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大粒水稻之遺傳研究

Ⅱ. 穀粒性狀之遺傳[1]

郭益全　劉　清[2]

摘要：以包括親本與正反交組合之9×9全互交F_1材料探討大粒水稻穀粒性狀之遺傳。數據經以Griffing及Jinks-Hayman等兩套不同方法分析，結果發現糙米粒長、粒寬、長寬比及千粒重等4穀粒性狀親本間之遺傳變異均極大，此變異係由累加性與顯性效應所引起，被評估之4個穀粒性狀之累加性效應均遠大於顯性效應。4個穀粒性狀之一般與特殊組合力均極顯著，且一般組合力效應又遠大於特殊組合力。4個穀粒性狀之狹義遺傳率均頗高，亦發現均存在有細胞質效應。經由同歸與變方分析估得4個性狀之顯性程度均屬部份或不完全顯性。正負等位基因之頻度在親本間之分布除粒長爲相等外，餘3性狀均不等。粒長及粒寬之顯性基因數約等於隱性基因數，而長寬比及千粒重等兩性狀之顯性基因數則多於隱性基因數。經藉迴歸圖析及親本顯性次序之判定，粒長、長寬比及千粒重爲單方向顯性，粒寬則爲雙方向顯性。

臺灣近年來雖因稻穀生產過剩而積極進行稻田轉作，但一個個更豐產水稻品種之育成仍是稻作育種之最重要目標之一，也是水稻育種工作者最主要挑戰之一。要增加水稻之產量可經由提高4個產量構成要素中之任一個，但不影響其他要素之表現而達成。松尾[9]認爲大粒爲最可能的高產要素；國內外研究顯示[13,17,18,19,22,30]大粒水稻之穀粒充實速率、澱粉累積效率、積儲供源比及穗部主要成分絕對轉流量等生理特性均以大粒爲優，而因爲現行中粒品種成熟收穫後尙有全穗總量20%之非構造性碳水化合物 (total nonstructual carbohydrates, TNC) 殘留莖稈[29]，故認爲經由增大穀粒體積謀求稻作增產有其生理理論基礎[29,30]；林[2]育成大粒豐產的臺中秈17號，由實際育種工作中證實大粒水稻品種確可提高稻作單位面積產量。

基此大粒種源之利用雖確爲超高產水稻品種選育之最可能途徑之一，但現存大粒種源往往集團乾物質產量較少[29,30]。其或爲一穗穎花數少[8,17,18,30]、或屬穗數少[29,30]、或係植株高大易倒伏[13,18]，很難直接利用。爲提供大粒水稻品種選育之遺傳育種基礎知識乃進行本項研究。前報[5]已報導抽穗期、株高、每株穗數及一穗穎花數等重要農藝性狀之遺傳行爲，本文則闡述穀粒性狀之遺傳，至於經濟產量、生物產量及收穫指數等3性狀之遺傳則於第3報論述之。

材料與方法

本研究全互交親本計有越光、豐錦、臺農67號、臺中65號、GP199、Pegonil、Khaokhaonio、Pb及 Nakkhaongo 等9個水稻品種。其包括正反交之72個F_1組合及9個親本於1984年一期作培植於

1.臺灣省農業試驗所　研究報告第1298號。

2.臺灣省農業試驗所農藝系助理研究員及前研究員（現任臺灣大學教授）。臺灣省　臺中縣　霧峰鄉。

本所萬豐試驗農場。田區排列採逢機完全區集設計（RCBD），2重覆。每小區5行，每行12株，行株距爲25×25cm。單本植。肥料用量 N-P_2O_5-K_2O爲 80—40—50 kg/ha。詳細之收穫、調製及調查方法如前報[5]。9個全互交親本於1984年一期作各穀粒性狀之表現如表1。

Table 1. Mean values of grain dimensions of brown rice of nine parental cultivars of rice

Parents	Grain length (mm)	Grain width (mm)	Length/width ratio	1000-grain weight (g)
Koshihikari (P-1)	5.08	2.75	1.85	17.93
Toyonishiki (P-2)	5.15	2.66	1.94	18.84
Tainung No. 67 (P-3)	5.07	2.90	1.74	19.00
Taichung No. 65 (P-4)	5.22	2.95	1.77	21.35
GP 199 (P-5)	6.94	3.27	2.12	28.02
Pegonil (P-6)	7.46	3.24	2.30	35.25
Khaokhaonio (P-7)	8.25	2.91	2.84	34.09
Pb (P-8)	8.32	3.03	2.75	37.04
Nakkhaongo (P-9)	7.31	3.25	2.25	33.37

全互交各遺傳介值之分析與估算係按 Hayman[15,16] 及 Jinks[21] 理論進行；一般及特殊組合力則仿 Griffing[14] 之 Method I 估算之；廣義及義狹遺傳力之估算則照 Mather and Jinks[24] 之公式計算。

結　　果

4個被研究穀粒性狀數據，經分別以 Griffing[14] 及 Jinks-Hayman氏[15,16,21] 兩類全互交表變方分析結果之變方成分對照表示於表2。由表2知，Griffing氏與Jinks-Hayman氏之分析結果頗爲一致。4個穀粒性狀均呈：Griffing 氏之一般及特殊組合力之均方與 Jinks-Hayman氏之a變因及b變因之均方皆極顯著，且一般組合力與 a變因之均方又分別遠大於特殊組合力與b變因之均方，此表示4個穀粒性狀有關遺傳基因之累加性與顯性效應對此4穀粒性狀之表現均扮有極重要之角色，且累加性效應又較顯性效應有更强之支配力。Griffing氏之正反交均方與Jinks-Hayman氏之c及d變因均方之顯著性，4個穀粒性狀中，除粒寬外亦均一致，一般而言，雌親之細胞質可能影響到此4個穀粒性狀之表現。另外，Jinks-Hayman氏變方分析之結果還指出：除粒寬之顯性方向爲雙方向外（b_1變因不顯著）。餘粒長、長寬比及千粒重等3性狀則爲單方向顯性（b_1變因極顯著）；此4穀粒性狀性狀有關基因之顯性效應，部份係由於正負效應等位基因在親本間之分布不均勻或不對稱所致（b_2變因極顯著）；同時，不歸諸於b_1及b_2變因之顯性效應，即累加性與累加性，累加性與顯性及顯性與顯性等三類遺傳基因之交感作用可能包含在此9×9之全互交組合中（b_3變因極顯著）。

每一親本4個穀粒性狀之一般組合與特殊組合力列於表3。概言之，大粒親本（P5—9）4穀粒性狀之一般組合多爲正值，反之，中粒親本（P1—4）4穀粒性狀之一般組合力則爲負值。唯僅就千粒重言，大粒親本 Pegonil (P-5) 之一般組合力爲正值親本中之最大者，而中粒親本 Koshihikari (P-1) 之一般組合力則係負值親本中之最小者。

特殊組合力方面，粒長、長寬比及千粒重等3性狀，似呈：中粒親本(P1—4)間及大粒親本(P5—9) 間之特殊組合力概爲正值，而中粒與大粒雜交 F_1 諸組合之特殊組合力則概爲負值，尤以粒長及長寬比兩性狀爲然。粒寬方面各類雜交組合特殊組合力之變異情形恰與前述另3個穀粒性狀者相反，呈

Table 2. Griffing and Hayman analysis of variance of grain dimensions of brown rice in 9×9 diallel crosses

Traits	Griffing			Hayman		
	Source	df	Mean square	Source	df	Mean square
Grain length	Block	1	—	Block	1	—
	Genotype	80	—	Genotype	80	—
	GCA	8	9.001**	a	8	18.001**
	SCA	36	0.111**	b	36	0.222**
				b_1	1	1.091**
				b_2	8	0.016**
				b_3	27	0.250**
	Reciprocal	36	0.005**	c	8	0.016**
				d	28	0.009**
	Error	80	—	Error	80	—
Grina width	Block	1	—	Block	1	—
	Genotype	80	—	Genotype	80	—
	GCA	8	0.232**	a	8	0.463**
	SCA	36	0.004**	b	36	0.008**
				b_1	1	0.002ns
				b_2	8	0.007**
				b_3	27	0.008**
	Reciprocal	36	0.001ns	c	8	0.002*
				d	28	0.001ns
	Error	80	—	Error	80	—
Length/width	Block	1	—	Block	1	—
	Genotype	80	—	Genotype	80	—
	GCA	8	0.628**	a	8	1.255**
	SCA	36	0.016**	b	36	0.032**
				b_1	1	0.140**
				b_2	8	0.010**
				b_3	27	0.035**
	Reciprocal	36	0.001**	c	8	0.003**
				d	28	0.002**
	Error	80	—	Error	80	
1000-grain weight	Block	1	—	Block	1	—
	Genotype	80	—	Genotype	80	—
	GCA	8	225.367**	a	8	450.733**
	SCA	36	1.445**	b	36	2.889**
				b_1	1	4.838**
				b_2	8	5.585**
				b_3	27	2.018**
	Reciprocal	36	1.758**	c	8	5.232**
				d	28	3.025**
	Error	80	—	Error	80	—

*, **: Statistically significant at 5 and 1% probablity levels, respectively.

Table 3. Estimates of Griffing's general combing ability and specific combining ability effects for grain dimensions of brown rice of the nine parental cultivars of rice

Traits	Parents	GCA effects	SCA							
			2	3	4	5	6	7	8	9
Grain length	P1	− 0.72	0.23	0.32	0.31	− 0.13	− 0.24	− 0.29	− 0.28	− 0.15
	P2	− 0.68		0.31	0.20	− 0.16	− 0.21	− 0.21	− 0.24	− 0.15
	P3	− 0.82			0.24	− 0.29	− 0.10	− 0.31	− 0.24	− 0.16
	P4	− 0.66				− 0.26	− 0.19	− 0.12	− 0.33	− 0.11
	P5	0.31					0.12	0.29	0.34	0.03
	P6	0.45						0.10	0.10	0.14
	P7	0.85							0.21	0.06
	P8	0.86								0.12
	P9	0.41								—
Grain width	P1	− 0.16	− 0.03	− 0.03	− 0.03	− 0.01	− 0.01	0.04	0.02	− 0.01
	P2	− 0.16		− 0.03	− 0.05	0.04	− 0.02	0.07	0.05	− 0.01
	P3	− 0.05			0.02	− 0.02	0.01	0.04	0.03	− 0.03
	P4	− 0.03				0.07	− 0.01	0.01	0.01	0.01
	P5	0.11					0.03	− 0.06	− 0.10	− 0.01
	P6	0.13						0.01	0.05	− 0.03
	P7	− 0.03							− 0.04	− 0.01
	P8	0.07								0.09
	P9	0.12								—
Length/width ratio	P1	− 0.13	0.08	0.11	0.11	− 0.04	− 0.07	− 0.11	− 0.10	− 0.03
	P2	− 0.12		0.11	0.10	− 0.08	− 0.05	− 0.11	− 0.11	− 0.04
	P3	− 0.24			0.06	− 0.08	− 0.02	− 0.13	− 0.09	− 0.02
	P4	− 0.19				− 0.11	− 0.05	− 0.05	− 0.11	− 0.02
	P5	0.03					0.01	0.13	0.16	− 0.02
	P6	0.06						0.02	− 0.01	− 0.05
	P7	0.31							0.10	0.02
	P8	0.23								0.03
	P9	0.05								—
1000-grain weight	P1	− 4.52	0.56	0.65	0.03	− 0.10	− 0.51	− 0.31	− 0.21	− 0.24
	P2	− 4.13		0.46	0.18	− 0.18	− 0.16	− 1.08	− 0.68	0.63
	P3	− 3.43			− 0.08	− 0.15	0.39	− 0.07	− 0.25	0.02
	P4	− 2.34				− 0.19	0.43	− 1.40	− 0.85	1.68
	P5	1.37					1.74	0.47	0.09	− 0.12
	P6	3.77						− 0.40	− 1.03	− 1.34
	P7	2.37							0.41	− 0.15
	P8	3.61								− 0.47
	P9	3.28								—

，中粒親本間及大粒親本間之特殊組合力多爲負值，而中粒與大粒親本雜交諸F_1諸組合之特殊組合力則概爲正值。由此似可推定此 4 個穀粒性狀之遺傳機制中，粒長、長寬比及千粒重者較相近，而粒寬性狀則稍異於此 3 性狀。

4 個穀粒性狀之W_r-V_r經純質性測驗 (homogeneity test) 結果，皆不顯著，表示本試驗 4 穀

粒性狀之資料符合 Hayman [16] 氏之遺傳假說，乃進一步估計 4 穀粒狀之遺傳成分（表 4）及遺傳系統（表 5），並繪製 4 穀粒性狀 W_r依V_r而變之迴歸圖（圖 1），以描述供試全互交親本之遺傳機制。

Table 4. Estimates of genetic components of variance and their standard deviations for grain dimensions of brown rice in 9×9 diallel of rice

Genetic component	Grainl ength	Grain width	Length/width ratio	1000-grain weight
D	2.0362** ± 0.0139	0.0493** ± 0.0008	0.1689** ± 0.0029	61.73** ± 0.43
H_1	0.2248** ± 0.0308	0.0089** ± 0.0017	0.0352** ± 0.0064	4.91** ± 0.94
H_2	0.2195** ± 0.0264	0.0065** ± 0.0014	0.0316** ± 0.0055	2.78** ± 0.81
h^2	0.2151** ± 0.0177	0.0003ns ± 0.0010	0.0275** ± 0.0037	0.93ns ± 0.54
F	0.0417ns ± 0.0325	0.0004ns ± 0.0018	0.0331** ± 0.0068	13.79** ± 1.00
E	0.0010ns ± 0.0044	0.0005ns ± 0.0002	0.0003ns ± 0.0009	0.05ns ± 0.14
D-H_1	1.8114** ± 0.0261	0.0404** ± 0.0014	0.1337** ± 0.0055	56.82** ± 0.80

*, **Statistically significant at 5 and 1% probability levels, respectively.
ns : Non-significant.

Table 5. Estimates of genetic systems for grain dimensions of brown rice in 9×9 diallel of rice

Estimates	Grain length	Grain width	Length/width ratio	1000-grain weight
$(H_1/D)^{1/2}$				
By graphic	0.3342	0.4534	0.4609	0.2862
By variance	0.3323	0.4249	0.4566	0.2812
$H_2/4H_1$	0.24	0.18	0.22	0.14
K_d/K_r	1.06	1.02	1.55	2.31
h^2/H_2	0.98	0.04	0.87	0.34
Heritabilities (%)				
Broad-sense	99.9	98.3	99.7	99.8
Narrow-sense	94.7	92.4	89.5	97.1
r of $(W_r+V_r)/Y_r$	0.97**	−0.12ns	0.87**	0.68*
Order of parental dominance	134296578[a]	718653924	213496578	92164387
Order of parental performance	876954321	596847321	786952143	867954321

*, ** : Statisttcally significant at 5 and % probability levels, respectively.
ns : Non-significant.
a : Parents codes : 1-Koshihkari, 2-Toyonishiki, 3-Tainung No. 67, 4-Taichung No. 65, 5-GP 199, 6-Pegonil, 7-Khaokhaonio, 8-Pb, 9-Nakkhaongo.

表 4 顯示粒長性狀之 D、H_1、H_2及h^2等遺傳變異成分均極顯著，因知累加性效應（D）與顯性效應（H_1、H_2及h^2）對水稻糙米粒長之表現甚爲重要。D-H 值爲極顯著之正值，顯示支配糙米粒長之有關基因之累加性效應極顯著地大於顯性效應。而環境效應（E）之影響則頗微小而不重要。F 成分爲不顯著之正值，顯示供試 9 × 9 全互交親本粒長性狀之遺傳體系中，顯性等位基位之頻度可能等於隱性等位基因之頻度。經比較本性狀親本間顯隱性基因總數之比值（K_d/K_r，表 5）爲1.06，雖略大於 1，而近於 1，由此不顯著之F成分及近於 1 之 K_d/K_r值，可認定，供試親本間糙粒米長有關基因羣中，顯性基因總數應等於隱性基因總數。經藉迴歸圖解法與變方分析，估得糙米粒長之平均顯性程度值〔$(H_1/D)^{1/2}$〕均在0.33左右（表 5）；而糙米粒長 W_r依V_r 而變之迴歸直線，切 W_r 軸於原點上方（圖 1），指出諸全互交親本控制糙米粒長之顯性基因的顯性程度爲不完全顯性或部份顯性。提

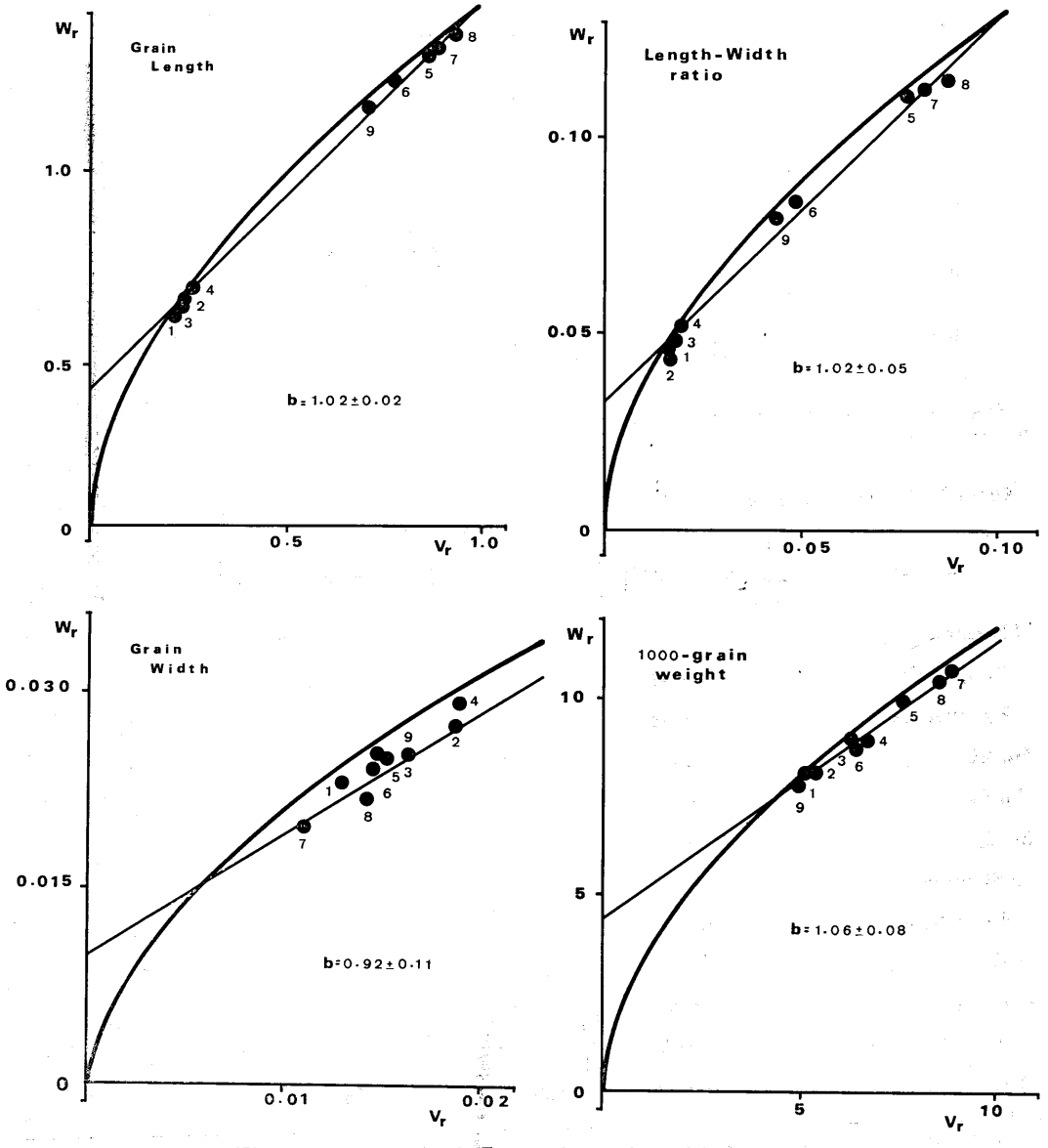


Fig. 1. W_r/V_r graph for grain dimensions of brown rice.
Parent codes : 1-Koshihikari, 2-Toyonishiki, 3-Tainung No. 67, 4-Taichung No. 65, 5-GP 199, 6-Pegonil, 7-Khaokaonio, 8-Pb, 9-Nakkhaongo.

供評估親本間目標性狀正（u）與負（v）等位基因平均相對頻度之$H_2/4H_1$的比值爲0.24（表5），接近於正負等位基因平均頻度相等之極限值0.25（按$u+v=1.0$, $uv=0.5\times0.5=0.25$）），因認定親本間有關糙米粒長之正與負等位基因平均相對頻度分布相等或對稱。唯此推定與全互交表變方分析結果本性狀極顯著之b_2值，所指出本性狀正與負等位基因相對頻度在諸親本間分布不均或不對稱之結果未能一致。供試全互交親本糙米粒長均值(Y_r)與相對應之W_r+V_r值成極顯著之正相關（$r=0.98$，表5），表示當W_r+V_r值增加時，Y_r值亦相對增加，此即Y_r值增加時，隱性基因數相對增加，亦即糙米粒長之增長伴隨隱性基因數目之增加。綜合本性狀Y_r與W_r+V_r間極顯著之正相關及極顯著之b_1僅（表2），再印證圖1知，本全互交供試親本中，糙米粒長短者爲顯性，而諸親本有關糙米粒長之顯性次序爲134296578，而親本之表現次序則爲867954321。本研究估得糙米粒長之廣義及狹義遺傳率均極高，表示早期選拔有效。本性狀具顯性效應基因羣數估值$h^2/H_2=0.98\div1.0$，表示粒長性狀可能有一對主效基因存在。按當有關基因僅具此許顯或無顯性（little or on dominance）時，此值不易檢出[27]；而當諸顯性基因效應符號正負相異時[27]、或有互補基因作用時[16]、或n個基因座之效應不等或非單方向顯性時[6]，此值易被低估。

粒寬性狀之累加性效應（D）與顯性效應（H_1及H_2）均極顯著，表示累加性與顯性效應對糙米粒寬之表現至爲重要。而粒寬之$D-H_1$值爲極顯著之正值，因知，控制粒寬表現之有關基因效應中，累加性效應遠大於顯性效應。環境因素（E）之影響則不顯著（表4）。H_1成分與H_2成份值不等，此可由提供評估親本間有關粒寬基因之正與負等位基因平均相對頻度分布是否相等之估值$H_2/4H=0.18$（表5），異於極限值0.25窺出端倪，配合本性狀極顯著之b_2變因（表2），故可明確地推定有關粒長性狀基因之正與負等位基因平均相對頻度在諸親本間之分布不均或不對稱。F成分不顯著（表4），表示在供試親本粒寬性狀之遺傳體系中，顯性基因之頻度可能等於隱性等位基因之頻度，經印證本性狀親本間顯隱基因總數之比值 $K_d/K_r=1.02\div1$(表5)，可肯定，供試親本間糙米粒寬有關基因羣中，顯性基因總數應等於隱性基因總數。經藉迴歸圖析及變方分析估得本性狀之平均顯性程度值〔$(H_1/D)^{1/2}$〕，介於1與零之間；W_r依V_r而變之迴歸直線切W_r軸於原點上方，獲知支配粒寬表現之有關基因呈部份或不完全顯性。供試全互交親本粒寬性狀之親本均值（Y_r）與對應之 W_r+V_r值之相關係數爲負值，但不顯著，顯示本研究供試材料有關粒寬性狀遺傳體系中，顯性方向爲雙方向，而與變方分析結果不顯著之b_1變因（表2）所蘊含之顯性方向不爲單方向者相印證。綜觀圖1及表1知粒寬中等者對較寬或較窄者爲相對顯性，而諸親本粒寬性狀之顯性次序爲 718653924，而親本之表現次序爲596847321。本性狀之廣義及狹義遺傳率均頗高，有利於選拔效果之確保。本研究粒寬性狀具主效基因羣數估值$h^2/H_2=0.04\div0$，顯示粒寬性狀似無主效基因羣存在。按當有關基因僅具些許顯性或無顯性時，此值不易檢出[27]，而顯性方向爲非單方向時，此值易被低估[6]。

長寬比即所謂粒形，其遺傳機制與粒長獨立[20]。本研究發現長寬比性狀之D、H_1、H_2及h^2等遺傳成分皆極顯著地異於零（表4），指出累加性（D）與顯性（H_1、H_2及h^2）效應對控制糙米之長寬比很重要。$D-H_1$爲極顯著之正值，表示支配糙米長寬比有關基因之累加性效應顯著地大於顯性效應，由此可推論長寬比之狹義遺傳率值應很大，而與利用諸遺傳成分估得之高的狹義及廣義遺傳率值相印證。環境成分（E）變方很小與零無顯著差異（表4），肯定環境因子對本研究目標性狀表現之影響，效應幾無。本性狀之F成分與零之差異極顯著，因認定本研究供試親本長寬比性狀之遺傳體系中，顯性等位基因之頻度可能多於隱性等位基因之頻度。經印證本性狀親本間顯隱基因總數之比值（K_d/K_r）爲1.55，遠大於1，綜合此極顯著之正F值及遠大於1之 K_d/K_r值，可認定本研究有關長寬比性狀之基因羣中，顯性基因羣數應遠多於隱性基因羣數。本性狀之 H_1與 H_2成分值似相差不大（表4），但其測定親本間有關本性狀基因之正負等位基因之平均相對頻度分布是否相等之估值，$H_2/4H_1=0.22$（表5），異於標準極限值0.25，且其變方分析中b_2變因亦極顯著，故推定本長寬比性狀有關基因之正與負等位基因平均頻度在諸親本間之分不均或不對稱。平均顯性程度值〔$(H_1/D)^{1/2}$〕介於

零與1之間（表5及圖1），指出支配長寬比性狀之基因呈部份或不完全顯性。供試材料糙米長寬比性狀之基因呈部份或不完全顯性。供試材料糙米長寬比性狀之親本的值（Y_r）與對應之W_r+V_r值成極顯著之正相關（表5），表示W_r+V_r值增加時，Y_r值相對增加，亦即親本長寬比增大時，隱性基因數目伴隨增加，配合全互交表變方分析指出顯性方向爲單方向之極顯著的b_1變因（表2），再印證表1及圖1，推得本研究長寬比性狀值小者對值大者爲相對顯性，供試親本本性狀之顯性次序爲2134 96578，表現次序則786952143。控制本性狀具主效之基因羣數估值$h^2/H_2=0.87\div1.0$，可知本性狀可能另有一羣主效顯性基因存在，按當諸顯性基因符號正負相異時[27]、或有互補基因作用時[16]、或n個基因座之效應不等及或非單方面顯性時[4]，此值易被低估。

千粒重是較穩定的品種特性之一，是水稻產量構成要素之一。表4數據顯示供試諸親本千粒重性狀之累加性效應（D）與顯性效應（H_1、H_2及h^2）均極顯著，指出累加性與顯性效應對水稻千粒重之多寡至爲重要。累加性效應與顯性效應之差異爲正值，且極顯著地異於零（表4），可知支配供試水稻材料千粒重多寡之有關基因效應中，累加性效應之支配力遠優於顯性效應。F 成分極顯著地異於零，且爲正值，表示供試材料支配千粒重之遺傳體系中，顯性等位基因多於隱性等位基因，此印證估計控制本性狀顯隱基因總數之比值$K_d/K_r=2.31$，故可肯定支配千粒重多寡之基因羣中，顯性基因羣數約爲隱性基因羣數之2倍餘。用於評估親本目標性狀正負等位基因平均頻度是否相等之$H_2/4H_1=0.14$遠低於極限標準值0.25，表示親本間控制千粒重表現有關等位基因之正與負等位基因平均頻分布不對稱或不均勻。經藉迴歸圖析（圖1）及變方分析（表2）估得本性狀之平均顯性程度值〔$(H_1/D)^{1/2}$〕，介於零與1之間，指出控制千粒重性狀之有關基因呈部份或不完全顯性。參試親本之千粒重的親本均值與對應之W_r+V_r值呈顯著之正相關，此即與變方分析結果極顯著之 b_1值（表2），同表研究中支配千粒重性狀之遺傳體系內，顯性方向實屬單方向性，而居於當親本千粒重增加時，W_r+V_r 值增加（即伴隨隱性基因數目增加），再參照圖1諸親本千粒重性狀在 W_r對V_r而變迴歸圖上之相對位置，確定參試材料中千粒重較輕者對重者應爲相對顯性，而本性狀之親本顯性次序爲92164387，表現次序則爲867954321。本性狀具主效之基因羣數無法估出（$h^2/H_2=0.34$），但本性狀之狹義率值則爲4穀粒性狀中之最高者。

Table 6. Simple correlation coefficients among grain dimensions of brown rice

Traits	Grain length	Grain width	Length/width ratio	1000-grain weight
Grain length	—	0.64**	0.95**	0.90**
Grain width			0.36**	0.80**
Length/width ratio				0.77**
1000-grain weight				—

**: Statistically significant at 1% probability level.

4穀粒性狀間之相關關係列於表6。由表知4個穀粒性狀間皆呈極顯著之正相關，此即，千粒重重者則米粒較長、較寬、長寬比大，反之粒子長則亦米粒較寬、長寬比大、千粒重較重。而由於長寬比是4個性狀中較難掌握之性狀，雖其屬導出性狀，會有較高之遺傳率，但在實際進行目標粒形（長寬比）選拔時，可能以其他較易掌握（與長寬比對照）之其他3穀粒性狀之一部或全部爲指標作考慮，即可能滿足吾人之育種目標。

討　　論

穀粒性狀雖可分爲粒長、粒寬、長寬比（粒形）及千粒重等，且彼此間往往有相關關係，但它們的遺傳行爲則被認爲是獨立的，且能與米粒外貌、顆粒澱粉含量、株型、休眠性及成熟期等品質與農藝狀作種種隨意之組合，因之米食人口對穀粒性狀之喜好才存有區域間之差異[20]，也因之穀粒性狀乃成爲一重要之經濟性狀，直接間接影響稻米之市場商品價值[11,12]。

據Chang and Li[11]及Chang and Somrith[12]之綜述，有關粒長之遺傳假說由單基因、雙基因及三基因等質的性狀，到多基因數量性狀並皆有之。綜述中並引述早期學者 Dave 對粒長顯性順序之觀察，其次序依次爲長粒＞中粒＞短粒＞極短粒。而本研究之結果則顯示短粒對長粒爲顯性，恰與早期學者Dave之觀察結果相反；與晚近短粒對長粒爲不完全顯性[3,7]或完全顯性[11,12]之遺傳假說近似或相同。Chang and Li[11]、Chang and smorith[12], Somrith *et al.*[28]、郭與謝[3]及郭等[4]指出粒長受累加性與顯性效應支配，而顯性方向則組合間互有不同[4,11,12]，間有遺傳基因之各類交感作用存在[3,11,12,28]，與本研究之結果恰相符合。粒寬、長寬比（粒形）及粒重均受數量基因之控制[11,12,20,26]，粒重及粒寬並發現有細胞質效應[4,11,12]，長寬比及粒重並有若干程度之遺傳基因的交感作用存在[4,7,28]，此類結果大致與本研究之結果相符。唯本研究估得 4 穀粒性狀之廣義及狹義遺傳均極高（表 5），遠高於 Somrith *et al.*[28]及Chang and Li[11]，而與Jennings *et al.*[20]及 McKenzie and Rutger[26]者相似。Jenning *et al*[20]提出粒形與粒長雖是數量遺傳，但因這些性狀固定得極早，如果在F_2集團選不到合意者，則在F_3世代也不可能發現理想的單株，應放棄這些材料，及早另作打算。亦即Jennings *et al.*[20]之建議與本研究發現 4 穀粒性狀有極高之遺傳率有相呼應之處。

據Mather and Poysa[25]，雖然 Griffing氏[14]與 Jinks-Hayman 氏[15,16,21]之全互交法雖各有其遺傳前提與解析，但數學上 Griffing氏之一般組合力（GCA）成分與 Jinks-Hayman氏之累加性成分a變因相等；特殊組力（SCA）成分及正反交效應（reciprocal）成分依次分別與b_1、b_2及b_3等三個顯性成分與c及 d等二個細胞質效應相當。考，Griffing 氏之分析實爲主效應（GCA）及交成效應（SCA）之嚴密地統計處理，僅行GCA與 SCA效應之變方與估值解析之，Jinks-Hayman氏之分析則在各遺傳前提下，行變方與共變方序列行統計與圖解法分析之，並作若干遺傳介量之估計。本研究經仿 Mather and Poysa[25]之理念，將Griffing氏與Jinks-Hayman氏全互交表變方分析結果之變方成分對照併列之（表 2），結果發現兩類分析方法所蘊含之遺傳訊息恰相合，由此實際數例支持 Mather and Poysa[25]及Liu[23]由理論所推定 Griffing氏與 Jinks-Hayman氏兩類分析法基本上爲等義之論證。

Hayman氏[16]全互交法有①親本爲二元體分離，②正反交無差異，③在全互交法內非等位基因具有獨立作用（無上位性），④無複等位基因，⑤純質結合體親本及⑥基因獨立分布親本間（無連鎖）等六個遺傳假說。據李[1]之綜論指出，由遺傳學之觀點言，Hayman 全互交假說中之基因獨立分布親本間（無連鎖）及非等位基因具有獨立作用（無上位性）等兩個前提不易被接受，Baker[10]認爲由全互交分析所得結果在遺傳上很難解釋上述兩前提，因此，Baker認爲由全互交分析用來說明等位基因之分布、顯性基因對數以及累加性和顯性遺傳變異等訊息，似僅具部分代表性，但 Mather and Jinks[24]則認爲上述前提若在統計上無法偵出時，由全互交法分析所得之遺傳訊息雖然有微小之偏差，但在一般與特殊組合力方面仍具價值。同文[1]指出基因之上位性存在時（即非等位基因間之效應未獨立而有基因間之交感作用存在時）會影響一般組合力與特殊組合力變方之估值，同時在親本數超過10個以上時，才可得正確各類估值，若當用較少數親本行全互交法分析時，則須利用統計上之固定模式爲恰當。而本研究是以F_1集團爲材料，自無連鎖之干擾。而遺傳變異成分之估計係按Hayman氏[15] 1954年全互交組合之理論與解析進行，理論上應屬固定型模式，雖親本數爲 9 個而未超過10個

以上，其各估值若有偏估，無疑偏差（inflated）有限。同時本研究之純質性測驗不顯著，W_r 依 V_r 而變之迴歸圖顯示 4 穀性性狀符合 Hayman [16] 氏非等位基因無交感作用與基因獨立分布親本間之前提迴歸直線斜率近於單位斜率 1 而異於零，圖 1），但因 b_3 變因顯著（表 2），故在闡釋等位基因之分布、顯性基因數以及累加性和顯性遺傳變方等訊息方面，可能須如 Baker [10] 所言，因其可能僅具部分代表性而須稍加保留。

Jinks-Hayman [15,16,21] 氏之全互交分析法，主要結果大致可分成三部分，①爲全互交表變方分析部分，②爲 W_r 依 V_r 而變之迴歸圖析部分及③各遺傳成分及系統之闡釋。往往由變方分析諸變因所顯示之訊息與由 W_r 對 V_r 而變之迴歸圖解，或由遺傳成分所蘊含之意義，常不能一致，本研究中亦有若干情況發生，如，4 個穀粒性狀之極顯著 b_3 變因顯示諸性狀應有各類交感作用存在（即非等位基因之作用未獨立，或無上位性），但 W_r 對 V_r 而變迴歸圖析，則認爲本研究之材料尚符合 Jinks-Hayman 氏 [15,16,21] 之非等位基因無交感作用與基因獨比分布親本間之前提等等，使下較肯定之結論頗費思量，唯因全互交法之分析僅須利用 F_1 世代材料，較少數之個體即可獲得相當多量之遺傳訊息，故本分析方法雖常有若干遺傳前提未能符合，若干遺傳訊息之闡釋過於抽象等缺點，但誠如 Mather and Poysa [25] 所說，本法仍爲大多數育種家及遺傳學家所一致使用，乃因本法實爲獲致大量數量性狀遺傳訊息之可資運用之極少數方法之一。

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Genetic Studies on Larger Kernel Size of Rice

II. Inheritance of Grain Dimensions of Brown Rice[1]

Yih-chuan Kuo and Ching Liu[2]

Summary

The inheritance of grain dimensions of brown rice of larger kernel size of rice were studied by means of a 9×9 diallel crosses including parents and reciprocal crosses. Data from the F_1 generation and parents were analyzed using the Griffing and the Jinks-Hayman methods of diallel analyses. The genetic variations of four grain traits, grain length, grain width, length/width and 1000-grain weight, were significant among the parents. Both additive and dominance effects were important for all four graifn traits. Furthermore additive effects were significantly larger than dominance effects for these grain traits studied. Highly significant general combining ability (GCA) and specific combining ability (SCA) effects were observed for these grain traits. The GCA effects were much more important than SCA effects. Estimated narrow-sense heritiabilities for all these grain traits were very high indicating that a major portion of phenotypic variabulity was controlled by additive effects. Maternal effects existed in all four grain traits. Degrees of dominance of four grain traits estimated by graphic and variance analyses showed partial or incomplete dominance. The average frequency of positive and negetive allel in parents were about equal for length/width, but not equal for the others. Number of dominant genes exceeded recessive genes for length/width and 1000/grain weight, however, both dominant genes and recessive genes were equal for grain length and grain width. Dircetions of dominance evaluated by regression plotting and the order of parental dominance were unidirection for grain length, length/width and 1000-grain weight and ambidirection for grain width.

