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复交组合种子性状杂种优势的预测方法

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摘要: 针对 $2n$ 种子和 $3n$ 胚乳数量性状的遗传特点, 在考虑种子核基因、细胞质基因和母体植株核基因 3 套遗传体系以及基因型 \times 环境互作效应的情形下, 分别提出了三交和双交组合种子性状杂种优势的预测方法, 给出了利用基因型值预测 F_n 代杂种优势的一般表达式。

关键词: 三交; 双交; 杂种优势预测; 种子遗传模型; 遗传效应分量; 基因型 \times 环境互作

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Approaches for predicting heterosis of quantitative seed traits based on multiple-cross mating designs.

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Abstract: According to the features of diploid and triploid inheritance pattern for quantitative seed traits, and considering three genetic systems of seed nuclear genes, cytoplasmic genes and maternal plant nuclear genes with genotype \times environment interactions, methods were proposed for predicting heterosis of seed characters based on the mating designs of three-way and four-way crosses. General formulae were derived for heterosis prediction of F_n generation by using the predicted genotypic values.

Key words: three-way crosses; four-way crosses (double cross); prediction of heterosis; genetic models for seed characters; components of genetic effects; genotype \times environment (GE) interactions

杂种优势预测是遗传育种学研究的一项重要的重要内容。Schnell 和 Cockerham^[1]综合评述了根据一定统计模型预测杂种优势的各类方法。由于杂种优势在不同环境下存在广泛的遗传变异^[2~4], 某一环境下的杂种优势应由两部分组成, 即不受环境影响的基因型优势 $H_M(F_n)$

和因环境不同而变异的环境互作优势 $H_{ME}(F_n)$, 可表示为杂种优势 = $H_M(F_n) + H_{ME}(F_n)$ ^[5]。现已提出了基于加性-显性模型^[5, 6]、加性-显性-上位性模型^[7]和种子模型^[5]分别预测单交组合农艺性状、种子性状杂种优势的新方法, 并在一些作物中得到了初步的应用。

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就复交方式而言,以往的研究侧重于三交和双交设计的遗传模型构建^[8~12]和农艺性状的杂种优势预测^[11, 12].与大多数农艺性状的遗传规律不同,关于种子及幼苗性状的遗传往往存在母体效应,这是因为种子的营养物质由母体植株提供,种子品质性状可能同时受到种子核基因、细胞质基因和母体植株核基因的控制^[5].本文在以前研究的基础上,针对三交和双交组合方式的遗传特点,提出复交设计种子数量性状的杂种优势预测方法,以期为农作物品质性状的遗传改良提供理论依据.

1 种子性状杂种优势预测的遗传模型

1.1 三交组合的种子模型

随机从某遗传群体中抽取一组纯系材料作为亲本,以三交方式(A×B)×C进行双列杂交,获得若干个三交组合.若假定不存在父体效应和上位性效应,且细胞质基因只通过母体稳定遗传,则第*i*个母本与第*j*个父本的杂交一代F_{1ij}和第*s*个亲本的第*k*种交配类型,在第*h*个环境、第*l*个区组中的平均表现型值可用线性模型^[10]表示.根据广义遗传模型建模原理^[5, 13],当*k*=2时,可写出三交一代F_{1ij}×P_s的遗传效应分量.对于双子叶植物如棉花、大豆、油菜的种子没有3*n*胚乳,其营养品质如蛋白质、油分等服从2*n*种子性状的遗传规律,其三交一代的遗传效应分量为:

$$G_{ijs2} = \frac{1}{2}A_i + \frac{1}{2}A_j + A_s + \frac{1}{2}D_{is} + \frac{1}{2}D_{js} + C_i + Am_i + Am_j + Dm_{ij}.$$

$$GE_{hjs2} = \frac{1}{2}AE_{hi} + \frac{1}{2}AE_{hj} + AE_{hs} + \frac{1}{2}DE_{his} + \frac{1}{2}DE_{hjs} + CE_{hi} + AmE_{hi} + AmE_{hj} + DmE_{hij}.$$

