser et al., 1998; Pertl et al., 2002; Hauser et al., 2003; Ammitzbøll et al., 2005; Allainguillaume et al., 2006)。转基因油菜与野萝卜杂交种的育性也随着代数的增加而提高(Chèvre et al., 1997; 1998)。

芥菜(*B. juncea*, 2n=36=AABB)和油菜有一个共同的A-基因组，因此两者具有较高的亲和性(Scheffler, Dale., 1994)。 转基因油菜和芥菜能在自然环境下自发杂交(Bing et al., 1996; Jørgensen et al., 1998)。野芥菜(wild *B. juncea*, 2n=36=AABB)

是广泛发生于我国长江流域、黄河流域以及西北地区的荒地及农田的重要杂草(Sun et al., 2018)。由于野芥菜与转基因油菜共有A-基因组，存在转基因油菜的抗性基因渗入野芥菜的可能性。在田间条件下抗除草剂转基因油菜和野芥菜能自发杂交(浦惠明等, 2005; 宋小玲等, 2007; Liu et al., 2010)，产生花粉育性较低的F_1，但F_1与野芥菜回交后，能形成适合度逐渐提高的回交后代(张庆玲等, 2017; 卞清等, 2017; 闫静等, 2018; Liu et al., 2010; Song et al., 2010)。最新研究表明不同地区的野芥菜具有遗传多样性，在11个SSR位点上观察到90个等位基因，具有广泛的等位基因多样性(Sun et al., 2018)。由于不同种群野芥菜之间存在差异，在与转基因油菜发生杂交时，不同后代适合度可能不同(Huangfu et al., 2009)。

前期Huangfu等(2011)研究了江苏句容市茅山、江苏南通市、青海西宁市和陕西西安市的野芥菜与抗草甘膦转基因油菜的杂交后代F_1的适合度发现，句容市、南通市、西宁市和西安市种群F_1的每角果饱粒数分别为0.25、0.19、0.15和0.18，句容市种群F_1的每角果饱粒数显著高于南通市、西宁市和西安市种群F_1，但F_1的繁育能力显著低于野芥菜。本课题组接着以F_1与4个不同种群野芥菜回交，得到正向回交2代(野芥菜为母本)和反向回交2代(野芥菜为父本)。本研究在温室和田间条件下测定了4个不同种群正向和反向回交2代的适合度。明确在相同环境下不同种群回交2代的适合度，以及各回交2代与各自的亲本野芥菜之间的差异。研究结果将为抗性基因从转基因油菜渗入不同种群野芥菜可能导致的生态后果提供依据，为转基因油菜环境释放的生态安全评估提供更深入的研究依据。

1 材料与方法

1.1 实验材料

4个种群野芥菜(*Brassica juncea*)的来源见表1，抗草甘膦转基因油菜(DS-Roughrider, Roundup Ready, event RT73, 加拿大)。以4种野芥菜为母本，抗草甘膦转基因油菜为父本，得到4种F_1，F_1和相应的野芥菜进行回交(正向: 野芥菜作母本为m; 反向: 野芥菜作父本为p)，分别得到正向和反向回交1代(BC1mF_1和BC1pF_1)，回交1代和相应的野芥菜进行回交，分别得到正向和反向回交2代(BC2mF_1和BC2pF_1)。

1.2 实验方法

温室试验在南京农业大学进行。经过41%草甘膦异丙胺盐水剂(农达, 美国孟山都公司生产) 1 400 g(a.i)/hm^{2}筛选后，选择发育良好的幼苗移栽盆钵。移栽后各材料的存活率均为100%。盆钵中所用土壤来源一致，均为菜园土，与腐殖质按质量比为1∶1混合均匀，所用盆钵大小一致(口径23 cm, 深24 cm)。每盆移栽1株。每种群野芥菜及各自的BC2F_1分别移栽30株。

筛选后选择发育良好的幼苗按照试验设计进行田间小区移栽。小区面积为3 m^2，移栽密度为5株/m^2，每小区移栽15株，重复3次，株距为40 cm，行距为50 cm。

1.3 抗性基因的分子检测方法

DNA提取、抗草甘膦基因5-烯醇式丙酮酰-莽草酸-3磷酸合成酶(5-enolpyruvyl-shikimate-3-phosphate synthase, *EPSPS*)的检测方法及体系参考郑爱