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去葉處理與栽植密度對大粒型水稻品種產量表現的影響[1]

魏夢麗　劉大江[2]

摘要：爲探討藉密植栽培增加大粒型水稻單位面積穗數以提高產量的可能性，及於抽穗期與抽穗後一週去除50%葉片，以明瞭穀粒充實期間光合成物質的供需平衡關係，本試驗採用大粒型水稻品種 Pegonil 與中粒型品種臺農67號爲材料，於抽穗後定期測定乾物質之累積與分佈，分析植株各器官全氮與非構造性碳水化合物（TNC）濃度的變化，並解析與產量表現間的關係。在第二期作的栽培環境下，臺農67號較 Pegonil 品種高產40%，穎花數與穗數爲導致差異的主要產量構成因素。於抽穗期去除50%葉片，對成熟期 Pegonil 穗重並無影響，但使臺農67號穗重減輕32%，抽穗後一週去葉使兩品種穗重分別降低14%與32%；去除部份葉片使穗部氮濃度降低，但對葉片與莖稈氮濃度的影響甚小，亦即氮素再轉移至穗部之量甚微，此一現象與同一時期莖稈 TNC 濃度大幅下降，顯示可能因光合成物質供應不足而降低根部活性，致使氮素供應不敷穀粒充實之需。密植栽培（行株距 30×7.5cm）較一般栽培（行株距 30×15cm）可提高 Pegonil 產量42%，唯仍較臺農67號低產20%；密植使單株穗數減少，但大幅增加單位面積穗數，且不影響其他產量構成要素的表現，顯示改良栽培方法以提高大粒型水稻產量的可行性。高族羣密度亦使穀粒氮濃度下降，在植株氮素供需與光合成物質的影響方面，可能與去葉處理具有相似的作用機制。本試驗中大粒型品種在抽穗後3週內，單穗乾物質、全氮與 TNC 的累積速率均顯著超過臺農67號，爲可資利用之優良生理特性，但穀粒充實期較短，穗內穎花累積 TNC 之均一性差距頗大，易導致產量效率（yield efficiency）之降低。

近年來由於水稻品種之改良，供源（source）能力已不爲限制產量的主要品種特性，增大積儲（sink）被認爲與提高產量有密切關係；Jones *et al.*[8] 即建議今後水稻品種改良應注重粒重或粒數的提高，Wei *et al.*[16] 經由對植株非構造性碳水化合物分配效率的研究，認爲如能增大穗部容積，本省第一期作水稻產量有再提高15—20%的可能。穀粒大小與水稻產量潛力及收穫指數均有正相關關係存在[1]，IRRI[7] 的報告指出千粒重爲39克時，水稻有最高產的表現；Wei *et al.*[17] 以 Mira 品種進行試驗，發現大粒型品種的產量雖因分蘖數少而低落，但單穗穀粒生產可超過栽培品種臺農67號26—39%，並建議可經由增加穀粒體積以謀求大幅提高本省稻作產量。

現有之大粒型水稻品種在本省栽培環境下，由於分蘖數與粒數少、結實率低、早熟、因株高而易倒伏及病蟲害抗性差等原因，並不具有經濟生產的條件；但在評估大粒型水稻產量潛能時，應考慮針對最大的產量限制因子—分蘖數少，採用適當的栽培密度；唯密植栽培的實際效果如何，以及光合成物質供需平衡關係的表現與機制如何，則迄今仍缺少試驗報告可資參考。

1.臺灣省農業試驗所　研究報告第1299 號。本計畫承行政院農業委員會補助經費（75農建—2.2—糧—133），本所農藝系張富洲先生與林淑雯小姐協助處理樣品及部份分析工作，謹致謝意。

2.本所農藝系助理與研究員。臺灣省　臺中縣　霧峰鄉。

本所作物遺傳與生理研究室多年來對大粒型水稻品種進行篩選與比較，發現籼型品種 Pegonil 的株高較矮（90—100cm）、分蘖數較多、千粒重高（介於 40—45g）而穩定，且糙米長寬比較低（2.33），遂選爲材料，用於培育臺農67號大粒型 isogenic 系統，初步結果甚爲理想（未發表資料）；同時又針對 Pegonil 品種進行各項栽培與生理研究，以瞭解其詳細特性。本試驗採用密植栽培與抽穗時期去除半數葉面積爲處理，探討對產量及其構成要素的影響，分析植株各器官重要成分在穀粒充實期間的濃度變化，及與產量表現間的關係。

材料與方法

本試驗於民國74年第二期作在臺中縣霧峰鄉本所試驗農場進行，以手植方式栽培水稻 Pegonil 與臺農67號兩品種，前者爲一大粒型品種，千粒重可達 45g，後者爲一中粒型推廣品種，千粒重約在 25g 左右。除特殊註明者外，栽植之行株距爲 30×15cm；插秧日期爲 8 月 2 日，肥料用量N：P_2O_5：K_2O 爲 100：60：50 kg/ha，分基肥與二次追肥施用，其他管理按慣行栽培法爲之。

試驗分爲兩部份進行；第一部份爲去葉試驗，係於水稻抽穗期及抽穗後一週，分別剪去兩個水稻品種每一葉片上端二分之一面積，合計 4 處理；第二部份爲栽培密度試驗，兩品種除以 30×15cm 行株距（合每公頃約22萬 2 千株）及 4 — 6 支苗移植栽培外，Pegonil 另以單本植及行株距 30×7.5cm（合每公頃44萬 5 千株）與單本植栽培，合計爲 4 處理。兩部份試驗於田間合併進行，採用完全逢機區集設計，三重複，小區面積爲 4.5×6m。

各試驗均自抽穗期起，每隔一週取樣一次，栽培密度試驗每次自每小區取樣10株，去葉處理試驗取樣 4 株（2×2），將植株區分爲葉片、莖稈（含葉鞘）及穗三部份，樣品置於 100°C 通風乾燥於 2 小時後，繼續以 80°C 乾燥48小時，測定乾物質重量；乾燥之樣品再經 Wiley mill 以40目篩磨粉，測定全氮與非構造性碳水化合物（TNC）濃度，前者係以 semi-micro Kjeldahl 法，後者係仿 Smith [11] 法分析。水稻成熟後，並自每小區取樣30株測定產量及其構成要素，穗部並區分爲充實與不充實穀粒及枝梗三部份，除秤量乾重外，亦分析全氮與 TNC 濃度。

結　果

本試驗進行期間的氣象資料列於表 1，水稻於 8 月 2 日插秧，大粒型品種 Pegonil 具有早熟特性，於 9 月24日抽穗，較臺農67號提早18日；Pegonil 品種於抽穗後 4 週即趨於成熟，但仍於抽穗後 5

Table 1. Mean temperature, sunshine duration, day-length and solar radiation at Wufeng (Taichung) area from July to December, 1985[a]

Item	July	Aug.	Sept.	Oct.	Nov.	Dec.
Temperature (°C)						
Mean	28.2	27.8	27.0	25.5	21.3	16.8
Maximum	33.5	34.0	32.0	30.4	28.1	25.9
Minimum	24.3	23.7	22.9	21.2	16.0	8.8
Sunshine Duration (hr)	6.7	6.7	8.3	8.3	7.9	7.6
Day-length (hr)	13.5	13.0	12.3	11.1	11.0	10.6
Solar Radiation ($cal/cm^2/day$)	405	328	348	315	276	274

[a] Data of temperature, sunshine duration and solar radiation are from Central Weather Bureau, ROC; day/length data are from Taiwan Provincial Food Bureau.

週收穫，臺農67號插秧至抽穗日數爲67日，亦於抽穗後5週收穫。水稻生育期間氣候良好，無嚴重病蟲害發生，植株生育健壯；但由表1之日射量資料推測，Pegonil 品種因抽穗較早，穀粒充實期間接受之日射量應較臺農67號爲高。

抽穗後 Pegonil 與臺農67號品種植株各部位乾物重變化示於表2之對照（CK）處理，每欉稻株之葉片、莖稈與穗部乾重，均以臺農67號爲高，顯示就全株而言，目前栽培最廣之臺農67號品種有較高的乾物質生產能力。葉片的乾重隨植株成熟而降低，但後期大幅減少的部份原因爲葉片枯萎脫落；莖稈乾重在抽穗後一週內有增加的趨勢，但隨後亦趨下降，降幅較大的時期，在 Pegonil 爲抽穗後1至2週，臺農67號爲2至3週；穗部因穀粒充實而乾重持續上升，Pegonil 在抽穗後2至3週的增加最爲明顯，第3週時已接近最高乾物質含量；臺農 67 號的表現則有不同，乾物累積速率以第1至3週最快，其後雖趨緩慢，但在試驗進行期間均維持增加的趨勢，亦即具有較長的充實時期（filling period）。

於抽穗時去除二分之一葉片，對莖稈乾物重變化的影響不大，除臺農67號收穫時經去葉處理植株莖稈乾重較低外，其他皆與對照植株相近（表2）。去葉有延緩大粒型品種 Pegonil 穗部乾物質累積的效果，亦即穀粒有效充實期間自3週延長爲接近5週，但充實速率同時下降，故最終穗重與對照處理相同。抽穗期去葉對臺農67號水稻穗部發育具有較明顯的影響，成熟期穗重爲每株 18.5g，較對照減少 9.1g，降幅達33%（表2）；又有縮短穀粒充實期間的作用，在抽穗後4週以後，穗部乾重已不再增加。抽穗後一週去除二分之一葉片，對臺農67號所造成的影響與抽穗時進行處理相同，均能

Table 2. Effects of 50% leaf-cutting on the changes in dry weight (g/plant) of different plant fractions of Pegonil and Tainung 67 rice varieties during grain-filling[a]

Variety	Plant Fraction	Time of Leaf-cutting Treatment (wks after heading)	Weeks after Heading 0	1	2	3	4	5
Pegonil	Leaf Blade	CK	5.7±0.9	5.2±0.5	3.8±0.6	2.6±0.3	—[b]	2.3±0.3
		0		2.9±0.7	2.3±0.7	1.5±0.1	—	1.0±0.2
		1			1.7±0.2	1.2±0.1	—	0.7±0.1
	Culm	CK	10.8±1.2	12.6±0.7	9.8±1.2	9.6±0.9	—	7.4±0.8
		0		11.4±1.5	8.4±1.2	7.7±0.8	—	9.0±0.7
		1			8.2±1.0	7.1±0.9	—	8.7±0.4
	Panicle	CK	2.7±0.5	6.1±0.9	9.5±0.5	17.9±1.9	—	18.1±2.2
		0		5.2±0.6	9.6±0.8	14.1±2.2	—	17.9±1.3
		1			10.1±2.3	12.4±0.7	—	15.6±1.0
Tainung 67	Leaf Blade	CK	7.0±0.3	6.5±0.3	5.4±0.2	4.8±0.6	3.1±0.3	2.4±0.2
		0		3.5±0.3	3.1±0.9	2.7±0.3	2.1±0.1	2.0±0.2
		1			2.8±0.4	2.8±0.3	2.1±0.2	1.7±0.3
	Culm	CK	17.7±0.3	18.7±1.0	17.4±0.8	14.9±1.2	14.0±1.6	14.2±0.6
		0		16.4±1.8	15.1±3.3	13.1±1.1	13.0±0.3	11.5±0.8
		1			15.6±1.5	15.1±3.3	13.4±1.6	11.1±1.1
	Panicle	CK	5.1±0.1	5.9±0.6	12.9±1.9	20.4±1.8	24.6±1.7	27.6±1.8
		0		4.9±0.8	10.7±1.9	15.2±0.8	18.6±0.9	18.5±1.5
		1			11.9±3.1	17.3±3.4	19.6±1.6	18.1±1.9

[a] Spacing was 30×15cm; transplanting rate was 4 to 6 seedlings per hill.

[b] Samplings were not made at the 4th week after heading for Pegonil variety.

使莖稈與穗部乾物產量下降，且不同時期處理間均無差異存在；Pegonil 品種穗重亦因抽穗後一週損失葉面積而下降，每株穗重減輕 2.5g，降幅爲10%，不若臺農67號顯著。

去葉處理對水稻植株各部位全氮濃度變化的影響列於表 3；在抽穗後一週以前，兩品種葉片氮濃度相近，介於2.3—2.6%之間，但隨後之濃度下降以 Pegonil 較爲明顯，第 3 週時僅爲1.3%，顯著低於臺農 67號之1.8%；成熟時臺農 67號葉片含氮量仍達全乾物重之1.33%，Pegonil 則已低至0.92%。抽穗時兩品種穗部氮濃度亦同，均爲1.2%，但 Pegcnil 穗部在穀粒充實期間可累積多量氮素，成熟時之濃度高達1.51%，遠較臺農67號（1.15%）爲高。

去葉處理對抽穗後葉片氮素濃度及其變化未能產生影響，但抽穗時去葉有使一週後莖稈氮濃度小幅上升的作用，唯此一現象在抽穗後第二週即已消失。去除部分葉片對氮素濃度表現最明顯的影響發生於穗部，抽穗期處理可使臺農67號穗部全氮濃度顯著降低，抽穗後一週處理，則兩品種穗部累積氮素都受到不利的影響（表 3）。

Table 3. Effects of 50% leaf-cutting on the changes in N concentrations (%) of different plant fractions of Pegonil and Tainung 67 rice varieties during grain-filling[a]

Variety	Plant Fraction	Time of Leaf-cutting Treatment (wks after heading)	Weeks after Heading 0	1	2	3	4	5
Pegonil	Leaf Blade	CK	2.57±0.24	2.26±0.15	1.65±0.13	1.30±0.18	—[b]	0.92±0.05
		0		2.25±0.15	2.06±0.20	1.38±0.19	—	1.00±0.06
		1			1.89±0.20	1.50±0.10	—	1.01±0.06
	Culm	CK	0.69±0.15	0.68±0.06	0.60±0.06	0.60±0.02	—	0.71±0.04
		0		0.78±0.12	0.81±0.00	0.69±0.05	—	0.72±0.09
		1			0.75±0.15	0.63±0.08	—	0.69±0.06
	Panicle	CK	1.24±0.16	1.64±0.11	1.57±0.05	1.38±0.06	—	1.51±0.18
		0		1.58±0.05	1.51±0.07	1.47±0.14	—	1.44±0.07
		1			1.47±0.16	1.27±0.02	—	1.32±0.00
Tainung 67	Leaf Blade	CK	2.41±0.12	2.23±0.10	1.89±0.07	1.81±0.10	1.45±0.06	1.33±0.02
		0		2.19±0.11	1.88±0.09	1.82±0.11	1.48±0.03	1.20±0.11
		1			1.88±0.12	1.62±0.12	1.47±0.00	1.20±0.10
	Culm	CK	0.57±0.06	0.55±0.02	0.58±0.04	0.64±0.06	0.59±0.02	0.53±0.03
		0		0.62±0.08	0.60±0.00	0.59±0.03	0.55±0.05	0.52±0.02
		1			0.60±0.07	0.59±0.10	0.49±0.04	0.60±0.02
	Panicle	CK	1.23±0.02	1.20±0.04	1.06±0.03	1.22±0.03	1.10±0.02	1.15±0.10
		0		1.22±0.04	1.04±0.06	1.09±0.02	1.04±0.06	0.88±0.12
		1			1.04±0.05	1.15±0.06	1.02±0.07	1.02±0.08

[a] Spacing was 30×15cm; transplanting rate was 4 to 6 seedlings per hill.

[b] Samplings were not made at the 4th week after heading for Pegonil variety.

與氮素濃度表現相反，大粒型品種 Pegonil 葉片內 TNC 濃度在抽穗後第 2 週以前均較臺農67號爲高，但成熟期之老化葉片內 TNC 濃度則以臺農67號較高（表 4）。抽穗時莖稈內含有多量之貯存性 TNC，兩品種之濃度介於23—25%之間，抽穗後一週內並有繼續累積與濃度上升的現象，以 Pegonil 爲例，可高達 29%；其後 TNC 濃度因再轉移作用而快速下降，第 2 週時爲17—19%，第 3 週已降至 8 %左右，收穫期 Pegonil 品種莖稈內 TNC 濃度僅爲 3 %，臺農67號稍高，但亦不及 7 %。穗爲水稻累積碳水化合物最主要的部位，其 TNC 濃度自抽穗後不斷上升，本試驗中成熟穗因

包含未充實穀粒、枝梗及內外穎等 TNC 含量較少的組織，TNC 濃度應低於穎果之濃度，Pegonil 之數值爲57%，臺農67號爲62%，以後者較高（表4）。

去葉處理對水稻莖稈與穗內 TNC 濃度的影響最爲顯著，抽穗時去除二分之一葉片，經過1、2與3週後，Pegonil 品種莖稈 TNC 濃度分別爲 20.6%、10.9% 與 2.1%，僅及對照植株（分別爲 29.0%、19.2%與7.7%）之30—70%，降幅極鉅。臺農67號水稻也有相似的表現，唯所受影響不若 Pegonil 品種顯著，處理後1至3週間，TNC 濃度約爲對照植株濃度的52—93%；但收穫期臺農67號莖稈內 TNC 含量僅有3.4%，恰爲未經去葉處理植株之一半（表4）。至於抽穗後一週進行去葉對莖稈 TNC 濃度造成的影響，則與抽穗期處理的結果相同，兩處理間無顯著差異存在。

Table 4. Effects of 50% leaf-cutting on the changes in TNC concentrations (%) of different plant fractions of Pegonil and Tainung 67 rice varieties during grain-filling[a]

Variety	Plant Fraction	Time of Leaf-cutting Treatment (wks after heading)	Weeks after Heading 0	1	2	3	4	5
Pegonil	Leaf Blade	CK	4.4±0.6	5.3±0.2	5.7±0.3	3.4±1.1	—[b]	0.9±0.3
		0		4.8±0.8	3.6±0.4	2.0±0.3	—	1.0±0.2
		1			4.1±0.7	2.0±0.3	—	1.1±0.3
	Culm	CK	22.7±3.6	29.0±0.2	19.2±3.3	7.7±3.5	—	3.1±1.1
		0		20.6±3.1	10.9±1.4	2.1±0.1	—	2.1±0.4
		1			10.2±0.2	2.2±0.6	—	2.6±0.5
	Panicle	CK	4.9±0.4	27.1±5.9	37.1±2.0	45.3±2.4	—	57.4±2.5
		0		28.1±5.2	—	40.9±2.3	—	53.0±1.2
		1			39.4±4.1	42.6±2.4	—	54.2±0.9
Tainung 67	Leaf Blade	CK	4.0±0.2	2.9±0.4	2.2±0.1	3.2±0.2	2.4±0.4	3.5±0.6
		0		2.9±0.4	2.1±0.2	2.9±0.2	2.2±0.3	2.7±0.4
		1			2.2±0.3	2.7±0.4	2.1±0.1	2.0±0.3
	Culm	CK	24.7±2.1	26.1±0.8	17.2±1.4	8.6±3.8	6.0±3.8	6.8±1.2
		0		24.3±3.7	12.5±4.8	4.5±0.9	2.2±0.8	3.4±0.5
		1			11.7±0.4	4.3±1.1	2.4±0.9	3.0±0.7
	Panicle	CK	6.2±0.2	15.3±2.6	—	37.3±0.8	48.9±4.6	61.9±1.2
		0		11.8±4.3	33.8±3.4	42.0±1.4	47.1±6.1	53.8±1.0
		1			36.4±5.3	46.1±2.5	46.9±4.8	53.4±1.4

[a] Spacing was 30×15cm; transplanting rate was 4 to 6 seedlings per hill.

[b] Samplings were not made at the 4th week after heading for Pegonil variety.

穀粒充實期間損失部分葉面積，可使臺農67號穀粒充實速率提高，但縮短有效充實時間之長度，由表4中穗部 TNC 濃度增加速度觀之，抽穗後三週內任一時間取樣分析的結果，均以經去葉處理植株的濃度較高，對照組較低，第三週以後的表現則相反，成熟時穗部 TNC 含量以未經去葉之植株爲高，與處理組間的差異極爲顯著。大粒種 Pegonil 品種之試驗結果相似，但所受影響的程度遜於中粒型品種臺農67號。

行株距試驗係以 Pegonil 品種爲材料，分爲30×15與 30×7.5cm 兩種處理，插秧所用苗數分爲多本（4—6支苗）與單本2種。各處理對抽穗與成熟期 Pegonil 植株各部位乾重的影響列於表5；行株距同爲 30×15cm 時，多本植稻株與單本植稻株比較，於抽穗期均具有較高的葉片、莖稈與穗重，但至成熟期已無差異。將族羣密度加倍（行株距爲 30×7.5cm），且以單本植栽培之處理

Table 5. Effects of spacing and transplanting rate on the changes in dry weight and concentrations of total nonstructural carbohydrates (TNC) and N of Pegonil rice plants between heading and maturity[a]

Plant Fraction	Plant Spacing (cm)	Seedling Number per Hill	Dry Weight(g/plant)		TNC (%)		N (%)	
			Heading	Maturity	Heading	Maturity	Heading	Maturity
Leaf Blade	30×15	4—6	5.7±0.9	2.3±0.3	4.4±0.6	0.9±0.2	2.57±0.24	0.92±0.05
	30×15	1	4.9±0.6	2.2±0.3	4.1±0.4	2.1±0.8	2.98±0.14	0.99±0.14
	30×7.5	1	3.4±0.2	1.7±0.2	4.4±0.2	2.1±0.3	2.85±0.22	0.99±0.09
Culm	30×15	4—6	10.8±1.2	7.4±0.8	22.7±3.6	3.1±1.2	0.69±0.15	0.71±0.04
	30×15	1	7.8±0.9	8.0±0.6	15.6±0.6	4.7±2.1	1.07±0.05	0.69±0.06
	30×7.5	1	5.8±0.7	5.6±0.8	17.1±2.3	5.8±2.2	1.03±0.13	0.65±0.08
Panicle	30×15	4—6	2.7±0.4	18.1±2.2	4.9±0.4	57.4±2.5	1.24±0.16	1.51±0.18
	30×15	1	1.3±0.3	17.3±2.7	6.4±0.5	60.4±4.1	1.67±0.06	1.52±0.07
	30×7.5	1	1.2±0.2	12.5±1.7	5.5±0.6	63.8±1.3	1.54±0.05	1.31±0.06

[a] Data are means of measurements from 30 plants (10 from each replication).

，每欉稻株乾重均較 30×15cm 處理植株爲低（表5），以成熟期爲例，莖稈重爲每株 5.6g，較30×15cm 行株距栽培之植株（8.0g）輕30%，穗部之差異相似，約爲28%；但如考慮族羣表現，密植栽培因株數加倍，乾物質生產量亦提高，估算成熟期穗與全株乾物產量均較 30×15cm 處理增加45%，稻穀產量之增加幅度亦達35%（表6）。

Table 6. Yield components and yield of Pegonil and Tainung 67 rice varieties sujected to different cultural treatments[a]

Variety	Plant Spacing (cm)	Seedling Number per Hill	Panicle Number per Hill	Spikelet Number per Hill	Ripened Grain (%)	1,000-Grain-Weight (g)	Panicle Fraction (g/plant)				Grain Yield (t/ha)
							Filled Grain	Unfilled Grain	Panicle Branch	Total	
Pegonil	30×15	4—6	10.0±0.9	43.0±3.8	82.0±5.1	45.3±1.3	15.7±2.0	2.8±0.6	0.6±0.1	19.1±1.8	3.5±0.4
	30×15	1	8.8±1.7	51.9±2.7	81.5±4.4	44.5±1.3	16.4±2.8	2.0±0.7	0.6±0.1	19.0±2.3	3.7±0.6
	30×7.5	1	6.5±0.6	47.3±4.7	82.8±4.4	44.5±3.2	11.3±1.7	1.6±0.4	0.4±0.1	13.3±1.5	5.0±0.7
Tainung 67	30×15	4—6	12.5±1.8	114.9±3.7	83.5±1.9	23.2±0.9	27.8±4.2	1.0±0.2	1.3±0.2	30.1±3.6	6.2±0.8

[a] Data are means of measurements from 90 plants (30 from each replication).

單本植（30×15cm）與密植栽培均可提高抽穗期葉片、莖稈與穗內氮濃度，但至成熟期則已無差異，密植栽培水稻穗部氮濃度並有下降現象（表5），與去葉處理的結果相似(參考表3)。在TNC濃度方面，栽培密度與移植苗數對抽穗期莖稈與成熟期穗部的效應最爲明顯，一般而言，單本植與密植可降低抽穗期莖稈 TNC 濃度，但提高成熟期穗部 TNC 濃度的作用（表5）。

行株距試驗另一項主要目的在瞭解對大粒型品種產量及其構成要素的影響，試驗結果列於表6。行株距 30×15cm 多本植處理之每株穗數爲 10.0，高於單本植之 8.8與密植栽培之6.5，但仍不如臺農67號之 12.5；各處理對 Pegonil 水稻每穗穎花數、結實率與千粒重未造成任何差異，亦即密植對產量的影響全由穗數決定。Pegonil 品種每穗穎花數僅爲 50個左右，不及臺農67號（115個）的一半，與穗數較少同爲產量遜於臺農67號的主要原因。Pegonil 品種之千粒重高達 45g，幾爲臺農 67號（23.2g）之兩倍。

行株距處理對充實穀粒、不充實穀粒與枝梗重量的影響列於表 6；由於密植栽培使穗數減少，每株水稻充實與不充實穀粒重量亦因粒數減少而降低，其充實粒重僅有 11.3g，爲 30×15cm 處理之 69%。品種間比較發現 Pegonil 不充實穀粒重佔全穗重之比例頗高達 10.5—14.7%，爲臺農67號（3.3%）之3.2至 4.5倍，顯示大粒型品種之充實效率較低。經由產量構成要素估算產量，30×15cm 與多本植處理爲 3.5t/ha，單本植爲 3.7t/ha，並無差異存在，密植處理的產量爲 5.0t/ha，亦即具有約30%的增產效果，但均不及臺農67號品種（6.2t/ha）高產（表 6）。

密植栽培可使 Pegonil 品種穗內充實穀粒 TNC 濃度升高，但全氮濃度降低，不充實穀粒內之含氮量亦有下降的趨勢；不同栽植密度對不充實穀粒 TNC 含量雖無影響，但三個處理的數值均在45%以上，遠高於臺農67號的17.5%（表 7），顯示大粒型品種穀粒對光合成物質的利用效率偏低，此外，Pegonil 品種枝梗內的氮濃度與莖稈部位相近，在 0.6%與 0.7%之間，亦無處理間效應；TNC 濃度極低，尚不及2.4%，與臺農67號比較（5.9%），呈現顯著的差異（表 7）。

Table 7. Concentrations (%) of N and total nonstructural carbohydrates (TNC) in different fractions of mature panicles of Pegonil and Tainung 67 rice plants

Variety	Chemical Constituent	Plant Spacing (cm)	Seedling Number per Hill	Filled Grain	Unfilled Grain	Panicle Branch
Pegonil	TNC	30×15	4—6	57.4±2.5	46.9±1.6	1.2±0.2
		30×15	1	60.4±4.1	45.5±2.2	1.8±0.1
		30×7.5	1	63.8±1.3	49.4±3.4	2.3±0.2
	N	30×15	4—6	1.51±0.18	1.66±0.07	0.66±0.05
		30×15	1	1.52±0.07	1.65±0.01	0.71±0.05
		30×7.5	1	1.31±0.06	1.50±0.11	0.64±0.04
Tainung 67	TNC	30×15	4—6	61.9±1.2	17.5±2.9	5.9±0.7
	N	30×15	4—6	1.15±0.10	1.01±0.02	0.63±0.04

討　論

本所作物生理研究室在對大粒型水稻進行的試驗中，曾採用 Mira 與 Arborio 品種爲材料，並發現兩品種間農藝性狀、產量與對環境適應性差異[4,17]；本試驗採用 Pegonil 品種，係因其具有株高較矮及千粒重高而穩定的特性，且用以培育臺農67號大粒型 isogenic line，頗具成功之故。試驗結果 Pegonil 在第二期作的產量偏低，密植栽培雖可大幅提高產量，但仍不及臺農67號的表現（表 6）。本研究室在74年第一、二期作曾以相同密植栽培處理進行另一項關於大粒型品種的生理研究，茲將其產量資料與本試驗結果（t/ha）併列於下，以供比較，括弧內之數值爲產量指數：

品　種	行　距　株	移植苗數	一　期　作	二　期　作	二　期　作（本試驗）
臺農 67 號	30×15cm	4—6	6.7(100)	5.8(100)	6.2(100)
Pegonil	30×15cm	4—6	5.2(78)	4.0(69)	3.5(57)
Pegonil	30×15cm	1	4.6(69)	3.8(66)	3.7(60)
Pegonil	30×7.5cm	1	7.3(109)	4.9(84)	5.0(81)

由上述資料得知，Pegonil 品種較不適於二期作栽培，與 Arborio 品種的適應性相同[17]，但與 Mira 品種較適於二期作環境的特性[16]有異，顯示品種間的差異。又因密植栽培使株數加倍，一期作可提高產量58%，二期作提高29—42%，一期作之產量並超越臺農67號，除表示大粒型品種確具高產潛力外，今後並應針對植株特殊農藝性狀，採用不同的栽培方法，以達到高產的目的。

穀類作物的產量由充實速率與充實期期間兩項因子共同決定[18]；由表 2 得知，臺農67號穗部乾重至抽穗後第 5 週始達高峰，充實期間頗長，爲一特殊現象，可能與穀粒充實期間溫度與日射量較低有關，Yoshida and Hara[20] 即曾指出，16—22°C 之低溫與低日射量可延長稃稻充實期間。由表 2 乾物重及表 6 一穗穎花數資料推算，大粒型品種 Pegonil 的穀粒有効充實期短，但以每一穀粒爲單位，充實速率應遠較臺農 67號爲高；周[2]以 7 個不同粒重水稻品種爲材料，獲得大粒品種在二期作具有較高充實速率之結果；Fujita *et al.*[6] 也報告充實速率隨穀粒粒重之加大而升高。

大粒型品種 Pegonil 如確實具有較高的充實速率與較短的有效充實時間，則在抽穗後三週內是否具有充份的光合作用能力（concurrent photosynthesis）或是否更依賴抽穗前預貯於莖稈中乾物質（pre-heading storage）之再轉移，以滿足穀粒充實的需要，值得予以探討。本試驗並未直接測定光合作用能力，但抽穗後一週內莖稈 TNC 濃度由22.7%急速上升至29%（表 4），且於抽穗期去除二分之一葉片，雖導致莖稈內 TNC 濃度下降（表 4），而與對照植株比較，莖稈與穗部乾重及成熟期穗部 TNC 濃度並未減少，表示可能仍有充份之光合成物質供應，唯仍不能確定其絕對光合作用能力高於臺農 67號品種。在對預貯性碳水化合物的利用方面，假設再轉移効率爲 70%[5]，則臺農67號成熟期穗部 TNC 有21%源於抽穗前之光合成產物，與以往的試驗結果[4]相近，Pegonil 則爲 24%；抽穗時與抽穗後一週行去葉處理，預貯性 TNC 的貢獻分別小幅上升至 27%與 29%，顯示葉面積減少一半時，Pegonil 仍以抽穗後之光合作用爲主要供源，對預貯性物質的依賴程度並未大幅上升，同時仍能維持相當的產量。反之，去葉處理使臺農67號穗重顯著降低（表 2），預貯性 TNC 對全穗 TNC 的貢獻增加至42%，表示光合成能力因葉面積減少而受到嚴重的阻礙。

抽穗時 Pegonil 與臺農67號葉片內氮濃度相同，隨後之下降幅度則以 Pegonil 較爲明顯，抽穗後第 2 及 3 週之濃度僅爲 1.65%與1.30%，遠低於臺農67號之1.89%與1.81%。Yoshida (1981) 估計維持水稻葉片高光合成能力的最低氮濃度爲 2 %，Tanaka[12] 也指出光合作用速率隨水稻葉片全氮濃度增加而上升，直至 3 %爲止；因此 Pegonil 品種葉片氮濃度在抽穗後急劇下降，有可能影響其生理活性[10]；換言之，光合作用能力雖能充份供應穀粒充實的需要，但以抽穗後全株乾物質累積量的觀點而言，其速率應仍低於臺農67號。

成熟期 Pegonil 穗部氮濃度（1.51%）遠較臺農 67號（1.15%）爲高（表 3），似爲大粒型水稻品種共有之特性[17]，也可能是抽穗後葉片氮濃度急劇下降的最主要原因，Thom *et al.*[13] 即曾報告，發育中穀粒的需氮量極大，除源於根部吸收作用之供應外，葉片內所含氮素亦向外轉移。但本試驗中去除二分之一葉片，減少葉片供應氮素能力後，穗部氮濃度雖有明顯下降，而葉片中之氮濃度却未較相當之對照組降低（表 3），顯然這種「再轉移」的現象並不單純。可能的解釋爲，葉面積減少後爲充份供應積儲對於光合成物質的需求，所餘葉片的活性上升，減緩氮素外移的速率；同時於損失葉面積，根部在競爭光合成物質方面，積儲强度（sink strength）更遜於穗部，在缺少能源供應的情況下，吸收能力下降，而使氮素供應更形不足，導致穗部氮濃度的下降。此外，去葉處理後，穗部乾物重與氮濃度並行降低，可能表示氮素與碳水化合物的累積亦互相影響與作用[9,14,15,17]。

在行株距試驗部份曾對產量構成要素進行詳細的調查，大粒型品種 Pegonil 的穗數雖低，但與臺農67號差距不大，一穗穎花數太少爲低產的最主要原因。在同爲 30×15cm之行株距下，多本植或單本植雖使後者穗數稍減，但穎花數增多，故產量相同（表 6）。密植（30×7.5cm）穗數明顯降低，但其他三項產量構成要素未受影響，因此單株產量雖然不如疏植者，公頃產量却爲最高（表 6）。經由比較 30×15cm 與 30×7.5cm 行株距而均以單本植之兩處理各項性狀，以全株乾重爲 10.4g，

爲疏植者（14.0g）之74%表5資料計算，顯然在抽穗以前，後者並不能充份利用環境資源；抽穗後由於植株已趨繁茂，空間成爲限制因子，故密植植株在穀粒全充實期間所增加之乾重僅約爲疏植者之70%，此一時期增加乾物重之量，爲密植最後穗重的75%，爲疏植最後穗重的78%，顯示在生育空間受到限制的情況下，水稻植株依賴再轉移物質的程度增加[18]。唯就本試驗之密植株而言，光合成能力雖受限制，應仍可供應穀粒充實的需要，此一推論可由穗部較高的 TNC 濃度（表5）得到證明。疏植與密植兩處理之乾物質收穫指數（dry matter harvest index）均爲0.63，氮收穫指數（nitrogen harvest index）均爲0.77，TNC 收穫指數（TNC harvest index）均爲0.96，處理間全無差異，亦與楊等[3]的數值相同，顯示在供試兩種不同密度的栽培方式下，生產效率（yield efficiency）相同，亦即密植具有可以使 Pegonil 品種增產的理論基礎。

對臺農67號與 Pegonil 品種穀粒充實度的調查，發現 Pegonil 品種不充實粒重占全穗重之10.5—14.7%，比例較高，臺農67號僅爲3.3%（表6）；又分析不充實穀粒 TNC 濃度，得知 Pegonil 高達45—50%，臺農67號爲17.5%，兩者亦有極顯著的差異（表7），顯示大粒型品種部份穀粒在充實的過程中，有過早中止充實或均一度欠佳的問題存在，估計穗內 TNC 含量中，有8—10%未能予以收穫，因此生產效率不如臺農67號；今後在謀求利用大粒型水稻種源時，應注意改善此一缺點。

綜合本試驗的結果，認爲單位面積粒數爲限制大粒型水稻品種 Pegonil 產量的最主要原因；抽穗期去除二分之一葉片對臺農67號產量有顯著影響，對 Pegonil 的作用較小，亦即就現有植株型態而言，Pegonil 品種具有充足的供源能力。密植栽培可提高大粒型水稻之產量，顯示以改良栽培方法提升大粒型品種的利用性應屬可行。大粒型水稻穀粒充實速率雖高，但充實期間短，又其充實均一性欠佳，造成穗部 TNC 的浪費，爲極待改良的缺點。

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Influence of Partial Leaf-Removal and Planting Density on the Yield Performances of Rice Plants Differing in Grain Weight[1]

M. L. Wei and D. J. Liu[2]

Summary

Studies were conducted to examine the possibility of enhancing grain yield of a large-grain variety, Pegonil, through increasing panicle number per unit area by dense planting(30×7.5cm vs. 30×15cm). Fifty percent leaf-cutting was also executed at either heading or 1 week after heading to investigate whether photosynthetic production was high enough to meet the needs of developing grains. Under the environmental conditions of the 2nd crop season, yield was 40% lower for Pegonil than for Tainung 67, a medium-grain variety, due mainly to fewer spikelet number per panicle and panicle number per hill. Leaf-removal at heading stage showed no effect on the mature panicle weight per hill, whereas a 32% reduction was observed in Tainung 67. Leaf-removal at 1 week after heading decreased panicle weight by 14% and 32%, repectively, for Pegonil and Tainung 67. Leaf-cutting caused a decrease of N concentration in the panicle, but not in the leaf blade and culm; indicating retranslocation of N to the panicle was insignificant. This, along with the low TNC concentration in the culm, suggested that photosynthetic production was unable to sustain high root activity, and hence the supply of N was not in an adequate state for the developing grains. Dense planting increased yield of Pegonil by 42%, which was still 20 % lower than the yield of Tainung 67. As panicle number per unit area was increased significantly while the other three yield components were unaffected, it indicated that grain yield of large-grain rice varieties could be increased substantially through cultural improvement. The large-grain variety Pegonil possessed high accumulation rates of dry matter, N ane TNC in the panicles during the first 3 weeks after heading. However, shorter effective grain-filling period and less uniform TNC deposition among spikelets within a panicle resulted in lower yield efficiency of Pegonil. Improvement should be made before the large-grain rice varieties were able to be grown commercially.