对于单子叶植物3*n*胚乳数量性状,例如稻米香味、糊化温度、直链淀粉含量;奥帕克-2玉米胚乳硬质度、蛋白质含量、赖氨酸含量等,需要采用胚乳性状遗传模型进行分析,其三交一代的遗传效应分量相应调整为:

$$G_{ijs2} = A_i + A_j + A_s + D_{is} + D_{js} + \frac{1}{2}D_{ii} + \frac{1}{2}D_{jj} + C_i + Am_i + Am_j + Dm_{ij}.$$

$$GE_{hjs2} = AE_{hi} + AE_{hj} + AE_{hs} + DE_{his} + DE_{hjs} + \frac{1}{2}DE_{hii} + \frac{1}{2}DE_{hjj} + CE_{hi} + AmE_{hi} + AmE_{hj} + DmE_{hij}.$$

上式中*A_i*、*A_j*或*A_s*~(0,σ_A²),是直接加性效应;*D_{ii}*、*D_{is}*或*D_{js}*~(0,σ_D²),是直接显性效应;*C_i*~(0,σ_C²),是细胞质效应;*Am_i*或*Am_j*~(0,σ_{Am}²),是母体加性效应;*Dm_{ii}*或*Dm_{ij}*~(0,σ_{Dm}²),是母体显性效应;*AE_{hi}*、*AE_{hj}*或*AE_{hs}*~(0,σ_{AE}²),是加性×环境互作效应;*DE_{hii}*、*DE_{his}*或*DE_{hjs}*~(0,σ_{DE}²),是显性×环境互作效应;*CE_{hi}*~(0,σ_{CE}²),是细胞质×环境互作效应;*AmE_{hi}*或*AmE_{hj}*~(0,σ_{AmE}²),是母体加性×环境互作效应;*DmE_{hii}*或*DmE_{hij}*~(0,σ_{DmE}²),是母体显性×环境互作效应.

1.2 双交组合的种子模型

设一组纯合亲本按双交方式(A×B)×(C×D)进行交配设计,在考虑细胞质和母体效应的情况下,若假定不存在父体效应和上位性效应,则任意4个独立亲本*i*、*j*、*s*、*t*组配的双交组合F_{1ijst}的第*k*种交配类型,在第*l*个区组中的平均表现型值可用线性模型^[10]表示.对于2*n*种子性状,其双交一代F_{1ijst}=F_{1ij}×F_{1st}的遗传效应分量为:

$$G_{ijst2} = \frac{1}{2}A_i + \frac{1}{2}A_j + \frac{1}{2}A_s + \frac{1}{2}A_t + \frac{1}{4}D_{is} + \frac{1}{4}D_{js} + \frac{1}{4}D_{it} + \frac{1}{4}D_{jt} + C_i + Am_i + Am_j + Dm_{ij}.$$

$$GE_{hijst2} = \frac{1}{2}AE_{hi} + \frac{1}{2}AE_{hj} + \frac{1}{2}AE_{hs} + \frac{1}{2}AE_{ht} + \frac{1}{4}DE_{his} + \frac{1}{4}DE_{hjs} + \frac{1}{4}DE_{hit} + \frac{1}{4}DE_{hjt} + CE_{hi} + AmE_{hi} + AmE_{hj} + DmE_{hij}.$$

对于3*n*胚乳性状,其双交一代的遗传效应分量相应调整为:

$$G_{ijst2} = A_i + A_j + \frac{1}{2}A_s + \frac{1}{2}A_t + \frac{1}{2}D_{ii} + \frac{1}{2}D_{jj} + \frac{1}{2}D_{is} + \frac{1}{2}D_{js} + \frac{1}{2}D_{it} + \frac{1}{2}D_{jt} + C_i +$$

$$Am_i + Am_j + Dm_{ij}.$$

$$GE_{hijs2} = AE_{hi} + AE_{hj} + \frac{1}{2}AE_{hs} + \frac{1}{2}AE_{ht} + \frac{1}{2}DE_{hii} + \frac{1}{2}DE_{hjj} + \frac{1}{2}DE_{his} + \frac{1}{2}DE_{hjs} + \frac{1}{2}DE_{hit} + \frac{1}{2}DE_{hjt} + CE_{hi} + AmE_{hi} + AmE_{hj} + DmE_{hij}.$$

三交和双交组合二倍体种子或三倍体胚乳性状的各遗传效应分量, 均可采用 AUP 法^[5] 进行无偏预测.