表1 野芥菜种群及采集地点

Table 1 Population of wild *Brassica juncea* and collection sites

种群名称 Name of population	采样点 Sampling sites	生境 Habits	经纬度 Longitude/Latitude
JR	江苏句容市 Jurong, Jiangsu	山顶 Top of mountain	119°10′/31°57′
NT	江苏南通市 Nantong, Jiangsu	小麦田 Wheat field	120°51′/32°01′
XN	青海西宁市 Xining, Qinghai	油菜田 Oilseed rape field	101°43′/36°34′
XI	陕西西安市 Xi'an, Shaanxi	玉米田 Corn field	109°03′/34°14′

琴等(2014)，引物见表2。

1.4 适合度成分测量

所测营养生长期指标包括株高、单株1次分枝数、茎粗。生殖生长期指标包括角果长、每角果饱粒数、单株有效角果数、单株种子重。测定方法参考王晓蕾等(2017)。莲座状直径测定方法：刚抽薹时，用直尺测量莲座状叶片的最大直径；叶绿素荧光测定方法：盛花期，用叶绿素荧光仪(Handy PEA植物效率分析仪)测定原初光能转化率*Fv*/*Fm*，每株取倒三叶的中部中脉两侧测定，5次重复。

1.5 数据的统计分析

回交2代与野芥菜的比较，以各自亲本野芥菜的各适合度成分为标准"1"，回交2代的各项适合度成分与亲本野芥菜相应适合度成分之比为回交2代该适合度成分的相对适合度值，总适合度值=Σ(各指标相对适合度值)/9。4个种群回交2代的比较，以南通市种群的回交2代适合度成分为标准"1"，方法同上。

2 结果与分析

2.1 分子检测

对抗草甘膦转基因油菜、4个种群野芥菜和$BC2F_1$进行PCR特异性引物扩增，得到527 bp的条带(图1)。各$BC2mF_1$和$BC2pF_1$扩增结果与抗草甘膦转基因油菜结果一致，在野芥菜中未检测到目的条带。

2.2 温室条件下的适合度比较

温室条件下各适合度指标的测定结果如表3。$JRBC2mF_1$的莲座状直径比野芥菜低3.16 cm；$JRBC2pF_1$的株高比野芥菜低15.24 cm，而单株1次分枝数和单株种子重量高于野芥菜1.9和1.352 g，$JRBC2mF_1$和$JRBC2pF_1$的总适合度为0.99和1.06，与野芥菜无显著差异。尽管$NTBC2mF_1$在株高和角果长显著高于野芥菜9.92%与6.75%，但是在莲座状直径、叶绿素荧光和茎粗显著低于野芥菜10.41%、2.77%和16.67%；$NTBC2pF_1$在株高、单株1次分枝数、角果长和每角果饱粒数都显著高于野芥菜17.17%、31.15%、10.91%和9.39%，而茎粗和单株有效角果数显著低于野芥菜20.83%和20.15%，$NTBC2mF_1$和$NTBC2pF_1$的总适合度为0.96和1.02，与野芥菜无显著差异。$XNBC2mF_1$在株高、莲座状直径和每角果饱粒数都显著低于野芥菜8.67%、21.51%和7.72%；$XNBC2pF_1$在角果长和单株种子重量显著高于野芥菜12.63%和44.71%，$XNBC2mF_1$和$XNBC2pF_1$的总适合度为0.92和1.08，与野芥菜无显著差异。尽管$XIBC2mF_1$在莲座状直径和角果长显著高于野芥菜27.94%和5.52%，但是在叶绿素荧光*Fv*/*Fm*、每角果饱粒数、单株有效角果数和单株种子重量分别低于野芥菜3.62%、6.38%和25.93%、和31.29%，达显著差异($P<0.5$)；$XIBC2pF_1$各项适合度指标均与野芥菜相当，因此$XIBC2mF_1$和$XIBC2pF_1$的总适合度为0.94和1.05，与野芥菜无显著差异。

表2 PCR序列扩增引物

Table 2 Primers for PCR sequence amplification

引物名称 Primer name	引物序列(5'~3') Primer sequence
EPSPS-F	AAGGCATTCATTCCCATTTG
EPSPS-R	TAACATCTTCACCTTCCAAAAG