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玉米雙對染色體轉座之成株農藝性狀對子實產量之影響[1]

劉孔生[2]　陳　成[3]

摘要：由於玉米之染色體轉座時會造成結實率下降，百粒重增加及子實重減少等影響，因此改變了各項產量構成要素之重要性。本試驗將全套之⊙6轉座異型接合組合種植於田間，試驗結果採用逐步複相關法進行分析，以比較染色體對產量構成要素之影響，由於⊙6組合之結實率僅25%，故除穗重外，影響產量最重要之因素爲百粒重，其次爲結實率。吐絲期與株高爲營養性狀，對子實產量之影響較小，如將穗重、百粒重及結實率等因素除去，方能顯示株高之重要性，至於吐絲期則無顯著之影響。

植物之染色體呈異型接合時，其部分雌配子染色體會發生重複與缺失 (13)，因此無法發育而導致稔實率下降 (14)。玉米之某一對染色體同時與其他的兩對染色體發生相互轉座（雙對染色體轉座，ring of six translocation 以⊙6代表）時，結實率將降至25% (3)。此時各子粒均有足够的空間及養分供應，能够充分的發育，使百粒重增加。而子實產量方面却由於積儲（sink）能力不足，使產量降低，因而改變了各項產量構成要素的重要性。爲求瞭解不同的染色體發生轉座時對產量構成要素之作用，本試驗以轉座系統爲材料進行交配，以探討⊙6染色體轉座對各項農藝性狀之影響，作爲日後利用轉座同源系，研究玉米產量時之參考。

材料與方法

本試驗以玉米全套染色體相互轉座系統（whole set of chromosomal reciprocal translocation stocks），爲材料（共計九系統，其參與轉座之染色體與斷點位置請參閱表1），進行全部組合（9×9）之交配，以產生81組之⊙6染色體轉座組合（見表2）之 F_1 種子。再於民國71年3月中旬將81組 F_1 組合種植於臺北市臺灣大學試驗農場。每組合種植一行，每行10株，爲避免植株之間發生生長競爭，使用90公分之行距，株距則爲30公分。田間設計採用順序排列，每五行種植一行H95自交系作爲對照，以校正由土壤差異所造成之影響。施肥分爲基肥與二次追肥，每次施用氮肥（N）50公斤、鉀肥（K_2O）60公斤及磷肥（P_2O_5）45公斤（以上爲每公頃用量，依田間面積換算後施用），基肥於播種前撒施，追肥則於播種後30天及60天條施，並進行培土。於雄穗抽出時，將各植株分別編號、掛牌，於每行中央生長正常者逢機選取四株，記錄吐絲期、測定株高，俟植株黃化後收取成熟果穗，烘乾秤量穗重、子實產量（子實重）及百粒重。同時測定果穗之子粒行數、每行粒數並計數子實數目，以計算結實率。

由於表2中之轉座組合，對角線部分實際上爲自交，其自交後裔不僅生長勢較差，染色體亦呈正

1.臺灣省農業試驗所　研究報告第 1300 號。本研究係第一作者博士論文之部分。

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表1 玉米第九對染色體與全套染色體相互轉座之同型接合體系統之名稱、代號及細胞學資料

Table 1. Name, code number and cytological information in whole set of chromosomal reciprocal translocation stocks.

轉座系統名稱 Name of tranlocation stock	代號 Code No.	相互轉座染色體對 Reciprocal translocation chromosome	斷點位置 Position of break point				標識基因 Marker gene
1—9_{4995}	T_1	1—9	1L	0.19	9S	0.20	wx/wx
2—9_b	T_2	2—9	2S	0.18	9L	0.22	wx/wx
3—9_c	T_3	3—9	3L	0.09	9L	0.12	wx/wx
4—9_g	T_4	4—9	4S	0.27	9L	0.27	wx/wx
5—9_a	T_5	5—9	5L	0.69	9S	0.17	wx/wx
6—9_b	T_6	6—9	6L	0.10	9S	0.37	wx/wx
7—9_b	T_7	7—9	7S	0.76	9S	0.19	wx/wx
8—9_d	T_8	8—9	8L	0.09	9S	0.16	wx/wx
9—10^b	T_9	10—9	10S	0.40	9S	0.13	wx/wx

表2 利用第九對染色體與全套染色體相互轉座之同型接合體系統正反交所得之72組⊙6染色體組合

Table 2. Totalling 72 (9×9-9) combinations of ⊙6 translocation heterozygotes from the crosses between the whole set (9-pair) reciprocal translocation stocks.

우 \ 숭	1—9	2—9	3—9	4—9	5—9	6—9	7—9	8—9	9—10
1—9	1—9	1—9—2	1—9—3	1—9—4	1—9—5	1—9—6	1—9—7	1—9—8	1—9—10
2—9	2—9—1	2—9	2—9—3	2—9—4	2—9—5	2—9—6	2—9—7	2—9—8	2—9—10
3—9	3—9—1	3—9—2	3—9	3—9—4	3—9—5	3—9—6	8—9—7	3—9—8	3—9—10
4—9	4—9—1	4—9—2	4—9—3	4—9	4—9—5	4—9—6	4—9—7	4—9—8	4—9—10
5—9	5—9—1	5—9—2	5—9—3	5—9—4	5—9	5—9—6	5—9—7	5—9—8	5—9—10
6—9	6—9—1	6—9—2	6—9—3	6—9—4	6—9—5	6—9	6—9—7	6—9—8	6—9—10
7—9	7—9—1	7—9—2	7—9—3	7—9—4	7—9—5	7—9—6	7—9	7—9—8	7—9—10
8—9	8—9—1	8—9—2	8—9—3	8—9—4	8—9—5	8—9—6	8—9—7	8—9	8—9—10
9—10	10—9—1	10—9—2	10—9—3	10—9—4	10—9—5	10—9—6	10—9—7	10—9—8	10—9

註：表中1—9～10—9等組合係估算之⊙6，實際測得之資料爲轉座材料自交之後裔，減數分裂時染色體呈二價體而非⊙6構造。

常之二價配對（Ⅱ），而非⊙6 構造，測定之結果將與其餘的轉座組合不同。以此等資料進行統計分析將產生誤差，因此利用下列估算等方法計算出估值：

$$i-9=\left[\sum_{j=1}^{9}(T_i\times T_j)+\sum_{j=1}^{9}(T_j\times T_i)\right]/16 \quad j=1,2,3,\cdots\cdots 8,10 \quad j\neq i$$

以此等估算之數值進行統計。

獲得之資料，利用臺灣大學電子計算機中心租用之CDC公司CYBER 825型電子計算機進行分析，以探討染色體轉座後營養性狀（吐絲期、株高）及生殖性狀（結實率、百粒重與穗重）對子實產量之影響。

統計時先依父本將資料合併（以母本爲重複），以消除母方親本之差異，求出各父本及父方之轉座效應。再依母本將資料合併，求出各母本及母方之轉座效應，最後將72組⊙6 轉座組合之資料合併，以明瞭一般⊙6 轉座對農藝性狀之影響。除上述資料外，試驗中亦加入同型接合轉座親本（二價體，Ⅱ），及估算之⊙6 組合作爲對照，共同比較。由於估算之 i — 9 組合（ i = 1，2，3，…… 8，10）均含有全部之轉座父本及母本，因此消除了各組合間之遺傳差異，僅餘染色體轉座效應，由此即可比較不同之染色體發生轉座時對農藝性狀之影響。

試驗調查所獲得的資料，先利用電子計算機硬式磁碟（hard disc）內所存之 MINITAB 程式檔（package）[16]，求出各農藝性狀與子實產量間之複迴歸方程式，由此方程式即可明瞭產量受各種農藝性狀影響之情形[4] 再由程式檔所計算出之各項均方求出複回歸決定係數（coefficient of determination, R^2），由R^2值之大小可判定各獨立變數所能代表隨變數之能力[12]。

最後利用貯存於計算機磁碟內之BMDP2R程式檔進行逐步複相關分析（Stepwise multivariate correlation analysis）[11]，以明瞭各獨立變數對於隨變數之重要性，求出影響子實產量最首要的因子，作爲育種選拔之指標[2,6]。此外亦利用電腦程式求出逐步複相關之相關係數，以表示各獨立變數可以增進應變數之比例，即可獲知各獨立變數所能增進相關性之程度[1]。

結果與討論

作爲土異控制之自交系 H95，其調查之各種性狀，經單向變方分析（one way ANOVA）得知土壤差異不顯著（資料未列出），證明田間地力、環境均一，因此參試材料之各項資料不需校正，可直接進行統計分析。

各項參試材料之吐絲期、株高、結實率、百粒重、穗重與產量之平均值與標準機差列於表 3。參試材料之雄親及雌親效應，係利用統計方法消去一親本效應，因此各項資料仍含有另一親之效應，並混有其轉座異型接合效應，對照比較時可判定各性狀是否具有母系效應（maternal effect），及推測各對染色體轉座於雌、雄親對於各農藝性狀之影響。對照處理中，⊙6 組合係利用統計方法估算而來，已除去雙親之遺傳差異，僅含有不同之染色體對之轉座異型接合效應；Ⅱ則將各個同接合轉座親本資料加以合併，因此不含⊙6 轉座異型接合效應，但具有親本遺傳背景之不同；總和資料則包含72組⊙6 F_1 及利用統計方法估算所得之 9 組⊙6（對照資料），不僅含有親本遺傳背景之差異，且具有各組⊙6 染色體轉座異型接合效應。因此比較總合資料及二項對照資料時；⊙6 與組合之間含有親本遺傳背景之差異，Ⅱ與總和之間則含有染色體轉座之差異，Ⅱ與⊙6 之間則有親本遺傳背景及雙染色體轉座同、異型接合之差異。由此三種資料，即可推測親本效應與染色體轉座異型接合對子實產量與各種農藝性狀間相關性之影響。

又由於玉米係異交作物，具有明顯之雜種優勢，因此自交系互相雜交後，一般會發生株高增加，雌穗增大、增長，雄穗分枝、花粉增多，子實數目增加，百粒重較重等現象[8]。因此在對照之Ⅱ（親本）與對照之⊙6，總和資料（F_1）之間尚有雜種優勢之差異，但表 3 所列之結果却有許多異常現象，比較總和、對照之⊙6（F_1）與對照之Ⅱ（親本）時，F_1 之吐絲期並未延長，株高增加不顯著，結實率顯著的下降，穗重與子實產量亦較低，僅百粒重增加。此乃由於試驗中使用之親本爲染色體

表3. 玉米⊙6組合之雄親、雌親效應於各轉座染色體對之吐絲期、株高、結實率、百粒重、穗重與子實重之平均及標準機差

Table 3. The mean and standard error of silking date, plant height, fertility, 100-seed weight, ear weight and kernel weight of male and female effects on translocation chromosomes in corn.

效應 Effect	轉座染色體對 Translocation chromosome	吐絲期（日） Silking date 平均±標準機差 $\bar{X}$±S. D.	株高（cm） Plant height 平均±標準機差 $\bar{X}$±S. D.	結實率（%） Fertility 平均±標準機差 $\bar{X}$±S. D.	百粒重（g） 100-seed wt. 平均±標準機差 $\bar{X}$±S. D.	穗重（g） Ear wt. 平均±標準機差 $\bar{X}$±S. D.	子實產量（g） Grain yield 平均±標準機差 $\bar{X}$±S. D.
雄親 Male parent	1—9	73.94±2.57	157.72±5.01	23.29±1.21	27.37±2.47	55.67±7.83	40.05±3.84
	2—9	77.06±2.92	154.67±3.34	23.48±1.28	27.72±2.82	55.68±7.70	41.14±3.44
	3—9	75.44±3.50	157.00±3.69	23.07±1.15	27.13±2.56	53.97±3.37	39.52±5.29
	4—9	77.86±3.15	154.92±3.81	23.11±1.24	27.62±3.04	55.88±7.51	41.58±3.72
	5—9	75.92±3.15	154.64±3.90	22.75±1.30	26.95±2.57	56.64±7.03	39.43±5.91
	6—9	73.36±2.70	160.44±5.19	22.85±1.45	27.64±2.30	59.92±3.70	40.78±3.67
	7—9	76.67±2.86	159.19±3.80	22.96±1.49	26.35±2.63	55.57±7.83	39.58±7.03
	8—9	75.39±2.50	161.94±3.27	22.59±1.42	27.37±3.11	54.47±3.52	38.70±3.68
	10—9	76.25±3.24	167.61±7.50	23.45±1.07	28.13±2.46	59.49±3.59	43.62±3.74
雌親 Female parent	1—9	74.83±2.85	153.56±3.91	23.32±1.31	27.43±2.89	57.75±3.06	41.75±5.61
	2—9	73.89±3.14	156.33±5.27	23.32±1.17	27.50±2.54	56.71±7.33	40.76±3.55
	3—9	75.39±2.37	156.86±3.78	23.05±1.42	26.84±3.31	54.88±3.75	40.74±9.44
	4—9	73.28±3.37	156.03±7.04	23.06±1.27	26.81±2.45	55.61±3.91	40.10±5.78
	5—9	76.08±2.67	156.03±3.83	23.03±1.39	27.50±2.57	54.48±3.57	39.54±4.65
	6—9	74.67±2.59	160.03±7.42	23.13±1.41	27.18±2.15	53.96±3.62	41.49±3.28
	7—9	76.67±3.35	161.69±3.84	22.78±1.38	26.86±2.37	54.92±7.73	40.02±7.03
	8—9	77.22±4.05	163.06±3.50	22.87±1.25	28.45±2.74	56.85±7.17	41.74±3.73
	10—9	74.86±3.66	164.56±3.45	23.00±1.28	27.70±2.87	54.12±3.17	38.25±3.41
總和	Pooled	75.77±3.23	158.68±7.72	23.06±1.32	27.36±2.69	55.81±7.22	40.49±3.62
對照 C. K.	Ⅱ	75.78±3.86	150.69±15.31	77.50±2.57	15.14±4.27	89.62±25.35	71.84±22.79
	⊙6	75.83±1.23	158.69± 4.83	23.06±0.55	27.36±1.34	55.81± 4.22	40.49±3.81

轉座同型接合體，因此親本在減數分裂時不會發生染色體缺失及重複，結實正常。而其相互交配所產生之F_1，則爲雙染色體轉座異型接合體，減數分裂時，大部分配子發生染色體缺失及重複，使結實率下降，穗重，子實產量亦隨之減少，至於百粒重則因結實率降低，每粒子實可獲得較多之養分而增加。吐絲期與株高未發生顯著之雜種優勢，可能由於多對染色體發生轉座異型接合時，會干擾基因間之平衡，使生長勢降低而抵消雜種優勢。因此在試驗中僅考慮染色體轉座後對於各農藝性之影響，F_1之雜種優勢則不討論。

在各平均值之標準機差方面，雄親與雌親效應間，各性狀之標準機差均極接近，因此母系效應對各性狀之變異性無顯著的影響。總和資料，對照之Ⅱ及⊙6三者之間，Ⅱ之機差最大、總合資料次之、⊙6最小，此乃由於Ⅱ含有九組遺傳背景不同之轉座系統，使機差增加；總合資料爲全互交之F_1，除含有親本遺傳背景之差異外，尚有轉座異型接合之效應，本應具有較大之機差，但由於玉米之F_1族羣對環境之適應性較强，使環境所引起之變異減少，又由於重複次數較多，使機差減少。⊙6組合，則由於先利用統計方法除去各組合間親本之差異，僅餘染色體轉座效應，再合併計算標準機差，故機差最小。又由於⊙6組合之資料係由全互交F_1估算而來，因此其平均值與總和資料之平均極爲接近。

子實產量與吐絲期、株高、結實率、百粒重及穗重等五種農藝性狀間之複迴歸列於表4，其中穗重之淨歸係數於各對染色體轉座均達於極顯著水準，顯示無論何對染色體發生轉座，穗重仍會影響子實重，又由於雄親與雌親效應一致，因此穗重與子實產量之關係不受正反交配母系效應影響。株高之淨迴歸係數於各染色體對轉座間亦達於極顯著，因此在營養性狀中，株高能配合穗重來影響子實產量，Ⅱ與總和資料之淨迴歸係數中，吐絲期、結實率與百粒重之顯著性並不一致，在總和資料均極顯著

表4：玉米雌雄親染色體轉座影響五農藝性狀（X_1, X_2, X_3, X_4, X_5）之複迴歸及淨迴歸係數分析與顯著性測驗

Table 4. Multiple regression analysis and significant test of partial regression coefficients of plant characters (X_1, X_2, X_3, X_4, X_5) on translocation and parental effects in corn.

效應 Effect	轉座染色體對 Translocation chromosome	截距 Intercept	吐絲期 (X_1) Silking date	株高 (X_2) Plant height	結實率(X_3) Fertility	百粒重(X_4) 100-seed wt.	穗重 (X_5) ear wt.	複迴歸決定係數 Coefficient of determination R^2
		a	b_1	b_2	b_3	b_4	b_5	
雄親 Male effect	1—9	−15.16	0.0494	−0.0951**	0.7630*	0.2350	0.7609**	0.93**
	2—9	−26.06	−0.0174	−0.0398	0.6708	0.2526	0.7117**	0.88**
	3—9	− 6.00	0.1548	−0.1638**	0.2647	0.4302 *	0.7744**	0.92**
	4—9	23.30	−0.0369	−0.1332	−0.9381	0.4766	0.9001**	0.70**
	5—9	−16.11	−0.0895	0.0567**	0.2293	0.3854**	0.6948**	0.95**
	6—9	−10.04	0.0069	−0.0250**	0.3175	0.0057	0.8242**	0.91**
	7—9	−10.17	0.0234**	−0.0696**	0.2568	0.2766	0.8253**	0.97**
	8—9	−43.69	0.0379	0.0573**	0.6919*	0.6277**	0.6872**	0.92**
	10—9	−24.43	0.0888**	0.0354**	0.2031	0.1597	0.7746**	0.96**
雌親 Female effect	1—9	−20.61	−0.0171**	−0.0108 *	0.5020*	0.2123	0.8271**	0.95**
	2—9	1.74	−0.0675	−0.0664	0.0346	0.2796**	0.8116**	0.98**
	3—9	− 9.92	0.2839**	−0.2129 *	−0.0518	0.7563	0.7935**	0.70**
	4—9	−12.76	−0.0731**	0.0215**	0.2440	0.2766	0.7560**	0.94**
	5—9	−14.48	0.1115 *	−0.0655**	0.4453	0.2710	0.6982**	0.86**
	6—9	−23.06	−0.1929 *	0.0587**	0.6059*	0.3492	0.8080**	0.93**
	7—9	−23.65	0.1198**	−0.0195**	0.0452	0.5110**	0.7808**	0.98**
	8—9	−22.85	−0.0237	−0.0141**	0.6981*	0.3960	0.7296**	0.93**
	10—9	−28.67	0.1078	−0.0342**	0.7700*	0.3671 *	0.6764**	0.92**
總和 Pooled		−18.21	0.0232**	−0.0256**	0.3775**	0.3773**	0.7519**	0.87**
對照 C. K.	Ⅱ	−25.68	0.2059	−0.0020**	0.0209	0.1158	0.8797**	0.99**
	⊙6	−15.31	0.1077	−0.0450**	−0.0069	0.3460 *	0.8148**	0.97**

註：迴歸方程式$y=a+b_1X_1+b_2X_2+b_3X_3+b_4X_4+b_5X_5$

，Ⅱ爲不顯著，此乃自交系（高結實率、百粒重輕）及組合F_1（低結實率，百粒重較重）三特性所造成（參閱表3之平均值）。⊙6與總和資料之間則有吐絲期及結實率二性狀不一致，因此吐絲期與結實率會受親本背景及染色體轉座之共同作用而改變其與子實產量之相關性，百粒重則僅有對照之Ⅱ不顯著，對照之⊙6達於顯著水準，總和資料達於極顯著，因此僅有親本效應會影響百粒重與子實產量之關係。至於Ⅱ與⊙6之間百粒重之顯著性不一致，則由於染色體發生雙對相互轉座之後結實率下降（結實率約 25%）(3)，使同穗中子粒數減少，而百粒重相對增加，導致百粒重對於子實產量發生顯著的效應。

表4所列之複迴歸決定係數於各項效應均達於極顯著，表示表中所列五項農藝性狀足以代表子實產量，爲產量構成要素。但各項性狀重要性並不相等，因此進行逐步複相關分析，其結果列於表5。由表中可知於諸農藝性狀中穗重對子實產量之影響最大，不僅於各項效應順位均排名首位，且增進R^2之百分比亦甚大，遠超過其他農藝性狀。表4中株高於各染色體對轉座時，對於子實產量有顯著的影響，表5中却非首要之獨立變值，乃由於穗重與子實產量相關太密切，株高性狀之變異也較大，進行逐步複相關分析時，爲統計程式所摒棄。表4中亦有許多農藝性狀達於顯著水準，進一步分析時，則並非決定子實產量之重要性狀，增進之R^2值極爲有限，因此認爲五性狀在共同分析時，僅穗重爲主要因子，其餘性狀對子實產量影響較小，如欲比較其餘四性狀，則應棄除相關性最密切之穗重性狀，再進行其他四性狀的分析。

四性狀複迴歸分析結果列於表6，於吐絲期、株高、結實率及百粒重諸性狀中，百粒重之淨迴歸係數於各對染色體轉座均達於極顯著，因此百粒重與子實產量之關係亦不受染色體轉座及母系效應之影響。至於其他性狀如結實率對子實產量，在某些轉座組合內具有顯著的影響。總和資料之淨迴歸係

表5：逐步複相關（五性狀）分析及顯著性測驗

Table 5. Stepwise multivariate (5-character) correlation analysis and significant tests.

效應 Effect	轉座染色體對 Translocation chromosome	首要獨立變值參與次序 Step number and number of independent variables included					增進 R^2 之百分率 Increase in R^2 (%)				
		1	2	3	4	5	X_1	X_2	X_3	X_4	X_5
雄親 Male parent	1—9	X_5	X_3						1.31		90.96
	2—9	X_5	X_3						1.88		84.80
	3—9	X_5									88.89
	4—9	X_5									64.00
	5—9	X_5	X_4							1.39	93.06
	6—9	X_5									89.85
	7—9	X_5	X_2					0.61			95.72
	8—9	X_5	X_4	X_3					1.28	4.03	86.80
	10—9	X_5	X_1				0.64				94.87
雌親 Female parent	1—9	X_5	X_3	X_4					1.06	0.82	92.63
	2—9	X_5	X_4	X_2				0.34		0.49	97.39
	3—9	X_5	X_4							4.76	63.48
	4—9	X_5									93.05
	5—9	X_5									82.16
	6—9	X_5	X_3						2.07		89.10
	7—9	X_5	X_4	X_1			0.35			1.42	96.07
	8—9	X_5									90.75
	10—9	X_5									88.27
總和 Pooled		X_5	X_4	X_3					0.54	1.11	84.80
對照 C. K	Ⅱ	X_5	X_1				0.14				99.32
	⊙♂	X_5	X_4							0.52	95.66

註：X_1, X_2, X_3, X_4, X_5見表4　未列出之變異數，不適供迴歸性狀，分析時爲統計程式所摒棄。

表 6：玉米雌雄親染色體轉座影響四農藝性狀（X_1, X_2, X_3, X_4）之複迴歸及淨迴歸係數分析與顯著性測驗

Table 6. Multiple regression analysis and significant test of partial regression coefficients of plant characters (X_1, X_2, X_3, X_4) on translocation and parental effects in corn

效應 Effect	轉座染色體對 Translocation chromosome	截距 Intercept	吐絲期 Silking date	株高 Plant height	結實率 Fertility	百粒重 100-seed wt.	複迴歸決定係數 Coefficient of determination
		a	b_1	b_2	b_3	b_4	R^2
雄親 Male parent	1—9	— 76.88	0.1381	0.0860	1.7530**	1.9120**	0.64**
	2—9	— 12.56	0.0129	— 0.0305	0.7171	1.6816**	0.55**
	3—9	— 21.30	— 0.1569	0.1502**	0.7334	1.1850**	0.41**
	4—9	— 2.46	— 0.3500	0.0305	0.9190	1.6479**	0.34**
	5—9	— 37.79	— 0.2828	0.1469**	1.7181**	1.3688**	0.62**
	6—9	— 40.23	— 0.1507	0.3494	0.1557	1.1739**	0.23
	7—9	— 94.55	0.1635	0.1663*	1.8851**	1.9672**	0.66**
	8—9	— 89.48	0.1685	0.1912	2.0357**	1.4076**	0.73**
	10—9	— 50.59	0.0594*	0.0549	1.5714 *	1.5507**	0.63**
雌親 Female parent	1—9	— 61.15	0.0056	0.2155	1.4724*	1.2782**	0.49**
	2—9	— 74.91	0.1859	0.0244	1.8055**	2.0231**	0.74**
	3—9	— 8.62	— 0.4057*	0.1315	0.4210	1.8481**	0.51**
	4—9	— 39.21	0.1388	0.1537*	0.2086	1.4892**	0.46**
	5—9	— 42.10	0.1629	0.1383**	0.7523	1.1036**	0.56**
	6—9	— 59.32	— 0.0971	0.2142	0.9422	1.9129**	0.54**
	7—9	— 105.53	— 0.0187*	0.2856**	2.1607**	1.9204**	0.78**
	8—9	— 48.34	— 0.1405	0.1234**	1.6576**	1.5075**	0.73**
	10—9	— 62.55	0.1318	0.1051	1.7945*	1.1685**	0.35*
總和 Pooled		— 47.33	— 0.0086	— 0.0909**	1.2845**	1.5756**	0.50**
對照 C. K.	Ⅱ	— 52.88	— 0.5826	0.4958**	0.4459	3.9366**	0.92**
	⊙6	— 36.02	— 0.1657	— 0.0323**	0.9510	2.2662*	0.71**

註：迴歸方程式 $y=a+b_1X_1+b_2X_2+b_3X_3+b_4X_4$

數亦極顯著，但對照之Ⅱ及⊙6則效應不顯著，顯示親本遺傳背景異同及不同染色體對轉座均會影響結實率與子實產量之關係，且由於雄親與雌親之顯著性大部分均一致，因此認爲母系效應不顯著。

株高之淨迴歸係數於總和及對照資料中均達於極顯著，因此株高亦爲決定子實產量之重要因子，再比較各對染色體轉座，却有多組資料不顯著，此可能由於不同染色體對發生轉座時，發生缺失及轉位效應不一，影響到株高與子實產量之關係，因此株高影響子實產量的因子很可能位於此轉座染色體。故於雄親方面，第一、第二、第四、第六、第八及第十對染色體可能含有株高影響子實產量的因子，而雌親則位於第一、第二、第三、第六及第十對染色體。

吐絲期方面，雄親之第十對、雌親之第三、第七對染色體，亦可能由於轉位效應，使原本不顯著之迴歸係數變成顯著，因此在這些染色體上亦可能含有吐絲期影響子實產量之因子。

複迴歸決定係數僅雄親之 6 — 9 染色體轉座不顯著，其餘爲顯著或極顯著，因此除雄親之 6 — 9 染色體轉座外，吐絲期、株高、結實率及百粒重已足以構成子實產量之構成要素，因此不需加入穗重作爲調查項目。至於 6 — 9 染色體轉座，四性狀中僅有百粒重達於極顯著水準，其餘效應均不顯著，使參與分析的性狀不足以代表子實產量，其原因可能由於第六對染色體係玉米之核仁染色體 [7]，發生轉座後會影響蛋白質合成而干擾株高與結實率性狀使變異加劇而稀釋對於子實產量之作用。

將穗重除去後四性狀之逐步複相關分析列於表 7，吐絲期、株高、結實率與百粒重之中以百粒重對子實產量之影響貢獻最大，於各項資料中均爲首要之獨立變值，增進之 R^2 值亦甚大，因此爲四性狀中最重要之產量構成要素。次要之獨立變值爲結實率，於多項資料位居第二，且增進之 R^2 值也不容

忽視。對照之Ⅱ其次要獨立變值爲株高，與總和資料（結實率）不同，可能由於Ⅱ之結實率正常恆定，因此結實率不再成爲影響子實產量之重要因子。對照之⊙6其株高與結實率均爲統計程式所摒棄，顯示當染色體發生轉座時固定變異的株高，及低結實率下（理論值25%），百粒重爲決定子實產量最重要之因子，總和資料則含有親本變異，故株高與結實率亦會影響子實產量。雄親效應之6—9染色體轉座，由於核仁染色體轉座後亦會影響百粒重之作用，因此 R^2增進量很少（13.82%）而其它性狀則因增進量過小而爲統計程式所摒棄。

將百粒重除去後再進行複迴歸分析，其結果列於表8，結實率之淨迴歸係數於總和資料及對照之Ⅱ均達顯著水準，對照之⊙6則不顯著，顯示染色體轉座後會使結實率對子實產量之作用減少，其原因可能由於染色體轉座使結實率下降 [9]，因此結實率無法再解釋子實產量，而Ⅱ則由於有正常的結實率，如受親本遺傳背景影響發生變動時，即會影響子實產量，總和資料則因親本之背景差異使結實率再度影響到子實產量。在雄親與雌親效應方面，結實率淨迴歸係數之顯著性並不一致，因此其顯著性不僅受正反交配母系效應，亦受不同轉座染色體對組合效應所影響。

表7：逐步複相關（四性狀）分析及顯著性測驗

Table 7. Stepwise multivariate (4-character) analysis and signifiant tests.

效應 Effect	轉座染色體對 Transloction chromosome	首要獨立變值參與次序 Step number and number of independent variables included				增進 R^2 之百分率 Increased in R^2 (%)			
		1	2	3	4	X_1	X_2	X_3	X_4
雄親 Male parent	1—9	X_4	X_3					10.10	53.51
	2—9	X_4							52.51
	3—9	X_4							37.17
	4—9	X_4	X_3						31.26
	5—9	X_4						17.70	40.17
	6—9	X_4							13.82
	7—9	X_4	X_3					13.57	49.81
	8—9	X_4	X_3					16.39	53.75
	10—9	X_4	X_3					9.32	53.08
雌親 Female parent	1—9	X_4	X_3	X_2			6.44	7.13	35.86
	2—9	X_4	X_3					8.96	64.06
	3—9	X_4	X_3						48.82
	4—9	X_4							42.13
	5—9	X_4	X_3					6.65	43.91
	6—9	X_4	X_2				7.40		41.90
	7—9	X_4	X_3	X_2			7.13	15.31	55.72
	8—9	X_4	X_3					11.84	59.13
	10—9	X_4	X_3					13.79	20.17
總合	pooled	X_4	X_3	X_2			1.09	6.60	41.97
對照 C. K.	Ⅱ	X_4	X_2	X_1		1.32	7.20		82.95
	⊙6	X_4							68.48

註：X_1, X_2, X_3, X_4見表6

株高之淨迴歸係數於總和資料及對照之Ⅱ達於極顯著，⊙6達於顯著，因此株高對於子實產量亦有顯著之影響，但於各項轉座染色體對之株高資料中，卻有多項淨迴歸係數不顯著，顯示不同染色體轉座及供爲雌、雄親時會影響株高及子實產量之關係，其交感因子很可能位於這參與轉座之染色體，亦即雄親方面位於第一、第二、第四、第六、第七、第八及第十對染色體，雌親方面則位於第一、第

表 8：玉米雌雄親染色體轉座影響三農藝性狀（X_1, X_2, X_3）之複迴歸及淨迴歸係數分析與顯著性測驗

Table 8. Multiple regression analysis and significant test of partial regression coefficient of plant characeters (X_1, X_2 , X_3) on translocation and parental effects in corn.

效應 Effect	轉座染色體對 Transloction chromosome	截距 Intercept	吐絲期 Silking date	株高 Plant height	結實率 Fertility	複迴歸決定係數 Coefficient of determination
		a	b_1	b_2	b_2	R^2
雄親 Male parent	1—9	— 60.92	0.2449	0.2261	2.0272*	0.18
	2—9	22.47	0.0625	0.0220	0.4449	0.01
	3—9	— 6.46	— 0.3158	0.4289**	0.1076	0.22
	4—9	29.05	— 0.3396	0.1927	0.3945	0.03
	5—9	— 10.84	— 0.2530	0.1683*	1.9101*	0.27*
	6—9	19.59	0.0661	0.1826	— 0.5670	0.06
	7—9	— 66.00	0.2796	0.3282	1.3886	0.17
	8—9	— 63.66	0.0273	0.2717	2.4928	0.32
	10—9	— 40.50	0.2033	0.1526	1.8345*	0.23
雌親 Female parent	1—9	— 37.48	0.4139	0.1460	1.1077	0.12
	2—9	— 35.50	0.2155	0.0751	2.0657*	0.13
	3—9	73.23	— 1.0623*	0.3301	— 0.1812	0.16
	4—9	— 5.09	0.3187	0.2404	— 0.7212	0.12
	5—9	— 24.57	0.0621	0.2788*	0.6897	0.23
	6—9	— 38.87	0.3303	0.1834	1.1394	0.14
	7—9	— 85.87	— 0.0733	0.4593**	2.5131**	0.39**
	8—9	— 56.98	— 0.0112	0.2982**	2.2277**	0.45*
	10—9	— 25.05	0.1183	0.1670	1.1726	0.10
總合	pooled	— 22.54	0.0887	0.1902**	1.1332*	0.10**
對照 C. K.	Ⅱ	— 356.72	0.5221	1.1778**	2.7290 *	0.61**
	⊙6	— 60.32	0.1341	0.2985 *	1.8763	0.21

註：迴歸方程式 $y=a+b_1X_1+b_2X_2+b_3X_3$

二、第三、第四、第六及第十對染色體。

總和資料及對照中Ⅱ之複迴歸決定係數極顯著，而對照之⊙6卻不顯著，表示染色體發生轉座後吐絲期、株高與結實率已不足以代表子實產量，在調查雙對染色體轉座異型接合組合之產量構成要素時，因低結實率子實發育在同一穗中無競爭存在故不可摒棄百粒重；Ⅱ之組合，由於結實率正常，因此結實率仍可解釋子實產量；而總和資料則因親本遺傳背景之作用，使雄親之5—9染色體轉座、雌親之7—9、8—9染色體轉座等組合影響結實率性狀而能解釋子實產量。

表9爲吐絲期、株高及結實率三性狀之逐步複相關分析，由於此三性狀對於子實產量之解釋能力較低，且組內變異增加，因此於多項染色體轉座資料，三性狀均爲統計程式所摒棄。總和資料與對照Ⅱ組合之間，參與之獨立變值雖然相同，次序卻相反，顯示染色體轉座會影響株高與結實率對子實產量之重要性。染色體轉座時結實率較低，同穗子實之間不發生競爭作用，每粒種子均可充分發育，因此百粒重甚接近，不會因結實率降低而增加，在此種情況下子實產量乃受結實率之影響，結實率高則子實產量亦重，使結實率成爲首要之獨立變值。在Ⅱ組合則由於結實率正常子粒多而互相競爭，結實率較低者，子實可獲得較多的養分，使百粒重增加，因此結實率對於子實產量之影響不大，而使株高成爲首要之獨立變數。

增進R^2值之百分率方面，各首要獨立變值之增進量亦甚低，顯示三性狀對子實產量之解釋能力均低，歸屬於親本遺傳背景及染色體之轉座效應發生各種變異。

表9：逐步複相關（三性狀）分析及顯著性測驗

Table 9. Stepwise multivariate (3-character) correlation analysis and significant tests.

效應 Effect	轉座染色體對 Translocation chromosome	首要獨立變值參與次序 Step number and number of independent variables included			增進 R^2 之百分率 Increased in R^2 (%)		
		1	2	3	X_1	X_2	X_3
雄親 Male parent	1—9	X_3					14.81
	2—9						
	3—9	X_2				18.56	
	4—9						
	5—9	X_3					22.50
	6—9						
	7—9						
	8—9	X_3					25.47
	10—9	X_3					15.71
雌親 Female parent	1—9						11.21
	2—9	X_3			10.91		
	3—9	X_1					
	4—9						
	5—9	X_2				18.03	
	6—9		X_2				
	7—9	X_3	X_2			19.48	19.59
	8—9	X_3				11.47	33.25
	10—9						
總合 pooled		X_3	X_2			4.97	5.22
對照 C. K.	Ⅱ	X_2	X_3			52.52	7.49
	⊙6	X_2				13.50	

註：X_1, X_2, X_3見表8

結實率、百粒重與穗重均爲植株成熟後方能測定之性狀，對於早期選拔並無助益，因此將此三性狀刪除，僅分析吐絲期與株高對子實產量之影響，其複迴歸分析結果列於表10。株高之淨迴歸係數於總和資料及對照之Ⅱ均達於極顯著，對照之⊙6則爲顯著，因此株高對於子實產量仍有極顯著之影響。再比較複迴歸決定係數與株高之顯著性，於各項染色體轉座組合，二者之顯著性均一致，因此在某些轉座之組合，株高可以決定子實產量。對照之⊙6組合，株高之淨迴歸係數顯著而複迴歸決定係數卻不顯著，可能由於吐絲期加入後 R^2 之機差自由度減少，使機差增加而導致不顯著。吐絲期之資料，僅有雌親之3—9染色體轉座達於顯著，推測可能係3—9染色體轉座時影響到吐絲期與子實產量之關係，使吐絲期發生顯著之作用。

表11爲吐絲期與株高之逐步複相關分析，其中雄親效應之3—9染色體轉座，雌親之5—9、7—9、8—9染色體轉座及總和資料，對照均以株高爲首要獨立變值，僅有雌親之3—9染色體轉座爲吐絲期，因此二性狀中以株高對子實產量較爲重要。在增進 R^2 之百分率方面，僅對照之Ⅱ增進值較高，顯示染色體轉座後會影響株高與子實產量之相關性。

影響子實產量之農藝性狀極多，本研究亦曾調查多種性狀，除結果中所列之五性狀外尚有穗高、穗數、穗長、充實期、每穗行數、每行粒數、子粒數等項目，但由於諸性狀間擁有顯著之正相關（例如株高與穗高、穗長與每行粒數、子粒數與結實率等），或有顯著之負相關（每穗行數×每行粒數與百粒重），加入分析不僅無意義且會干擾分析結果，因此摒棄不用。子實充實期之長短亦會影響子實

表10：玉米雌雄親染色體轉座影響二農藝性狀（X_1, X_2）之複迴歸及淨迴歸係數分析與顯著性測驗

Table 10. Multiple regression analysis and significant test of partial regression coefficents of plant characters (X_1, X_2) on translocation and parental erfects in corn.

