作 物 育 種 原 理

—作物育種之兩個基本遺傳法則—

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前　言

人類之所以栽培作物，無非是要利用該等作物之莖、葉、花、果實或種子等來滿足人類物質或精神上之需求。而人類對這些被使用部份質或量之改進開始的很早，一般咸認：史前人類蒐集植物可食用部分，進而人為栽種即是作物育種之濫觴。此後，人類文明進步，作物育種方法確立，遺傳理論闡揚，而被人類使用之植物就被稱為作物；而作物的莖、葉、花、果實或種子等等就被稱之為性狀。

習慣上，作物之性狀常依—控制該性狀之基因數目暨環境對該基因表現之相對重要性等兩因子—而被歸類為質的性狀或量的性狀。唯，嚴格來說，週延地判斷一種性狀之被歸類為質的性狀或量的性狀有時也相當不易；同時，就作物言，往往也發現若干性狀之表現係同時受質和量的基因所控制。因之，嚴格地區分某些性狀之為質或量的性狀，在某些狀況下亦無特殊意義。話雖如此，然，一般咸同意：質的性狀的表現係受一對或少數主效基因所控制，且該等基因之表現也較不受環境所影響，而該性狀之頻度分布則是分立不連續的；量的性狀則呈連續性分布，其表現則受多數微效基因所控制，而這些基因之個別效應微小且其表現受環境之影響則頗為強烈。換言之，作物性狀之表現（P）係由遺傳（G）及環境（E）來共同決定；而遺傳與環境效應對各該性狀表現之相對重要性則依性狀別而不同。

作物育種學就是：經藉改變或組合作物之遺傳組成，來人為地操控目標作物若干質或量的性狀之表現，而使該作物之綜合表現能儘可能地契合人們需求的一門科學。因之，作物育種學是現今多元化作物生產上不可或缺的一個環結。在傳統育種操作中，作物遺傳組成之改變或組合概經由雜交（天然或人為）或突變（天然或人為）所達成，故，作物之常態繁殖及花粉授與方法與各該作物遺傳組成改變或組合之方法有極其密切之關係存在。一般，作物依常態繁殖方法可大別為二大類：（一）無性繁殖作物：利用植物體之營養部分以接木、壓條、扦插、分株、分球、組織培養或其他等無性繁殖方法以產生新的個體；及（二）有性繁殖作物：需藉開花時，雌雄配子之融合來繁殖新的個體。而有性繁殖作物又可依花粉自然授與之方式而區分為：自交作物（self-pollinated or autogamous crops）；屢異交作物（often cross-pollinated or partly allogamous crops）；及異交作物（cross-pollinated or allogamous crops）等三種。故而，此二類作物或此三種作物在遺傳組成之改變

或組合，在實際傳統育種操作方法上是殊有不同，唯，在實際育種操作方法上雖有不同，但在遺傳操控方面所涉及之遺傳法則，則不論目標性狀之屬質的性狀或係量的性狀，則大致仍尊循：孟德爾及後來遺傳學者等之基本遺傳法則。

孟德爾遺傳定律是奧國僧侶孟德爾（Gregor Johann Mendel）由豌豆實驗所發現，其論文雖早在1865年就已經發表，但並未引起當時學界之注意（後人推測此可能與該論文係用當地語文撰寫有關）。直至孟氏死後，而於本世紀初（1900's）該定律才被再發現。如今，孟德爾遺傳定律已被公認為現代遺傳學之基石；而孟德爾本人則被認為是遺傳學之父。孟德爾遺傳定律可大別成兩個法則，孟氏的第一個遺傳定律是所謂的分離律（the principle of segregation）；而孟氏的第二個遺傳定律則是所謂的獨立組合律（the principle of independent assortment）。目前，自交作物的一般育種理論或異交作物連續自交時目標性狀之遺傳行為多可由孟德爾之遺傳定律來解說。

哈弟—溫柏格（Hardy-Weinberg或Castle-Hardy-Weinberg equilibrium）定律（均衡）敘述在設定之內外在條件下，族群內基因及基因型頻度之變化情形。當某些條件符合時，族群內基因頻度代代保持不變；而基因型之頻度也呈現一定之比率。而在某些特定條件下，族群內基因及基因型頻度則依一定之方向改變。哈弟—溫柏格定律（均衡）向被認為是族群遺傳（population genetics）之核心理論，也是異交作物傳統育種之重要理論基石之一。