2 三交组合种子性状杂种优势的预测方法

2.1 基于三交组合的 2n 种子模型

$$\begin{aligned} \text{令 } \omega_A &= (A_j - A_s), \Delta_{D_{is}} = D_{is} - \frac{1}{2}(D_{ii} + D_{ss}), \Delta_{D_{js}} = D_{js} - \frac{1}{2}(D_{jj} + D_{ss}), \Delta_{D_{ij}} = D_{ij} - \frac{1}{2}(D_{ii} + D_{jj}), \omega_C = (C_i - C_s), \omega_{Am} = (Am_j - Am_i), \Delta_{Dm_{is}} = Dm_{is} - \frac{1}{2}(Dm_{ii} + Dm_{ss}), \Delta_{Dm_{js}} = Dm_{js} - \frac{1}{2}(Dm_{jj} + Dm_{ss}). \end{aligned}$$

对双子叶植物二倍体种子数量性状而言, 各世代的平均优势为:

$$\begin{aligned} H_M(F_1) &= G(F_{1ijs}) - \frac{1}{2}[G(F_{1ij}) + G(P_s)] = \frac{1}{2}[(D_{is} + D_{js}) - (D_{ij} + D_{ss})] + \frac{1}{2}(C_i - C_s) + (Am_j - Am_s) + [Dm_{ij} - \frac{1}{2}(Dm_{ii} + Dm_{ss})] = \frac{1}{2}(\Delta_{D_{is}} + \Delta_{D_{js}} - \Delta_{D_{ij}}) + \frac{1}{2}\omega_C + (Am_j - Am_s) + [Dm_{ij} - \frac{1}{2}(Dm_{ii} + Dm_{ss})]. \end{aligned}$$

$$\begin{aligned} H_M(F_2) &= G(F_{2ijs}) - \frac{1}{2}[G(F_{1ij}) + G(P_s)] = (\frac{1}{4}D_{is} + \frac{1}{4}D_{js} + \frac{1}{8}D_{ii} + \frac{1}{8}D_{jj} - \frac{1}{2}D_{ij} - \frac{1}{4}D_{ss}) + \frac{1}{2}(C_i - C_s) + \frac{1}{2}(Am_j - Am_i) + \frac{1}{2}[(Dm_{is} + Dm_{js}) - (Dm_{ii} + Dm_{ss})] = \frac{1}{4}(\Delta_{D_{is}} + \Delta_{D_{js}} - 2\Delta_{D_{ij}}) + \frac{1}{2}\omega_C + \frac{1}{2}(Am_j - Am_i) + \frac{1}{2}[(Dm_{is} + Dm_{js}) - (Dm_{ii} + Dm_{ss})]. \end{aligned}$$

$$\Delta_{D_{is}} - 2\Delta_{D_{ij}}) + \frac{1}{2}\omega_C + \frac{1}{2}\omega_{Am} + \frac{1}{2}[(\Delta_{Dm_{is}} + \Delta_{Dm_{js}}) - \frac{1}{2}(Dm_{ii} - Dm_{jj})].$$

$$\begin{aligned} H_M(F_3) &= G(F_{3ijs}) - \frac{1}{2}[G(F_{1ij}) + G(P_s)] = (\frac{1}{8}D_{is} + \frac{1}{8}D_{js} + \frac{3}{16}D_{ii} + \frac{3}{16}D_{jj} - \frac{1}{2}D_{ij} - \frac{1}{8}D_{ss}) + \frac{1}{2}(C_i - C_s) + \frac{1}{2}(Am_j - Am_i) + \frac{1}{4}[(Dm_{is} + Dm_{js}) - (\frac{3}{2}Dm_{ii} - \frac{1}{2}Dm_{jj} + Dm_{ss})] = \frac{1}{8}(\Delta_{D_{is}} + \Delta_{D_{js}} - 4\Delta_{D_{ij}}) + \frac{1}{2}\omega_C + \frac{1}{2}\omega_{Am} + \frac{1}{4}[(\Delta_{Dm_{is}} + \Delta_{Dm_{js}}) - (Dm_{ii} - Dm_{jj})]. \end{aligned}$$