效應 Effect	轉座染色體對 Translocation chromosome	截距 Intercept	吐絲期 Silking date	株高 Plant height	複迴歸決定係數 Coefficient of determination
		a	b_1	b_2	R^2
雄親 Male parent	1—9	— 30.27	0.3100	0.3005	0.05
	2—9	34.11	0.0375	0.0268	0.00
	3—9	— 3.10	— 0.3194	0.4249**	0.22*
	4—9	35.70	— 0.3062	0.1919	0.03
	5—9	12.05	— 0.2187	0.2844	0.12
	6—9	0.93	0.0732	0.2149	0.04
	7—9	— 26.03	0.3088	0.2634	0.09
	8—9	15.67	— 0.1189	0.1975	0.04
	10—9	— 8.59	0.3110	0.1700	0.12
雌親 Female parent	1—9	— 1.78	0.3978	0.0896	0.05
	2—9	37.64	0.0582	— 0.0083	0.01
	3—9	70.85	— 1.0759*	0.3252	0.16
	4—9	— 19.74	0.3148	0.2297	0.09
	5—9	— 15.15	0.1518	0.2765*	0.19
	6—9	— 12.09	0.2691	0.2092	0.08
	7—9	— 55.00	0.3836	0.4058*	0.20*
	8—9	— 25.05	0.0751	0.4452**	0.31**
	10—9	— 9.21	0.1655	0.2131	0.04
總和 pooled		2.16	0.1047	0.1916**	0.05**
對照 C. K.	Ⅱ	— 89.32	— 0.0182	1.0786**	0.53**
	⊙6	— 15.23	0.1311	0.2885*	0.14

註：迴歸方程式 $y=a+b_1X_1+b_2X_2$

產量 [10,15]，但測定充實期之長短時誤差甚大，且本試驗所使用之九組轉座材料充實期均極接近（於三月中旬播種時，充實期約28天），因此組合內變異常大於組合間之變異，使充實不再成爲產量構成要素，本試驗乃摒棄充實期不參加分析。

染色體轉座後結實率下降可能會影響脫粒率，因此分析資料時加入穗重進行分析，結果顯示穗重與子實產量仍呈高度正相關。由於一般玉米品種之脫粒率差異不大，轉座對脫粒率亦無影響，故日後調查時擇一即可。

一般之玉米品種，營養生長較佳之植株，株高較高，產量亦較多，因此在同一品種內株高與產量呈正相關 [5]，但試驗結果中五性狀之複迴歸顯著性測驗却有部分資料其株高之淨迴歸係數呈負值（見表 4），可能由於株高較高者，其雌穗穗軸重量亦較重，由於具有高低結實率之因素，使子實產量並未成比例增加，因此脫粒率降低，如利用穗重爲獨立變數，則株高較高者，子實產量會高估，加入株高爲獨立變數時，爲使複迴歸方程式能符合，株高之淨迴歸值乃成爲負值。將穗重性狀除去後，穗軸重即不再發生影響，因此表 6。表 8 及表10中株高之淨迴歸係數即爲正值，子實產量隨株高而增加。

表11：逐步複相關（二性狀）分析及顯著性測驗

Table 11. Stepwise multivariate (2 character) correlation analysis and significant tests.

效應 Effect	轉座染色體對 Translocation chromosome	首要獨立變值參與次序 Step number and number of independent variables included		增進 R^2 之百分率 Increased in R^2 (%)	
		1	2	X_1	X_2
雄親 Male parent	1—9				
	2—9				
	3—9	X_2			18.56
	4—9				
	5—9				
	6—9				
	7—9				
	8—9				
	10—9				
雌親 Female parent	1—9				
	2—9				
	3—9	X_1		10.91	
	4—9				18.03
	5—9	X_2			
	6—9				16.05
	7—9	X_2			30.65
	8—9	X_2			
	10—9				
總和	pooled	X_2			5.05
對照 C. K.	Ⅱ	X_2			52.52
	⊙6	X^2			13.50

註：X_1, X_2見表10

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Effect of Agronomic Characters on the Grain Yield of Corn Hybrids Derived from Double Chromosomal Translocations[1]

Kong-Sheng Liu[2] and Cheng Chen[3]

Summary

Chromosomal translocations in corn usually caused the decrement in seed fertility, hence alternated the yield components, as a result, the 100-seed weight would be increased while the total grain yield decreased. In this experiment hybrid combination of whole set of ⊙6 translocation heterozygotes were grown in the field to investigate the effects of chromosomal translocation on the yield components. Ther results showed that: 100-Seed weight as well as ear weight, were the most important factor on grain yield. Ear fertility was inferior to 100-seed weight and ear weights owing to the low fertility (25%) of the ⊙6 individuals. Vegetative characters such as silking date and plant height, had less influences on yield. The influence of plant height appeared only when the effects of 100-seed weight and fertility were omitted. However, silking date showed no effect on grain yield if 100-seed weight and fertility were omitted.

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Effects of N Fertilization on the Growth and Yield of Two Maize Hybrids[1]

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Abstract : A single-cross maize hybrid, Tainung No. 351, and a double-cross hybrid, Tainan No. 11, were grown in the field at a density of 58,800 plants/ha in the fall of 1983. N rates of 75, 150, 225 and 300 kg/ha were supplied in the form of ammonium sulfate. Samplings were made at a two-week interval starting from mid-silking to maturity. Leaf area and N and total nonstructural carbohydrate (TNC) concentrations were determined in plant fractions. The purposes of this study were to compare the physiological differences between the two hybrids and to clarify the physiological basis of the high yield potential of Tainung No. 351. Results showed that increased N fertilization delayed the dates of heading and silking. Grain yield of Tainung No. 351 increased with increasing N level, due mainly to higher kernel number per ear which could compensate for the loss of lower 100-kernel weight. N had positive effects on plant N concentration, leaf area and dry matter accumulation. N use efficiencies (unit grain yield per unit N supplied) of Tainung No. 351 were 90.5 and 27.3 at N rates of 75 and 300 kg/ha, respectively. Corresponding values for Tainan No. 11 were 68.9 and 19.9. Yield efficiencies (unit grain yield per unit leaf area) were 3.06 and 2.96 g/dm^2 for Tainung No. 351 and 3.50 and 3.17 g/dm^2 for Tainan No. 11 at N rates of 150 and 300 kg/ha, respectively. Within 2 weeks after silking, stalk and cob acted as temporary sinks to store N and TNC for the subsequent needs of grain filling. TNC concentration was above 13% in the stalk of mature Tainung No. 351 plants but was below 3% in Tainan No. 11. This fact indicated that carbohydrate translocation of the high-yielding Tainung No. 351 was less efficient. Yield could be further enhanced through increasing kernel weight. Limiting factors to grain yield of Tainan No. 11 were presumed to be both source capacity and sink size. Experimental results suggested that nutritional requirements of Tainung No. 351 was high. Appropriate dense planting might be a good measure under satisfactory conditions to increase leaf area and photosynthetic ability. Further understanding of the interaction between N and C metabolism was important in order to increase kernel number and kernel weight simultaneously and hence the yield of Tainung No. 351.

The overproduction of rice has caused problems to the national economy of this country in recent years. Maize, with its high yield potential and wide adaptability, is

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the most promising crop in substituting for part of the paddy rice. Grain yield of the commercial, double-cross maize varieties in Taiwan averaged at only 3.5 t/ha. In 1984, Taiwan Agricultural Research Institute released a single-cross maize variety, Tainung No. 351, which can yield 6 t/ha of grain on an islandwide basis. The new variety is expected to dominate the acreage within a few years.

As a single-cross hybrid, Tainung No. 351 is uniform in plant development and possesses very strong growth vigor compared with the double-cross hybrids. Higher grain yield of maize can be obtained by increasing biological yield and the efficiency of partitioning dry matter to the economic organ (i.e., high harvest index). However, it is known that for maize, modern hybrids perform better only when grown under high levels of fertilizers. As a consequence, the increased productivity is usually associated with a drop in the efficiency of nutrient utilization [2,3]. Nitrogen plays a very important role in the grain production of maize. Differences in N utilization among genotypes have been demostrated, not only in differential response to N fertilizer, but also in differences in absorption and in utilization of absorbed N [4,9,13]. Thus Tainung No. 351 may be a superior, N efficient hybrid compared with Tainan No. 11.

This study investigated the responses of Tainung No. 351 and Tainan No. 11 hybrids to different levels of N fertilization. In addition to yield components, several physiological characters were also studied in order to obtain detailed information on maize grown in Taiwan. Hopefully, the results of this experiment can provide useful suggestion to the future improvement of varieties and cultural practices.

Materials and Methods

This experiment was conducted at the experimental farm of Taiwan Agricultural Research Institute. A single-cross maize hybrid, Tainung No. 351 (TA 80-2598 × TA 80-1410), and a double-cross hybrid, Tainan No. 11((2027-3-5 × LY 22-4) × (PH9-DMR × AME III)), were selected as experimental materials. Kernels of the maize hybrids were overplanted at a spacing of 85×20 cm on Sept. 27, 1983 and thinned to 58,800 plants/ha (one plant per hill) after emergence. Nitrogen rates of 75, 150, 225 and 300 kg /ha were supplied in the form of ammonium sulfate. Forty percent each of N was applied at planting and 25 days after emergence (DAE) which occurred on Oct. 2, 1983. The remaining 20% was applied 44 DAE. Rates of P_2O_5 and K_2O supplied at planting were 70 and 90 kg/ha, respectively. Each experimental unit consisted of nine-row plot containing 41 plants per row. Randomized complete block design was employed with three replications.

Samplings were made at a two-week interval starting from mid-silking to maturity. Five plants per plot were harvested for the first five samplings (silking to 8 weeks after silking) and 15 plants were taken from each plot for the last sampling for yield determination. The plants were divided into the following parts immediately after harvest: tassel, stalk, upper leaves (leaf blades from nodes above the ear position), ear leaves, husks, cob and grain. Leaf area and N concentration of each plant fraction were determined. Concentration of total nonstructural carbohydrates (TNC) was analyzed in

grain and stalk internodes above and below the ear node only. Yield components investigated included ear length, unfilled ear length, kernel row number, kernel number per ear, 100-kernel weight and shelling rate. Grain yield was expressed in the unit of kg/ha. Since all the filled grains were collected, results showed a relatively high kernel number per ear and low 100-kernel weight.

Leaf area was measured with a LI-3000 leaf area meter (LI-COR Co., USA). Plant parts were dried at 80°C for 48 hrs in an air-drafted oven. Dried samples were then ground in a Wiley mill by using a 40-mesh screen for chemical analyses. Nitrogen was analyzed by the Kjeldahl method. TNC was analyzed according to the method of Smith [16]. Ground samples were first hydrolyzed with takadiastase ("Clarase" 40,000, courtesy of Miles-Kyowa Co., Japan) at 40°C for 44 hrs, and reducing sugars were measured by the Shaeffer-Somogyi copperiodometric titration method. This method of hydrolysis for the determination of TNC has been demonstrated by Streeter and Jeffers [17] and tested by this laboratory as most acceptable for precision, accuracy and recovery of standard added to the samples.

Results

Some agronomic and yield characters of maize hybrids grown under different levels fo N fertilization were shown in Table 1. There was a tendency that N application could delay tasseling and silking. The duration between tasseling and mid-silking was 9 days for Tainung No. 351 and 4—5 days for Tainan No. 11. The growth duration (

Table 1. Some agronomic and yield characters of maize hybrids grown under different levels of N fertilization[a]

Character	Tainung No. 351				Tainan No. 11			
	N_1	N_2	N_3	N_4	N_1	N_2	N_3	N_4
Days to Tasseling	50	51	51	53	43	43	45	47
Days to Silking	59	59	60	62	48	48	50	51
Days to Harvest	137	137	139	139	128	128	129	130
Plant Height (cm)	177	182	182	181	181	185	180	181
Ear Length (cm)	14.7	15.0	15.6	15.4	14.6	15.3	15.3	16.0
Unfilled Ear Length (cm)	2.4	2.2	2.3	1.8	2.3	2.2	2.2	2.1
Kernel Row Number	14.7	14.4	14.9	15.1	12.9	12.8	12.7	12.2
Kernel Number per Ear	621	598	670	791	529	599	615	567
100-Kernel Weight (g)	19.0	20.2	18.5	18.0	17.9	17.7	16.9	16.9
Shelling Rate (%)	81.5	79.8	80.5	79.7	81.2	82.0	80.5	81.8
Grain Yield (t/ha)	6.79	7.01	7.83	8.19	5.17	6.10	5.35	5.97
Harvest Index	0.53	0.50	0.51	0.49	0.54	0.56	0.53	0.55

[a] N_1 : 75 kg-N/ha, N_2 : 150 kg-N/ha, N_3 : 225 kg-N/ha, N_4 : 300 kg-N/ha,

days from emergence to harvest) was 9-10 days longer for Tainung No. 351 than for Tainan No. 11 but no fertilizer effect was observed. Plant height was almost the same for the two hybrids and again, no significant difference among N treatments existed.

Ear length was 14.6-15.4 cm and unfilled ear length was 1.8-2.4 cm for the two varieties. Tainung No. 351 had more kernel rows on the ear (average 14.8) than Tainan No. 11 (average 12.7). Consequently, the former hybrid had more kernels per ear than the latter. Nitrogen rate had a positive effects on kernel number per ear for Tainung No. 351 but the relationship was less clear for Tainan No. 11. On the contrary, heavy N fertilization tended to decreased 100-kernel weight. For example, weight of 20.2 g and 18.0 g were observed for N treatments of 150 and 300 kg/ha, respectively, for Tainung No. 351. A similar trend was also found in Tainan No. 11.

Table 1 also showed that shelling rate was comparable between the two hybrids. Tainung No. 351 was more responsive to fertilization in showing increased grain yield with increasing N rate. Grain yield was 6.79 t/ha at 75 kg-N/ha and over 8 t/ha at 300 kg-N/ha. The relationship was less significant for Tainan No. 11 as the highest yield recorded was 6.10 t/ha for plants supplied with 150 kg-N/ha. Grain yield decreased somewhat at higher N rates. Harvest indices were generally above 0.50 while higher values were observed for Tainan No. 11.

Changes in leaf area per plant during grain development as a result of N fertilization were shown in Table 2. In general, N showed positive influences on the leaf area of both hybrids. For Tainung No. 351, leaf area increased from 27.4 to 47.1 dm^2/plant

Table 2. Effects of N fertilization on the leaf area (dm^2/plant) during grain filling of maize hybrids

*Hybrid	Week after Silking	N Applied (kg/ha)			
		75	150	225	300
Tainung No. 351	2	27.4	38.9	33.3	47.1
	4	31.9	39.1	38.9	42.5
	6	33.2	38.3	44.7	39.8
	8	30.3	31.5	34.6	37.4
Tainan No. 11	2	27.8	29.6	31.9	32.0
	4	26.3	26.8	31.5	31.2
	6	24.7	25.6	26.9	29.0
	8	23.8	26.5	30.6	31.5

as N increased from 75 to 300 kg/ha, when measurement was made at 2 weeks after silking. However, exceptions were four in that 150 kg-N/ha treatment had higher leaf areas than 225 kg-N/ha treatment, at least during the first 4 weeks after silking. In most cases, the decrease of leaf area with the advance of grain development was minor. The most significant reduction was found in Tainung No. 351 supplied with 300 kg-

N/ha where a 20% decrease occurred between 2 to 8 weeks after silking. Comparison between the two hybrids indicated that although plan height was similar, Tainung No. 351 had higher leaf area values than Tainan No. 11, especially under the highest N fertilization rate. In addition, maximum leaf area was obtained at 225 kg-N/ha for Tainan No. 11, suggesting that further increase in N fertilization was uneffective for both leaf development (Table 2) and grain yield (Table 1). On the other hand, the single-cross Tainung No. 351 performed better when grown under the highest level of N-fertilizer.

The influences of N fertilization on the N concentrations in different plant parts of maize hybrids Tainung No. 351 and Tainan No. 11 were shown in Tables 3 and 4, respectively. Although there was a general tendency that higher N level could increase

Table 3. N concentrations (%, dry basis) in different plant fractions of maize hybrid Tainung No. 351 as affected by levels of N fertilization

Plant Fraction	N Level (kg/ha)	Weeks after Silking					
		0	2	4	6	8	11
Upper Leaf Blade[a]	75	2.49	2.84	2.59	2.40	1.97	1.23
	150	2.61	2.65	2.52	2.35	2.12	1.32
	225	2.60	2.97	2.63	2.24	2.08	1.50
	300	2.92	2.61	2.56	2.31	2.16	1.52
Ear Leaf Blade	75	2.64	2.54	1.96	2.30	1.77	1.29
	150	2.55	2.39	2.23	2.26	1.92	1.35
	225	2.74	2.49	2.39	2.24	2.03	1.69
	300	2.95	2.48	2.45	2.41	2.17	1.63
Stalk	75	0.56	0.56	0.46	0.43	0.35	0.30
	150	0.70	0.55	0.55	0.45	0.33	0.30
	225	0.66	0.61	0.47	0.50	0.39	0.28
	300	0.69	0.69	0.51	0.54	0.36	0.29
Husk	75	1.17	0.83	0.63	0.46	0.38	0.25
	150	1.25	0.98	0.58	0.57	0.50	0.25
	225	1.49	0.94	0.63	0.54	0.46	0.25
	300	1.26	0.82	0.70	0.67	0.56	0.24
Cob	75	2.28	1.64	1.69	1.08	0.81	0.28
	150	2.48	1.56	1.80	1.26	0.93	0.57
	225	2.91	1.74	1.90	1.12	0.94	0.55
	300	2.58	1.83	2.30	1.29	1.02	0.50
Grain	75		2.54	2.54	1.93	1.58	1.35
	150		2.52	2.31	1.91	1.66	1.48
	225		2.61	2.15	2.04	1.63	1.56
	300		2.77	2.79	2.28	1.68	1.58

[a] Leaf blades from nodes above the ear position.

Table 4. N concentrations (%, dry basis) in different plant fractions of maize hybrid Tainan No. 11 as affected by levels of N fertilization

Plant Fraction	N Level (kg/ha)	Weeks after Silking					
		0	2	4	6	8	11
Upper Leaf Blade[a]	75	2.74	2.55	2.75	2.60	2.11	1.31
	150	2.39	2.68	3.02	2.56	2.52	1.35
	225	3.30	2.91	2.74	2.48	2.37	1.57
	300	2.38	2.79	2.83	2.53	2.44	1.34
Ear Leaf Blade	75	2.83	2.64	2.42	2.20	2.01	1.25
	150	3.39	2.87	2.56	2.31	2.26	1.32
	225	3.16	2.86	2.37	2.43	2.33	1.56
	300	3.37	2.82	2.41	2.50	2.52	1.50
Stalk	75	0.77	0.62	0.62	0.52	0.35	0.29
	150	0.88	0.93	0.74	0.59	0.41	0.29
	225	0.82	0.81	0.69	0.56	0.48	0.44
	300	0.88	0.78	0.70	0.61	0.66	0.34
Husk	75	1.24	0.84	0.60	0.53	0.39	0.20
	150	1.38	0.83	0.74	0.53	0.39	0.22
	225	1.66	1.02	0.70	0.55	0.47	0.28
	300	1.48	0.81	0.77	0.65	0.65	0.23
Cob	75	2.58	1.60	1.18	1.17	0.72	0.32
	150	2.63	1.88	1.22	0.99	0.93	0.36
	225	2.94	1.56	1.21	1.05	0.92	0.28
	300	2.89	1.57	1.23	1.06	1.19	0.25
Grain	75		2.16	2.59	1.64	1.31	1.16
	150		2.17	2.82	1.72	1.57	1.35
	225		2.16	2.54	1.60	1.76	1.48
	300		2.27	2.55	1.55	1.76	1.49

[a]Leaf blades from nodes above the ear position.

N concentrations, the results were not consistent when each sampling was taken into consideration. No significant difference in leaf N concentration was found between ear leaf and upper leaf blades for Tainung No. 351. Nitrogen decreased during grain-filling for both hybrides, particularly during the last 4-5 weeks of sampling (6 to 11 weeks after silking). Leaf N decreased from 2.4-3.4 % at silking to 1.3-1.7 % just be-

fore harvest. Stalk contained less N than leaf blade. Stalk N concentrations ranged between 0.5-0.8 % at silking and were about 0.3—0.4 % at maturity.

The husks had about 1.5% of their dry weight as N at the time of silk emergence. The decrease of husk N concentration was continuous throughout grain development but the most obvious decline was found in the first 2 weeks after silking. Mature ear contained less than 0.3% N in the husks(Tables 3 and 4). Nitrogen concentration in the cob (2.5-3.0 %) was comparable to that in the leaf blade at silking. However, the decline during grain-filling was much more significant. Translocation of N out of the cob was most prominent during the last 2—3 weeks of sampling. The concentration of cob was about 0.5% for Tainung No. 351 and only 0.3% for Tainan No. 11 when plant approached maturity.

Highest grain N concentration of Tainung No. 351 hybrid was recorded when first sampling was made at 2 weeks after silking. In other words, N concentration of grain decreased continuously during grain-filling. It declined rapidly between 4 and 8 weeks after silking which was in accordance with the rapid increase of grain dry weight. Statistical analysis showed no significant difference in grain N for N rates above 150 kg/ha. Grain N concentration was lower when only 75 kg-N/ha was applied (Table 3). Similar pattern was also found in Tainan No. 11 (Table 4). The only differences were that there was an increase in grain N between 2 to 4 weeks after silking and N concentration in the mature grain of Tainan No. 11 was lower than that of Tainung No. 351.

No significant effect of N fertilization on the concentration of total nonstructural carbohydrates (TNC) was found among N treatments. However, the changing pattern of TNC concentration in the stalk was different from that of N and differences existed

Table 5. Concentrations (%, dry basis) of total nonstructural carbohydrates in the stalk and grain of maize hybrids as affected by levels of N fertilization

Hybrid	Plant Fraction	N Level (kg/ha)	Weeks after Silking					
			0	2	4	6	8	11
Tainung No. 351	Stalk[a]	75	25.1	32.4	36.3	29.2	34.0	12.8
		150	23.9	35.2	33.5	34.7	21.9	15.1
		225	24.9	26.0	29.3	32.7	31.3	13.0
		300	24.7	30.4	31.9	32.4	29.5	13.0
		Mean	24.6	31.0	32.8	32.2	29.2	13.5
	Grain	75	37.2[b]	31.7	37.4	65.8	70.6	76.0
		150	39.1	29.3	39.4	67.8	73.9	76.0
		225	38.0	21.4	54.5	67.2	71.5	73.8
		300	40.4	27.2	46.5	60.0	66.2	74.1
		Mean	38.7	27.4	44.4	65.2	70.6	75.0

Table 5. (continued)

Hybrid	Plant Fraction	N Level (kg/ha)	Weeks after Silking					
			0	2	4	6	8	11
Tainan No. 11	Stalk[a]	75	23.8	25.7	41.1	18.7	13.4	3.2
		150	22.7	27.0	44.9	25.4	20.6	2.6
		225	22.7	26.9	39.4	22.9	29.8	3.2
		300	24.3	24.4	39.1	20.9	25.8	2.7
		Mean	23.4	26.0	41.1	22.0	22.4	2.9
	Grain	75	37.6[b]	23.0	47.9	66.2	72.0	77.9
		150	37.3	24.5	45.8	67.9	73.3	79.8
		225	40.4	27.4	43.5	66.6	67.2	72.9
		300	40.3	28.8	41.5	64.4	67.3	76.3
		Mean	38.9	25.9	44.7	66.3	70.0	76.7

[a]—Including stalk internodes above and below ear node only.

[b]—Including cob for sampling at the time of silking.

between the two hybrids (Table 5). For Tainung No. 351, mean TNC concentrations in the stalk internodes just above and below the ear node across N treatments were 24.6, 31.0, 32.8, 32.2, 29.2 and 13.5% at 0, 2, 4, 6, 8 and 11 weeks after silking, respectively. There was a slight increase in the first two weeks and a marked decrease in the last two weeks of grain development. For Tainan No. 11, stalk TNC concentration increased from 23.4% to 41.1% within 4 weeks after silk emergence but dropped back to 22.0% in the next 2 weeks. Although the highest stalk TNC concentration of Tainan No. 11 (41.1%) exceeded that of Tainung No. 351 (32.8%), it was much lower in the mature plant (2.9%) than that of Tainung No. 351 (13.5%).

Increase of TNC concentration in the grains during the whole filling period was almost the same for the two hybrids. The cob contained 39% TNC when analyzed at silking time. TNC concentration of the young grains (two weeks after silking) was about 27% and the linear increase thereafter lasted for 4 weeks. The incraese levelled off afterwards and the mature grain contained 75-77% of TNC on a dry weight basis.

Discussion

According to the Corn Breeding Laboratory of Taiwan Agricultural Research Institute, Tainung No. 351 is 10-20 days longer in growth duration and 20 cm taller in plant height than No. 11 when sown in late September. This experiment failed to find any difference in plant height between the two hybrids. Experiments conducted by this laboratory in the fall crop season of 1983 showed that Tainan No. 11 could grow as tall as Tainung No. 351 in many locations of Taiwan (unpublished data). Moleba and Hart[11]

also reported no difference in plant height between N rates of 150 and 300 kg/ha. Daynard and Muldoon [5] indicated that taller plants tended to anthese and silk earlier and produce more grain. Remison and Fajemisin [14] stated that N application hastened flowering of maize plants. In this aspect, the authors found that the influence of plant height on flowering and yielding characters must be restricted within variety. In addition, N application delayed rather than hastened the time of tasseling and silking (Table 1). The difference between this experiment and Remison and Fajemisin's result might be due to genotypic variation.

The interval between tasseling and silking was longer for Tainung No. 351 (9 days) than for Tainan No. 11 (4-5 days) (Table 1). One weakness of the high yielding Tainung No. 351 is the high proportion of unfilled ear length and this is suggested by many agronomists, among other reasons, as a result of the longer interval between tasseling and silking which makes the pollens unavailable to the silks. In view of the almost equal length of unfilled ear of the two hybrids and the unpublished results showing unfilled ear length was significant only when very high grain yield was recorded in Tainung No. 351, it is presumed that factors causing the unfilling of upper grains of the ear are complex. The balance between source supply and sink demand is a more reasonable explanation for such a phenomenon.

Grain yield of Tainung No. 351 was higher when more N fertilizer was applied (Table 1). The yield increase was primarily a result of increasing kernel number, as 100 -kernel weight decreased at high N level. Peaslee [12] reported that in corn hybrids, the relative effects of severe N stress were greater on kernel number than on kernel weight. Both characters declined at low N fertilization. 100-kernel weight of this experiment (ca. 20 g) was comparable to that of Badu-Apraku *et al.* [1] but was far below the values (30—40g) reported by Molebu and Hart [11] and Peaslee [12]. Although a negative correlation existed between the number and weight of kernels, yield of Tainung No. 351 should be able to be enhanced further by increasing kernel weight to some extent without a concurrent sacrifice of kernel number.

The double-cross Tainan No. 11 was less responsive to N because grain yield decreased with N levels over 150 kg/ha. Both kernel weight and kernel number restricted grain yield of this variety under high N fertilization. According to Johnson and Tanner [7] and Tollenaar and Daynard [18], final kernel number is established near the time when linear increase in grain weight begins. It is therefore important to provide the maize plants with sufficient nutrients during early grain growth to assure yield depression caused by fewer kernels would not occur.

Moll *et al.* [10] defined N use efficiency as grain production per unit of N supplied to the soil. They found that the mean N use efficiencies of 8 hybrids were 95.7 with 56 kg-N/ha and 26.5 with 224 kg-N/ha of fertilization. Results of this experiment showed that for Tainung No. 351, N use efficiencies were 90.5 and 27.3 with N rates of 75 and 300 kg/ha, respectively. Corresponding values of Tainan No. 11 were 68.9 and 19.9. In other words, the single-cross Tainung No. 351 can use N more efficiently than the double-cross hybrid Tainan No. 11. However, both hybrids showed a

drastic decrease in N use efficiency as the amount of N fertilizer applied increased.

Remison and Lucas[15] reported that leaf area index (LAI) was maximum at mid-silking and the decrease afterwards was very rapid. They recorded LAI of 2.5 at 2 weeks after silking and yield of 4.0 t/ha for maize grown with 75 kg/ha of N in Nigeria. Leaf area was also low in this experiment. The highest leaf area recorded (Table 2) corresponded to LAI less than 3. However, yield of 6-8 t/ha for Tainung No. 351 was obtained. Possible reasons for the low leaf area may be that only the green portion of the leaf was measured 2 weeks after silking and the lowermost leaf blades wilted earlier due to rainfall in early growth season. Yield efficiencies, defined by Moleba and Hart[11] as grain yield per unit leaf area, were 3.06 and 2.96 g/dm^2 for Tainung No. 351 supplied with 150 and 300kg-N/ha, respectively. Corresponding values for Tainan No. 11 were 3.50 and 3.17 g/dm^2. The efficiencies were higher than the result (2.78 g/dm^2) obtained by Moleba and Hart[11] with similar growth conditions (60,000 plants/ha and 200 kg-N/ha) in Kansas, USA. However, LAI of maize crop should be increased to 4-5 in order to provide sufficient photosynthetic surface for dry matter production and hence increasing the yield[11].

Concentration of leaf N of both hybrids were near the lower sufficiency level of 2.75% proposed by Jones, Jr.[8]. The decrease in N concentrations of the leaves, stalk, husks and cob during grain development was an indication that a large amount of N was retranslocated to the developing grains. Hay *et al.*[6] estimated that about 60% of the final N in maize kernels was present in the vegetative tissues at pollination, the remaining 40% was obtained from the soil subsequently. The cob had very high N concentration (2.5-3.0 %) at the time of silk emergence (Tables 3 and 4). TNC concentration in the cob could also reach 40% on a dry weight basis at silking. These facts suggested that cob acted as an important temporary sink to store N and carbohydrates to meet the needs of subsequent development of adjacent grains.

TNC concentration in the stalk continued to increase for several weeks after silking, indicating that the stalk possessed the function of sink for TNC during this period. Although the grain-filling of Tainung No. 351 depended more on the contribution of stalk dry weight under heavy N fertilization (unpublished data), TNC concentration in the stalk did not show significant decrease until 8 weeks after silking. On the other hand, stalk TNC of Tainan No. 11 started to decline at 4 weeks after silking. Judged by the dry weight and TNC concentration data, it was proposed that Tainung No. 351 is more photosynthetically active than Tainan No. 11. Stalk of mature Tainung No. 351 plant still contained more than 13% of its dry matter as TNC whereas the value was below 3% for Tainan No. 11 (Table 5). The results showed that a certain amount of TNC in the stalk of Tainung No. 351, which had 100-kernel weight of only 20 g, was unavailable to be transported to the grains. Yield should be increased if the efficiencies of production and distribution of TNC by the plant could be increased simultaneously.

In conclusion, the results of this experiment suggested that nutritional requirements for Tainung No. 351 is high. This hybrid is more responsive to N by showing higher grain yield at higher levels of N fertilization. Grain yield per unit of N supplied to the

soil was also higher for Tainung No. 351 than for Tainan No. 11. Appropriate dense planting might be a good measure under fertile soil condition to increase leaf area and photosynthetic ability. Further understanding of the interaction between N and C was important in order to increase kernel number and kernel weight simultaneously through the efficient utilization of photosynthates and hence to increase the yield of Tainung No. 351.

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氮肥用量對兩個雜交玉米品種生長與產量的影響[1]

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摘 要

試驗採用單雜交玉米品種臺農351號與雙雜交品種臺南11號爲材料，於1983年秋作在田間栽培，密度爲每公頃58,800株，氮肥用量爲75、150、225與300 kg/ha ；於玉米吐絲（mid-silking）期開始每隔2週取樣一次，測度葉面積與植株各器官氮素及非構造性碳水化合物 （TNC） 濃度變化，並調查產量性狀，目的在比較兩個玉米對氮素反應的生理性差異，以及探討臺農 351號高產的理論基礎。試驗結果發現增加氮肥用量可延遲抽穗與吐絲日期，提高臺農 351號種子產量，但臺南11號之產量却以150 kg-N/ha 處理最高；產量提高的主要原因爲一穗粒數增加，足以補償粒重降低的損失而有餘。在75與300 kg-N/ha 處理時，臺農351 號的氮利用效率（產量／施用氮量）爲90.5與27.3，較臺南11號之68.9與19.9爲高；但於150與300 kgN/ha 處理，臺南11號的產量效率（產量／單位葉面積）爲3.50與3.17g/dm²，遠較臺農351號之3.06與2.96g/dm²爲高，各器官氮素濃度有隨施氮量增加而提高的趨勢，且於種子充實期間大幅下落。莖與穗軸在吐絲後2週內具有暫時貯存氮素與TNC的功能，可供應隨後種子發育的需要。吐絲以後臺南11號莖稈內TNC 濃度較臺農351號爲高，但下降之時間較早，幅度亦大；成熟時臺農351號莖稈內仍含有13%以上的 TNC ，但臺南 11 號僅爲 3 %以下，顯示前者雖爲高產品種，但粒重未臻理想，應謀增加粒重而更提高產量；後者之供源 （source） 能力與積儲（sink） 容量均有不足，可能並爲產量限制因子。試驗結果認爲臺農 351號玉米品種對營養要素的需求量較高，建議栽植密度宜適量提高，以增加葉面積與生產乾物質能力，對氮素與碳素間相互作用的關係亦應再予瞭解，以求在同時增加粒數與粒重的情形下達到更高產的目標。

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藥用植物種子之形態與發芽研究[1]

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摘要：本研究共選用14科24種藥用植物的種子，經由發芽觀察，計有11種植物可在室溫下順利發芽。豆科與錦葵科植物之種子，經由種皮穿刺或硫酸處理後發芽，顯示硬實現象爲其休眠之主要原因。白花菜種子之休眠機制主要在於種皮外層，可用硫酸、硝酸鉀及充分浸種等處理而促進發芽；另外光照亦能抑制白花菜之發芽。枸杞屬於室溫中容易發芽之藥用植物，其最適最低及最高發芽溫度應爲 28、16及 32°C。柴胡之發芽速度頗不整齊，可能與胚發育程度不同及內生荷爾蒙平衡有關，經用低溫層育可稍加改進其發芽勢，其中尤以四星期之層育效果較佳，但仍須進一步研究。另外 9 種發芽率低落者，經用1% TTC (2, 3, 5-triphenyl tetrazolium chloride) 溶液檢定，發現其活力大多不盡理想，顯示種子自採收後之調製、貯藏應加以重視，藉以確保種子活力。

生藥之利用在我國已有數千年歷史，本省每年在中醫成藥及製劑的消費值約在臺幣80億元以上，但其中藥材却大多仰賴進口，每年耗費大額外匯 (4)。本省境內平原，丘陵及高山處處皆是，且氣候類型上兼具熱帶、亞熱帶、溫帶及寒帶等特徵，很適合各類藥材之栽培，若能建立本省自有之生藥材生產體系，除了增進國民健康，增加農民的收益外，將可減少鉅額外匯支出。本所近年來正積極自國外及省內各地蒐集藥用植物種源，以便進一步發展藥用作物。由於種子之優劣及種子發芽過程之是否旺盛與整齊將是藥用植物生產成功的先決條件，所以特作研究室擬就所蒐集藥用植物之種子，就其形態及活力加以調查，並探討各種促進種子發芽的方法，俾便對往後藥用植物栽培有所助益。

材料與方法

一、供試材料：

扁決明等24種藥用植物（表１），除柴胡爲新鮮種子外，其餘種子於 0—4°C 冰箱中冷藏已６—12個月。

Table 1. Classification and healing parts of 24 medicinal plants (1.5.6)

Scientific name	Family	Medicinal parts
Cassia occidentalis L.	*Leguminosae*	Seeds
Uraria macrostachys Wall	*Leguminosae*	Whole plant
Azukia angularts (willd.) Owhi	*Leguminosae*	Seeds

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Scientific name	Family	Medicinal parts
Hibiscus mutabilis L.	*Malvaceae*	Leveas
Urena lobata L. var. *albiflora* Kan.	*Malvaceae*	Roots
Abutilon indicum (L.) Sweet	*Malvanaceae*	Whole plant
Lycium halimifolium Miller.	*Solanaceae*	Whole plant
Solanum aculeatissimum Jacq.	*Solanaceae*	Roots and Seeds
Datura stramonium L.	*Solanaceae*	Corolla
Leonurus sibiricus L. var. *albiflors* Miqrel	*Labiatae*	Whole plant
Salvia plebeia R. Br.	*Labiatae*	Whole plant
Angelica acutiloba Kitagawa	*Umbelliferae*	Roots
Bupleurum falcatum L.	*Umbelliferae*	Roots
Taraxacum officinale Weber	*Compositae*	Whole plant
Xanthium surtmarium L. var. *jiaponica* (Widder) Hara.	*Compositae*	Whole plant
Gynostemma pentaphyllum (Thunb) Makino	*Cucurbitaceae*	Leaves
Trichosanthes cucumeroides Maxim.	*Cucurbitaceae*	Roots and Seeds
Cleome gynandra L.	*Capparidaccae*	Whole plant
Asclepias curassavica L.	*Asclepiadaceae*	Whole plant
Coptic japonica (Thunb) Makino	*Ranunculaceae*	Roots and Seeds
Alpinia specisa (Wendl.) K, Schumann	*Zingiberaceae*	Roots and Seeds
Canna flaccida Rosc.	*Cannaeeae*	Roots
Digitalis purpurea L.	*Scrophulariacae*	Leaves
Sapindus mukorossi Gaerthl.	*Sapindaceae*	Seeds

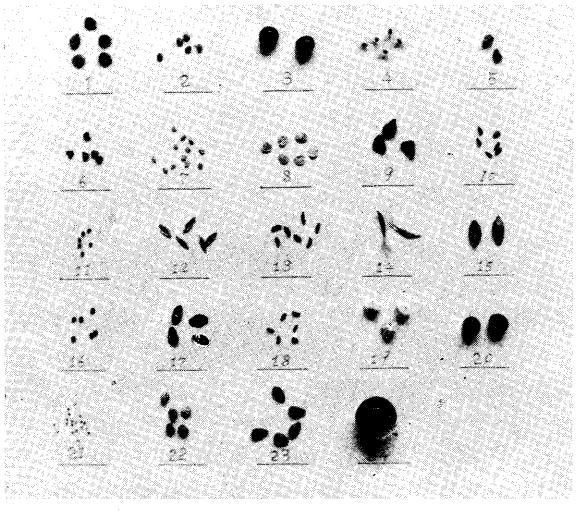
二、試驗方法：

形態觀察：記錄種子之外型、色澤、長寬厚、種子型以及胚長度等。發芽觀察：種子先以1%次氯酸鈉（NaHClO）浸種消毒10分鐘，復以蒸餾水清洗10分鐘，置於11公分培養皿之濾紙上於室溫中行紙上發芽觀察，並記錄其發芽型（germinational type）、發芽日數及發芽情型。硬實處理：經發芽觀察若發現硬實者以種皮穿刺（scarification）處理未發芽種子，記錄其效果，復以硫酸（Merck, 97—95%）處理5—20分鐘，探討其最佳處理時間。活力檢定：發芽率低落之種子於室溫下浸種16—18小時後，置於1%TTC（2, 3, 5-triphenyl tetrazolium chloride）溶液（30°C）6—8小時，依胚及胚乳染色情形判別其活力，探討發芽不良之部份原因。藥劑處理：以KNO_3（0.2～1%）及GA_3（400ppm）直接添加於培養皿中或GA_3（1000ppm）浸種24小時等處理，探討KNO_3及GA_3對種子發芽之影響。低溫層育：將種子置於含有飽和水分之濾紙上於0—4°C之冰箱中2—8星期，探討其對柴胡發芽率及發芽勢之影響。發芽適溫探討，於不同溫度之恆溫箱中（8, 12, 16, 20, 24, 28, 32, 36°C）就發芽率及發芽勢兩方面測定其發芽之最適、最高及最低溫度。本試驗除了發芽觀察試驗未設重複外，其餘試驗重複數2—4，每重複種子數20—50粒。發芽勢以達到種子發芽總數之一半所需要的時間（T_{50}）爲準[12]，其計算公式：$T_{50}=t_i+\frac{(N+1)/2-n_i}{(n_j-n_i)}\times(t_j-t_i)$，N爲發芽總數，發芽數

累計，當$n_i < (N+1)/2 \leq n_j$時，t_i及t_j各爲n_i及n_j時之時間。

結果與討論

由圖1可明顯看出24種藥用植物種子在外觀上具有明顯的差異。種子大小（長度）由毛地黃（*D. pnrpurea*）之0.8mm以至於無患子（*S. mukorossi*）之1.0cm兩者差異甚大。根據 Atwater [9] 報導



Length of the line below the seeds is 1.5cm.