本文之目的即在：將此兩基本遺傳法則在質的性狀之遺傳方面做一溫故性與綜合性地再強調，期與與會學者專家共收溫故而悟新之功。至於量的性狀之遺傳則不在討論範圍之內。而為討論方便起見，茲按自交作物—自花授粉不施淘汰（self-pollination without selection）、自花授粉並施淘汰（self-pollination with selection）；異交作物—異花授粉不施淘汰（cross-pollination without selection）、授粉前施淘汰（selection before pollination）及授粉後施淘汰（selection after pollination）等項分別敘述；並以自花與異花授粉族群選拔效應之綜述為總結，敬請與會賢達不吝指教。

自交作物—自花授粉不施淘汰

茲以雜交某基因座上兩等位基因（alleles）不同的兩個純質（homozygous）親本的後裔分離情況來說明之。設，親本-1某一質的性狀之基因型為BB，而親本-2則為bb。此兩親本之雜交第一代F_1植株，因從兩親本各獲得成對染色體組中之一組（或稱各獲得某基因成對等位基因中之一個等位基因），其基因型是為Bb；同時，這F_1植株所產生單元體花粉粒及卵所攜帶兩等位基因（B與b）之比例為1：1。而當這F_1植株自交時，單元體之花粉粒與卵結合而產生各基因型比例為1 BB：2 Bb：1 bb的F_2後裔。此後，因為在每一世代之自交過程中，純質之植株將均僅產生如己的純質後裔；反之，異質之植株則均產生各基因型比例為1 BB:2 Bb:1 bb的後裔。

如此，連續自交使該族群純質後裔之頻度增加，而異質後裔之頻度降低，而此等頻度之變化完全遵循孟德爾遺傳定律並示如圖1。由圖列知，在自交作物自花授粉不施淘汰之族群中，異質後裔之個體數以—每自交一代遞減1/2之比例—隨自交代數之增加而遞降，而在當 n（自交之世代數）趨近無窮大時，族群中異質後裔之個體數將趨近於零而不等於零，而兩純質後裔之和將趨近於百分之百而不為百分之百。

而在自交的任何世代中，將任一世代（n） 之異質植株行自交一次時，其後裔（是為 n+1 世代）各基因型分離之比例必與F_1植株行自交時之族群（即F_2族群）相同；而當自交二次時，其後裔（即 n+2 世代）各基因型分離之比例必與F_1植株行自交時之族群相同（即F_3族群）。此即，如於F_6世代的異質植株行自交時，該異質植株之後裔族群（即F_7族群）各基因型之頻度將分別為1 BB : 2 Bb : 1 bb，此比例正與由F_1植株自交所成F_2世代之後裔，其族群各基因型分離成1BB : 2Bb : 1 bb之比例相同。而如果再任由這F_6異質植株所成F_7族群續行自交而不施任何淘汰，則這個族群（即F_3族群）各基因型之頻度將分別為3 BB : 2 Bb : 3 bb，而與F_3族群各基因型之分離比例相同。

如此，具有分離後裔之植株（即異質植株）的頻度，將依選拔世代異質個體之頻度而定；而異質植株後裔基因型與表現型之頻度，則依該異質植株選出後之自交世代數而定。因之，後裔被培育之世代數暨該後裔被選出以成立系統之世代數，是為育種家極為重視之兩個數字。

	Parent 1		Parent 2
	BB	×	bb
F_1		Bb	
F_2	1/4 BB	1/2 Bb	1/4 bb
F_3	3/8 BB	1/4 Bb	3/8 bb
F_4	7/16 BB	1/8 Bb	7/16 bb
.	.	.	.
.	.	.	.
F_{n+1}	$1/2[1-(1/2)^n]$	BB $(1/2)^n$ Bb	$1/2[1-(1/2)^n]$ bb

圖 1. 雙元體物種單基因之分離。

Fig. 1. Segregation of a single gene in a diploid species. The fraction given for each genotype is the frequency expected on the average for each generation of self-pollination.

茲以假想之某自交作物一對抗病基因之例子來例釋系統間及系統內各基因型之分離情形，並假定等位基因 R 對 r 為完全顯性。以下例題供進一步思考：

1. What is the frequency of susceptible plants in the self-pollinated population without selection in the F_2 and F_4generations ?