2.3 田间条件下的适合度比较

田间条件下各适合度指标的测定结果如表4。$JRBC2mF_1$的单株有效角果数比野芥菜多275.38个，其他指标均与野芥菜相当，总适合度为1.17，与

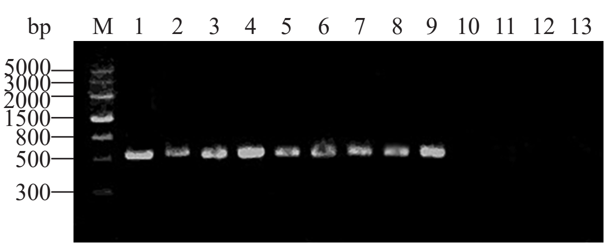

图1 PCR扩增抗草甘膦转基因油菜、4个种群野芥菜及其回交2代的*EPSPS*基因

Figure 2 PCR amplification of *EPSPS* gen from glyphosate-tolerant oilseed rape, 4 population wild *B. juncea* and their second backcross generations

M：DL5000 DNA Marker；1：抗草甘膦转基因油菜；2~5：$BC2mF_1$(句容市，南通市，西宁市，西安市)；6~9：$BC2pF_1$(句容市，南通市，西宁市，西安市)；10~13：野芥菜(句容市，南通市，西宁市，西安市)

1: Transgenic glyphosate-tolerant oilseed rape; 2~5: $BC2mF_1$ (JR, NT, XN, XI); 6~9: $BC2pF_1$ (JR, NT, XN, XI); 10~13: Wild *B. juncea* (JR, NT, XN, XI)

野芥菜相当；JRBC2pF_1的株高、莲座状直径、茎粗、单株有效角果数和单株种子重量高于野芥菜22.74%、64.57%、48.57%、132.18%和187.44%，使得JRBC2pF_1的总适合度为1.52，显著高于野芥菜。NTBC2mF_1的每角果饱粒数、单株有效角果数和单株种子重量显著高于野芥菜49.88%、67.52%、233.25%，使得NTBC2mF_1的总适合度为1.43，显著高于野芥菜(P<0.5)；NTBC2pF_1的叶绿素荧光*Fv*/*Fm*低于野芥菜0.046，而茎粗比野芥菜粗0.4 cm，NTBC2pF_1的总适合度为1.12，与野芥菜无显著差异。XNBC2mF_1的莲座状直径比野芥菜低3.57 cm，而每角果饱粒数比野芥菜多3.05粒，XNBC2mF_1总适合度为1.06，与野芥菜无显著差异；尽管XNBC2pF_1的莲座状直径低于野芥菜37.49%，但是每角果饱粒数、单株有效角果数和单株种子重量高于野芥菜48.93%、81.58%和155.01%，使得XN-

表3　温室条件下4个种群野芥菜及其与抗草甘膦油菜回交2代的适合度成分及总适合度比较

Table 3　Comparison on fitness components and composite fitness of 4 populations wild *Brassica juncea* and their second backcross generations with glyphosate-resistant oilseed rape in greenhouse