Fig. 1. Seed shape of 24 medicinal plants (The order is as Table 1)

，形態相似的種子具有相類似的休眠與發芽型式（germination and dormancy patterns），雙子葉草本植物中，無胚乳種子之胚已成熟，其休眠原因大多因種皮（seed coat）或胚乳膜（endosperm membrane）對於水分、溶液及氣體等之通透度（permeability）不良或因種皮內含有發芽抑制物質所造成；而有胚乳種子之休眠除了以上原因外，尙有因胚之發育不全所造成之形態休眠（morphology dormancy）及胚乳內含抑制物質等原因。因此，由種子之胚乳及子葉等基本構造劃分之不同種子型（seed patterns），可作爲發芽試驗之初步依據。參試材料中屬於單子葉者計有2種，雙子葉無胚乳者計12種；雙子葉有胚乳者計10種（表2）。同一科之植物其種子型可能不同，例如在唇形科（*Labiatae*）中之白花益母草（*L. siqiricue*）爲有胚乳種子，而荔枝草（*S. plebeia*）却爲無胚乳種子。另外荔枝草種子經浸水後，種皮外層產生透明膠質層（mucilaginous layer），一般認爲在水分吸收之同時，此一膠質層有助於氧氣及其它氣體的通透，但是此層如何形成目前並未十分清楚 [9]。在試驗過程中亦曾發現不具膠質層之荔枝草種子，但未發芽。種子之發芽型基本上可分爲(1)地下發芽型（hypogeal germination），即種子發芽時子葉留於地表下(2)地上發芽型（epigeal germination），即發芽時子葉突出於地表。參試材料中單子葉植物都屬於地下發芽型，而雙子葉有胚乳植物則爲地上發芽型，在無胚乳種子亦以地上發芽型居多，只有赤小豆（*A. angularts*）爲地下發芽型（表2）。但是種子型與發芽型間似乎沒有一定的關係。於室溫下進行種子發芽試驗，發現扁決明（*C. occidentalis*）等11種可順利發芽（發芽率高於 50%）（表2）。其中無患子及柴胡（*B. falcatum*）之發芽開始日數較長，無患子係因硬實而延長發芽日數，而柴胡則可能因胚之發育不全而延遲發芽。由表2中可知柴胡、馬利筋（*A. curassavica*），枸杞（*L. halimifolium*），小顚茄

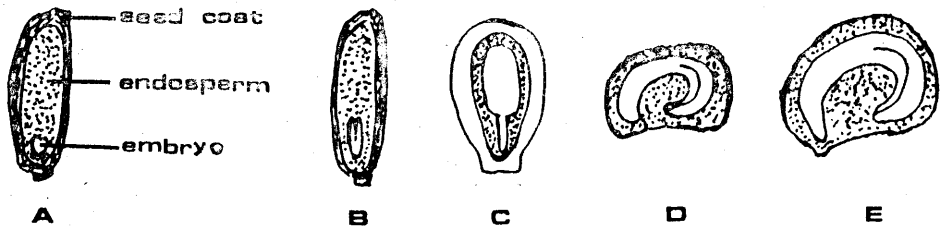
Table 2. Seed pattern and germination under room temperature of 24 medicinal plants

Scientific name	Seed* pattern	Days to germ.	Germ. *		Effect of scarification
			type	rate	
C. occidentalis	2	1	2	+	+
U. macrostachys	2	1	2	−	+
A. angularts	2	1	1	+	+
H. mutabilitis	2	3	2	−	+
U. lobata	2	2	2	−	+
A. indicum	2	7	2	−	
L. halimifolium	3	2	2	+	
S. aculeatissium	3	3	2	+	
D. stramonium	3	—	—	−	
L. sibiricus	3	—	—	−	
S. plebeia	2	3	2	+	
A. acutiloba	3	16	2	−	
B. falcatum	3	19	2	+	
T. officinale	2	3	2	−	
X. strumarium	2	2	2	+	
G. pentaphyllum	2	5	2	−	
T. cucumeroides	2	13	2	−	
C. gynandra	3	1	2	−	
A. curassavica	3	3	2	+	
C. japonica	3	—	—	−	
A. speciosa	1	18	1	−	
C. flaccida	1	5	1	+	−
D. purourea	3	6	2	+	+
S. mukorossi	2	14	2	+	+

*Seed pattern : "1" Monocotyledon, "2" Dicotyledon with residual endosperm, "3" Dicotyledon with endosperm.

*Germination type : "1" Hypogeal germination, "2" Epigeal germination.

*Germination rate : "+" Above 50%, "−" Below 50%.



A : *C. Japonica*, B : *B. falcatum*, C : *A. curassavica*,
D : *L. hallmifolium*, E : *S. aculeatissimume*

Fig. 2. Different embryo shape of endospermic seeds of medicinal plants.

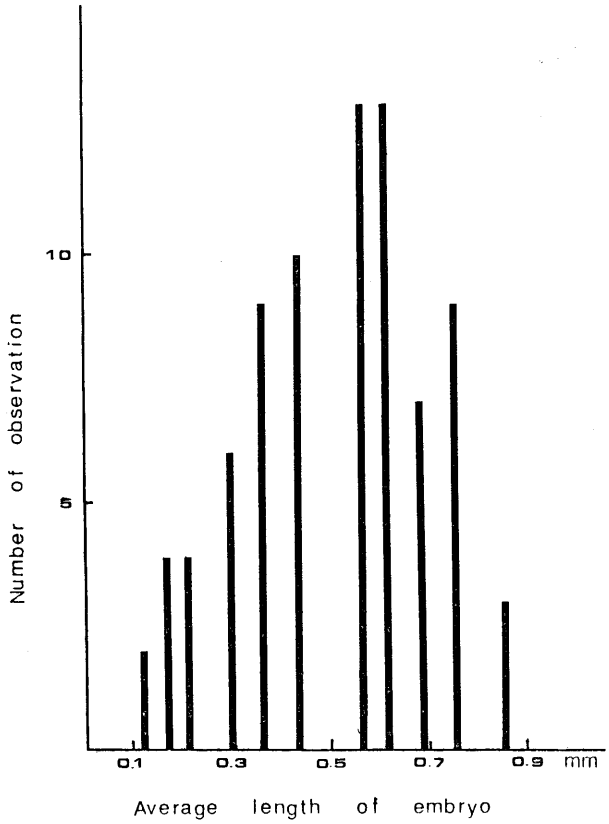


Fig. 3. Distribution of embryo length of *Bupleurum falcatum* L.

(*S. aculeatissimum*) 等4種同屬雙子葉有胚乳種子，但在胚發育形態上具有明顯的差異（圖2），後三者之胚形態已臻成熟，而柴胡胚發育則尚未成熟。此或許如 Atwater [9] 所稱，繖形科（*Umbelliferae*）之種子在脫離植株時，其胚發育未臻成熟，此類種子之發芽需要一段時日之胚發育後方具有發芽的能力，且胡柴之胚發育在同一批種子中（80個樣品）亦有明顯的差異（圖3），胚長度有由0.13mm 至0.86mm之變域，因此造成柴胡日後發芽日數較長及發芽不整齊的因素之一。如何促使柴胡發芽快速整齊，值得進一步研究。另在解剖觀察中發現黃連（*C. joponica*）之胚更形細小（圖2），胚之發育形態約在心臟形（heart-shaped）至魚雷形（torpedo-shaped）間 [10]，胚長度僅佔種子長度之⅒左右。朱 [2] 之譯述指出此類種子必須經過3—4個月後熟作用，胚始能發育完全而發芽。

室溫發芽試驗中，發現扁決明等 8 種種子具有硬實現象（表 2），經用種皮刻傷（scarification）處理後，除月桃（*A. speciosa*）外均可促進發芽。顯示，扁決明（*C. occidentalis*）、狐狸尾（*U. macrostachys*）、木芙蓉（*H. mutabilis*）、白花虱母（*U. lobata*）、磨盤草（*A. indicum*）（以上爲豆科（*Leguminosae*）及錦葵科（*Malvaceae*）藥用植物）、黃花曇華（*C. flaccida*）及無患子等僅因種皮限制水分吸收而無法發芽或延遲發芽。此依前人研究[7]：豆科與錦葵科之種子常有硬實現象，克服之法除了應用種皮刻傷外，尚可應用加熱、變溫或硫酸等處理。前 5 種種子經以濃硫酸處理之結果如表 3 所示，除了木芙蓉因濃硫酸處理 5 分鐘失去發芽力外，其餘 4 種植物種子在發芽率及 T_{50}（發芽勢）上皆有明顯的改良效果，其中扁決明、狐狸尾以濃硫酸處理 10分鐘、白花虱母15分鐘後之發芽率都達95%以上，其 T_{50} 甚至僅爲不處理之 1／10；而磨盤草之處理時間似可加長；木芙蓉種子若以硫酸處理時濃度宜低。

Table 3. Effect of pre-sowing H_2SO_4 treatment on germination of five medicinal plants with hard seed

Treatment (Mins)	*C. occidentalis*		*U. macrostachys*		*H. mutabilis*		*U. lobata*		*A. indicum*	
	A*	B*	A	B	A	B	A	B	A	B
0	70.0	77.7	0	—	47.0	115.0	55.0	132.0	5.0	—
5	90.0	17.7	89.3	108.1	0	—	80.0	37.5	15.0	174.0
10	95.0	14.3	96.3	11.0	0	—	90.0	25.5	37.5	156.0
15	—	—	—	—	—	—	100.0	12.9	60.0	51.2
20	—	—	—	—	—	—	—	—	60.0	28.0

*A : Germination rate (%), B : Hours needed to 50% of total germination.

Table 4. TTC test of 9 medicinal plants

Medicinal plant	Treatment	Seed vigor (%)**		
		++	+	−
A. speciosa	1*	0	5.0	95.0
A. speciosa	2*	83.3	8.3	8.3
C. gynandra	1	1.0	3.0	96.0
C. gynandra	2	98.0	1.0	1.0
L. sibiricus	1	4.4	44.9	50.7
D. purpurea	1	4.3	12.7	82.9
G. pentaphyllum	1	16.1	29.8	58.2
D. stramonium	1	0	0	100.0
T. officinale	1	18.2	0	81.8
T. cucumeroides	2	50.0	27.8	22.2
A. acutiloba	1	13.0	1.4	85.7

*1 : Intact seed, 2 : Cutted seed.

**++ : Strong-vigor, + : little-vigor, − : No-vigor.

另以1%TTC 溶液檢定在室溫發芽試驗中發芽率低落種子之活力。依其胚乳及胚染色情形判別[14]，大部份發芽率低落的藥用植物種子活力皆有偏低的現象，其中尤以曼陀羅（*D. stramonium*）最爲嚴重，其活力爲零（表4），甚至其胚之形態萎縮或已不復見。此顯示種子自採收後調製及貯藏之技術有待改進提昇，以確保種子活力。在表4中月桃及白花菜（*C. gynandra*）之完整種子及縱切種子之活力表現有明顯的差異，顯示在完整種子狀態下，其種皮有阻礙水分進入種子內部的可能。月桃之外種皮甚爲堅硬，且於解剖顯微鏡下可見其種臍爲一厚層木栓化組織所塡塞，此可能爲其吸水障礙原因。前文中（表2）亦曾針對月桃之硬實外殼施以種皮刻傷處理，但無法改進其發芽。白花菜種子經解剖觀察得知其爲環狀胚（peripheral embryo）種子，此類種子之發芽主要受種皮的控制[9]，Koller[15]亦指稱此類種子之外種皮具有高滲透價（high osmotic value）物質，此物質將阻礙水分進入種子內部，種子因而無法發芽；應用洗濯或浸種可將此一物質除去而促使發芽。此外尙可應用種皮割傷，照光及KNO_3等處理達到發芽的目的。白花菜經用相關處理之結果如表5所示，充分的浸種（7天）及濃硫酸處理（0.5～1.5分鐘）之發芽效果良好，且發芽快速整齊，但硫酸處理2.5分鐘白花菜即失去發芽力，故以濃硫酸處理之時間不宜過長。以KNO_3不同濃度處理亦有明顯的效果，且以高濃度（1%）之效果較佳。但是照光（3600lux, 16hrs/day）處理不僅無法促進其發芽，反而有抑制的現象，並且抵消了KNO_3的作用。此與Koller[15]在*Atripley dimorphostegia* 之試驗結果相類似，其發芽需要滲透壓之調節，但亦在光照下受到抑制。以$GA_3$400ppm 取代蒸餾水之處理於光照下培養仍未見發芽（表5）。此與Chen[11]之試驗結果略有出入，其指出光抑制發芽之種子（*Nemoplnila msignis*）可用 GA_3（5×10^{-4}M）之處理而在光照下發芽。另取在照光下不發芽種子（3週）經用濃硫酸處理後於光照及黑暗中培養，光照組仍無發芽的現象，而在黑暗中之發芽率亦僅有4%。以上顯示白花菜種子之休眠原因可能有種皮對於水分吸收的阻礙及照光抑制等2種機制。

Table 5. Influence of GA_3, KNO_3 and pre-sowing H_2SO_4 treatments on germination rate of *Cleome gynandra* L.

Germ. condition	CK	GA_3 (400ppm)	KNO_3		H_2SO_4 (Mins)			
			1.0%	0.2%	0.5	1.0	1.5	2.5
Dark	9.0d*	2.0f	31.0bc	23.0c	—	—	—	—
Dark**	26.0c	—	—	—	43.6ab	50.8a	51.4a	0.0 f
Light***	0.0 f	0.0 f	0.0 f	0.0 f	—	—	—	—

*Means with the same letter are not significantly different ($p\leq.05$), using Duncan's New Multiple Ravge Test.

**Seeds presoaked in water for seven days then dried in air.

***Light intensity : 3600 lux, 16 hours per day.

枸杞種子之發芽溫度探討，結果如表6所示，由8°C至36°C之發芽溫度中，5個參試品種（系）在發芽率及發芽勢的表現頗爲一致。從表中可明顯得知32°C及16°C 應爲所有參試枸杞品種（系）發芽之最高及最低溫度。惟溫度由20°C降至16°C時，到達T_{50}所須時間即呈大幅增加，其中尤以貢杞（Kung-chi）增加達130小時最爲明顯，由此一結果指出，貢杞之發芽較不適於低溫。5個參試品種（系）中，就發芽率而言，以貢杞最爲良好，其自16°C～32°C之平均發芽率達98.5%，而丙杞（Ping-chi）之平均發芽率僅爲54%左右，另就發芽勢（T_{50}）而言，則以甲杞（Chia-chi）爲優。綜合發芽率及發芽勢之表現，28°C應爲所有參試枸杞品種（系）發芽之最適溫度（表6）。

Table 6. Effect of temperature on germination of *Lycium halimifolium* M.

Varities	8°C		12°C		16°C		20°C		24°C		28°C		32°C		36°C	
	A*	B*	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Kung-chi	0	—	15.3	—	94.0	219	100.0	85.3	99.3	74.8	100.0	59.1	99.3	62.3	21.5	—
Chia-chi	0	—	16.7	—	90.0	108	96.7	74.2	96.0	59.5	94.0	58.7	97.3	59.5	25.0	—
Heieh-chia-chi	0	—	20.6	—	82.0	145	94.0	83.4	92.6	83.9	97.3	59.6	95.3	60.3	16.5	—
Heieh-i-chi	0	—	12.0	—	82.0	142	85.3	82.2	92.0	61.1	92.6	59.1	88.0	75.3	12.6	—
Ping-chi	0	—	12.7	—	53.0	222	49.0	153.0	49.0	138.0	60.0	144	57.0	170.0	2.0	—

*A : Germination rate (%), B : Hours needed to 50% of total germination.

Table 7. Effect of cold stratification on seed germination under room temperature of *Bupleurunl falcatum* L.

Treatment	Days to germ.	Final germ. (days)	T_{50}* (days)	T_{75}* (days)	Germ. rate (%)
CK	19	53	33.8	46.3	84.5
Cold stratification (0—4°C) for 13 days	18	41	35.0	37.5	86.2

*T_{50}, T_{75} : Times to 50% and 75% of total germination, respectively.

柴胡爲重要藥材，其種子發芽率及發芽勢之改進一直爲其栽培研究之重要課題之一。以本所所採柴胡之新鮮種子於室溫下之發芽情形如表 7 所示，表中顯示柴胡新鮮種子之發芽率達84.5%頗爲良好，只是其發芽起始日數（19日）稍嫌過長，且其發芽速度頗不整齊，此將在實際栽培管理上造成不便。前文中(圖 3)亦曾就柴胡胚發育上之差異推論其爲柴胡發芽不整齊之可能因素。本研究室曾以開花後50、57、64、71天等不同成熟度之柴胡種子於室溫下進行發芽觀察，其結果（未發表）以57天之發芽率及發芽勢表現最爲良好，50天者次之，64及71天之表現最差、顯示胚之大小並不是唯一影響發芽勢之因素，可能與種子內生荷爾蒙之平衡或種皮通透性有關。在採收時期胚發育未臻成熟之雙子葉有胚乳種子，其胚之後熟作用可能被胚乳內之抑制物質所抑制，此外柴胡之種皮可能爲半透性（semi-permeability）。[9] GAs 或低溫層育 (cold stratification) 等處理有助於胚發育[2,8,9]，因此應用低溫層育 (0—4°C) 處理 2 星期，試圖改善柴胡種子發芽不整齊現象，其結果列於表 7，柴胡經13天期之低溫層育處理後於室溫下發芽，可明顯縮短T_{75}的時間，但對T_{50}及起始發芽日數却無促進作用。由於繖形科植物種子之發芽適溫在20°C左右[9,13]。因此，另以臺東採回並且陰乾後於0—4°C 冰箱貯存 2 個月之柴胡種子爲材料，給予GA_3及 2、4、8 星期之低溫層育等處理，在16、20及 24°C 三種溫度下經 35 天培養之結果列如表 8 及表 9。比較表 8 與表 7 之結果，可明顯發現貯存後之柴胡種子發芽率較新鮮種子爲低，此與邱[3] 所述，柴胡種子隔年發芽率低弱有著相同的趨勢，顯示柴胡種子之貯存條件十分重要，有必要加以探討。表 8 中亦顯示，種子大小與發芽率有密切關係，即較大之種子（種子直徑1.19—1.0mm）具有較高的發芽率。就溫度而言，在對照組中由16°C至24°C間，柴胡發芽率（表 8）呈遞減，而T_{50}（表 9）所需時間漸增的現象，顯示柴胡發芽溫度以 16°C 較爲畤恰。

Table 8. Effect of GA_3 and cold stratification on germination rate of *Bupleurunl falcatum* L.

Seed size (ϕ, mm)	Temp. °C	Germination rate (%)				
		CK	GA_3 1000ppm	Cold stratification (0—4°C)		
				2 weeks	4 weeks	8 weeks
1.19—1.0	20	45.0ab*	26.3cd	43.4ab	50.0a	37.5abc
1.0—0.84	20	24.0cd	25.0cd	36.7abc	48.0a	28.0cd
1.0—0.84	16	35.0adc	25.0cd	—	50.0a	45.0ab
1.0—0.84	24	13.3d	21.3cd	26.7cd	31.3bc	—

*Means with the same letter are not significantly different ($p \leq .05$), using Duncan,s New Multiple Range Test.

Table 9. Effect of GA_3 and cold stratification on speed of germination of *Bupleurunl falcatum* L.

Seed size (ϕ, mm)	Temp. °C	Speed of germination (T_{50}, days)				
		CK	GA_3 1000ppm	Cold stratification (0—4°C)		
				2 weeks	4 weeks	8 weeks
1.19—1.0	20	17.95bcd*	19.58bc	15.70de	12.76ef	16.20de
1.0—0.84	20	17.65cd	17.85cd	13.31ef	11.24f	12.93ef
1.0—0.84	16	16.33cde	20.30abc	—	10.05f	11.54f
1.0—0.84	24	23.97a	21.88ab	24.33a	18.33bcd	—

*Mean with the same letter are not significantly different ($p \leq .05$), using Duncan's New Multiple Kange Test.

$GA_3$1000ppm浸泡24小時之處理，只在24°C中表現較對照組良好外，其他並無預期效果。添加 cytokinins的效果如何，尚待進一步研究。

由低溫層育處理 2 、 4 及 8 星期之結果指出（表 8 、表 9），無論在發芽率或 T_{50} 均以 4 星期處理組表現最爲良好，且低溫層育的效果對於小種子較爲顯者。在低溫層育 4 星期中 1.19—1.0mm者發芽率由對照組之45%增至 50%，約增加 5 % ，但未達顯著水準 ，而 1.0—0.84mm 者由 35%、24%及13.3%（三個溫度對照組）增至50%、48%、31.3%，增加幅度較大，且均達顯著水準。 8 星期之低溫層育，結果皆較 4 星期層育者差，是否因層育過程太長，導致其胚活力降低，有待進一步探討。

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Studies on the Seed Morphology and Germination of 24 Medicinal Plants[1]

H. C. Huang, M. F. Hu and S. Y. Liu[2]

Summary

This study was conducted with seed observation and germination of 24 species medicinal plants from 14 families. The results indicated that the seeds of 11 species such as *Lycium halimifolium* M. could easily germinate at room temperature. Its optimum, highest and lowest temperature for germination were 28°C, 32°C and 16°C, respectively. Hard-seed was a major fator that prohibited seed of Leguminosae and Malvaceae like *Uraria macrostachys* W. from germination. The dormancy of *Cleome gynandra* L. might result from outer coverings and light inhibition. Many methods such as treatments of soaking in water (7 days) or H_2SO_4(97—95%, 0.5—1.5 minutes)and KNO_3 (0.2—1.0%) could minimize seed dormancy and enhance germination in dark condition. The seed germination of *Bupleurum falcatum* L. was not uniformly, and could last for 50 days at room temperature. Stratification at 0—4°C for four weeks could significantly enhance its germination rate and shorten its germination time. According to the results of TTC test, there were nine poor germination species, which showed litter or no vigor of seeds. This result indicated that the storage technique of seeds should be emphasized to main tain high vigor.

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Variance Component Analysis of Unbalanced Diallel Crosses[1]

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Abstract : This paper presents an efficient and stable method for estimating variance components from an unbalanced diallel crosses. The method follows the general procedure for computing the sums of squares in a random model by formulating testable hypotheses as if all effects were fixed and then compute the corresponding sums of squares. Expected sums of squares are derived from the expectations of quadratic forms of the observations. Estimable functions for effects in the model are generated by using the Cholesky decomposition of the reduced X'X matrix on the grounds that the sequential reduction is suitable in obtaining the sums of squares of general combining abilities, specific combining abilities, maternal effects and reciprocal effects in an unbalanced diallel crosses. As far as the sampling properties of the estimated variance components are concerned, no other method has yet been proved to be more optimal uniformly than the present one. Same computational method can also be used to handle the mixed diallel model with a little modification in the expected values of the sums of squares. Computing covariance components can be done virtually the same way as computing the variance components. Numerical examples are given to illustrate the computational procedurs.

Introduction

Any set of matings among p individuals, strains or inbred lines which can be arranged into sets of symmetrical two-way classifications by parentage may be called a diallel crosses. Many and seemingly different diallel analyses have been presented in the literature. Diallel analyses differ in four main ways - in the sampling assumptions of the experimental materials, in the postulated underlying genetic mechanism, in the methods of estimation, and in the parental heterozygosity.

Kempthorne (1956) has discussed these methods of analysis in terms of variances of inbred parents, crossbred offspring and the covariance between parents and offspring. Griffing (1956) has classified the four different diallel crossing methods from which at least a p(p-1)/2 set of crosses can be obtained. He also discussed the analysis of

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each in terms of the variance of general and specific combining abilities under two alternative assumptions with regard to the sampling nature of the experimental material. Theoretically, the important difference among these four methods depends upon whether not selfings are included. Griffing (1956) suggested that the term "diallel" should be used for those methods which include the selfings and the term "modified diallel" be used for those methods which do not. It was shown that with the modified diallel methods, unbiased estimates of the population variances can be obtained from mean squares of the appropriate analysis of variance (Griffing, 1958). Kempthorne (1956) derived the expectation of mean squares for a complete homozygous diallel. He showed that these mean squares alone could not yeild unbiased estimates of the desired parameters. Griffing (1958) also reached the similar conclusion for other diallel methods.

Maternal and recpirocal (sex-linkage) effects among the progenies of a set of homozygous diallel crosses has been examined by Wearden(1964). He derived the expected mean squares for three different analyses under two different models, assuming in each case either maternal or reciprocal effects. Topham (1966) has examined the implications of both effects occuring in the same material under the fixed model. Cockerham and Weir (1977) have given a quadratic analysis of reciprocal crosses of inbred lines for the balanced factorial and diallel mating designs.

Estimation of variance components in a diallel crosses is a special case of general problem of estimating variance components. Searle (1971) has given a good review on the topics in variance component estimation. Hartley's (1967) method of "synthesis" was one of the first methods developed for computing the coefficients in the expected values of mean squares for the mixed model. Gaylor et al. (1970) described the computation of expected values arising from the set of mean squares of the Forward Doolittle. Speed and Hocking (1974) developed the most computationally simple techniques to date and Goodnight and Speed (1980) modified the Speed and Hocking's technique to improve the computational efficiency.

Unbalanced data are those in which the numbers of observations in the subclasses of the model are not all the same, including cases where there are no observations in some subclasses. In contrast, balanced data are those in which the numbers of observations in all subclasses of the model are equal. Unequal subclass numbers always cause the different classes of effects to be non-orthogonal. This means that the different kinds of effects, such as general combining abilities and specific combining abilities, cannot be seperated directly without entanglement. In order to free these effects from confounding, it is necessary to consider all of the effects simultaneously. With equal subclass numbers, the effects are all mutually orthogonal and the statistics obtained directly from the class or subclass totals are equivalent to those obtained by the simultaneous consideration of all effects.

Diallel analysis with unbalanced data have not been discussed in detail before. In only one case (Harvey, 1960) have attempts been made to analyze diallel crosses data in the unbalanced case, without missing subclasses. The method of estimating variance components from an unbalanced diallel crosses will be discussed in this paper.

The Model

A diallel crosses with unbalanced data will be considered for estimating the variance components. There will be n_{ij} ($n_{ij} \geq 0$) observations of each cross in a completely randomized environmental design. More complicated environmental designs can be readily accomodated.

The model for the phenotypic value may include maternal, reciprocal (or sex-linkage) and environmental effects as well as the genotypic value which is usually composed of the general combining and specific combining abilities. The model can therefore be written as:

$$y_{ijk}=\mu+g_i+g_j+s_{ij}+m_i+r_{ij}+e_{ijk}, \quad (i \neq j) \quad \cdots\cdots [1]$$

where

μ = population mean of the crossbreds,

$g_i(g_j)$ = general combining ability effect for the i^{th} (j^{th}) parent,

s_{ij} = specific combining ability effect for the cross between the i^{th} and j^{th} parents such that $s_{ij} = s_{ji}$,

m_i = maternal effect of the i^{th} parent,

r_{ij} = reciprocal (sex-linkage) effect involving the reciprocal crosses between the i^{th} and j^{th} parents such that $r_{ij} = -r_{ji}$,

e_{ijk} = environmental effect associated with the ijk^{th} individual observation of the crossbreds.

Under the assumptions of the model (Random Model), all terms (except μ) are taken as being normally distributed with zero means and their respective variances.

Following Searle (1971), [1] can be represented by a general random model as:

$$Y=\mu 1+\sum_{i=1}^{k} X_i\beta_i+e \quad \cdots\cdots [2]$$

$$=X\beta+e$$

where

(1) Y is an n-vector of observations,

(2) 1 is an n-vector of 1's, $X_1, \cdots, X_k$ are nxm_i known matrices and $X=[1 \mid X_1 \mid \cdots \mid X_k]$,

(3) μ is general mean,

(4) The vectors $\beta_i (i=1, \cdots, k)$ are assumed independent of each other and are distributed $N(0, \sigma_i^2 I_{mi})$,

(5) e is an n-vector of random error and are assumed $N(0, \sigma_e^2 I)$.

On making the above normality assumptions.

$E(Y)=\mu 1$,

$$Var(Y)=\sum_{i=1}^{k} X_i X_i'\sigma_i^2+I\sigma_e^2.$$

Computing Sums of Squares

The qeneral procedure for computing the sums of squares (SS) in a random model is to formulate testable hypotheses as if all effects were fixed and then compute the corresponding SS.

Letting (1) $\beta=\begin{pmatrix}\mu\\ \beta_1\\ \vdots\\ \beta_k\end{pmatrix}$

(2) $(X'X)^-$=any generalized inverse of $(X'X)$

(3) $b=(X'X)^-(X'Y)$

(4) L=any matrix of full row rank in the row space of X,

then

$$SS_L=SS(H_0: L\beta=0)$$
$$=(Lb)'(L(X'X)^-L')^{-1}(Lb)$$
$$=Y'Q_LY \quad \cdots\cdots [3]$$

where $Q_L=X(X'X)^-L'(L(X'X)^-L')^{-1}L(X'X)^-X'$.

Expected Values of Sums of Squares

Equation [3] is a quadratic form in Y and any symmetric quadratic form Y'QY has (Searle, 1971) :

$$E(Y'QY)=\mu^2 1'Q1+\sum_{i=1}^{k} tr\,(X_i'QX_i)\sigma_i^2+tr(Q)\sigma_e^2 \quad \cdots\cdots [4]$$

Letting $X=[1 \mid X_1 \mid \cdots \mid X_k]$, all of the matrices except Q needed in [4] are submatrices of X'QX. It is easily seen that, from [4], only the elements of $X'Q_LX$ are needed to evaluate the expected value of [3] if [2] is assumed to be the true model.

Since L is in the row space of X, from the theory of estimability

$$L=L(X'X)^-X'X$$

and therefore

$$X'Q_LX=L'(L(X'X)^-L')^{-1}L.$$

Let U=Cholesky decomposition (upper) of $L(X'X)^-L'$,

(i.e., $L(X'X)^-L'=U'U$)

then $X'Q_LX=L'(L(X'X)^-L')^{-1}L$

$$=L'(U'U)^{-1}L$$
$$=C'C \text{ , where } C=(U')^{-1}L$$
$$=\begin{pmatrix} C_0'C_0 & C_0'C_1 & \cdots & C_0'C_k\\ C_1'C_0 & C_1'C_1 & \cdots & C'_1C_k\\ \vdots & \vdots & \vdots & \vdots\\ C_k'C_0 & C_k'C_1 & \cdots & C_k'C_k\end{pmatrix}$$

From [4], we have

$$E(SS_L)=C_0^2\mu^2+\sum_{i=1}^{k} tr\,(C_i'C_i)\,\sigma_i^2+n_L\sigma_e^2$$

$$=C_0^2\mu^2+\sum_{i=1}^{k} SSQ(C_i)\sigma_i^2+n_L\sigma_e^2 \quad \cdots\cdots [5]$$

where SSQ (C_i) = sum of squares of the elements of the C_i submatrix,
and n_L = the number of rows in L.

It is seen from [5] that C'C need not be computed and the matrix $C=(U')^{-1}L=[C_0 \mid C_1 \mid \cdots \mid C_k]$ of the same dimensions of L is all that is needed for computing the expected values of SS_L.

Reducing Dimensionality

Let the model in [2] be written as

$$Y=X\beta+e$$

$$=[X_1 \mid X_2]\begin{pmatrix}\beta_1\\ \beta_2\end{pmatrix}+e$$

where X_1 has full column rank and $X_2=X_1M$ for some matrix M.
Imposing $\hat{\beta}_2=0$, we have

$$X'X=\left(\begin{array}{c|c} X_1'X_1 & X_1'X_2 \\ \hline X_2'X_1 & X_2'X_2 \end{array}\right),\quad (X'X)^-=\left(\begin{array}{c|c} (X_1'X_1)^{-1} & 0 \\ \hline 0 & 0 \end{array}\right)$$

where $X_1'X_1$ has full row rank , equal to r(X), and $(X'X)^-$ is a g2-inverse of X'X.

Since $L(X'X)^-L'=[L_1 \mid L_2]\left(\begin{array}{c|c} (X_1'X_1)^{-1} & 0 \\ \hline 0 & 0 \end{array}\right)\begin{pmatrix}L_1'\\ L_2'\end{pmatrix}$

$$=L_1(X_1'X_1)^{-1}L_1'$$
$$=U'U, \text{ (Cholesky decomposition)}$$

then $C=(U')^{-1}L=[C_0 \mid C_1 \mid \cdots \mid C_k]$
Similarly,

$$SS_L=(Lb)'(L(X'X)^-L')^{-1}(Lb)$$
$$=(L_1b_1)'(L_1(X_1'X_1)^{-1}L_1')^{-1}(L_1b_1)$$

where $b=(X'X)^-(X'Y)=\begin{pmatrix}(X_1'X_1)^{-1}(X_1'Y)\\ 0\end{pmatrix}=\begin{pmatrix}b_1\\ 0\end{pmatrix}$

and $E(SS_L)=C_0^2\mu^2+\sum_{i=1}^{k} SSQ(C_i)\sigma_i^2+n_L\sigma_e^2$

Thus without affecting anything, imposing restrictions reduces the computational burden significantly.