   The frequency of susceptible plants (rr) is 1/4 in F_2 and 7/16 in F_4

2. What is the frequency of resistant plants in the self-pollinated population without selection in the F_2 and F_4 generations ?

   The frequency of resistant plants is the sum of the frequencies of RR and Rr plants. Thus, the frequency of resistant plants in F_2 is 1/4 + 1/2 = 3/4; in $F_4$is 7/16 + 1/8 = 9/16.

3. What frequency of $F_{2:3}$ lines would have segregating progeny ?

   The frequency of lines that segregate is equal to the frequency of heterozygous plants in the generation in which they were derived. The frequency of heterozygous plants (Rr) in F_2 is 1/2; therefore, the frequency of segregating $F_{2:3}$ lines is 1/2.

4. What frequency of $F_{2:5}$ lines would have segregating progeny ?

   The frequency of heterozygous plants (Rr) in F_2 is 1/2; therefore, the frequency of segregating $F_{2:5}$ lines is 1/2.

5. What is the frequency of susceptible plants in an $F_{2:3}$ line that is segregating for the R gene ?

   A heterozygous F_2 plant is equivalent genetically to an F_1; therefore, segregation among progeny from an F_1 is equivalent to segregation among F_3 progeny from a heterozygous F_2 (1/4 RR : 1/2Rr : 1/4 rr). The frequency of susceptible plants (rr) in a segregating $F_{2:3}$ line is 1/4.

6. What is the frequency of susceptible plants in an $F_{9:11}$line that is segregating for the R gene ?

   A heterozygous F_9 plant is equivalent genetically to an F_1. The segregation among F_{10} progeny from an F_9 plant is equivalent to that among F_2 progeny of an F_1 plant (1/4 rr plants). Segregation among F_{11} progeny from an F_9 plant would be equivalent to that of F_3 progeny from an F_1 plant (3/8 rr plants). The frequency of susceptible plants in a segregating $F_{9:11}$ line is 3/8

自交作物—自花授粉並施淘汰

自花授粉族群單一基因之—基因型暨表現型頻度—可經人為或天然淘汰而改變之。當就隱性基因型植株選拔完全有效時，僅經一世代之淘汰，顯性等位基因即可被有效地從族群中剔除。但要從族群中有效地剔除隱性等位基因，則相當困難，因為此隱性等位基因常被異質個體之顯性等位基因所隱蔽而不易察知。

當就某顯性等位基因實際行選拔時，淘汰後當世代之隱性基因型頻度可依下述步驟來估算之，茲以於 F_2 世代某顯性等位基因實際行選拔為例而例釋之。

STEP 1. Compute the sum of the frequencies of homozygous dominant and heterozygous individuals in the generation in which selection is conducted.

F_2= 1/4 BB : 1/2 Bb : 1/4 bb

Sum of BB + Bb =1/4 + 1/2 = 3/4

STEP 2. Divide the frequency of homozygous dominant individuals before selection by the sum obtained in step 1 to obtain the frequency of homozygous dominant individuals after selection.

$$\frac{1/4\ BB}{3/4\ (BB + bb)} = 1/3\ BB$$

STEP 3. Divide the frequency of heterozygous individuals before selection by the sum obtained in step 1 to obtain the frequency of heterozygous individuals after selection.

$$\frac{1/2\ Bb}{3/4\ (BB + bb)} = 2/3\ Bb$$

STEP 4. The frequency of homozygous recessive individuals in the generation after selection is equal to one-fourth the frequency of heterozygous individuals after selection (step 3) because the heterozygotes segregate 1/4 BB : 1/2 Bb : 1/4 bb.

2/3 Bb × 1/4 = 1/16 bb in F_3

STEP 5. The frequency of heterozygous individuals in the generation after selection is equal to one-half the frequency of heterozygous individuals after selection (step 3).

2/3 Bb × 1/2 = 1/3 Bb in F_3

STEP 6. The frequency of homozygous dominant individuals in the generation after selection is equal to the frequency of homozygous dominant individuals after selection plus one-fourth the frequency of heterozygous individuals after selection.