依次类推, 二倍体种子 F_n 代的平均优势 $H_M(F_n)$ 为:

$$\begin{aligned} H_M(F_n) &= G(F_{n ijs}) - \frac{1}{2}[G(F_{1ij}) + G(P_s)] = (\frac{1}{2})^n (\Delta_{D_{is}} + \Delta_{D_{js}} - 2^{n-1}\Delta_{D_{ij}}) + \frac{1}{2}\omega_C + \frac{1}{2}\omega_{Am} + (\frac{1}{2})^{n-1}[(\Delta_{Dm_{is}} + \Delta_{Dm_{js}}) - 2^{n-3}(Dm_{ii} - Dm_{jj})]. \end{aligned}$$

其中, $n \geq 2$. 同理, 二倍体种子 F_n 代的平均优势互作离差 $H_{ME}(F_n)$ 为:

$$\begin{aligned} H_{ME}(F_n) &= GE(F_{nhijs}) - \frac{1}{2}[GE(F_{1hij}) + GE(P_{hs})] = (\frac{1}{2})^n (\Delta_{DE_{his}} + \Delta_{DE_{hjs}} - 2^{n-1}\Delta_{DE_{hij}}) + \frac{1}{2}\omega_{CE} + \frac{1}{2}\omega_{AmE} + (\frac{1}{2})^{n-1}[(\Delta_{DmE_{his}} + \Delta_{DmE_{hjs}}) - 2^{n-3}(DmE_{hii} - DmE_{hjj})]. \end{aligned}$$

式中, $n \geq 2$. 由此可见, 二倍体种子性状的遗传较为复杂, 其平均优势不仅与直接显性效应有关, 而且与细胞质、母体加性、母体显性及其与环境互作效应均有关系.

2.2 基于三交组合的 3n 胚乳模型

对单子叶植物三倍体胚乳数量性状而言, 各世代的平均优势为:

$$\begin{aligned} H_M(F_1) &= G(F_{1ijs}) - \frac{1}{2}[G(F_{1ij}) + G(P_s)] = \frac{1}{2}(A_j - A_s) + (D_{is} + D_{js} - D_{ij} + \frac{1}{2}D_{jj} - \frac{3}{2}D_{ss}) + \frac{1}{2}(C_i - C_s) + (Am_j - Am_s) + [Dm_{ij} - \end{aligned}$$

$$\frac{1}{2}(Dm_{ii} + Dm_{ss})] = \frac{1}{2}\omega_A + [(\Delta_{D_{is}} + \Delta_{D_{js}} - \Delta_{D_{ij}}) - \frac{1}{2}(D_{ss} - D_{jj})] + \frac{1}{2}\omega_C + (Am_j - Am_s) + [Dm_{ij} - \frac{1}{2}(Dm_{ii} + Dm_{ss})].$$

$$H_M(F_2) = G(F_{2ijs}) - \frac{1}{2}[G(F_{1ij}) + G(P_s)] = \frac{1}{2}(A_j - A_s) + \frac{1}{2}(D_{is} + D_{js} - 2D_{ij} + D_{jj} - D_{ss}) + \frac{1}{2}(C_i - C_s) + \frac{1}{2}(Am_j - Am_i) + \frac{1}{2}[(Dm_{is} + Dm_{js}) - (Dm_{ii} + Dm_{ss})] = \frac{1}{2}\omega_A + \frac{1}{2}[(\Delta_{D_{is}} + \Delta_{D_{js}} - 2\Delta_{D_{ij}}) - \frac{1}{2}(D_{ii} - D_{jj})] + \frac{1}{2}\omega_C + \frac{1}{2}\omega_{Am} + \frac{1}{2}[(\Delta_{Dm_{is}} + \Delta_{Dm_{js}}) - \frac{1}{2}(Dm_{ii} - Dm_{jj})].$$

$$H_M(F_3) = G(F_{3ijs}) - \frac{1}{2}[G(F_{1ij}) + G(P_s)] = \frac{1}{2}(A_j - A_s) + \frac{1}{4}(D_{is} + D_{js} - 4D_{ij} + \frac{1}{2}D_{ii} + \frac{5}{2}D_{jj} - D_{ss}) + \frac{1}{2}(C_i - C_s) + \frac{1}{2}(Am_j - Am_i) + \frac{1}{4}[(Dm_{is} + Dm_{js}) - (\frac{3}{2}Dm_{ii} - \frac{1}{2}Dm_{jj} + Dm_{ss})] = \frac{1}{2}\omega_A + \frac{1}{4}[(\Delta_{D_{is}} + \Delta_{D_{js}} - 4\Delta_{D_{ij}}) - (D_{ii} - D_{jj})] + \frac{1}{2}\omega_C + \frac{1}{2}\omega_{Am} + \frac{1}{4}[(\Delta_{Dm_{is}} + \Delta_{Dm_{js}}) - (Dm_{ii} - Dm_{jj})].$$