实验材料 Experiment material	株高/cm Plant height	莲座状直径/cm Diameter of plant rosette	叶绿素荧光*Fv*/*Fm* Chlorophll fluorescence *Fv*/*Fm*	茎粗/cm Stem diameter	单株1次分枝数 The first branch number/plant	角果长/cm Silique length	每角果饱粒数 Seed number /silique	单株有效角果数 Silique number /plant	单株种子重量/g Total seed weight /plant	总适合度 Composite fitness
JR BC2mF_1	129.54±2.80a	19.64±0.93b	0.81±0.01a	0.94±0.04a	6.30±0.37b	4.12±0.04a	15.54±0.15a	283.20±12.86a	6.46±0.41ab	0.99a
JR BC2pF_1	112.86±2.49b	24.62±0.79a	0.83±0.01a	0.96±0.05a	8.80±0.29a	3.99±0.05a	15.15±0.23a	311.80±14.09a	6.97±0.38a	1.06a
野芥菜 Wild *B. juncea*	128.10±2.94a	22.80±0.72a	0.80±0.01a	0.98±0.07a	6.90±0.50b	4.00±0.05a	14.95±0.34a	290.10±26.41a	5.61±0.47b	1.00a
NT BC2mF_1	106.97±4.05a	18.51±0.79b	0.81±0.01b	0.80±0.04b	6.10±0.28b	4.11±0.06a	14.73±0.24b	285.20±12.11ab	5.92±0.30a	0.96a
NT BC2pF_1	114.03±2.50a	19.16±0.66ab	0.81±0.01ab	0.76±0.05b	8.00±0.49a	4.27±0.07a	16.43±0.28a	251.20±9.78b	6.36±0.34a	1.02a
野芥菜 Wild *B. juncea*	97.32±2.72b	20.66±0.53a	0.83±0.02a	0.96±0.05a	6.10±0.23b	3.85±0.13b	15.02±0.17b	314.60±15.40a	6.41±0.40a	1.00a
XN BC2mF_1	114.62±4.13b	17.19±1.01b	0.82±0.01a	0.92±0.05b	5.90±0.23a	3.75±0.06b	14.23±0.32b	283.00±16.67a	4.31±0.40b	0.92b
XN BC2pF_1	128.61±3.14a	20.18±0.84a	0.82±0.01a	1.08±0.04a	6.80±0.47a	4.19±0.08a	15.72±0.26a	304.45±14.78a	7.09±0.41a	1.08a
野芥菜 Wild *B. juncea*	125.50±3.92a	21.90±0.73a	0.82±0.01a	0.98±0.04ab	6.80±0.39a	3.72±0.07b	15.42±0.36a	291.60±11.46a	4.90±0.34b	1.00ab
XI BC2mF_1	118.71±3.08b	22.12±1.19a	0.80±0.02b	0.90±0.07a	6.00±0.45b	4.40±0.07a	16.73±0.22b	269.80±12.71b	5.25±0.35b	0.94b
XI BC2pF_1	127.30±2.34a	19.79±0.95ab	0.840±0.01a	1.02±0.05a	7.40±0.31a	4.30±0.06ab	17.13±0.39ab	395.25±23.46a	7.53±0.58a	1.05a
野芥菜 Wild *B. juncea*	124.89±2.36ab	17.29±0.53b	0.83±0.01a	0.92±0.04a	6.60±0.22ab	4.17±0.04b	17.87±0.24a	364.25±17.90a	7.64±0.32a	1.00ab

JR/NT/XN/XI BC2mF_1和BC2pF_1：句容市、南通市、西宁市、西安市种群正向回交2代和反向回交2代；数据为平均值±标准误。同列不同字母表示野芥菜与其后代差异显著(P<0.05)；下同

JR/NT/XN/XI BC2mF_1 和 BC2pF_1: Jurong/Nantong/Xining/Xi'an of forward and reverse the second backcross generations; Values are $\overline{X}$±*SD* error. The different letters within the same column denote significant differences among wild *Brassica juncea* and its backcross generations at P<0.05; The same below

BC2pF$_1$的总适合度为1.33，显著高于野芥菜(P<0.5)。虽然XIBC2mF$_1$的株高高于野芥菜25.53%，但是XIBC2mF$_1$的单株种子重量和每角果饱粒数低于野芥菜57.34%和25.55%，达显著差异(P<0.5)；XIBC2pF$_1$的株高比野芥菜高17.4 cm，莲座状直径比野芥菜粗4.57 cm，而XIBC2pF$_1$的单株种子重量低于野芥菜10.775 g，XIBC2mF$_1$和XIBC2mF$_1$总适合度为0.92和0.96，与野芥菜无显著差异。

2.4 4个种群野芥菜回交后代间的总适合度比较

在温室条件下，JRBC2mF$_1$的总适合度明显大于XNBC2mF$_1$和NTBC2mF$_1$，而与XIBC2mF$_1$相当；XIBC2pF$_1$的总适合度显著高于NTBC2pF$_1$ (P<0.5)，但与JRBC2pF$_1$和XNBC2pF$_1$相当(图2A)。田间条件下，JRBC2mF$_1$、NTBC2mF$_1$和XIBC2mF$_1$的总适合度相当，均显著高于XNBC2mF$_1$ (P<0.5)；JRBC2pF$_1$的总适合度最大，明显高于NT-BC2pF$_1$、XNBC2pF$_1$和XIBC2pF$_1$ (P<0.5)(图2B)。

3 讨论

抗除草剂转基因油菜的发展十分迅速，但也隐藏着一系列生态风险，其中抗性基因渗入到野生近缘种的问题备受关注(Scheffler et al., 1994; Gressel., 2010; Liu et al., 2013; 闫静等, 2018)。转基因作物和野生近缘种发生初始杂交是抗性基因渗入野生近缘种的决定性因素(Darmency et al., 1998;