1/3 BB + (2/3 Bb X 1/4) = 1/3 + 1/6 = 1/2 BB in F_3

如此，在F_3 世代（於F_2 世代行隱性等位基因之淘汰）各基因型之頻度為：

1/2 BB : 1/3 Bb : 1/6 bb

以下節錄二個例題供進一步思考。設 R為某抗病之等位基因，R 對r 為完全顯性。

1. What is the frequency of susceptible plants in the F_4 generation after selection for resistance among F_3 plants?

Step 1. The genotypic frequency in the F_3 is

3/8 RR : 1/4 Rr : 3/8 rr

The frequency of selected genotype is 3/8 RR + 1/4 Rr =5/8

Step 2. The frequency of RR after selection is

$$\frac{3/8\ RR}{5/8(RR+Rr)} = 3/5\ RR$$

Step 3. The frequency of Rr after selection is

$$\frac{1/4\ Rr}{5/8(RR+Rr)} = 2/5\ Rr$$

Step 4. The frequency of susceptible rr individuals in F_4 is

2/5 Rr × 1/4 = 1/10 rr

2. Susceptible plants are rouged from the population in the F_4 generation early in the season. At maturity, individual F_4 plants are harvested. What frequency of the $F_{4:5}$ lines would segregate for resistance.

Step 1. The genotypic frequency in the F_4 is

7/16 RR : 1/8 Rr : 7/16 rr

RR + Rr = 9/16

Step 2. Does not apply.

Step 3. The frequency of segregating $F_{4:5}$ lines is equal to the frequency of heterozygous plants after selection in F_4.

$$\frac{1/8\ Rr}{9/16\ (RR+Rr)} = 2/9\ Rr$$

The frequency of segregating $F_{4:5}$ lines would be "2/9".

異交作物—異花授粉不施淘汰

經藉逢機異花授粉所成族群某性狀的遺傳組成視該族群該性狀的等位基因之頻度而異。當某族群由某世代繁衍至下一世代時，某性狀之基因暨基因型頻度維持不變，則此族群稱呈哈弟—溫柏格均衡。在一呈哈弟—溫柏格均衡之族群，該性狀基因型之頻度將由方程式 p2 + 2p(1-p) + (1-p)2表示之。此處，p表某等位基因之頻度；(1-p)表另一等位基因之頻度 。

假設在二元植物異花授粉之族群中，兩等位基因為 Y 與 y 的單一基因控制種皮之顏色；而等位基因：Y 之頻度為 0.3。則當此族群在呈哈弟—溫柏格均衡時YY，Yy，及 yy 各基因型之頻度為何? 考慮此一問題時，首先令 Y 等位基因

之頻度為 p； y 等位基因之頻度為 (1-p)。則，p = 0.3；(1-p) = 1-0.3 = 0.7。如此，

YY : Yy : yy = (0.3)2 : 2(0.3)(0.7) : (0.7)2

=0.09 : o.42 : 0.49

而任何族群達哈弟—溫柏格均衡要件，據Hartl and Clark (1989)所述為：

1.The organism in question is diploid,

2.Reproduction is sexual,

3.Generations are nonoverlapping

4.Mating is random

5.Population size is very large.

6.Migration is negligible

7.Mutation can be ignored.

8.Natural selection does not affect the gene under consideration.

茲以由四親本所成假想之異花授粉族群為例以例釋之。設該四親本中之兩個的基因型為 Bb，另兩個為 BB。則等位基因 B之頻度為 0.75，等位基因 b 之頻度為 0.25。當四親本行自交暨反交以外之所有儘可能的交配時，該族群各基因型之頻度如下。

	Genotypes		
	BB	Bb	bb
Bb-1×Bb-2 =	1	2	1
Bb-1×BB-1 =	2	2	
Bb-1×BB-2 =	2	2	
Bb-2×BB-1 =	2	2	
Bb-2×BB-2 =	2	2	
BB-1×BB-2 =	4		
Total	13	10	1
Genotypic frequency	0.54	0.42	0.04
Hardy Weinberg equilibrium	0.56	0.38	0.06

在這種交配方式下，該族群各基因型之頻度顯然並未符合哈弟—溫柏格均衡。而在當將四親本之自交暨反交等兩種交配方式納入交配清單時，則此族群各基因型之頻度即符合哈弟—溫柏格均衡。