依次类推,三倍体胚乳 F_n 代的平均优势 $H_M(F_n)$ 为:

$$H_M(F_n) = G(F_{n ijs}) - \frac{1}{2}[G(F_{1ij}) + G(P_s)] = \frac{1}{2}\omega_A + (\frac{1}{2})^{n-1}[(\Delta_{D_{is}} + \Delta_{D_{js}} - 2^{n-1}\Delta_{D_{ij}}) - 2^{n-3}(D_{ii} - D_{jj})] + \frac{1}{2}\omega_C + \frac{1}{2}\omega_{Am} + (\frac{1}{2})^{n-1}[(\Delta_{Dm_{is}} + \Delta_{Dm_{js}}) - 2^{n-3}(Dm_{ii} - Dm_{jj})].$$

这里, $n \geq 2$. 由上式可见,与二倍体种子性状的平均优势相比较,三倍体胚乳性状的平均优势除与直接显性、细胞质、母体加性、母体显性效应有关以外,还与直接加性效应有关,包含了全部遗传效应分量.

同理,三倍体胚乳 F_n 代的平均优势互作离

差 $H_{ME}(F_n)$ 为:

$$H_{ME}(F_n) = GE(F_{n ijs}) - \frac{1}{2}[GE(F_{1ij}) + GE(P_s)] = \frac{1}{2}\omega_{AE} + (\frac{1}{2})^{n-1}[(\Delta_{DE_{his}} + \Delta_{DE_{hjs}} - 2^{n-1}\Delta_{DE_{hij}}) - 2^{n-3}(DE_{hii} - DE_{hjj})] + \frac{1}{2}\omega_{CE} + \frac{1}{2}\omega_{AmE} + (\frac{1}{2})^{n-1}[(\Delta_{DmE_{his}} + \Delta_{DmE_{hjs}}) - 2^{n-3}(DmE_{hii} - DmE_{hjj})].$$

这里, $n \geq 2$. 二倍体种子和三倍体胚乳的平均优势除以群体平均数即可得到群体平均优势. 其超亲优势可仿平均优势类推.

3 双交组合种子性状杂种优势的预测方法

3.1 基于双交组合的 $2n$ 种子模型

令 $\Delta_{\bar{D}} = \frac{1}{4}(\Delta_{D_{is}} + \Delta_{D_{js}} + \Delta_{D_{it}} + \Delta_{D_{jt}})$, 其中 $\Delta_{D_{is}} = D_{is} - \frac{1}{2}(D_{ii} + D_{ss})$, $\Delta_{D_{js}} = D_{js} - \frac{1}{2}(D_{jj} + D_{ss})$, $\Delta_{D_{it}} = D_{it} - \frac{1}{2}(D_{ii} + D_{tt})$, $\Delta_{D_{jt}} = D_{jt} - \frac{1}{2}(D_{jj} + D_{tt})$, $\omega_C = C_i - \frac{1}{4}(C_i + C_j + C_s + C_t)$, $\Delta_{\bar{Dm}} = \frac{1}{4}(\Delta_{Dm_{is}} + \Delta_{Dm_{js}} + \Delta_{Dm_{it}} + \Delta_{Dm_{jt}})$, 其中, $\Delta_{Dm_{is}} = Dm_{is} - \frac{1}{2}(Dm_{ii} + Dm_{ss})$, $\Delta_{Dm_{js}} = Dm_{js} - \frac{1}{2}(Dm_{jj} + Dm_{ss})$, $\Delta_{Dm_{it}} = Dm_{it} - \frac{1}{2}(Dm_{ii} + Dm_{tt})$, $\Delta_{Dm_{jt}} = Dm_{jt} - \frac{1}{2}(Dm_{jj} + Dm_{tt})$.