表4 田间条件下4个种群野芥菜及其与抗草甘膦油菜回交2代的适合度成分及总适合度比较

Table 4 Comparison on fitness components and composite fitness of 4 populations wild *Brassica juncea* and their second backcross generations with glyphosate-resistant oilseed rape in field

实验材料 Experiment material	株高/cm Plant height	莲座状直径/cm Diameter of plant rosette	叶绿素荧光 Fv/Fm Chlorophll fluorescence	茎粗/cm Stem diameter	单株1次分枝数 The first branch number/plant	角果长/cm Silique length	每角果饱粒数 Seed number/silique	单株有效角果数 Silique number/plant	单株种子重量/g Total seed weight/plant	总适合度 Composite fitness
JR BC2mF$_1$	95.30±5.78b	16.38±1.18b	0.83±0.01a	1.07±0.18b	8.40±0.56b	3.94±0.08a	16.13±0.65a	781.38±106.52b	15.80±4.03b	1.17b
JR BC2pF$_1$	109.85±3.24a	27.17±3.09a	0.79±0.01b	1.56±0.20a	10.60±0.60a	3.81±0.17a	15.53±0.92a	1174.83±78.87a	24.66±2.26a	1.52a
野芥菜 Wild *B. juncea*	89.50±3.57b	16.51±1.05b	0.82±0.01ab	1.05±0.09b	9.40±0.43ab	3.96±0.05a	14.08±0.49a	506.00±54.61c	8.58±1.39b	1.00b
NT BC2mF$_1$	88.67±4.29a	20.15±1.25a	0.78±0.01ab	1.07±0.03ab	7.70±0.47a	3.97±0.13a	13.63±0.81a	715.33±99.55a	12.55±1.66a	1.43a
NT BC2pF$_1$	89.85±3.36a	19.59±1.35a	0.74±0.02b	1.27±0.15a	8.80±0.85a	3.62±0.10a	10.84±0.66b	353.88±40.69b	5.85±2.07b	1.12ab
野芥菜 Wild *B. juncea*	82.78±5.83a	19.37±1.35a	0.79±0.01a	0.87±0.13b	8.10±0.55a	3.70±0.25a	9.28±0.41b	427.00±119.52b	3.77±1.01b	1.00b
XN BC2mF$_1$	77.12±3.40a	14.30±0.92b	0.77±0.02a	0.66±0.06a	6.90±0.50a	3.50±0.06b	12.45±0.35b	314.00±6.35b	7.39±0.09ab	1.06b
XN BC2pF$_1$	86.95±6.19a	11.17±0.62b	0.79±0.01a	0.84±0.15a	8.20±0.59a	4.05±0.01a	14.00±0.60a	587.40±61.19a	11.09±1.20a	1.33a
野芥菜 Wild *B. juncea*	81.08±4.98a	17.87±1.63a	0.81±0.01a	0.69±0.08a	8.00±0.64a	3.42±0.05b	9.40±0.58c	323.50±61.37b	4.35±0.84b	1.00b
XI BC2mF$_1$	112.10±5.10a	16.28±1.13b	0.80±0.01a	1.10±0.08a	8.60±0.40a	3.92±0.08a	9.73±0.54b	584.38±64.69a	8.94±1.86b	0.92a
XI BC2pF$_1$	106.70±4.33a	20.31±1.56a	0.80±0.01a	1.05±0.18a	8.90±0.82a	3.93±0.12a	10.88±1.57ab	620.83±189.59a	10.17±3.30b	0.96a
野芥菜 Wild *B. juncea*	89.30±5.22b	15.74±1.13b	0.78±0.02a	1.07±0.11a	8.10±0.57a	3.82±0.12a	13.07±0.41a	873.83±99.42a	20.94±1.77a	1.00a