	Genotypes		
	BB	Bb	bb
Six single cross in above table	13	10	1
Reciprocals of the six single crosses	13	10	1
Bb-1 self	1	2	1
Bb-2 self	1	2	1
BB-1 self	4		
BB-2 self	4		
Total	36	24	4
Genotypic frequency	0.56	0.38	0.06
Hardy-Weinberg equilibrium	0.56	0.38	0.06

由此可知逢機交配（random mating）對異交族群達哈弟—溫柏格均衡之影響。當然，Hartl and Clark (1989) 所述任何族群達哈弟--溫柏格之均衡要件，對族群達哈弟—溫柏格均衡之影響程度互有不同。單一要件之影響程度也視其它內外在條件之搭配而異，同時，目標性狀若與其他極易受外在栽培條件影響之性狀相關或連鎖時，可能亦將影響該族群各基因或基因型之頻度。再者，作物育種之目的是在操控目標族群之基因頻度往預期之方向改變。故，育種族群不符族群達哈弟—溫柏格之均衡要件。通常，異交作物任由異花授粉不施淘汰之族群可稱為哈弟—溫柏格均衡之族群，尤以老舊傳統農家異交作物品種（族群）為然 。

異交作物—異花授粉前施淘汰

異交作物異花授粉前施淘汰，因係當選植株之雌雄配子才有機會交配產生後裔，故可稱為雌雄親本均受控制之交配方式；而異交作物異花授粉後施淘汰，因僅雌配子係來自當選之植株，雄配子則來自族群中任何植株，故這種交配方式僅雌性親本受控制。因之，在操控目標族群之基因頻度往預期方向改變之效應方面，異花授粉前施淘汰者概較授粉後施淘汰者為佳。茲將估算異交作物異花授粉前施淘汰，目標族群之基因頻度往預期方向改變之數學估算步驟列述於下，估算過程中係假設淘汰隱性等位基因。

Step 1. Calculate the genotypic frequency in the population before selection with the equation $p_o^2 + 2\,p_o(1-p_o) + (1-p_o)^2$, where, p_o = frequency of the dominant allele and $1-p_o$ = frequency of recessive allele before selection.

Step 2. Eliminate the homozygous recessive individuals represented by the component $(1-p_o)^2$, and add the frequencies of the homozygous dominant and heterozygous individuals: $p_o^2 + 2\,p_o(1-p_o)$.

Step 3. Compute the frequency of the dominant allele after selection by using the relationship.

$$p_1 = \frac{p_o^2 + p_o(1-p_o)}{p_o^2 + 2\,p_o(1-p_o)}$$

where p_1 = frequency of the dominant allele after one generation of selection.

Step 4. Calculate the frequency of the recessive allele after selection as $1-p_1$ or as

$$1-p_1 = \frac{p_o(1-p_o)}{p_o^2 + 2\,p_o(1-p_o)}$$

Step 5. Compute the genotypic frequency in the population after selection as

$$p_1^2 + 2\,p_1^2(1-p_1^2) + (1-p_1^2)_2$$

茲以假想之逢機交配族群抗性基因例釋之，此例中等位基因 R 對 r 為顯性，並假定進行淘汰前原始族群 R 等位基因之頻度為 0.2 ，而 r 為 0.8，其數學估算步驟分述於下。

Step 1. Since the original population were random-mated without selection, the gene frequencies would not change. Union of the sperm and egg cells can be diagrammed as

		Female	
		0.2 R	0.8 r
Male	0.2 R	0.04 RR	0.16 Rr
	0.8 r	0.16 Rr	0.64 rr

The genotypic frequency in the population would be

0.44RR + 0.32 Rr + 0.64 rr

That is equivalent to the equation:

$$p_o^2 + 2\,p_o(1-p_o) + (1-p_o)2 = (0.2)2 + 2\,(0.2)(0.8) + (0.8)2$$

Step 2. Elimination of the homozygous recessive individuals before pollination results in a population consisting of 0.04 RR + 0.32 Rr = 0.36 of the original population.