Generating Estimable Functions

In order for a hypothesis H_0: $L\beta=0$ to be testable, $L\beta$ must first be estimable. For any L we say that $L\beta$ is estimable if and only if a linear combination of the Y's exists which has an expected value of $L\beta$. Since any linear combination of the Y's, say KY, has $E(KY)=KX\beta$, then for $L\beta$ to be estimable, L must be a linear combination of the rows of the X matrix. In other words, L must be in the row space of X. This leads to the definition that: $L\beta$ is estimable if and only if there exists a K such

that L=KX (Goodnight, 1978).

It is clear from the above definition of estimability that if an L is to be constructed such that $L\beta$ is estimable, then only linear combinations of the rows of X need be considered. In fact any linear combination of the rows of X yields an L such that $L\beta$ is estimable. Thus the X matrix or any matrix (with the same row rank of X) constructed from row operations on X may be used as a generating set for constructing any and all L's. Obviously an infinite number of L's can be generated. For a given model, an entire set of L's must be generated, one L for each effect in the model.

As far as the estimation of variance components in a diallel crosses is concerned, the simplest sets of L's is generated by computing the Cholesky decomposition matrix of X'X, and letting the L's for each effect be the non-zero rows associated with that effect.

Cholesky decomposition matrix of full rank matrix X'_1X_1 is obtained most conveniently by first computing the Forward Doolittle matrix from $X_1'X_1$:

$$X_1'X_1 \xrightarrow{\text{Forward Doolittle}} A_1, \text{ (upper triangular matrix).}$$

If each row of A_1 is divided by the square root of its diagonal element to produce a matrix Z_1, then Z_1 is the Cholesky decomposition matrix of $X_1'X_1$ with $X'_1X_1=Z_1'Z_1$.
For symmetric positive semi-definite matrix X'X,

$$\text{let } X'X=\left(\begin{array}{c|c} X'_1X_1 & X'_1X_2 \\ \hline X'_2X_1 & X'_2X_2 \end{array}\right) \text{ and } X_1'X_1=Z_1'Z_1$$

where $X_1'X_1$ has full rank.

$$\text{If } Z=\left(\begin{array}{c|c} Z_1 & (Z_1')^{-1}(X_1'X_2) \\ \hline 0 & 0 \end{array}\right), \text{ then } X'X=Z'Z.$$

(i.e., Z is the Cholesky decomposition matrix of X'X.)
Therefore $[Z_1 \mid (Z'_1)^{-1}(X'_1X_2)]$ can be used to generate the entire set of L's, one L for each effect in the model.

$$\text{If } L=[Z_1 \mid (Z'_1)^{-1}(X'_1X_2)] = \left(\begin{array}{c} L_0 \\ \hline L_1 \\ \hline \vdots \\ \hline L_s \\ \hline \vdots \\ \hline L_k \end{array}\right) = \left(\begin{array}{c|c} L_{01} & L_{02} \\ \hline L_{11} & L_{12} \\ \hline \vdots & \vdots \\ \hline L_{s1} & L_{s2} \\ \hline \vdots & \vdots \\ \hline L_{k1} & L_{k2} \end{array}\right)$$

then (1) $L_s(X'X)^-L_s'=L_{s1}(X_1'X_1)^{-1}L'_{s1}=I$ (identity matrix)

(2) $C_s=L_s=[C_{s0} \mid C_{s1} \mid \cdots \mid C_{sk}]$

(3) $SS_{Ls}=SS(H_0 : L_s\beta=0)=(L_sb)'(L_s(X'X)^-L'_s)^{-1}(L_sb)$

$=(L_{s1}b_1)'(L_{s1}(X_1'X_1)^{-1}L'_{s1})^{-1}(L_{s1}b_1)$

$=(L_{s1}b_1)'(L_{s1}b_1)$ ..... [6]

where $b=\left(\begin{array}{c} b_1 \\ \hline 0 \end{array}\right)=\left(\begin{array}{c} (X_1'X_1)^{-1}(X'_1Y) \\ \hline 0 \end{array}\right)$

(4) $E(SS_{Ls}) = C^2_{s0}\mu^2+\sum_{i=1}^{k} SSQ(C_{si})\sigma_i^2+n_{Ls}\,\sigma_e^2$ ..... [7]

The computational burden is further reduced if the Cholesky decomposition matrix of X'X is used for generating the L's.

Numerical Examples

The data given in Table 1 were used to illustrate the computational procedures developed in this paper. Suppose the data represent average daily gains of the progenies of a 4×4 diallel crosses in an animal breeding program. Data set 1 is balanced with 4 progenies for each cross. The other data sets are all unbalanced (unequal numbers of progenies for each cross), but with different structures to include some missing-subclass (cross) cases. Data set 2 has every cross present. Data set 3 has a cross (2×4) missing. Data set 4 has a cross (2×4) and a corresponding reciprocal cross (4×2) missing. Data set 5 has 2 crosses (2×4 and 2×1) of the same female parent missing.

Table 1. Data usde in numerical examples

Cross (F×M)	Data set						
	1	2	3	4	5	6	7
1×2	114	114	114	114	114	114	114
	119	119	119	119	119	119	119
	132	132	132	132	132	132	132
	148	148	148	148	148	148	148
1×3	126	126	126	126	126	126	126
	125	125	125	125	125	125	125
	113	113	113	113	113	113	113
	119	—	—	—	—	—	—
1×4	104	104	104	104	104	104	104
	108	108	108	108	108	108	108
	104	104	104	104	104	104	104
	100	100	100	100	100	100	100
2×1	127	127	127	127	—	127	—
	128	128	128	128	—	128	—
	114	—	—	—	—	—	—
	122	—	—	—	—	—	—
2×3	137	137	137	137	137	137	137
	135	135	135	135	135	135	135
	126	126	126	126	126	126	126
	131	131	131	131	131	131	131

Table 1. (續)

Cross (F×M)	Data set						
	1	2	3	4	5	6	7
2×4	115	115	—	—	—	—	—
	101	101	—	—	—	—	—
	101	101	—	—	—	—	—
	112	—	—	—	—	—	—
3×1	112	112	112	112	112	112	112
	133	133	133	133	133	133	133
	113	113	113	113	113	113	113
	124	—	—	—	—	—	—
3×2	134	134	134	134	134	134	134
	138	138	138	138	138	138	138
	129	129	129	129	129	129	129
	128	128	128	128	128	128	128
3×4	112	112	112	112	112	—	—
	111	111	111	111	111	—	—
	97	—	—	—	—	—	—
	107	—	—	—	—	—	—
4×1	100	100	100	100	100	100	100
	114	114	114	114	114	114	114
	94	94	94	94	94	94	94
	117	117	117	117	117	117	117
4×2	116	116	116	—	116	116	116
	114	114	114	—	114	114	114
	106	106	106	—	106	106	106
	110	—	—	—	—	—	—
4×3	97	97	97	97	97	97	97
	98	98	98	98	98	98	98
	103	103	103	103	103	103	103
	96	96	96	96	96	96	96
No. of obs.	48	40	37	34	35	35	33

Data set 6 has 2 crosses (2×4 and 3×4) of the same male parent missing. Data set 7 has 3 crosses (2×4, 2×1 and 3×4) missing, of which 2 crosses have the same female parent and 2 crosses have the same male parent. [Table 1]

For model in [1], the reduced X'X matrix for generating estimable functions and the estimable functions generated by the Cholesky decomposition of the reduced X'X matrix were given in Table 2 and Table 3, respectively, for data set 1 only to save space. Values for other data sets were obtained in a similar manner. Restrictions on general combining abilities (gca) and on maternal effects (me) were imposed by the usual way. Restrictions on specific combining abilities (sca) were applied on the last effect of every female parent first, then applied the remaining constraint on effect

Table 2. Reduced X'X matrix of data set 1 for generating estimable functions

Effect	Source of variation											
	mean(μ)	gca(g)			sca(s)		me(m)			re(r)		
μ	48	24	24	24	8	8	12	12	12	0	0	0
g_1	24	24	8	8	8	8	12	4	4	0	0	0
g_2	24	8	24	8	8	0	4	12	4	0	0	0
g_3	24	8	8	24	8	8	4	4	12	0	0	0
g_4	24	8	8	8	0	0	4	4	4	0	0	0
s_{12}	8	8	8	0	8	0	4	4	0	0	0	0
s_{13}	8	8	0	8	0	8	4	0	4	0	0	0
s_{14}	8	8	0	0	0	0	4	0	0	0	0	0
s_{23}	8	0	8	8	0	0	0	4	4	0	0	0
s_{24}	8	0	8	0	0	0	0	4	0	0	0	0
s_{34}	8	0	0	8	0	0	0	0	4	0	0	0
m_1	12	12	4	4	4	4	12	0	0	4	4	0
m_2	12	4	12	4	4	0	0	12	0	-4	0	4
m_3	12	4	4	12	0	4	0	0	12	0	-4	-4
m_4	12	4	4	4	0	0	0	0	0	0	0	0
r_{12}	0	0	0	0	0	0	4	-4	0	8	0	0
r_{13}	0	0	0	0	0	0	4	0	-4	0	8	0
r_{14}	0	0	0	0	0	0	4	0	0	0	0	0
r_{23}	0	0	0	0	0	0	0	4	-4	0	0	8
r_{24}	0	0	0	0	0	0	0	4	0	0	0	0
r_{34}	0	0	0	0	0	0	0	0	4	0	0	0

which have the highest i+j value (i and j stand for the female and male parent indices, respectively). Restrictions on reciprocal effects (re) were applied on the last effect of every male parent first, then applied the remaining constraint on effect which have the highest i+j value . For data with i×j cross missing, an additional constraint must be applied on the i×j reciprocal effect, simply because this reciprocal effect is no longer estimable. For data with both i×j and j×i crosses missing, two additional constraints must be employed. One for the i×j specific combining ability and the other for the i×j reciprocal effect, since both these two effects are no longer estimable.

Table 3. Estimable functions of data set 1 generated by Cholesky decomposition of reduced X'X matrix ($\times 10^{-3}$)

Effect	Source of variation											
	mean(μ)	gca(g)			sca(s)		me(m)			re(r)		
μ	6928	0	0	0	0	0	0	0	0	0	0	0
g_1	3464	3464	0	0	0	0	0	0	0	0	0	0
g_2	3464	-1155	3266	0	0	0	0	0	0	0	0	0
g_3	3464	-1155	-1633	2828	0	0	0	0	0	0	0	0
g_4	3464	-1155	-1633	-2828	0	0	0	0	0	0	0	0
s_{12}	1155	1155	1633	0	1633	0	0	0	0	0	0	0
s_{13}	1155	1155	- 817	1414	-817	1414	0	0	0	0	0	0
s_{14}	1155	1155	- 817	-1414	-817	-1414	0	0	0	0	0	0
s_{23}	1155	-1155	817	1414	-817	-1414	0	0	0	0	0	0
s_{24}	1155	-1155	817	-1414	-817	1414	0	0	0	0	0	0
s_{34}	1155	-1155	-1633	0	1633	0	0	0	0	0	0	0
m_1	1732	1732	0	0	0	0	2450	0	0	0	0	0
m_2	1732	- 577	1633	0	0	0	-817	2309	0	0	0	0
m_3	1732	- 577	- 817	1414	0	0	-817	-1155	2000	0	0	0
m_4	1732	- 577	- 817	-1414	0	0	-817	-1155	-2000	0	0	0
r_{12}	0	0	0	0	0	0	1633	-1155	0	2000	0	0
r_{13}	0	0	0	0	0	0	1633	577	-1000	-1000	1732	0
r_{14}	0	0	0	0	0	0	1633	577	1000	-1000	-1732	0
r_{23}	0	0	0	0	0	0	0	1732	-1000	1000	- 577	1633
r_{24}	0	0	0	0	0	0	0	1732	1000	1000	577	-1633
r_{34}	0	0	0	0	0	0	0	0	2000	0	1155	1633

From the estimable functions generated by the Cholesky decomposition of the reduced X'X matrix, sums of squares (SS) and the expected values of SS for general combining abilities, specific combining abilities, maternal effects and reciprocal effects were easily computed from [6] and [7], respectively, and were listed in Table 4. Estimated values of varianae components were summarized in Table 5. Some estimates were negative, but this was largely due to the sampling error of the data itself and

Table 4. Sums of squares (SS) and expected values of SS for estimable functions generated by Cholesky decomposition of reduced X'X matrix

S. O. V.	Data set	DF	SS(H_0:Lβ=0)	Coefficients in Exp(SS)					
				μ^2	σ_g^2	σ_s^2	σ_m^2	σ_r^2	σ_e^2
mean(μ)	1	1	644960.33344	48	48.00000	8.00000	12.00000	0.00000	1
	2	1	542657.02494	40	40.00000	6.80000	10.10000	0.20000	1
	3	1	509539.56744	37	37.24324	6.62162	9.70270	0.45946	1
	4	1	472001.05876	34	35.05882	6.94118	8.88235	0.23529	1
	5	1	477244.82846	35	35.37143	6.42857	9.68571	0.82857	1
	6	1	484747.45762	35	35.37143	6.42857	9.34286	0.82857	1
	7	1	452439.27307	33	33.27273	6.21212	9.30303	...	1
gca(g)	1	3	5542.37500	0	48.00000	24.00000	12.00000	0.00000	3
	2	3	5239.89583	0	40.00000	20.00000	10.33333	0.66667	3
	3	3	4974.73876	0	36.75675	18.82282	10.18619	1.87387	3
	4	3	4889.03939	0	32.94118	20.20168	8.59384	0.71709	3
	5	3	4768.53881	0	34.62857	17.90476	10.31429	3.40952	3
	6	3	5030.02137	0	34.62857	17.90476	10.65714	3.40952	3
	7	3	4851.37311	0	32.72727	16.78788	10.94697	...	3
sca(s)	1	2	191.29167	0	0.00000	16.00000	0.00000	0.00000	2
	2	2	134.70417	0	0.00000	13.20000	0.23333	0.46667	2
	3	2	81.15201	0	0.00000	11.55556	0.77778	2.00000	2
	4	1	73.36012	0	0.00000	6.85714	0.19048	0.38095	1
	5	2	70.34094	0	0.00000	10.66667	1.33333	3.42857	2
	6	2	178.81316	0	0.00000	10.66667	1.33333	3.42857	2
	7	2	153.89583	0	0.00000	10.00000	1.75000	...	2
me(m)	1	3	87.18750	0	0.00000	0.00000	24.00000	24.00000	3
	2	3	48.58302	0	0.00000	0.00000	19.33333	19.76246	3
	3	3	73.56640	0	0.00000	0.00000	16.33333	20.07312	3
	4	3	73.56640	0	0.00000	0.00000	16.33333	20.07312	3
	5	3	86.20833	0	0.00000	0.00000	13.66667	21.07246	3
	6	3	16.05978	0	0.00000	0.00000	13.66667	21.07246	3
	7	3	16.12500	0	0.00000	0.00000	11.00000	...	3
re(r)	1	3	155.81250	0	0.00000	0.00000	0.00000	24.00000	3
	2	3	253.79198	0	0.00000	0.00000	0.00000	18.90420	3
	3	2	168.64194	0	0.00000	0.00000	0.00000	12.59355	2
	4	2	168.64194	0	0.00000	0.00000	0.00000	12.59355	2
	5	1	155.25000	0	0.00000	0.00000	0.00000	6.26087	1
	6	1	0.81522	0	0.00000	0.00000	0.00000	6.26087	1
	7	–	...	–	...	...	...	...	–
error(e)	1	36	2143.00000	0	0.00000	0.00000	0.00000	0.00000	36
	2	28	1827.00000	0	0.00000	0.00000	0.00000	0.00000	28
	3	26	1696.33333	0	0.00000	0.00000	0.00000	0.00000	26
	4	24	1640.33333	0	0.00000	0.00000	0.00000	0.00000	24
	5	25	1695.83333	0	0.00000	0.00000	0.00000	0.00000	25
	6	25	1695.83333	0	0.00000	0.00000	0.00000	0.00000	25
	7	24	1695.33333	0	0.00000	0.00000	0.00000	0.00000	24

had not much to do with the computational method employed. Negative estimates occurred in even the balanced data (Table 5).

Table 5. Estimated values of μ^2 and variance components

Data set	Estimated values of					
	μ^2	σ_g^2	σ_s^2	σ_m^2	σ_r^2	σ_e^2
1	13325.19271	110.20312	4.51476	− 2.85938	− 0.94878	59.52778
2	13438.79583	128.62971	0.39998	−10.75056	3.07032	65.25000
3	13637.45220	134.76743	−3.51535	−11.20286	3.02971	65.24359
4	13734.09118	144.49875	0.90032	−11.16717	2.53681	68.34722
5	13498.40773	142.96354	−6.84836	−30.11073	13.96238	67.83333
6	13708.86010	135.88499	7.13694	2.78966	−10.70428	67.83333
7	13565.85548	145.27819	4.37667	−17.79924	···	70.63889

Although data used in this paper vary considerably in degree of unbalancedness, the estimated values of variance components for each effect are fairly consistent among 7 data sets. This demonstrates the stable nature of the computing algorithm developed in this paper.

Discussion

Estimating variance components from unbalanced data is not as straightforward as from balanced data. Several methods of estimation are available. Most of these methods reduced to the analysis of variance method for balanced data. Only a few comparative studies have been made on the relative merits of the different methods (Bush and Anderson, 1963; Anderson and Crump, 1967 and Kussmaul and Anderson, 1967). None of the methods has yet been clearly established as superior to the others. All of the methods involve relative cumbersome algebra. Discussion of unbalanced data can therefore easily deteriorate into a "welter of symbols" (Searle, 1971).

Methods 1 and 3 of Henderson (1953) and complete least-squares analysis are frequently used for estimating variance components from unbalanced data under the random model. All of these methods use, in one way or another, quadratic forms of the observations. The general methodology is to obtain expected values of quadratic forms and to equate them to their observed values. This is exactly what is done with sums of squares, which are quadratic forms of the observations, in the analysis of variance method for balance data. Whereas with balanced data their is obviously only one set of quadratic forms, they lead to estimators that are unbiased and have minimum variance properties. There are many sets of quadratic forms that can be used for unbalanced data. The simplest way to evaluate these estimators would be to compare their sampling variances , but to compare the sampling variances of different estimators is difficult because the variances themselves involve the true variance components even if

normality is assumed. It should be noted that although the change from balanced data to unbalanced data might appear relatively small on the surface, it causes enormous change in the tractability of methods and the properties of estimators. Comparative studies of different estimators arising from different quadratic forms, analytically or numerically, are therefore not simple because of the algebric complexity of unbalanced data involved. No particular set of quadratic forms has yet been established as more optimal than any other set. The only universal outcome of these different methods is that they all provide unbiased estimators. Unlike testing fixed effects where appropriate F-statistic is a problem, unbiased variance components can always be estimated by equating the expected values of quadratic forms to their observed values. Therefore an efficient and stable method for computing the observed values of quadratic forms and their expected values is most desirable.

Variance component estimators derived by the method presented in this paper are linear combinations of quadratic forms of the observations. Each quadratic form can be expressed in the form Y'QY for an appropriate Q-matrix and hence its sampling variance can be derived from application of $\mathrm{Var}(Y'QY)=2\ \mathrm{tr}(QV)+4\mu^2 1'QVQ1$, where $V=\mathrm{Var}(Y)=\sum_{i=1}^{k} X_iX_i'\sigma_i^2+I\sigma_e^2$, and the sampling covariance between any two quadratic forms can be derived from $\mathrm{Cov}(Y'QY, Y'RY)=2\ \mathrm{tr}(QVRV)+4\mu^2 1'QVR1$. In this way the sampling variance of linear combinations of these quadratic forms can be obtained, although the details are somewhat lengthy, involving considerable matrix manipulation.

The use of the Cholesky decomposition matrix of X'X in generating the estimable functions for effects in an unbalanced diallel crosses, as used in this paper, is proven to be both efficient and stable as well as appropriate. Methods 1 and 3 of Henderson and complete least-squares analysis, unreparametrized or reparametrized, should not be used in design matrix structure as unbalanced diallel. This is because in an unbalanced diallel, general combining abilities should not be adjusted for specific combining abilities and maternal effects should not be adjusted for reciprocal effects. Therefore sequential reductions, which is the outcome of the use of the Cholesky decomposition matrix of X'X, is proper in obtaining the sums of squares of general combining abilities, specific combining abilities, maternal effects and reciprocal effects in an unbalanced diallel crosses.

Although the diallel crosses model used in this paper is assumed random, same computational method can also be used to handle the mixed model with a little modification in the expected values of the sums of squares. Besides, computing sums of cross-products from an unbalanced data is analogus to computing sums of squares, therefore computing covariance components can be done virtually the same way as computing variance components. As far as the sampling properties of the estimated variance components are concerned, no other method has yet been proved to be more optimal uniformly than the present one.

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不均衡全互交之變方成分分析[1]

劉 清[2]

摘 要

本文提出一種有效且穩定的方法來估算不均衡全互交資料之變方成分。本法先將所有效應視爲固定型以構成可測擬說（testable hypothesis），後再計算逢機型模式中各項效應之平方和，平方和之期望值是由觀測值二次形（quadratic form）之期望值導出。模式中各項效應之可估函數（estimable function）是由減縮（reduced）X′X矩陣經Cholesky分解而得來，此因在不均衡全互交資料中，逐次減縮法（sequential reduction）最適合用來計算一般組合力、特殊組合力、母系效應及反交效應等之平方和。就估算所得之變方成分的取樣性質（sampling properties）而言，尚未有其它方法經證實較本法一致爲優。本文之計算方法亦可應用於混雜型全互交模式，僅需將平方和之期望值部份作些許修改。由於變方成分計算與變積成分計算之共同性，本法亦可用來估算變積成分。文中附有數例以說明計算過程。

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Component Analysis of Heterozygous Diallel Crosses[1]

Ching Liu[2]

Abstract : By constructing separate models for selfings and crossbreds based on their genotypic values, the genetic components analysis of Hayman and the combining ability analysis of Griffing for a diallel crosses were proved to be essentially equivalent and were combined to provide estimates of various genetic parameters of the sampled population from a heterozygous diallel. Difference in estimation of genetic parameters between homozygous diallel and heterozynous diallel were indicated.

Introduction

Any set of matings among p individuals, strains or inbred lines which can be arranged into sets of symmetrical two-way classifications by parentage may be called a diallel crosses. Many and seemingly different diallel analyses have been presented in the literature. Diallel analyses differ in four main ways-in the sampling assumptions of the experimental materials, in the postulated underlying genetic mechanism, in the methods of estimation, and in the parental heterozygosity.

Yates (1947) has given a statistical analysis by using the principles of analysis of variance for the factorial experiment; this has been modified and stated in terms of biometrical genetic parameters by Jinks and Hayman (1953) and further by Hayman (1954a, b, 1958, 1960) and Jinks (1954). Hayman (1954a) has defined five components (h, D, H_1, H_2, and F) of genetic variance in a homozygous diallel crossing system exhibiting additive and dominance, but no epistatic variance. The method of Jinks and Hayman (1953) emphasizes the analysis of genetic variances for a diallel crosses of inbred lines. They used diagrammatic methods to estimate the ratio of additive genetic variance to non-additive genetic variance in order to determine the mean level of dominance for a quantitative character. Dickinson and Jinks (1956) have extended the method of Jinks and Hayman to diallel crosses involving parental heterozygosity but the use of their method requires information about the parents which is not generally available.

Kempthorne (1956) has discussed these methods of analysis in terms of variances of inbred parents, crossbred offspring and the covariance between parents and off-

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spring. Griffing (1956) has classified the four different diallel crossing methods from which at least a p(p-1)/2 set of crosses can be obtained. He also discussed the analysis of each in terms of the variance of genral and specific combining ability under two alternative assumptions with regard to the sampling nature of the experimental material. Theoretically, the important difference among these four methods depends upon whether or not sefings are included. Griffing (1956) suggested that the term "diallel" should be used for those methods which include the sefings and the term "modified diallel" be used for those methods which do not. It was shown that with the modified diallel methods, unbiased estimates of the population variances can be obtained from mean squares of the appropriate analysis of variance (Griffing, 1958). Kempthorne (1956) derived the expectation of mean squares for a complete homozygous diallel. He showed that these mean squares alone could not yield unbiased estimates of the desired parameters. Griffing (1958) also reached the similar conclusion for other diallel methods.

As far as the random model (Eisenhart's Model II) is concerned, the five genetic components of variation defined by Hayman (1954a) are a set of linear transformations of the variances of general and specific combining ability and three other parameters. The combining ability analysis of Griffing (1956, 1958) can be extended to cover the analysis of genetic components of Hayman (1960) by constructing seperate models for selfings and crossbreds for both the homozygous diallel as well as the heterozygous diallel.

Problem of parental heterozygosity in a diallel crosses has scarcely been touched. The intent of this study is to establish basic models that can be further developed to evaluate the complete set of variance components and the genetic constitution of the sampled population.

Models and Analyses

Genotypic Models

The hypotheses listed below either hold in many inheritance mechanisms or are useful simplifications. We assume :

(a) Diploid segregation,

(b) No epistacy,

(c) No multiple allelism.

Let the genotypic values of three genotypes TT, Tt and tt at the t^{th} locus be denoted by d_t, f_t and $-d_t$ respectivly. And let these three genotypes be denoted by a variable θ_t which takes the value 1, 0, and -1 respectively (Hayman, 1954b). Then, if the genotype controlling a metric character is denoted by $\theta=(\theta_1, \theta_2, \cdots, \theta_q)$ and there is no epistacy, the genotypic value is

$$\sum_{t}^{q}[d_t\theta_t+f_t(1-\theta_t^2)] \quad \cdots\cdots (1)$$

as may be seen merely by substituting $\theta_t=1$, 0 and -1 in turn.

Some general results on this representation are ;

(a) The individual with genotype θ_t produces gametes L and t with frequencies $(1+\theta_t)/2$ and $(1-\theta_t)/2$, respectively.

(b) The cross $\theta_i \times \theta_j$ produces progeny TT, Tt and tt with frequencies

$(1+\theta_{it})(1+\theta_{jt})/4$, $(1-\theta_{it}\theta_{jt})/2$ and $(1-\theta_{it})(1-\theta_{jt})/4$,

respectively. These are the probabilities that $\theta_t = 1$, 0 or -1 in the progeny.

(c) In the progency of the cross $\theta_i \times \theta_j$,

$$\begin{aligned}E(\theta_t) &= (1)(1+\theta_{it})(1+\theta_{jt})/4+(0)(1-\theta_{it}\theta_{jt})/2 \\ &\quad +(-1)(1-\theta_{it})(1-\theta_{jt})/4 \\ &= (\theta_{it}+\theta_{jt})/2,\end{aligned}$$

$$\begin{aligned}E(1-\theta_t^2) &= 1-E(\theta_t^2) \\ &= 1-[(1)^2(1+\theta_{it})(1+\theta_{jt})/4+(0)^2(1-\theta_{it}\theta_{jt})/2 \\ &\quad +(-1)^2(1-\theta_{it})(1-\theta_{jt})/4] \\ &= (1-\theta_{it}\theta_{jt})/2\end{aligned}$$

The expected genotypic value of the progeny is

$$E\sum_t^q [d_t\theta_t + f_t(1-\theta_t^2)] = [d_t E(\theta_t) + f_t E(1-\theta_t^2)]$$

$$= \sum_t^q [d_t(\theta_{it}+\theta_{jt}) + f_t(1-\theta_{it}\theta_{jt}]/2$$

(d) The expected genotypic values for selfing and crossbred in the diallel crosses are :

$$\left.\begin{aligned}Y_{ii} &= \sum_t^q [2d_t\theta_{it} + f_t(1-\theta_{it}^2]/2 \\ Y_{ij} &= \sum_t^q [d_t(\theta_{it}+\theta_{jt}) + f_t(1-\theta_{it}\theta_{jt})]/2, \quad (1 \neq j)\end{aligned}\right\} \cdots\cdots (2)$$

In the homozygous diallel the selfings are identical with the parents. This is not so, however, in the heterozygous diallel. The heterozygous×heterozygous selfings show a fall in expected genotypic value equal to $\sum_t^q f_t/2$, as can be proved easily with a one-gene, two-allele model. Thus the selfings in the heterozygous diallel may be regarded as fictitious parents.

Let the frequencies of two allels L and t at the t^{th} locus be deoted by u_t and $v_t (u_t + v_t = 1)$, respectively.

Hence :

$$\left.\begin{aligned}E(\theta_{it}) &= u_t - v_t \\ E(\theta_{it}^2) &= u_t^2 + v_t^2 \\ E(\theta_{it}\theta_{jt}) &= (u_t - v_t)^2 \\ V(\theta_{it}) &= 2u_t v_t \\ V(\theta_{it}^2) &= 2u_t v_t (u_t^2 + v_t^2) \\ V(\theta_{it}\theta_{jt}) &= 4u_t v_t (u_t^2 + v_t^2) - 4u_t^2 v_t^2 \\ Cov(\theta_{it}, \theta_{jt}) &= 0\end{aligned}\right.$$

$$\begin{aligned}
&Cov(\theta_{it}, \theta_{it}^2)=2u_tv_t(u_t-v_t)\\
&Cov(\theta_{it}, \theta_{it}\theta_{jt})=2u_tv_t(u_t-v_t)\\
&Cov(\theta_{it}, \theta_{i't}\theta_{jt})=0\\
&Cov(\theta_{it}, \theta_{jt}^2)=0\\
&Cov(\theta_{it}^2, \theta_{jt}^2)=0\\
&Cov(\theta_{it}^2, \theta_{it}\theta_{jt})=2u_tv_t(u_t-v_t)^2\\
&Cov(\theta_{it}\theta_{jt}, \theta_{it}\theta_{jt})=2u_tv_t(u_t-v_t)^2\\
&Cov(\theta_{it}\theta_{jt}, \theta_{i't}\theta_{j't})=0
\end{aligned} \quad \cdots\cdots (3)$$

By applying the expectations in (3), we have :

$$\begin{aligned}
&\mu_0=E(Y_{ii})=\sum_t^q[d_t(u_t-v_t)+f_tu_tv_t]\\
&\mu_1=E(Y_{ij})=\sum_t^q[d_t(u_t-v_t)+2f_tu_tv_t]\\
&g_i=E(Y_{it})-\mu_1=\sum_t^q[d_t-f_t(u_t-v_t)][\theta_{it}-(u_t-v_t)]/2\\
&z_{ii}=Y_{ii}-\mu_0-2g_i\\
&\quad=\sum_t^q[2f_t(u_t-v_t)\theta_{it}+f_t\theta_{it}^2-f_t+6f_tu_tv_t]/2\\
&s_{ij}=Y_{it}-\mu_1-g_i-g_j\\
&\quad=\sum_t^q[f_t[u_t-v_t)\theta_{it}+f_t(u_t-v_t)\theta_{jt}-f_t\theta_{it}\theta_{jt}-f_t\\
&\qquad+4f_tu_tv_t]/2
\end{aligned} \quad \cdots\cdots (4)$$

The genotypic models in (2) can therefore be vritten as :

$$\begin{aligned}
&Y_{ij}=\mu_0+2g_i+z_{ii}\\
&Y_{ij}=\mu_1+g_i+g_j+s_{ij},\quad (i\#j)
\end{aligned} \quad \cdots\cdots (5)$$

Where :

μ_0 = population mean of the selfings.

μ_1 = population mean of the crossbreds.

$g_i(g_j)$ = general combining ability effect for the i^{th} (j^{th}) parent.

z_{ij} = remaining discrepancy in the i^{th} selfing.

s_{ij} = specific combining ability effect for the cross between the i^{th} and j^{th} parents such that $s_{ij}=s_{ji}$.

It should be pointed out that, by constructing seperate models for selfings and crossbreds, g_i is general combining ability as defined by Sprague and Tatum (1942). Also the s_{ij} fits their definition of specific combining ability, for they defined these effects as deviations from the mean of the F_1's.

Define five genetic components of variation similar to those used by Hayman[1] (1954a) as

$$\left.\begin{aligned} D &= 2\sum_{t}^{q} u_t v_t d_t^2 \\ H_1 &= 2\sum_{t}^{q} u_t v_t (u_t^2 + v_t^2) f_t^2 \\ H_2 &= 4\sum_{t}^{q} u_t^2 v_t^2 f_t^2 \\ F &= 4\sum_{t}^{q} u_t v_t (u_t - v_t) d_t f_t \\ h &= \sum_{t}^{q} u_t v_t f_t \end{aligned}\right\} \quad \cdots\cdots (6)$$

From (3), (4) and (6), it can be shown, after some afgebraic simplifications, that :

$$\left.\begin{aligned} &E(g_i) = E(z_{ii}) = E(s_{ij}) = 0 \\ &\mu_1 - \mu_0 = h \\ &(\mu_1 - \mu_0)^2 = h^2 \\ &V(g_i) = \sigma_g^2 = (D + H_1 - H_2 - F)/4 \\ &V(z_{ii}) = \sigma_z^2 = H_1/4 \\ &Cov(g_i, z_{ii}) = \sigma_{gz} = -(H_1 - H_2)/4 + F/8 \\ &V(s_{ij}) = \sigma_z^2 = H_2/4 \end{aligned}\right\} \quad \cdots\cdots (7)$$

All other covariances are zero.

It is obvious that h, D, H_1, H_2, and F are a set of linear transformations of $\mu_1 - \mu_0$, σ_g^2, σ_z^2, ρ_{gz} and σ_s^2 as mentioned before.

It is seen from (1) that the genotypic value of the s^{th} individual in a random mating population can be expressed by

$$Y_s = \sum_{t}^{q} [d_t \theta_{st} + f_t (1 - \theta^2_{st})].$$

Let the average effect of the t^{th} gene substitution be denoted by

$$\alpha_t = d_t - f_t (u_t - v_t), \quad \text{(Falconer, 1981)}$$

then the breeding value and the dominance deviation of the s^{th} individual can be expressed by

$$\begin{aligned} b_s &= \sum_{t}^{q} [(\theta_{st} - 1) u_t \alpha_t + (\theta_{st} + 1) v_t \alpha_t] \\ &= \sum_{t}^{q} \alpha_t [\theta_{st} - (u_t - v_t)] \end{aligned}$$

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[1]The five components (h, D, H_1, H_2 and F) defined here are not same as those (h', D', H_1', H_2' and F') defined by Hayman (1954a). The relationship between these two sets of components is :

$h' = 4h$, $D' = 2D$, $H_1' = 2(H_1 + H_2)$, $H_2' = 4H_2$, $F' = 2F$.

and

$$d_s=[Y_s-E(Y_s)]-b_s$$
$$=\sum_t^q f_t[2u_tv_t+(u_t-v_t)\theta_{st}-\theta^2_{st}]$$

respectively.

By applying (3) and (6), we have

$$\left.\begin{aligned} V(b_s)&=\sigma_a^2=D+H_1-H_2-F\\ V(d_s)&=\sigma_d^2=H_2\\ Cov(b_s,\ d_s)&=0\end{aligned}\right\} \quad \cdots\cdots (8)$$

Where σ_a^2 and σ_d^2 are the additive and dominance variances respectively. From (7) and (8), we have derived the relations that:

$$\left.\begin{aligned} \sigma_a^2&=4\sigma_g^2\\ \sigma_d^2&=4\sigma_s^2\end{aligned}\right\} \quad \cdots\cdots (9)$$

This result (9) is to be distinguished from that of a homozygous diallel. In a homozygous diallel $\sigma_a^2=2\sigma_g^2$ and $\sigma_d^2=\sigma_s^2$.

Genetic Constitution of Sampled Population

The genetic components of variation can be estimated from the proposed models. Certain properties of the population under investigation can then be investigated in the following manner.

(a) Mean level of dominance

Mean level of dominance can be estimated by the expression

$$\sqrt{(H_1+H_2)/D.}$$

This reduces to

$$\sqrt{2\Sigma u_tv_tf_t^2/2\Sigma u_tv_td_t^2}$$

which becomes $\bar{f}/\bar{d}$ if the q loci have equal effects. Whereas if the loci have unequal effects, the estimated dominace ratio is automatically weighted in favor of those with largest effects and those with allelic frequency nearset to 0.5. As unequal effects may be the usual case and we can only deal with the combined effects of all the loci, the loci with greater effects will contribute more information to the weighted estimate than the loci at low frequency and/or with small effects (Dickinson and Jinks, 1956).

In addition to the above, with similar reasoning

$$\sqrt{H_2/D^2}=\sqrt{4\Sigma u_t^2v_t^2f_t^2/4\Sigma u_t^2v_t^2d_t^4}=\bar{f}/\bar{d}^2$$

These estimates of $\bar{f}/\bar{d}$ and $\bar{f}/\bar{d}^2$ can be solved simultaneously for $\bar{f}$ and $\bar{d}$.

(b) Average level of heterozygosity and allelic frequencies The expression

$$H_2/(H_1+H_2)$$

gives a weighted estimate of the average level of heterozygosity. This reduced to

$$4\Sigma u_t^2 v_t^2 f_t^2 / 2\Sigma u_t v_t f_t^2$$

which becomes $2\bar{u}\bar{v}$ if the q loci have equal effects. Whereas if the loci have unequal effects, this estimate will be the average level of the heterozygosity at loci showing dominance since the ratio is confined to terms in f^2, The loci showing greater dominance will also contribute relatively more to this weighted estimate than those showing little dominance. In addition, this estimate will be weighted in favor of loci with allelic frequency nearest to 0.5. Hence biased estimation of the average heterozygosity will occur whenever the level of heterozygosity differes from one locus to another which may in reality be the situation. In addition to the above. $\bar{u}+\bar{v}=1$. These equations of $\bar{u}$ and $\bar{v}$ can be solved simultaneously for $\bar{u}$ and $\bar{v}$.