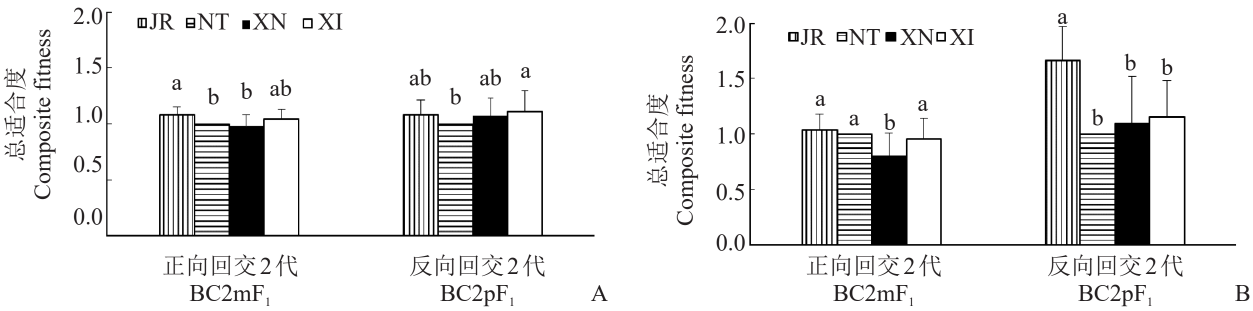

图2 温室(A)和田间(B)条件下抗草甘膦转基因油菜与4个种群野芥菜的回交2代总适合度的比较

Figure 2 Comparison on composite fitness of the second backcross generations between 4 populations wild *Brassica juncea* and glyphosate-resistant oilseed rape in greenhouse (A) and in field (B)

JR：句容市；NT：南通市；XN：西宁市；XI：西安市。不同字母表示正向或反向回交2代之间差异显著(P＜0.05)；下同

JR: Jurong; NT: Nantong; XN: Xining; XI: Xi'an. The different letters denote BC2mF_1 or BC2pF_1 significant differences at P＜0.05; The same below

Hall et al., 2000; Wilkinson et al., 2009)。前人研究表明，在田间条件下，转基因油菜能与芥菜或野芥菜自发杂交。Bing等(1996)研究了甘蓝型油菜和芥菜在混种条件下杂交频率为3.13%。抗草甘膦转基因油菜与野芥菜在田间隔行种植条件下抗性基因的漂移率达到0. 014% (宋小玲, 2007)。因此商业化种植转基因抗除草剂油菜前需要全面深入评估其抗性基因向野芥菜的渗入。

抗性基因渗入还依赖于杂交或回交后代的适合度(Tang et al., 2018)。由于转基因油菜的近缘种芜菁(AA)和芥菜(AABB)与油菜有一个共同的A基因组，亲缘关系较近，因此已经有较多关于转基因油菜与这两种近缘种后代的适合度研究的报道。Halfhill等(2005)发现，在温室条件下，抗虫转基因油菜和芜菁的回交2代子1代的单株干生物量和单株种子重量显著低于芜菁。Ammitzbøll等(2005)报道在田间条件下，抗除草剂转基因油菜和芜菁回交1代的适合度比F_1有明显的提高。Snow等(1999)研究发现，抗除草剂转基因油菜和芜菁的回交3代的单株种子量与芜菁相当。就野芥菜，已有的报道表明，抗除草剂转基因油菜与江浦种群野芥菜的回交后代适合度会随着回交次数和自交代数的增加而提高(Song et al., 2010; 王建等, 2016; 王晓蕾等, 2017; 卞清等, 2017; 闫静等, 2018)。Tsuda等(2012)以转基因油菜和野芥菜为材料，研究发现F_1的结实率较低，但随着回交代数的增加结实率不断提高，回交2代和回交3代的结实率趋近于野芥菜。转基因油菜与不同近缘种的杂交和回交后代的适合度不同，这可能是由于亲本之间基因组的同源性差异引起的。

本课题组前期研究发现，西宁市、西安市、南通市和句容市4个种群野芥菜与抗草甘膦转基因油菜F_1的每角果饱粒数显著低于野芥菜(Huangfu等, 2011)。本研究继续评估了4个种群正向和反向回交2代的适合度，结果表明，4个种群的正向和反向回交2代在温室条件下均与野芥菜的适合度相似，在田间条件下均与野芥菜相似或高于野芥菜。特别是田间条件下，适合度较高的JRBC2pF_1，单株能够产生1 174个有效角果，每角果产生14粒饱满种子，单株能产生约16 436粒饱满种子；即使是适合度较低的XNBC2mF_1，单株也能产生约3 768粒种子。理论上讲，转基因油菜与野芥菜的回交后代染色体数不稳定，处于20(2A)+8(B)+0-8(B)+0-9(C)之间。在后代自交或回交的减数分裂过程中，C染色体组由于没有同源染色体配对逐渐丢失，后代染色体逐渐稳定，适合度也因此不断提高(Tsuda et al., 2012; 闫静, 2016)。回交2代产生的数量庞大的种子洒落之后可能会在土壤中建立种子库，并成为自生苗的来源。因此抗草甘膦转基因油菜向野芥菜的基因逃逸风险不容忽视。