对二倍体种子性状而言,各世代的平均优势为:

$$H_M(F_1) = G(F_{1ijst}) - \frac{1}{4}[G(P_i) + G(P_j) + G(P_s) + G(P_t)] = \frac{1}{4}[(D_{is} + D_{js} + D_{it} + D_{jt}) - (D_{ii} + D_{jj} + D_{ss} + D_{tt})] + \frac{1}{4}[3C_i - (C_j + C_s + C_t)] + \frac{1}{2}[(Am_i + Am_j) - (Am_s + Am_t)] +$$

$$[Dm_{ij} - \frac{1}{4}(Dm_{ii} + Dm_{jj} + Dm_{ss} + Dm_{uu})] = \Delta_{\bar{D}} + \omega_C + \frac{1}{2}[(Am_i + Am_j) - (Am_s + Am_t)] + [Dm_{ij} - \frac{1}{4}(Dm_{ii} + Dm_{jj} + Dm_{ss} + Dm_{uu})].$$

$$H_M(F_2) = G(F_{2ijst}) - \frac{1}{4}[G(P_i) + G(P_j) + G(P_s) + G(P_t)] = \frac{1}{8}[(D_{is} + D_{js} + D_{it} + D_{jt}) - (D_{ii} + D_{jj} + D_{ss} + D_{uu})] + \frac{1}{4}[3C_i - (C_j + C_s + C_t)] + \frac{1}{4}[(Dm_{is} + Dm_{js} + Dm_{it} + Dm_{jt}) - (Dm_{ii} + Dm_{jj} + Dm_{ss} + Dm_{uu})] = \frac{1}{2}\Delta_{\bar{D}} + \omega_C + \Delta_{\bar{Dm}}.$$

类似地, 双交 F_n 代的平均优势 $H_M(F_n)$ 为:

$$H_M(F_n) = G(F_{nijst}) - \frac{1}{4}[G(P_i) + G(P_j) + G(P_s) + G(P_t)] = (\frac{1}{2})^{n-1}\Delta_{\bar{D}} + \omega_C + (\frac{1}{2})^{n-2}\Delta_{\bar{Dm}}.$$

这里 $n \geq 2$, 即除 F_1 代外, 其余各世代均可用此通式预测二倍体种子性状的杂种优势. 同理, 双交组合的平均优势还应包括互作离差部分, 即 $H_M(F_n) + H_{ME}(F_n)$. 自 F_2 代开始, $2n$ 种子性状 F_n 代的平均优势互作离差 $H_{ME}(F_n)$ 为:

$$H_{ME}(F_n) = (\frac{1}{2})^{n-1}\Delta_{\bar{DE}} + \omega_{CE} + (\frac{1}{2})^{n-2}\Delta_{\bar{DmE}}.$$

$2n$ 种子性状的群体平均优势可表示为:

$$H_{PM}(F_n) + H_{PME}(F_n) = \frac{1}{\mu}[H_M(F_n) + H_{ME}(F_n)] = \frac{1}{\mu}[(\frac{1}{2})^{n-1}(\Delta_{\bar{D}} + \Delta_{\bar{DE}}) + (\omega_C + \omega_{CE}) + (\frac{1}{2})^{n-2}(\Delta_{\bar{Dm}} + \Delta_{\bar{DmE}})].$$

3.2 基于双交组合的 $3n$ 胚乳模型

对三倍体胚乳性状而言, 各世代的平均优势为:

$$H_M(F_1) = G(F_{1ijst}) - \frac{1}{4}[G(P_i) + G(P_j) + G(P_s) + G(P_t)] = \frac{1}{4}(A_i + A_j - A_s - A_t) + \frac{1}{2}[(D_{is} + D_{js} + D_{it} + D_{jt}) - \frac{1}{2}(D_{ii} + D_{jj} + 3D_{ss} + 3D_{uu})] + \frac{1}{4}[3C_i - (C_j + C_s + C_t)] + \frac{1}{2}(Am_i +$$

$$Am_j - Am_s - Am_t) + [Dm_{ij} - \frac{1}{4}(Dm_{ii} + Dm_{jj} + Dm_{ss} + Dm_{uu})].$$

$$H_M(F_2) = G(F_{2ijst}) - \frac{1}{4}[G(P_i) + G(P_j) + G(P_s) + G(P_t)] = \frac{1}{4}[(D_{is} + D_{js} + D_{it} + D_{jt}) - (D_{ii} + D_{jj} + D_{ss} + D_{uu})] + \frac{1}{4}[3C_i - (C_j + C_s + C_t)] + \frac{1}{4}[(Dm_{is} + Dm_{js} + Dm_{it} + Dm_{jt}) - (Dm_{ii} + Dm_{jj} + Dm_{ss} + Dm_{uu})] = \Delta_{\bar{D}} + \omega_C + \Delta_{\bar{Dm}}.$$