(c) Number of loci showing diminance

The expression

$$4h^2/H_2 = 4(\Sigma u_t v_t f_t)^2 / 4\Sigma u_t^2 v_t^2 f_t^2$$

gives an estimate of the number of loci showing dominance provided that certain assumptions are made. Assuming that q′ loci involved exhibit unidirectional dominance and have equal effects, the expression becomes

$$4(\Sigma u_t v_t f_t)^2 / 4\Sigma u_t^2 v_t^2 f_t^2 = (q' u_t u_t f_t)^2 / q' u_t^2 v_t^2 f_t^2 = q'^2/q' = q'$$

An underestimate of q′ will occur if either or both assumptions are not valid. Thus, when all loci do not exhibit unidirectional dominance, positive and negative values of f cancel out in h, with a consequent reduction in the estimated value of q′. In addition, inequality of effects at the q′ loci will also give a lower estimate. Since the present estimate is confined to a ratio of terms in f, it obviously gives a lower bound of the number of loci showing doming dominande and is biased in favor of those of greater dominance (Dickinson and Jinks 1956).

(d) Dominance level over loci

An estimate of this is given by the expression

$$F/2\sqrt{D(H_1 - H_2)}$$

provided that certain assumptions are made. If the ratio of f to d and the difference of u and v are constants over all loci, then the absolute value of this expression will be 1. However, if either or both assumptions are not valid, then the absolute value of this expression will be close to 0. Hence, regardless of the dominance level this ratio can be used to measure the extent to which the dominance level varies from one locus to another (Mather and Jinks, 1971).

Conclusion

Development of an effective breeding program for a given species depends upon knowledge of the kinds and magnitudes of variability which contribute to differences among individuals. Additive, dominance and epistatic genetic variances are particularly important in understanding the inheritance mechanisms of the economically important

characters.These genetic variances can only be estimated from covariance between relatives (e. g., between parent and offspring, between full-sibs, between half-sibs, etc.). Covariances between relatives can only be estimated from experiments based on controlled crosses with specific mating designs. Due to restrictions of time, space, cost and biological limitations, some of the mating designs for estimating genetic variances are confined to those dealing with one common generation of parental materials originating as a random sample from a single random population. Nested, factorial and diallel designs are well known and are commonly used. All of the above designs permit estimates of covariance between full-sibs and between half-sibs which can be interpreted in terms of genetic variances of the sampled population. Although diallel designs are relatively difficult to use in some breeding program, they should be particularly useful when a complete evaluation of variance components is desired including those due to selfing, maternal and reciprocal effects.

Genetic variances are estimated from the covariances between relatives which in turn are estimated from the functions of variance components. Therefore efficient estimates of genetic variances depends entirely on efficient estimates of variance components.

Constructing seperate models for selfings and crossbreds besed on their genotypic values, the genetic components analysis of Hayman and the combining ability analysis of Griffing can be combined to provide estimates of various genetic parameters of the sampled population from a heterozyous diallel.

In practice, estimates of the genetic components of variation and other parameters derived from them may not be very precise. This is not only because of the lack of knowledge about the true genetic mechanisms that control the inheritance of the traits studied but also because of the sizable amount of of environmental variation usually associated with the measurements themselves. Interpretations and applications of these genetic parameters should be carefully made. Different traits may need different models to explain their variation and incompatible results may indicate the incorrectness of the model used.

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異質型全互交之成分分析[1]

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摘　　要

本文依據異質型全互交自交後代與雜交後代不同基因型值分別建立其數學模式以證明在全互交分析上 Hayman 氏之遺傳成分分析法與 Griffing 氏之組合力分析法基本上爲等義的，且綜合此二種分析法來分析異質型全互交以對取樣族羣提供各項遺傳介量之估值。文中亦指出異質型全互交與同質型全互交在遺傳介量估算上之差異。

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柑桔葉片同功異構酶之研究

I. 本省重要柑桔葉片之電泳分析與葉齡對分析結果之影響[1]

吳明哲　卓俊銘[2]

摘要：本研究以目前本省最重要的六個柑桔栽培種—椪柑、桶柑、柳橙、檸檬、葡萄柚和柚子等二年生植株之葉片爲材料，藉電泳分離技術，探討 Peroxidase, Esterase, Superoxide dismutase 與 Glutamate oxaloacetate transaminase 等四種酵素之同功異構酶基因型之差異，做爲將來育種上珠心胚苗與有性胚苗鑑定之依據，以提高育種效率。此外，由於不同成熟度葉片之生理狀況可能不同，本研究亦同時探討葉齡對於電泳分離結果之可能影響。

試驗結果顯示，Peroxidase 在 Rf 0.35, 0.37 之條帶，Esterase 在 Rf 0.3 之條帶，Superoxide dismutase 在 Rf 0.29, 0.32, 0.36, 0.39 之條帶均有明顯之種間遺傳差異存在，可做爲鑑別之依據。Glutamate oxaloacetate transaminase 電泳分離結果，可明顯分出兩羣獨立基因座（GOT-1 和 GOT-2）所控制之同功異構酶，除椪柑與桶柑之類型相同外，其餘受測柑桔種間均存有不同之類型。由於受測柑桔種間有此種明顯之差異存在，且由於電泳方法的建立，具有操作簡單，快速的優點，此等技術在未來本省柑桔雜交育種上，具有實際應用於珠心胚苗與有性胚苗早期鑑定之價值。

不同葉齡的電泳分離結果顯示，Peroxidase 與 Superoxide dismutase 以完全成熟葉，Esterase 以嫩葉，Glutamate oxaloacetate transaminase 以不完全成熟葉爲最清晰完整。此外，本研究結果顯示桶柑之 Esterase 同功異構酶基因型介於椪柑與柳橙之間，葡萄柚之 Glutamate oxaloacetate transaminase 同功異構酶基因型介於柚子與柳橙之間。彼等種間之血緣關係，有待進一步之探討。

多胚性（polyembryony）在柑桔種中是極普遍的現象[8,17]，由於其有性胚苗與珠心胚苗通常無法從外觀上加以分辨，如果沒有早期區別有性胚苗與珠心胚苗的方法，在柑桔育種上，勢必同時需培育大量珠心胚苗，並且需等到多年後開花結實時才能分辨[19]。長久以來，珠心胚苗與有性胚苗的分辨方法即爲柑桔育種家所極欲突破的技術。例如利用枳殼的三葉性狀，柚類的大翼葉或檸檬的紅色頂梢等具有顯性遺傳之性狀，而採用枳殼、柚類或檸檬作爲父本，使其有性胚苗在外觀上帶有父本特徵，可和珠心胚苗明確區分；又如利用單胚性品種作母本，免除實生苗中含有珠心胚苗的困擾。凡此皆不失爲有效分辨珠心胚苗與有性胚苗的方法，有助於提高育種效率。然而此種選擇具有特殊遺傳性狀之父本或母本的方法，却嚴重地限制了雜交親本的利用價值，實乃一大缺失。

自從1970年以來，國外逐漸開發出運用電泳（gel electrophoresis）技術以分離同功異構酶（isoenzyme）的方法，以應用於柑桔有性胚苗與珠心胚苗的早期鑑別工作上[5,9,10,11,20,22]。Torres 等人[21]認爲有些柑桔同功異構酶（isoenzyme）是受對等顯性基因（codominant genes）所控制的

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，較少受環境影響；而且同一品種的幼株和老株之葉片中的同功異構酶均爲相同；因此極力推薦以電泳作爲鑑別柑桔有性胚苗與珠心胚苗的方法。此種方法在育種之早期（幼苗期）即可有效地利用。本研究以本省最常見的六種柑桔之葉片作材料，探討以電泳分離數種酵素之同功異構酶的方法，應用在有性胚苗與珠心胚苗之鑑別工作上的可行性。此外，亦嚐試以不同成熟度的葉片作材料，以明瞭葉片的不同生理狀況對電泳分離結果之影響。

材料與方法

本試驗以椪柑 (Citrus reticulata Var. Ponkan)、桶柑 (Tankan, a tangor?)、柳橙 (C. sinensis Var. Liuchen)、Eureka 檸檬 (C. limon Var. Eureka)、葡萄柚 (C. paradisi Var. Ruby) 和柚子 (C. grandis Var. Wentan) 等柑桔二年生植株之葉片作爲供試材料；於民國75年1月至3月間，正當春梢萌發時進行採樣。所採葉片共分三類：1）嫩葉一最近所抽新梢上之幼嫩葉片；2）不完全成熟葉一前一季枝梢上之青綠色葉片；3）完全成熟葉一前兩季枝梢之墨綠色葉片。葉片取下之後，立即以清水洗淨，用吸水紙拭乾，裝進塑膠袋中，再置入—20°C 之冷凍櫃，冷凍時間爲1天—2週。

電泳操作以聚丙烯醯胺 (polyacrylamide) 爲膠體，在直立式平板膠體之儀器 (vertical gel slab apparatus, BRL V16—2) 中進行，平板膠體之大小爲 16×20cm，厚度爲 1.5mm，每次操作四塊平板膠體，膠體之冷却使用 2°C 冷水之循環裝置。緩衝液 (buffer) 之系統採用 Ornstein, Davies[6,14] 之不連續性法 (discontinuous buffer system)，上下電泳槽之緩衝液爲 0.025M Tris, 0.192M Glycine, pH8.3。分析膠體 (resolving gel) 和層積膠體 (stacking gel) 之聚丙烯醯胺濃度分別爲7.5%和4.5%；其緩衝液則分別爲 1.5M Tris-HCl, pH8.8 和 0.5M Tris-HCl, pH6.8。使用平口老虎鉗萃取葉片之汁液，每一樣品使用 15ul 萃取液。每塊膠體使用 30mA 之電流，需時4—5小時。

所分析之酵素種類及其染色方法如下：

1）Peroxidase：0.1g O-dianisidine, 100ml 之 0.2M acetate buffer (pH5.0) 和2滴35%之 H_2O_2[4]。

2）Esterase：0.1g Fast Blue RR salt, 40ml H_2O, 10ml 之 0.2M Na_2HPO_4 (pH8.8), 50ml 之 0.2M NaH_2PO_4 (pH4.6), 20mg α-naphthyl acetate[4]。

3）Superoxide dismutase (SOD)：200mg MTT, 0.4ml TEMED, 1mg riboflavin, 200ml 之 50mM NaH_2PO_4 (pH7.5)[24]。

4）Glutamate oxaloacetate transaminase (GOT)：100mg α-Ketoglutarate, 200mg aspartic acid, 10mg pyridoxal-5-P, 150mg Fast Blue BB salt, 100ml之0.1M Tris (pH8.5)[23]。

每一種酵素之分析均重複兩次以上。

結　　果

試驗結果顯示柑桔葉片之 Peroxidase, Esterase 等之同功異構酶數目甚多，電泳分離結果之類型 (pattern) 複雜 (圖 1a, 2a)；而 Superoxide dismutase (SOD) 和 Glutamate oxaloacetate transaminase (GOT) 之同功異構酶數目少，電泳分離結果之類型較清楚 (圖 3a, 4a)，上述四種酵素之同功異構酶電泳分離結果均另以繪圖方式表示 (圖1b，2b，3b，4b)。爲便於比較起見，僅繪出明顯且種間差異顯著之具有代表性條帶 (band，每一條帶代表一同功異構酶)，對於較不清楚或較不確定之條帶均不繪出。

圖 1a, 1b 爲供試之六種柑桔嫩葉，不完全成熟葉，完全成熟葉之 Peroxidase 電泳分離結果。

三種不同葉齡之葉片以完全成熟葉之分離結果較完整，種間之比較則以桶柑和柳橙類似(均有Rf 0.4, 0.42, 0.45, 0.49, 0.63等之條帶），葡萄柚和柚子較類似（均有 Rf 0.35, 0.4, 0.42, 0.45, 0.57等之條帶)，椪柑(有 Rf 0.37, 0.4, 0.42, 0.45, 0.57, 0.81 等之條帶)，和檸檬（有 Rf 0.35, 0.37, 0.4, 0.42, 0.45, 0.49, 0.54, 0.57, 0.63 等之條帶）則較爲特殊。

Esterase 之分析結果以嫩葉最爲清楚和完整（圖 2a, 2b）。桶柑、柳橙、葡萄柚、柚子等均具有 Rf 0.26, 0.3, 0.33 等之條帶，椪柑和檸檬只有 Rf 0.26, 0.33 等之條帶。椪柑、桶柑和檸檬具有 Rf 0.38, 0.4 之條帶，柳橙、葡萄柚和柚子則均缺乏或模糊不清。所有材料中，僅檸檬具有 Rf 0.58, 0.62. 0.65 之條帶。

SOD 是負面染色 (negative staining) 的一種酵素，圖 3a, 3b 顯示，經電泳分離出來的結果，似乎以完全成熟葉最爲完整。以 Rf 0.3, 0.32, 0.36, 0.39之條帶而言，葡萄柚和柚子類型最爲相似（均有 Rf 0.3, 0.32 之條帶），檸檬除了 Rf 0.3, 0.32之條帶外，另具有 Rf 0.36之條帶。椪柑僅有 Rf 0.32 之條帶，桶柑具有 Rf 0.29, 0.36 之條帶，柳橙則具有 Rf 0.36, 0.39 之條帶。

GOT（圖 4a, 4b）是本試驗中所測之酵素中同功異構酶數目最少，電泳分離結果最單純明瞭，且遺傳背景已經了解的酵素，根據 Torres 等人之報告[21]，Rf 0.21, 0.24, 0.28之條帶應屬同一基因座 (GOT-1)，Rf 0.35, 0.37, 0.39, 0.43 之條帶屬另一基因座 (GOT-2)。供試之六種柑桔中除葡萄柚外，不同葉齡之葉片電泳分離結果均相同，葡萄柚之嫩葉和完全成熟葉 Rf 0.21, 0.24之條帶則均模糊不清。椪柑和桶柑之電泳分離結果相同（均有 Rf 0.21, 0.39, 0.43 之條帶）。和椪柑、桶柑比較，柳橙則在GOT-2 缺少 Rf 0.43之條帶。檸檬在 GOT-1 有 Rf 0.21, 0.24, 0.28之條帶，在 GOT-2 有 Rf 0.35, 0.37, 0.39之條帶，葡萄柚雖有 Rf 0.21, 0.24, 0.28之條帶，在 GOT-2 却僅有 Rf 0.39之條帶，柚子則在 GOT-1 僅有 Rf 0.28之條帶，在 GOT-2 僅有0.39之條帶。

結　　論

由圖1，2，3，4可見，同一柑桔種內，不同葉齡之材料，在每一種所測試之酵素中，所得電泳分離之同功異構酶類型均相同，然而其條帶數目與清晰度有時因葉齡而異。Peroxidase 與 SOD 之電泳結果以完全成熟葉（圖1，3），Esterase 以嫩葉（圖2），GOT 則以不完全成熟葉（圖4）爲最清晰完整。此種現象可能係由於葉片生理狀況之不同而影響酵素之活性[12,13]。根據Torres 等人之看法[21]，同一栽培種的酵素之同功異構酶類型並不受樹齡影響，認爲電泳分析可作爲早期鑑別柑桔珠心胚苗與有性胚苗之依據。而本試驗結果顯示柑桔葉齡有時會影響同功異構酶電泳分離條帶之數目與清晰度，故對分析樣品之葉齡應愼加選擇，方可獲得正確之鑑定。

除葉齡之因素外，由於電泳分離條帶之數目與清晰度與同功異構酶之有效含量有關[16]，因此材料萃取方法亦可能影響試驗結果。本試驗之材料僅以最簡單之方法萃取，而且未經酵素純化過程，電泳分離結果難免受到一些材料本身即已存在之化合物，如酚類化合物 (phenolic compounds) 等之影響。儘管如此，圖1—4之結果確能顯示不同柑種之酵素中，有不少顯著而試驗重覆相當一致之同功異構酶，可做爲鑑別種間差異之遺傳指標 (genetic markers)。因此，本試驗所採用之材料處理方法，雖省略繁雜之酵素純化過程，然却可在大量雜交後代之鑑定上，達到快速，簡單而且正確之實用目的。

圖1所示之 Peroxidase 電泳分離結果，檸檬、葡萄柚、柚子具有 Rf 0.35 之條帶，而椪柑、桶柑、柳橙無，椪柑、檸檬具有 Rf 0.37 之條帶，而其餘四種並無，因此 Rf 0.35, 037 之條帶，似可成爲鑑別種間差異之遺傳指標。圖2所示 Esterase 之結果，桶柑、柳橙、葡萄柚、柚子均具有 Rf 0.3 之條帶，而椪柑、檸檬則無，Rf 0.3 之條帶亦似可成爲鑑別種間差異的遺傳指標。然而 Peroxidase 和 Esterase 之同功異構酶數目甚多，電泳分離之結果甚爲複雜，從本試驗結果無法辨識出這兩種同功異構酶是由多少個基因座 (gene loci) 所控制，同一基因座有多少個對偶基因 (

alleles），以及某一個同功異構酶是由多少個小分子（subunit）所組成[16]。Soost 等人[18]認爲 Peroxidase 和 Esterase 之電泳結果雖然相當複雜，無法做遺傳分析，可是如果電泳結果是相當一致的，種間遺傳上之差異仍可用來鑑定有性胚苗，只是有些有性胚苗有時會出現和母本與珠心胚苗相同之電泳結果，本試驗之結果似可印證此一論點。

圖3所示之 SOD 結果顯示 Rf 0.29, 0.32, 0.36, 0.39之條帶可成爲種間差異之遺傳指標，此外 Rf 0.56 之條帶爲檸檬所獨具，其餘五個柑種均告闕如，因此該條帶似可成爲檸檬遺傳特性之指標。

GOT-1 僅有兩個對偶基因 F 和 S，每一同功異構酶由兩個小分子組成[21]，本試驗結果顯示（圖4）椪柑、桶柑、柳橙在 GOT-1 各僅有一條帶且在相同位置，其基因型應爲 SS，柚子在 GOT-1 亦僅有一條帶，然在不同位置，其基因型應爲 FF，檸檬與葡萄柚有三條帶且彼此之距離相等，其基因型應爲 FS（兩個條帶爲同質雙元體 FF 和 SS，另一個爲異質雙元體 FS，電泳移動速率介於 FF 和 SS 之間）。GOT-2 在本試驗之六個柑桔種中出現三個對偶基因 F、M、S，此基因控制之同功異構酶到底是由一個小分子或兩個小分子組成仍然未知，然而很可能是由兩個小分子組成而且 F 和 M 無法合成異質雙元體（heterodimer），椪柑與桶柑各均僅有兩個條帶，依此推論其基因型是 FM。檸檬在 GOT-2 則具有三個等距之條帶，依此推論，其基因型應爲 MS，且其 M 和 S 可合成異質雙元體(兩個同質雙元體 MM 和 SS，另一個爲異質雙元體 MS，電泳移動速率介於 MM 和 SS 之間）。Torres 等人[21]稱此爲雙元體演化成單元體或單元體演化成雙元體之過渡階段的一種現象。柳橙、葡萄柚、柚子在 GOT-2 則均僅有一條帶其基因型應爲 MM。

電泳分離同功異構酶之方法，除可應用在柑桔珠心胚苗與有性胚苗之鑑定外，亦可做爲分類研究之依據[15]。桶柑在分類上之歸屬，多年來一直懸而未決，由於其性狀介於寬皮柑類與橙類之間，一般認爲桶柑應屬於一種天然橘橙（tangor）[1,2,3,7]。本試驗所做 Esterase 電泳結果（圖2）顯示，桶柑之同功異構酶類型介於椪柑與柳橙之間（它和柳橙同具 Rf 0.26, 0.29, 0.33 之條帶，和椪柑同具 Rf 0.38, 0.4 之條帶），此結果或可做爲前人所推斷之佐證。葡萄柚一般認爲是柚子之突變種[17,25]，本試驗之 GOT 電泳結果（圖4）則顯示它具有柚子與甜橙之特性。

本試驗所用之材料皆屬本省最重要之柑桔類，將來在雜交育種上極可能作爲主要親本。本試驗結果既顯示，此等材料以電泳分析，確具有可資分辨種間差異之同功異構酶，故此項技術在未來本省柑桔雜交育種上，應可應用於珠心胚苗與有性胚苗之早期鑑定，以提高育種與選拔效率。

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圖 1. 柑桔葉片 Peroxidase 之同功異構酶電泳分離結果。1—3 爲椪柑，4—6 爲桶柑，7—9 爲柳橙，10—12 爲檸檬，13—15爲葡萄柚，16—18爲柚子。每組之第一個材料爲嫩葉，第二個材料爲不完全成熟葉，第三個材料爲完全成熟葉。Rf 0 爲分析膠體之起點。(a) 照相結果。(b) 繪圖結果。

Fig. 1. Peroxidase isoenzyme banding patterns from leaf extracts of 2-year-old citrus plants. Ponkan (Citrus reticulata) is in the lane of 1-3, Tankan (a tangor?) in the lane of 4-6, Liuchen (C. sinensis) in the lane of 7-9, lemmon(C. limon var. Eureka)in the lane of 10-12, grapefruit (C. paradisi var. Ruby) in the lane of 13-15, and wentan (C. grandis) in the lane of 16-18. The young leaf is in the first lane, the incompletely mature leaf in the second lane and the completely mature leaf in the third lane of every species. Rf 0 is the origin of the resolving gel. (a) The photographic picture. (b) The drawing picture.

圖 2. 柑桔葉片 Esterase 之同功異構酶電泳分離結果。材料之位置安排如圖 1 所述。Rf 0 爲分析膠體之起點。(a) 照相結果。(b) 繪圖結果。

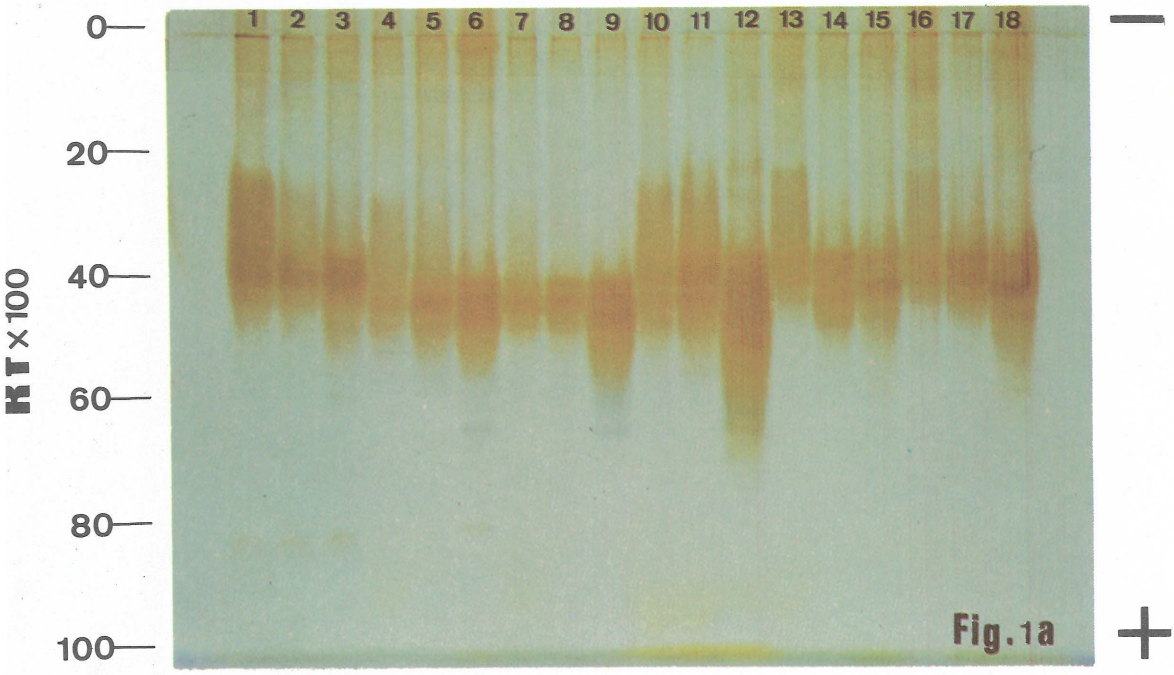
Fig. 2. Esterase isoenzyme banding patterns from leaf extracts of 2-year-old citrus plants. The arrangement of samples is as described in Fig. 1. Rf 0 is the origin of the resolving gel. (a) The photographic picture. (b) The drawing picture.

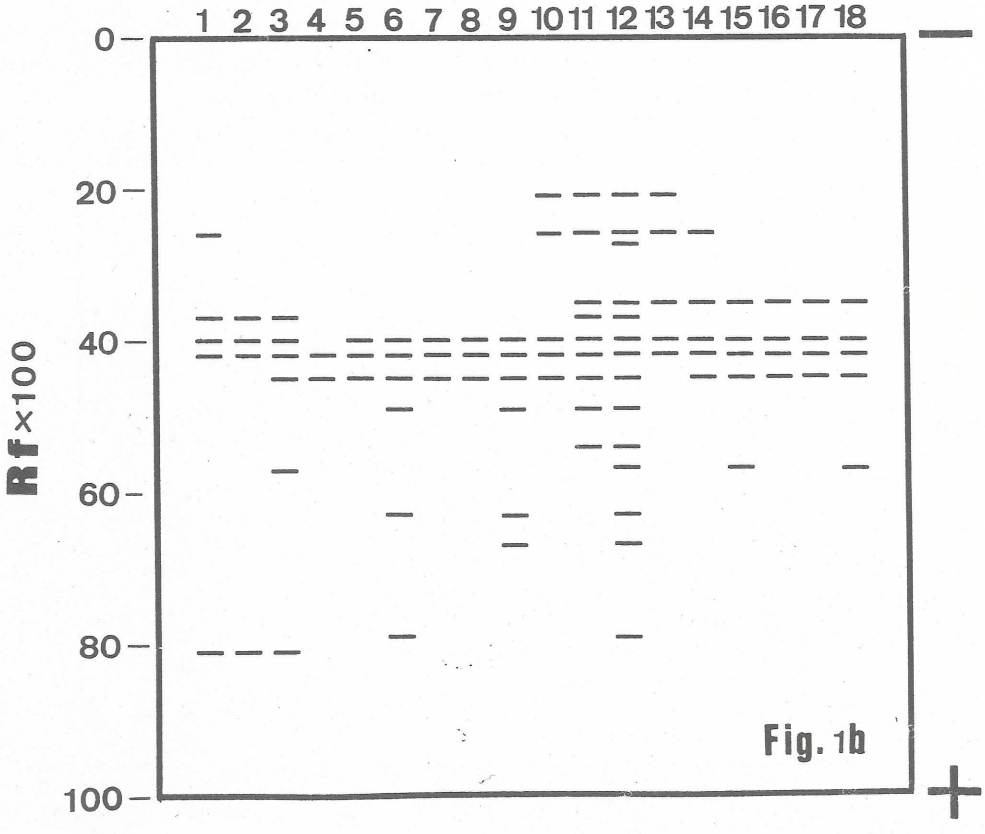
圖 3. 柑桔葉片 Superoxide dismutase (SOD) 之同功異構酶電泳分離結果。材料之位置安排如圖 1 所述。Rf 0 爲分析膠體之起點。(a) 照相結果。(b) 繪圖結果。

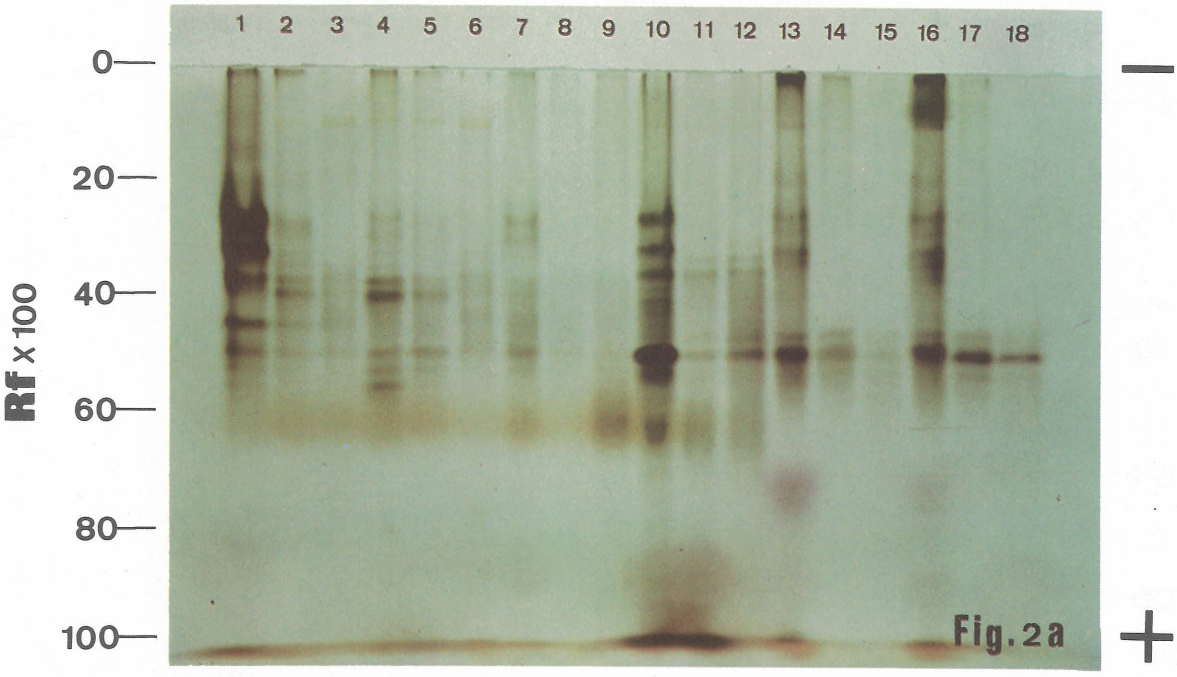
Fig. 3. Superoxide dismutase isoenzyme banding patterns from leaf extracts of 2-year-old citrus plants. The arrangement of samples is as described in Fig. 1. Rf 0 is the origin of the resolving gel. (a) The photographic picture. (b) The drawing picture.

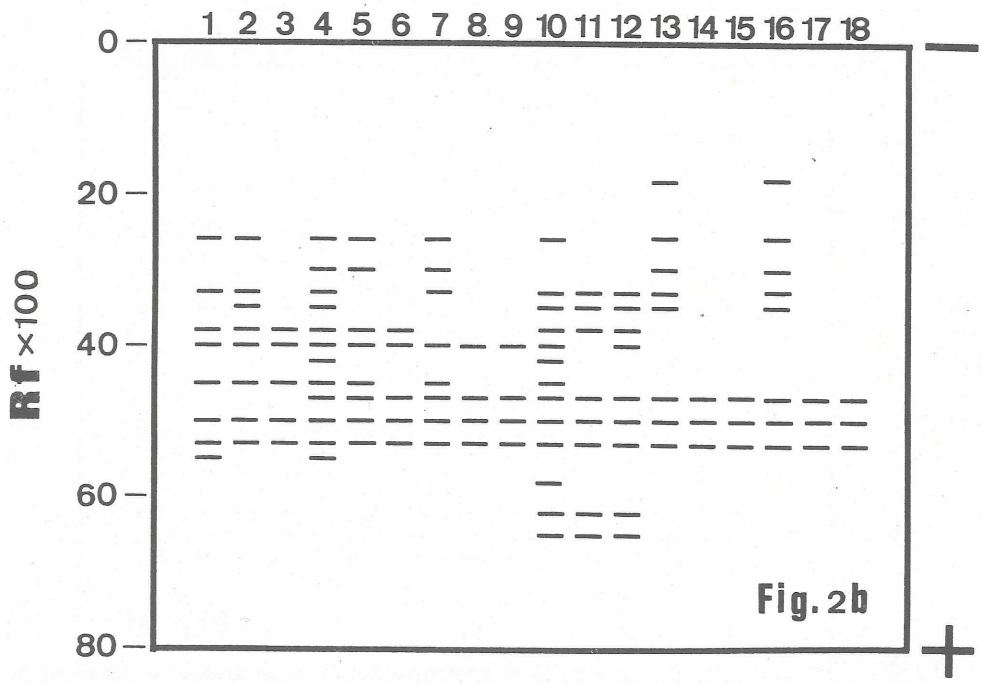
圖 4. 柑桔葉片 Glutamate oxaloacetate transaminase (GOT) 之同功異構酶電泳分離結果。材料之位置安排如圖 1 所述。Rf 0 爲分析膠體之起點。(a) 照相結果。(b) 繪圖結果。

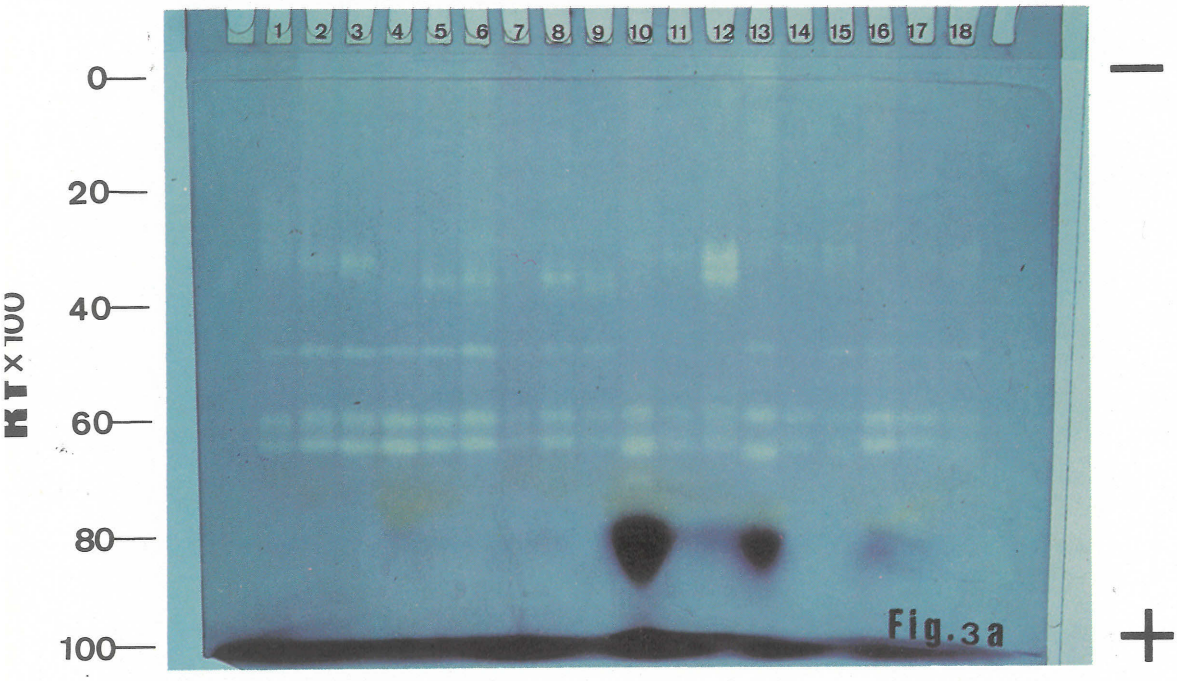
Fig. 4. Glutamate oxaloacetate transaminase isoenzyme banding patterns from leaf extracts of 2-year-old citrus plants. The arrangement of samples is as described in Fig. 1. Rf 0 is the origin of the resolving gel. (a) The photographic picture. (b) The drawing picture.