Step 3. The homozygous dominant individuals produce gametes with the allele R, and half the gametes produced by the heterozygotes carry the R allele. The frequency of the R allele in the gametes available for fertilization would be

$$\frac{0.04\ RR + 1/2\ (0.32\ Rr)}{0.36\ (RR + Rr)} = 0.56\ R$$

This is equivalent to

$$p_1 = \frac{p_o^2 + p_o(1-p_o)}{p_o^2 + 2\ p_o(1-p_o)} = \frac{(0.2)2 + (0.2)(0.8)}{(0.2)2 + 2(0.2)(0.8)} = 0.56\ R$$

Step 4. The gametes that do not have the R allele must have the r allele. Therefore, the frequency of r is 1- 0.56R = 0.44, which is equivalent to $1-p_1$. An alternative procedure is to consider that half the gametes of the heterozygous carry the r allele. The frequency of r can be calculated as

$$\frac{1/2\ (0.32\ Rr)}{0.36\ (RR + Rr)} = 0.44\ r$$

Step 5. The gametes produced by selected individuals would have the frequency of 0.56 R and 0.44 r. Every gamete would have an equal chance to combine with every other gamete, which can be diagrammed as

		Female	
	0.56 R		0.44 r
0.56 R	0.31 RR		0.25 Rr
Male			
0.44 r	0.25 Rr		0.19 rr

The genotypic frequency in the new population would be

0.31 RR + 0.50 Rr + 0.19rr

That is equivalent to

$$p_1^2 + 2\ p_1(1-p_1) + (1-p_1)^2 = (0.56)^2 + 2(0/56)(0.44) + (0.44)^2$$

異交作物—異花授授粉後施淘汰

由於異交作物異花授粉前施淘汰系雌雄親本均受控制之交配方式；而異交作物異花授粉後施淘汰之交配方式僅雌性親本受控制。因之，在操控目標族群之基因頻度往預期方向改變之效應方面，異花授粉前施淘汰者概為授粉後施淘汰者之兩倍。有關估算異交作物異花授粉後施淘汰，目標族群之基因暨基因型頻度改變之數學估算步驟除步驟 5外，餘與估算異交作物異花授粉前施淘汰者同。茲以前例解析之。

Step 1 to 4. Calculation of the frequency of the dominant and recessive allele applies only to the female gametes. There is no selection of the male parent; therefore, there is no change in the frequency of alleles among male gametes.

Step 5. The frequency of alleles from the selected female parent is equal to p_ and 1-p_, while the frequency from the unselected male parent is po and 1-po. The genotypic frequency in the next generation can be calculated as

$$p_0p_1 + [p_0(1-p_1) + p_1(1-p_0)] + (1-p_0)(1-p_1)$$

With selection after pollination, the gene frequency for the selected female becomes $R = p_1 = 0.56$ and $r = 1-p_1 = 1-0.56 = 0.44$.

The gene frequency for the unselected male remains at $R = p_o = 0.2$ and $r = 1-p_o = 1-0.2 = 0.8$.

The union of gametes to form the new population can be diagrammed as

		Female	
		0.56 R	0.44 r
Male	0.2 R	0.11 RR	0.09 Rr
	0.8 r	0.45 Rr	0.35 rr

The genotypic frequency is 0.11 RR + 0.54 Rr + 0.35rr

That is equivalent to

$$p_0p_1 + [p_o(1-p_1) + p_1(1-p_o)] + (1-p_o)(1-p_1) =$$
$$(0.2)(0.56) + [(0.2)(0.44) + (0.56)(0.8)] + (0.8)(0.44)$$

綜合上述授粉前施淘汰及授粉後施淘汰的典型例子（表 1）知，在當原始族群之基因型頻度為0.04 RR : 0.32 Rr : 0.64 rr ；基因頻度為 R = 0.2，r = 0.8 之族群進行授粉控制時，授粉前施淘汰所成新族群之基因型頻度則成為 0.31 RR : 0.50 Rr : 0.19 rr；基因頻度變為 R = 0.56，r = 0.44。 而授粉後施淘汰成新族群之基因型頻度變為0.11 RR : 0.54 Rr : 0.35 rr； 基因頻度則成為 R = 0.38，r = 0.62。此例強調

出一個重要之作物育種原則：即在逢機授粉之族群中，授粉前施淘汰對新成族群基因頻度改變之效應是為授粉後施淘汰者之兩倍。此一作物育種原則在輪迴選種方面是一個極其重要之考量因子。

表1. 異花授粉作物原始暨衍生族群基因頻度之改變。

Table 1. Change in gene frequency of original and subsequent populations in a hypothetic cross-pollinated population.