类似地, 双交 F_n 代的平均优势 $H_M(F_n)$ 为:

$$H_M(F_n) = G(F_{nijst}) - \frac{1}{4}[G(P_i) + G(P_j) + G(P_s) + G(P_t)] = (\frac{1}{2})^{n-2}\Delta_{\bar{D}} + \omega_C + (\frac{1}{2})^{n-2}\Delta_{\bar{Dm}}.$$

这里 $n \geq 2$, 与二倍体种子性状相类似, 自 F_2 代开始, 各世代杂种优势遵循一定的规律递减, 可用通式予以表示. 双交组合杂种优势的预测公式与单交组合杂种优势的预测公式^[5]形式上相似, 但所表述的具体遗传组成分量不同. 双交组合较某一优良自交系或某一优良单交组合的超亲优势也可类似地推导.

同理, 双交组合 $3n$ 胚乳性状的平均优势互作离差部分为:

$$H_{ME}(F_n) = (\frac{1}{2})^{n-2}\Delta_{\bar{DE}} + \omega_{CE} + (\frac{1}{2})^{n-2}\Delta_{\bar{DmE}}.$$

$3n$ 胚乳性状的群体平均优势可表示为:

$$H_{PM}(F_n) + H_{PME}(F_n) = \frac{1}{\mu}[H_M(F_n) + H_{ME}(F_n)] = \frac{1}{\mu}[(\frac{1}{2})^{n-2}(\Delta_{\bar{D}} + \Delta_{\bar{DE}}) + (\omega_C + \omega_{CE}) + (\frac{1}{2})^{n-2}(\Delta_{\bar{Dm}} + \Delta_{\bar{DmE}})].$$

4 结 语

根据二倍体种子和三倍体胚乳性状的遗传特点, 本文给出了预测三交和双交组合杂种平均优势及其与环境互作优势的通用公式, 可用于种子性状杂种优势的遗传分析. Xu 和 Zhu^[7]曾定义 Δ_D 为显性杂种优势, Δ_{AA} 为加性 \times 加性上位性杂种优势, Δ_{DE} 为显性 \times 环境互作杂种优

势, Δ_{AAE} 为加性 \times 加性 \times 环境互作杂种优势. 类似地, Δ_{Dm} 和 Δ_{DmE} 可分别定义为母体显性杂种优势和母体显性 \times 环境互作杂种优势. 一般地, 种子和胚乳性状杂种优势的遗传分析比农艺性状的遗传更为复杂, 几乎包括了全部的遗传效应分量. 此外, 需要指出的是, 杂种优势的预测结果因公式推导的出发点不同而有差异, 以三交组合为例, 以亲本单交种和另一自交系为基础推导时, $2n$ 种子性状的平均优势与直接加性效应无关, 以 3 个亲本自交系为基础推导时则有关, 后者可由下式看出:

$$H_M(F_1) = G(F_{1ijs}) - \frac{1}{3}[G(P_i) + G(P_j) + G(P_s)] = \frac{1}{6}(2A_s - A_i - A_j) + \frac{1}{6}(3D_{is} + 3D_{js} - 2D_{ii} - 2D_{jj} - D_{ss}) + \frac{1}{3}(2C_i - C_j - C_s) + \frac{1}{3}(Am_i + Am_j - 2Am_s) + \frac{1}{3}(3Dm_{ij} - Dm_{ii} - Dm_{jj} - Dm_{ss}).$$

$$H_M(F_2) = G(F_{2ijs}) - \frac{1}{3}[G(P_i) + G(P_j) + G(P_s)] = \frac{1}{6}(2A_s - A_i - A_j) + \frac{1}{24}(6D_{is} + 6D_{js} - 5D_{ii} - 5D_{jj} - 2D_{ss}) + \frac{1}{3}(2C_i - C_j - C_s) + \frac{1}{6}(2Am_s - Am_i - Am_j) + \frac{1}{6}(3Dm_{is} + 3Dm_{js} - 2Dm_{ii} - 2Dm_{jj} - 2Dm_{ss}).$$