亲本的基因型对后代的适合度也有影响(Simard et al., 2005)。Guèritaine等(2002)发现野萝卜为母本的回交6代比抗草丁膦转基因油菜为母本的回交6代的适合度高100倍。郑爱琴等(2014)以两种抗除草剂转基因油菜和野芥菜为材料，分别杂交得到F_1，将F_1与5种常规栽培油菜回交，发现在不同回交后代的茎粗、有效角果数和地上部干生物量存在差异。本研究中4个种群野芥菜的基因型

不同，可能是导致回交2代之间适合度不同的原因之一。温室条件下，JRBC2mF$_1$的总适合度显著高于NTBC2mF$_1$和XNBC2mF$_1$，XIBC2pF$_1$的总适合度显著高于NTBC2pF$_1$。田间条件下，JRBC2mF$_1$、NTBC2mF$_1$和XIBC2mF$_1$的总适合度相当，均显著高于XNBC2mF$_1$，JRBC2pF$_1$的总适合度高于其他3个种群。因此要注意避免转基因向不同种群野芥菜的基因渗入，特别要关注向后代适合度较高的野芥菜种群的基因渗入。

除亲本基因型的影响外，适合度也与环境因素有关，如种植比例、竞争和选择压等(Hauser et al., 2003; Halfhill et al., 2005; Londo et al., 2010)。Hauser等(2003)研究甘蓝型油菜、芜菁、F$_1$和回交1代在混种条件(2∶4∶1∶1)和单种条件下的单株种子量，发现甘蓝型油菜、芜菁和回交1代在单种条件下比混种条件下产生更多的种子，F$_1$在混种时比单种产生更多的种子。Mercer等(2007)发现，无竞争条件下野生向日葵(*Helianthus annuus*)与抗磺酰脲类转基因向日葵的杂交1代与野生向日葵的种子量比与小麦(*Triticum aestivum*)竞争条件下均显著提高。Londo等(2010)发现草甘膦雾滴漂移时，抗草甘膦转基因油菜的适合度以及其与芜菁回交1代的适合度比无抗草甘膦雾滴漂移时提高。本研究并没有对竞争条件、不同密度条件以及除草剂选择压下的适合度进行评价，有待于进一步研究。

本研究发现，在温室条件下4个种群野芥菜回交2代的总适合度与野芥菜相当，但在田间条件下JRBC2pF$_1$、NTBC2mF$_1$和XNBC2pF$_1$的总适合度显著高于相应的野芥菜，主要是由于这3种回交2代在田间条件下的单株有效角果数及单株种子重量提高导致的，这说明环境条件对4种野芥菜回交2代的适合度影响并不完全相同。这3种回交2代在田间的结实率更高，因此在田间条件下生存定植的可能性更大。

Snow等(1999)研究抗草丁膦油菜和芜菁的回交3代的在无选择压下的适合度，结果表明，抗性植株和敏感植株的生存和繁殖能力没有明显差异，说明无选择压下的适合度的优势不一定是转基因带来的。杂交产生亚基因组后也能表现出优势(朱家立, 2010; Qian et al., 2005; 2007)。由于本研究仅在无除草剂选择压下研究了抗草甘膦转基因油菜与野芥菜的抗性回交2代的适合度，因此还需要研究受体油菜与野芥菜回交2代的适合度，比较转基因油菜和受体油菜与野芥菜回交2代适合度的差异。但如果在草甘膦选择压下，受体油菜与野芥菜的回交2代由于没有抗性基因而无法存活，抗草甘膦转基因油菜与野芥菜的回交2代的表达抗性的植株却能存活下来，因此抗草甘膦转基因油菜的抗性基因向野芥菜渗入可能带来的生态风险应该受到关注。

4 结论

4个种群野芥菜的正向和反向回交2代无论是在温室还是在田间条件下均具有与野芥菜相似或高于野芥菜的适合度，因此都具有在野外生存定植的可能性。虽然回交2代适合度受野芥菜基因型的影响，但这些回交2代单株至少能产生3 700粒饱满种子，这些种子洒落田间，在土壤中形成种子库，萌发后还能与野芥菜不断回交从而完成抗性基因向野芥菜的渗入。在大面积种植转基因油菜时，务必要防范转基因向各种群野芥菜的基因漂移，特别要关注向后代适合度较高的野芥菜种群的基因漂移。

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