	Gene frequency	
	R	r
Original population	0.2	0.8
Selection after pollination	0.38	0.62
Selection before pollination	0.56	0.44

自花與異花授粉族群之選拔效應

自花授粉族群單一基因之—基因型暨表現型頻度—可經人為或天然淘汰而改變之。當就隱性基因型植株選拔完全有效時，僅經一世代之淘汰，顯性等位基因即可被有效地從族群中剔除。但要從族群中有效地剔除隱性等位基因，則相當困難，因為此隱性等位基因常被異質個體之顯性等位基因所隱蔽而不易察知已如前述。而在異花授粉族群中，當某些條件符合時，如就隱性基因型植株選拔完全有效暨授粉前施淘汰等，顯性等位基因僅經一世代之淘汰也可被有效地從該異花授粉族群中被有效地剔除。此即，若就隱性基因型植株選拔完全有效時，自花授粉作物與異花授粉授粉前施淘汰一樣，均能僅經在一個世代之淘汰而將該顯性等位基因自族群中剔除。但，對顯性等位基因行選拔則不然，因族群中異質植株之隱性等位基因為另一顯性等位基因所遮掩，而無法有效地自該族群中剔除該隱性等位基因。

理論上，在自花授粉族群植株之任一個配子無例外地被嚴格限制必與各該植株之任一個配子相結合；但在異花授粉族群植株之任一個配子則很有可能是與來自族群中任一植株之配子相結合。因之，在自花授粉族群中，純質顯性個體僅產生純質顯性之後裔；而在異自花授粉族群中，純質顯性個體所接受之花粉很有可能是來自異質植株之隱性或顯性等位基因。故，就顯性等位基因行選拔時，其對衍生族群基因型之選拔效應在自花授粉族群與異花授粉授粉前施淘汰則有不同。兩族群基因型改變之概況示如表 2。由表知，就本例之結果是：兩族群基因頻度

不變，而在兩族群基因型頻度方面則異花授粉授粉前施淘汰者之效應較自花授粉族群者小。衍生之意義應是：相同之遺傳條件下，自花授粉作物之育種時效應較異花授粉授粉前施淘汰者有利。

表2. 授粉前就顯性等位基因選拔在自花及異花授粉族群之選拔效應。

Table 2. Effect of selection among plants before pollination or a dominant allele in a self-pollinated and in a cross-pollinated populations.

	SELF-POLLINATED POPULATION	
	Before selection	
Gene frequency		Genotypic frequency
R = 0.5 : r = 0.5		0.25 RR : 0.50 Rr : 0.25 rr
		Self-pollinated (Discard)
	After selection	
R = 0.67 : r = 0.33		0.50 RR : 0.33 Rr : 0.17 rr
	CROSS-POLLINATED POPULATION	
	Before selection	
Gene frequency		Genotypic frequency
R = 0.5 : r = 0.5		0.25 RR : 0.50 Rr : 0.25 rr
		Cross-pollinated (Discard)
	After selection	
R = 0.67 : r = 0.33		0.45 RR : 0.44 Rr : 0.11 rr

結　　語

傳統作物育種雖因各該作物之繁殖方式、生長特性、被利用部份及各目標性狀遺傳機制之不同，在實際育種操作方法上或可能有所不同，但在遺傳操控方面所涉及之遺傳法則，則不論目標性狀之屬質的性狀或係量的性狀，則大致仍尊循：孟德爾及後來遺傳學者等之基本遺傳法則。本文即在討論作物育種中，質的性狀所遵循的此兩個重要之遺傳法則。經藉自花與異花授粉作物基因暨基因型在原始暨衍生族群之改變來數學地例釋此兩個遺傳法則。所舉例子說明在異花授粉族群中，授粉前施淘汰對基因頻度改變之效應為為授粉後施淘汰者之兩倍。就選拔族群中隱性基因型而言，自花授粉作物與異花授粉授粉前施淘汰一樣，均能在僅歷一個世代即可將該顯性等位基因自該族群中剔除。但，對顯性基因型行選拔則不然，因族群中異質植株之隱性等位基因為另一顯性等位基因所遮掩，而無法有效地自該族群中剔除該隱性等位基因。

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