$3n$ 胚乳性状平均优势的预测公式与 $2n$ 种子性状的恰恰相反, 以 3 个亲本自交系为基础推导时与直接加性效应无关:

$$H_M(F_1) = G(F_{1ijs}) - \frac{1}{3}[G(P_i) + G(P_j) + G(P_s)] = \frac{1}{2}(2D_{is} + 2D_{js} - D_{ii} - D_{jj} - 2D_{ss}) + \frac{1}{3}(2C_i - C_j - C_s) + \frac{1}{3}(Am_i + Am_j - 2Am_s) + \frac{1}{3}(3Dm_{ij} - Dm_{ii} - Dm_{jj} - Dm_{ss}).$$

$$H_M(F_2) = G(F_{2ijs}) - \frac{1}{3}[G(P_i) + G(P_j) + G(P_s)] = \frac{1}{2}(D_{is} + D_{js} - D_{ii} - D_{jj}) + \frac{1}{3}(2C_i -$$

$$C_j - C_s) + \frac{1}{6}(2Am_s - Am_i - Am_j) + \frac{1}{6}(3Dm_{is} + 3Dm_{js} - 2Dm_{ii} - 2Dm_{jj} - 2Dm_{ss}).$$

References:

- [1] Schnell F W, Cockerham C C. Multiplicative vs. Arbitrary gene action in heterosis[J]. *Genetics*, 1992, 131: 461-469.
- [2] Knight R. The relation between hybrid vigour and genotype \times environment interaction[J]. *Theor Appl Genet*, 1973, 43: 318-322.
- [3] Virmani S S, Aquino R C, Khush G S. Heterosis breeding in rice (*Oryza sativa* L.) [J]. *Theor Appl Genet*, 1982, 63: 373-380.
- [4] Young J B, Virmani, S S. Heterosis in rice over environments[J]. *Euphytic*, 1990, 51: 87-93.
- [5] ZHU Jun (朱军). *Analysis Methods for Genetic Models* (遗传模型分析方法)[M]. Beijing: China Agricultural Press, 1997, 12-55, 104-111, 175-201. (in Chinese)
- [6] ZHU Jun, JI Dao-fan, XU Fu-hua (朱军, 季道藩, 许馥华). A genetic approach for analyzing intra-cultivar heterosis in crops[J]. *Acta Genetica Sinica* (遗传学报), 1993, 20(3): 262-271. (in Chinese)
- [7] Xu Z C, Zhu J. An approach for predicting heterosis based on an additive, dominance and additive \times additive model with environment interaction[J]. *Heredity*, 1999, 82(5): 510-517.
- [8] Rawlings J O, Cockerham C C. Triallel analysis[J]. *Crop Sci*, 1962, 2(3): 228-231.
- [9] Rawlings J O, Cockerham C C. Analysis of double cross hybrid populations[J]. *Biometrics*, 1962, 18: 229-244.
- [10] XU Zi-cheng, ZHU Jun (许自成, 朱军). Genetic models with additive-dominance-maternal effects and Monte Carlo simulation analysis for three-way and four-way crosses[J]. *Acta Agronomica Sinica* (作物学报), 2000, 26(1): 40-46. (in Chinese)
- [11] XU Zi-cheng, ZHU Jun (许自成, 朱军). An ADAA model and its analysis method for agronomic traits based on the double-cross mating design[J]. *Acta Genetica Sinica* (遗传学报), 2000, 27(3): 247-256. (in Chinese)
- [12] XU Zi-cheng, ZHU Jun (许自成, 朱军). Genetic Models and Heterosis Prediction for Triallel Mating Design[J]. *Journal of Biomathematics* (生物数学学报), 2001, 16(2): 448-455. (in Chinese)
- [13] Cockerham C C. Random and fixed effects in plant genetics[J]. *Theor Appl Genet*, 1980, 56: 119-131.