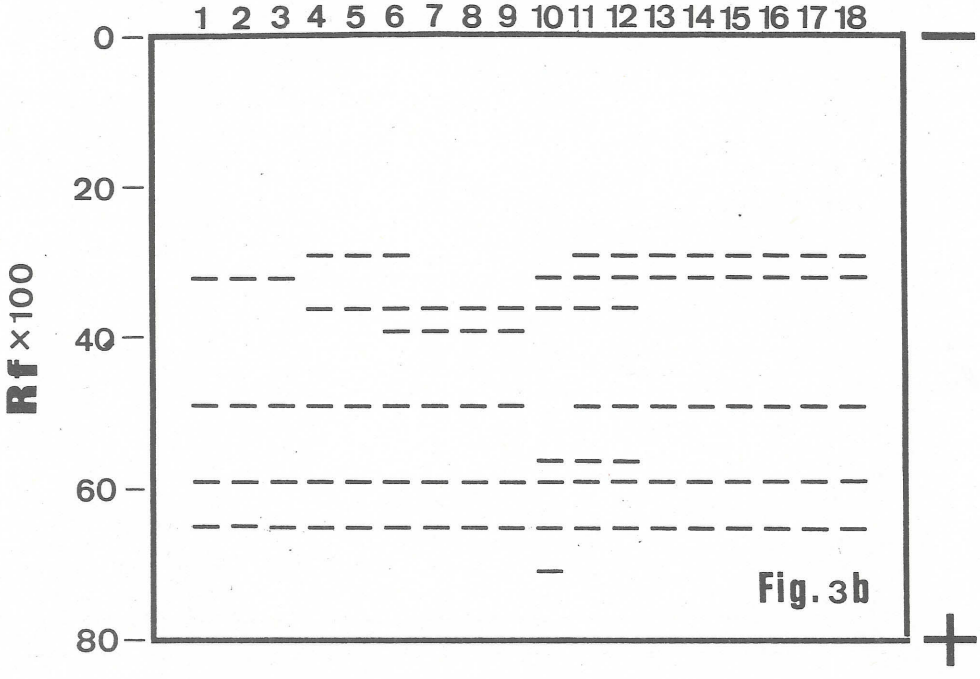

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
0
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Rf×100
−
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Fig. 1a

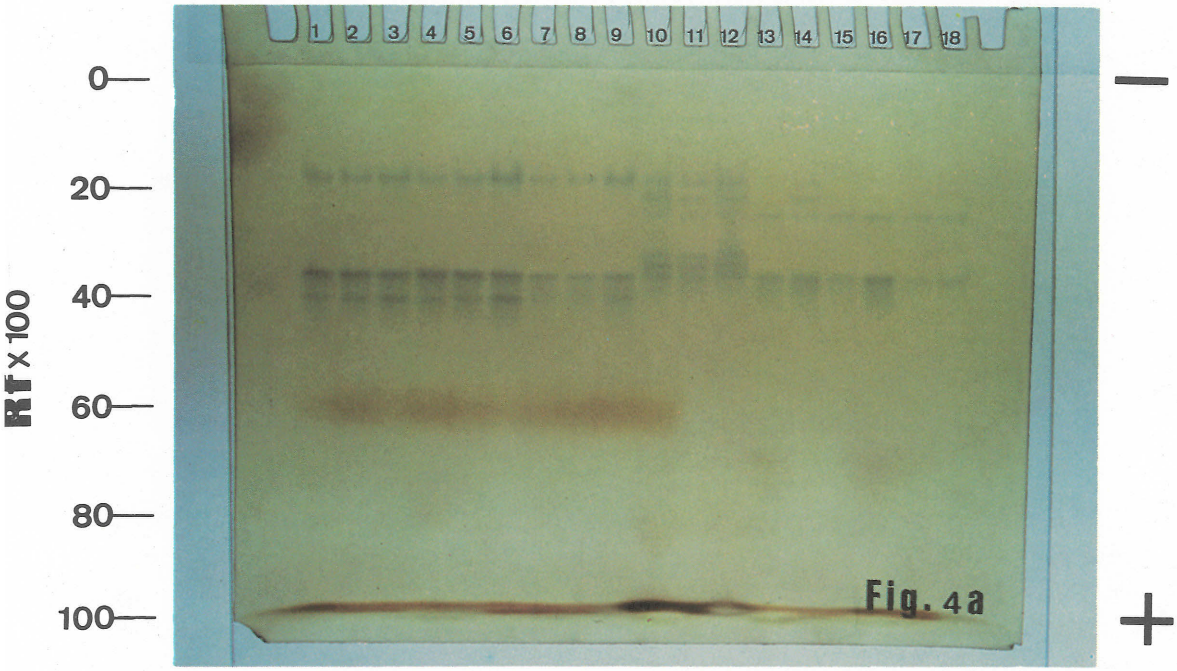

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Fig. 1b

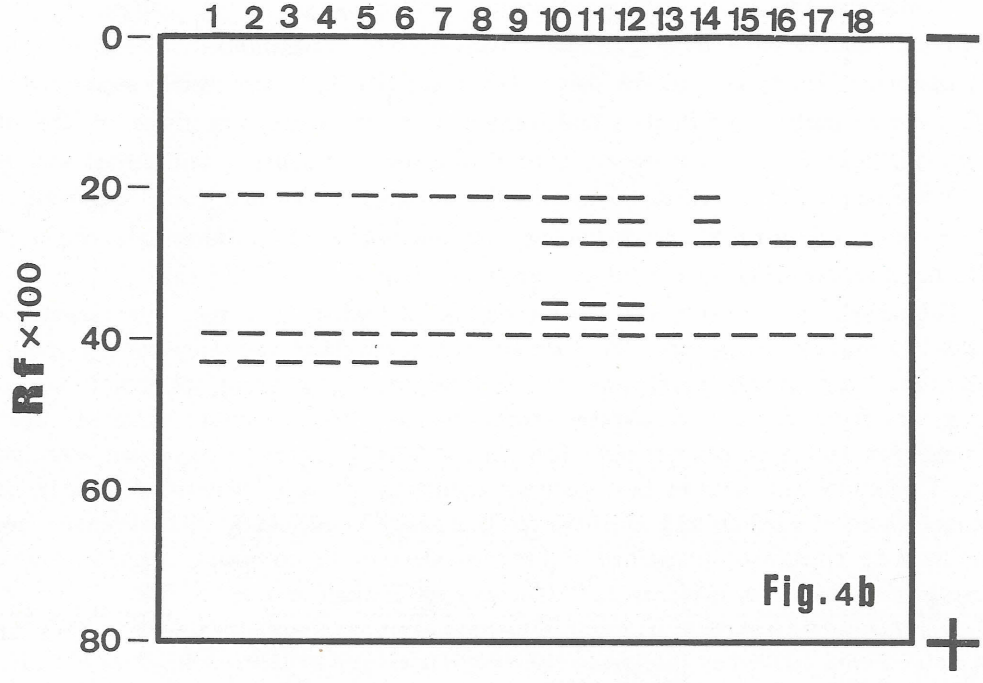

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
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Rf x100
−
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Fig. 2a


1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
0
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80
Rf x100
−
+
Fig. 2b


1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
0
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Fig. 3a


1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
0
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Rf×100
−
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Fig. 3b


1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
0
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40
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Rf × 100
−
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Fig. 4a


1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
0
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80
Rf × 100
−
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Fig. 4b

Studies on the Isoenyzmes of Citrus Leaves

I. The Gel Electrophoretic analysis of Six Important Citrus Species in Taiwan and the Effect of Leaf Age[1]

Min-Tze Wu and Jung-Ming Jwo[2]

Summary

Leaves from 2-year-old plants of six important citrus species in Taiwan…Ponkan (Citrus reticulata), Tankan (a tangor?), Liuchen (C. sinensis), Lemmon (C. Limon. var. Eureka), grapefruit (C. paradisi var. Ruby) and Wentan (C. grandis), were used as the plant materials for identification of the isoenzyme genotypes of peroxidase, esterase, superoxide dismutase and glutamate oxaloacetate transaminase. The objective of this study was to look for the genetic differences among certain citrus species. The effect of leaf age on isoenzyme banding patterns was also tested.

The results indicated that bands of Rf 0.35, 0.37 on peroxidase, band of Rf 0.3 on esterase, and bands of Rf 0.29 , 0.32, 0.36, 0.39 on superoxide dismutase could be the genetic markers for distinguishing differences among certain citrus species. From the isoenzyme banding patterns of glutamate oxaloacetate transaminase, two groups of iso enzymes controlled by two genetic loci (GOT-1 and GOT-2) were clearly separated. The GOT banding patterns of Ponkan and Tankan were the same, but those of the other 4 were different. Referring to the evidence of differences among certain citrus species in isoenzyme genotypes identified by means of the above simple and rapid electrophoretic method, it is believed that this technology can be applied to differentiate the zygotic from nucellar seedlings in the future citrus breeding work in Taiwan.

The clearness of isoenzyme banding was influenced by leaf age. Zymograms from completely mature leaves were the clearest for peroxidase and supeoxide dismutase, while those from young leaves was for esterase and those from incompletely mature leaves was for glutamate oxaloacetate transaminase . The choice of different ages of leaf samples should be emphasized when such an electrophoretic experiment was conducted. This study also showed that esterase isoenzyme banding pattern of Tankan is in between those of Ponkan and Liuchen, the glutamate oxaloacetate transaminase isoenzyme banding pattern of grapefruit in between those of Wentan and Liuchen. However, it needs more study to evidence the taxonomy of Tankan and grapefruit.

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Purification and Serology of an Isolate of Zucchini Yellow Mosaic Virus[1]

C. H. Huang, S. H. Hseu and Y. J. Chao[2]

Abstract: An isolate of zucchini yellow mosaic virus, ZYMV-7, was purified and its antiserum produced. Systemic leaves from inoculated zucchini plants taken 9-10 days after inoculation had the highest virus concentration, and were used in virus purification. Yields of purified virus estimated by spectrophotometer were 18-22 mg/100g leaf tissues. The O. D. ratio of A260/280 from several separate preparations ranged from 1.27 to 1.31. The purified virus preparation obtained from the first isopycnic centrifugation in cesium sulfate was found contaminated with host proteins, however, the contaminated materials could be removed by a second isopycnic centrifugation. The reciprocal titers of antiserum against homologous antigens in crude leaf extracts and purified virus preparations were 2048 and 4096, respectively, in ring interface precipitin tests. The titer of this antiserum against crude sap antigens was 16 in SDS-immunodiffusion tests. Antisera collected at several bleedings reacted with host constituents weakly, but the addition of 2% bovine serum albumin to the antisera or to agar medium completely removed the non-specific reactions in SDS-gel diffusion tests. Antiserum to ZYMV-7 produced precipitin bands with all 10 ZYMV isolates, i. e., ZYMV-1 to ZYMV-9 from Taiwan, and ZYMV-FL from Florida. There were no serological relationships of ZYMV-7 with WMV-1 and WMV-2 (Florida isolate). However, an antiserum to WMV-2, obtained from University of Florida, reacted with ZYMV isolates strongly but formed definite spurs with WMV-2 in SDS-gel diffusion tests, indicating that ZYMV isolates from Taiwan are different from WMV-2 Florida isolate but have some serological relations to certain types of WMV-2.
(Key words: purification, serology, zucchini yellow mosaic virus)

Introduction

More than 25 viruses, including at least 7 belonging to potyvirus group, are found naturally in cucurbits (16,22). Among them zucchini yellow mosaic virus (ZYMV) first described by Lisa et al. in 1981 from Italy is a relatively new potyvirus (15). The virus has also been reported to occur in France (11), the United States (19,22) and Lebanon

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(13). In Taiwan, cucumber mosaic virus(CMV) (4,27), watermelon mosaic virus type-1 (WMV-1) (12), cucumber green mottle mosaic virus (CGMMV) (26) and Loofah mosaic virus (LoMV) (3) have been reported infecting cucurbitaceous plants. In 1982, we observed a disease which produced severe mosaic and rugose symptoms on leaves and distortion and malformation of fruits of cucumber plants. On the basis of symptoms, host range and serological relationships, we proposed that zucchini yellow mosaic virus is the cause of the disease (9). Recently, in screening of 54 cucumber cultivars/lines for resistance to cucurbit viruses, Yang (27) found that ZYMV is the most destructive to cucumber crops.

Lisa et al. (15) have characterized and purified ZYMV. Recently, Provvidenti et al. (19) have also purified the cytoplasmic inclusion proteins from ZYMV infected plants. However, because of the tendency of the virus to aggregate, difficulties are often encountered in purifying the virus, especially for a high yield. In comparative studies, Huang and Hseu (10) found that different ZYMV isolates greatly influenced the virus yield under same purification procedure, although these isolates displayed serological identity in SDS-immunodiffusion tests (9). This paper deals with a selected ZYMV isolate which we purified and consistently gave high yields of purified virus by the procedure of Gonsalves and Ishii with some modifications (8).

Materials and Methods

Source and maintenance of the virus isolate: The ZYMV isolate used mostly in this study referred to as ZYMV-7 (9) was originally obtained from leaves of infected cucumber plants grown in the experimental field of Taiwan Agricultural Research Institute. It had passed through three serial transfers from a local lesion host, *Chenopodium amaranticolor*, to zucchini plants. The isolate produced severe mosaic and leaf distortion on zucchini, and latent infection on *Pisum sativum* 'Alaska'. It was generally maintained and propagated on zucchini plants through this study.

Determination of virus concentration in zucchini: To determine the time required for the virus to reach highest concentration in systemically infected leaves of zucchini plants, leaves were sampled from three inoculated plants at 2-day intervals. About six discs (0.5cm in diameter) were taken from each leaf by a cork borer. Then, the leaf discs were pooled, weighed, and ground in 10 volumes of 0.05M potassium phosphate buffer, pH 7.5, (w/v). The crude extract was inoculated to two *C. amaranticolor* plants for producing local lesions. The relative virus concentration in systemically infected leaves was estimated by counting the number of lesions 10-14 days after inoculation.

Purification: The purification procedure for ZYMV was a modification of that described by Gonsalves and Ishii (8) for purifying papaya ring-spot virus. Systemically infected leaves were harvested from greenhouse-grown zucchini plants 9-10 days after inoculation with ZYMV. The leaf tissue was homogenized with a Waring blendor (Model 31BL42) in 0.25M potassium phosphate buffer (2ml/g tissue), containing 0.01M disodium ethylenediaminetetraacetate (EDTA) and 0.1% Na_2SO_3, pH 7.5. Chloroform and carbon tetrachloride, each at 0.5ml/g tissue, were added slowly as the tissues were being

ground. The homogenate was centrifuged at 5,000 rpm (Hitachi RPR-12) for 5 min, and the supernatant centrifuged again at 8,000 rpm for 15 min in same rotor. PEG (polyethylene glycol, M. W. 6,000) was added to the supernatant at the rate of 8g/100ml. The mixture was stirred for 1-2 hr and was centrifuged at 10,000g for 20 min in a Hitachi RPR-16 rotor. The resulting pellets were resuspended in 0.1M potassium phosphate buffer plus 0.01M EDTA, pH 7.5, and stirred for another hour. Before the second PEG treatment (5% PEG and 0.3M NaCl), the resuspended virus was centrifuged at 4,000-5,000 rpm for 10 min to remove the host constituents. The virus was precipitated after second PEG treatment, and the pellets were finally resuspended in 0.05M potassium phosphate buffer, pH 7.5, and stirred overnight.

Upon isopycnic centrifugation, the virus suspension was mixed with 26% cesium sulfate (w/w), or with 30% cesium chloride. Centrifugation was performed at 38,000 rpm for 22-24 hr at 6°C in a Hitachi RP-65T rotor ($w^2t = 1.28 \times 10^{12}$ rad^2/s). After centrifugation, the virus zone was collected by a small pipet. The purified virus was diluted to five times its volume with phosphate buffer, and again centrifuged at 10,000g for 10 min. The virus preparation was dialyzed overnight against 0.05M phosphate buffer to remove Cs salt for spectrophotometry, or it was given another cycle of isopycnic centrifugation.

The purity and quantity of the purified virus preparations were determined by a Hitachi spectrophotometer (Model 220S). In one trial, the absorption profile was measured at 254 nm with UV monitor (Gilson LC detector, Model 111) coupled with Gilson CRP fractionator for virus sample from the second cycle of isopycnic centrifugation in Cs_2SO_4.

Production of antiserum: All antisera to ZYMV-7 were produced in one rabbit by injecting virus purified after one cycle of isopycnic centrifugation. The rabbit was given a series of four intramuscular injections at weekly intervals, and a booster at 6 wk after the final injection. The immunized rabbit was bled weekly, starting 1 wk after the last injection. Antibodies reacting with host proteins were removed by adding 2% of bovine serum albumin (BSA) (Sigma Co.) to the sera, and usually incubating the mixture overnight at 4°C. All sera were stored in the presence of 0.02% sodium azide at −20°C.

Serology: The titer of antiera was determined either by ring interface precipitin test (2), and or by SDS-immunodiffusion test (14,20) against homologous virus. Serological reactions were determined among the following ZYMV isolates: ZYMV-1 to ZYMV-9 from Taiwan (9), and ZYMV-FL (FC1119) from Florida. In addition, WMV-1 and WMV-2 (Florida isolate) were also included for the purpose of comparisons. Both ZYMV-FL and WMV-2 were kindly provided by Dr. D. E. Purcifull, University of Florida. The agar medium for immunodiffusion tests consisted of 0.8% Noble agar, 1% sodium azide and 0.3% dodecyl sulfate sodium (SDS) (14,22). In some cases 2% bovine serum albumin was incorporated into the medium to remove the non-specific reaction (4,20,23). Crude antigens were prepared from fresh leaves of inoculated zucchini plants by grinding 1ml/g tissue in distilled water, followed by adding 1ml of 3% SDS,

and filtered through cheesecloth. Generally, the whole procedure was completed within one hour.

Results

Virus concentration in zucchini: Leaf extracts prepared from systemic leaves of inoculated zucchini plants were assayed for virus concentration by inoculation to *Chenopodium amaranticolor*. The local lesions produced on *C. amaranticolor* showed that virus content increased gradually in zucchini during the first 6 days, and then it increased rapidly. A peak virus concentration was reached in systemically infected plants about 8-10 days after inoculation under the growth chamber conditions (25°C) (Fig. 1). Therefore, leaves were usually harvested at this time and used for virus purification and serological studies.

Purification: In our earlier purification attempts, virus suspension was mixed with 30% Cs_2SO_4 for isopycnic centrifugation, the virus zone appeared at about 1.5cm below the meniscus after centrifugation for 22-24 hr using Hitachi RP-65T rotor tubes. It was close to the host green components and needed a great care to collect it by a small pipet. Later, the virus suspension was mixed with 26% Cs_2SO_4. After isopycnic run the virus zone was located just below the middle of the tube and was well separate from the green materials. The purified virus was easily collected from Cs salt gradient.

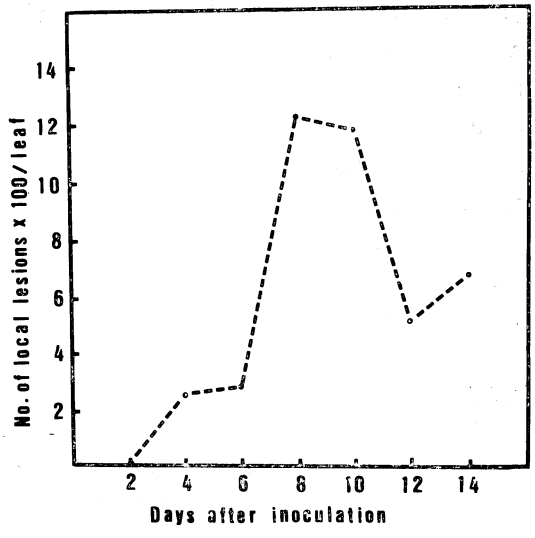


Fig. 1. Virus concentration of zucchini yellow mosaic virus in relation to the time of infection in zucchini plants under the constant temperature at 25°C The relative virus concentration was estimated by counting the local lesions produced on*Chenopodium amaranticolor*

The purity and quantity of the purified virus preparations were analyzed by spectrophotometer. Virus recovered from the first isopycnic centrifugation was found contaminated with host proteins. However, a second cycle of isopycnic centrifugation yielded highly purified virus (Fig. 2). The absorption of several separate preparations of the purified virus was lowest at 246-247 nm and highest at 260 nm, and the O. D. ratio of A260/280 ranged from 1.27 to 1.31 (uncorrected for light scattering). Assuming $E^{0.1\%}_{260}=2.4$ (21), yield of the purified virus was estimated to be 18-22mg/100g leaf tissues.

In one additional trial for comparing virus stability in cesium sulfate and cesium chloride solutions, the virus suspension was mixed with Cs salts. After isopycnic centrifugation, virus preparations from both Cs salts were inoculated to *C. amaranticolor* after dialysis. At O. $D._{259}=0.593$, the purified virus from CsCl gradient produced 1835

lesions/leaf, and at O. D.$_{260}$=0.528, that from Cs_2SO_4 gradient produced 1378 lesions/leaf. These results indicated that ZYMV-7 is stable in both Cs salts.

Serology: In ring interface precipitin tests the reciprocal titers of antiserum, taken from the third bleeding, were 2048 and 4096 against homologous antigen in crude leaf extracts and purified preparations, respectively. This antiserum reacted with healthy plant extracts at 1:4 dilution. Reacting with crude antigen in SDS-immunodiffusion gel, the antiserum had a titer of 16. There were no precipitin band formation when it was tested against healthy plant extracts. However, antisera collected from several bleedings reacted with host proteins weakly (Fig. 3, b). Generally, we added 2% BSA into the agar medium to remove the nonspecific reactions (Fig. 3, a).

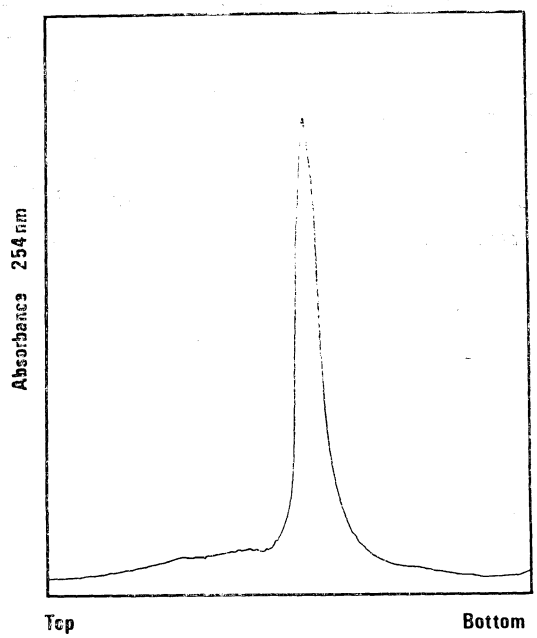


Fig. 2. Absorption profile of the purified zucchini yellow mosaic virus from the second cycle of isopycnic centrifugation in Cs_2SO_4.

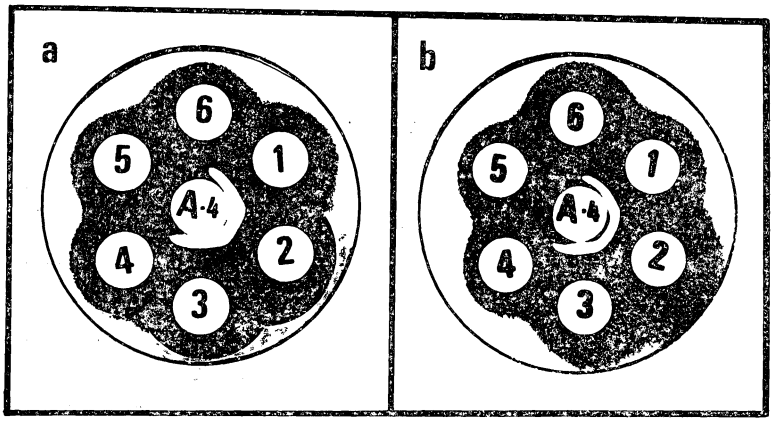


Fig. 3. Serological reactions of zucchini yellow mosaic virus (ZYMV), watermelon mosaic virus-1 (WMV-1), and watermelon mosaic virus-2 (Florida isolate) with antiserum to ZYMV-7.
The central wells (A-4) contained antiserum to ZYMV-7 collected 4 wk after the last injection. The peripheral wells contained SDS-treated antigens: 1: ZYMV-4; 2: ZYMV-FL (Florida isolate); 3: ZYMV-7; 4: WMV-2 (Florida isolate); 5: WMV-1; 6: leaf extracts from healthy zucchini plants.
The medium for pattern (b) consisted of 0.8% Noble agar, 0.3% SDS, and 1% NaN_3, whereas medium for pattern (a) consisted of the above constituents plus 2% BSA. The non-specific reaction was observed in (b), however, it disappeared in (a).

ZYMV-1 to ZYMV-9, and ZYMV-FL appeared to be serologically identical in SDS-gel diffusion tests. Except that ZYMV-2 sometimes formed a weak precipitin line, they formed strong precipitin bands without spur reaction when tested against antiserum to ZYMV-7 (Fig. 4, a, b) or antiserum to ZYMV-Italy (Fig. 4, c) (provided by Dr. V. Lisa, Italy). There were no serological relations between ZYMV-7 and WMV-1 or WMV-2 (Florida isolate) (Fig. 3). However, an antiserum to WMV-2 obtained from Dr. D. E. Purcifull which reacted with WMV-2 Florida isolate strongly, also produced precipitin bands when tested against ZYMV-4, ZYMV-7 and ZYMV-FL (Fig. 4, d). These results indicate that ZYMV isolates from Taiwan were serologically related to certain types of WMV-2.

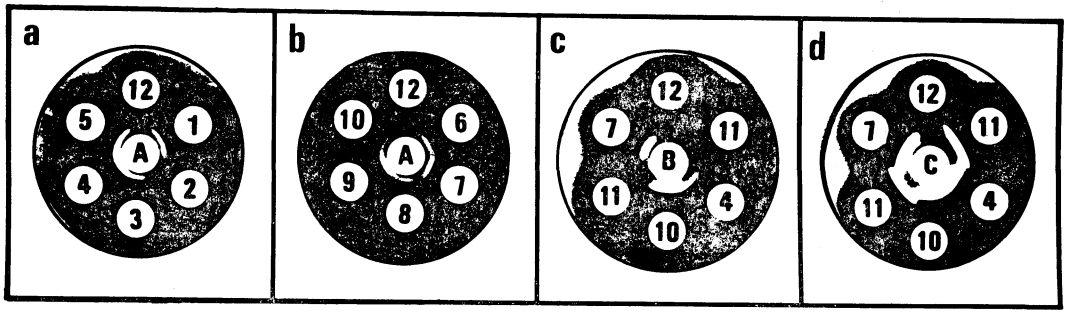


Fig. 4. Serological comparisons of zucchini yellow mosaic virus isolates and watermelon mosaic virus-2 (Florida isolate) in SDS-immunodiffusion tests.
The central wells (A) contained antiserum to ZYMV-7, (B) antiserum to ZYMV-Italy (kindly provided by Dr. V. Lisa), and (C) antiserum to WMV-2 (kindly provided by Dr. D. E. Purcifull). The peripheral wells contained SDS-treated antigens from zucchini leaves infected with: ZYMV isolates Nos. 1-9 from Taiwan; 10=ZYMV-FL (Florida isolate); 11 : WMV-2 (Florida isolate); 12=healthy zucchini squash leaves.

Discussion

Aggregation of virus particles during purification has been considered a limiting factor in obtaining higher yields of purified virus in the PVY group (8, 15, 17, 24, 25). ZYMV, a potyvirus recently reported by Lisa et al. (15), is no exception. The use of chloroform for clarification or of high molarity buffers for resuspension did not improve the yields of the virus (15). In our initial purification attempts, an isolate designated ZYMV-4 (9) was selected and the yield of purified virus was low, probably due to the losses of virus from aggregation during purification; however, when ZYMV-7 was proceeded through the same procedure, a relative high yield of purified virus was obtained, suggesting that different ZYMV isolates greatly affect the yield of virus in purification (10).

The addition of EDTA to extraction or resuspending buffers to reduce virus aggregation had been proposed (5, 8, 24, 25). Deigado-Sanchez and Grogan (5) obtained an UV absorption spectrum typical of nucleoprotein for purified virus resuspended in borate buffer plus 0.01M EDTA. Our initial experiments showed that the addition of Na-EDTA at 0.01M in purified virus preparations changed the UV spectra. It also affected the value of O. $D._{260/280}$. Therefore, while EDTA was used to prevent virus aggregation,

its effect on spectrophotometric measurement should be taken into account.

The purified virus preparations from either the first or the second isopycnic centrifugation gave an identical UV absorption curve; however, the virus preparations from one isopycnic centrifugation were still contaminated with host proteins as previously observed by others (1, 8, 24). The value of $A_{260/280}$ ranging from 1.27 to 1.31 in our studies was a little high, presumably due to contamination with host nucleic acids by the use of phosphate buffer (6, 21), but it fitted into the range of 1.2-1.37 reported for other potyviruses (7, 18).

Our ZYMV isolates and the Florida isolate ZYMV-FL appeared to belong to the same serogroup in SDS-immunodiffusion tests. They were not serologically related to WMV-1 or WMV-2 (Florida isolate). Lisa et al. (15) found that ZYMV reacted with two antisera against Italian isolates of WMV-2. Purcifull et al. (22) pointed out that antiserum to WMV-2 collected at late bleedings could reacted with ZYMV (Florida isolate 1119) antigen. In our studies, an antiserum to WMV-2, provided by Dr. D. E. Purcifull, reacted with our ZYMV isolates but formed spur reactions. This result confirmed that ZYMV isolates were serologically, but distinctly, related to certain isolates of WMV-2 as reported previously (15, 22).

Since ZYMV has not been extensively investigated in Taiwan, the collection of more ZYMV isolates from different crops and study of their serological relationships to WMV-2 are necessary. ZYMV has been reported to be the most destructive virus to cucumber plants (27); breeding programs designed to develop ZYMV-resistant varieties should evaluate cross progenies against a wide range of ZYMV isolates.

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矮南瓜黃化嵌紋病毒之純化與血清學特性之研究[1]

黃秋雄　許秀惠　趙玉珍[2]

摘　要

將 Gonsalves 及 Ishii 純化木瓜輪點病毒所使用之等密度平衡離心法 (isopycnic centrifugation)略加修改，可成功地純化矮南瓜黃化嵌紋病毒(zucchini yellow mosaic virus, ZYMV)。以接種 ZYMV-No. 7 分離株之矮南瓜爲純化材料，估計每百克病葉可獲得22毫克之純化病毒。紫外光吸收比值$A_{260/280}$約在1.27至1.31之間。所純化之病毒懸浮液適量混合輔助劑 (adjvuant) 後注射入小白兎使產生抗血清。利用界面環沈澱法，將抗血清與本病毒之粗汁液及純化之病毒反應，測得血清力價分別爲2048及4096。

本省九個ZYMV分離株及一個美國佛州ZYMV-FL分離株，以SDS-瓊脂免疫擴散法來探討各分離株血清類緣關係，結果發現所有分離株均與 ZYMV-No. 7抗血清形成明顯沈澱帶且互爲融合，證明各分離株均有相同血清類緣關係，但與 WMV-1 或 WMV-2 (佛州分離株) 無關。進一步試驗，發現本省之ZYMV 分離株與一個來自佛州大學之 WMV-2 抗血清有血清類緣關係。由是可知，本省之ZYMV 分離株異於 佛州一個 WMV-2 分離株，但與 WMV-2 部份分離株有血清類緣關係。

(關鍵字：病毒純化，血清學研究，矮南瓜黃化嵌紋病毒)。

1.臺灣省農業試驗所　研究報告第 1306 號

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中華農業研究（Jour. Agric. Res. China）35(4)：504～510（1986）

臺灣葡萄汁液傳播性黃斑病毒病之發生[1]

楊一郎　鄧汀欽[2]　陳脈紀[3]

摘要：本省田間葡萄呈現黃斑型病徵之病毒病害，於1982年在臺中地區發現。可經汁液接種感染草本檢定植物 *Chenopodium amaranticolor* 等13種，形成局部斑點（local lesion）、黃斑（yellow spot）、斑紋（mottling）及嵌紋（mosaic）等病徵。經重複單斑分離，並由其寄主病徵反應及血清反應得到五個分離株。回接到巨峰健全實生苗亦形成黃斑病徵。應用葡萄檢定品種（*Vitis* indicator），分別得到嫁接傳播及土壤傳播之分離株，並在檢定葡萄品種上，形成黃斑或葉脈黃化病徵。各病毒之檢定植物病葉材料，經以 grape fanleaf virus（GFLV), tomato ringspot virus（TmRSV), grape Bulgarian latent virus（GBLV）及grape chrome mosaic virus（GCMV）四種抗血清之ELISA測定結果，其中兩個分離株與TmRSV抗血清有正反應。經電子顯微鏡觀察結果，在病株粗汁液與組織切片中，發現直徑26—30nm之球型病毒。由以上結果顯示此兩個分離株病毒，爲 TmRSV 之系統（strain）。

葡萄病毒病害普遍發生於世界各葡萄產地，其種類甚多，已報告者有葡萄扇葉病（fanleaf）、捲葉病（leafroll）及木栓化病（corky bark）等20餘種[3,4,5,6,7,8,9,10,18]。葡萄爲無性繁殖作物，且大部分由國外引種，致帶毒苗木之擴散蔓延，形成葡萄產業之嚴重損失[3,5,7,9,11]。葡萄病毒病，在不同品種上與不同季節環境下，有不同病徵反應，亦易在高溫季節隱避病徵（masking），且多數爲土壤線蟲傳播性病毒[3,5,7,9,10,17]。田間葡萄品種，因病毒病徵隱避或生理病或元素缺乏症之混淆，致不易判別其病徵，故除扇葉病毒羣（fanleaf group viruses）爲可經由汁液傳染之病毒[3,6,7,9,19]外，其餘病毒皆需賴費時之葡萄屬檢定品種（*Vitis* indicator plants）之嫁接檢定[4,7,9,15,17]。本省葡萄病毒病害，尚少有資料可稽[2]。惟各試驗單位之品種圃及各地田間栽培品種，係由國外引進[2]，且有多數品種顯現季節性之疑似病毒病徵[2]。本試驗乃對本省葡萄黃斑型病徵之病毒病材料，所做檢定結果提出報告，藉供研究及防除本省葡萄病毒病之參考，並期提供本省葡萄病毒病之檢疫資料。

材料與方法

汁液接種：

1982年在本省臺中地區主要葡萄產地，調查田間葡萄病毒病，在栽植地區發現多數黃斑型（yellow mottle）似病毒病病株。採取其幼葉，加入5倍量之 0.1M phosphate buffer（PH 7.0內含2％ nicotine），經研磨後，以紗布過濾，以此粗汁液爲接種源，並以棉花球棒進行汁液接種在 *Chenopodium amaranticolor, Ch.quinoa, Gomphrena globosa, Petunia hybrida, Datura stramonium, Phaseolus vulgaris, Nicotiana glutinosa, N. rustica, N. debneyi, N. benthamiana, N.*

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tabacum 'Burley 21', *N. tabacum* 'Havana 425', *N. tabacum* 'Van-Hicks', *Lycopersicum esculentum* 'TN1', *Cucumis sativus* 'Pixie' 等15種草本檢定植物[3,5,6,19]。在網室內觀察其病徵發展，並進行局部病斑之單斑分離及再接種。另以健全巨峰葡萄果實採取種籽，並以消毒土壤育成健全實生苗。將上述單斑分離後所得之病斑材料，分別以汁液接種法，回接到巨峰健全實生苗。

嫁接及田間土壤傳播試驗：

1982年由美國加州大學Dr. A. C. Goheen引進無病毒葡萄屬檢定植物三品種（LN-33, Rupestris St. George, Cabernet Franc）各10支。經以消毒之碎石繁殖，再繁殖在盛有消毒土壤之植缽供試。以上述培育之無病毒葡萄屬檢定植物三品種之芽枝，分別在春季前，嫁接在新社區巨峰葡萄黃斑病株上[4,7,18]。另將該葡萄屬檢定品種27苗，分別種植在上述病株間，經兩年觀察其嫁接檢定及病株之土壤傳播結果[1,7,10,17]。

血清反應測定：

1983年分別由意大利及美國引進 grape fanleaf virus (GFLV), tomato ringspot virus (TmRSV), grape Bulgarian latent virus (GBLV) 及grape chrome mosaic virus (GCMV) 之抗血清。並以分離得之葡萄5個病毒分離株，分別接種在*N. debneyi*, *N. glutinosa*及*Cucumis sativus*上出現之病葉爲病毒材料，將該病葉加5倍量之phosphate buffer (pH7.0)，研磨後以紗布過濾之，並以ELISA方法，重複進行上述材料之測定三次，分析其血清反應結果與病毒類型[5,6,8,11]。另以上述病汁液接種於草本植物，供爲純化材料。

電子顯微鏡觀察：

以5個病毒分離株之紅葉局部斑點進行陰染法，另取*N. tabacum* 'Burley 21'上之病斑並以超薄切片法，進行電子顯微鏡（JEOL-200CX型）觀察，檢查病毒型態、大小、存在情形及分析該病毒類型[,6,7,9,10,11]。

耐稀釋度測定：

以上述5個病毒分離株之*N. debneyi*病葉，加10倍量phosphate buffer (pH 7.0) 研磨，以紗布過濾其粗汁液後，分別以其10^{-1}，10^{-2}，10^{-3}，10^{-4}，10^{-5}及10^{-6}之稀釋汁液，接種在檢定植物*Ch. amaranticolor*及*N. debneyi*，定期記錄各病徵反應，藉以明瞭各病毒分離株之耐稀釋度 (dilution end-point)，本試驗重複三次。

結果及討論

汁液接種：

供試田間葡萄黃斑病葉（圖A），經供試15種草本檢定植物之汁液接種及單斑分離接種試驗結果，分別呈現局部斑點、系統性斑紋、黃斑、嵌紋等病徵及部分無感染反應。依其在寄主植物上之反應及病徵型而分爲五個類型之病毒分離株。各分離株，分別回接到健全巨峰實生苗亦呈現黃斑型病徵。結果如表1。

依上述試驗結果，證實本省田間巨峰葡萄黃斑型病株，係汁液傳播性病毒。可使*Ch. amaranticolor*等3種植物呈現局部壞疽斑點（圖B及C）。於草、胡瓜及番茄等10種植物，形成斑紋、黃斑或嵌紋等系統性病徵（圖D、E、F及G），2種植物無感染反應。上述草本植物中，經血清反應測知，G614分離株在千日紅及 *N. benthamiana* 之病毒濃度最高，可供爲純化材料。

嫁接及田間土壤傳播試驗：

田間病株，經嫁接傳播試驗結果，在供試葡萄屬檢定品種接穗上顯現黃斑型病徵[4,7,18]。巨峰葡萄發病田之田間土壤傳播試驗結果，在觀察2年間，葡萄屬檢定品種27株中，有7株顯現葉脉黃化病徵[5,7,10,17]。由於大多數葡萄病毒，係經由土壤線蟲媒介傳播[3,5,7,9,10,17]，及根據本省葡萄線蟲調查報告[1]，並由本試驗之土壤傳播結果，推測本病毒似經由病田土壤中存在之 *Xiphinema* spp. 線蟲

表1. 葡萄黃斑病毒經汁液接種在草本檢定植物之病徵反應。

Table 1. Symptom responses of herbaceous indicator plants to virus isolates of grape yellow mottle by sap inoculation.

Indicator plants	Inocula				
	G608	G612	G614	G615	G675
Chenopodium amaranticolor	LL*	LL	LL	LL	LL
Ch. quinoa	LL	LL	LL	LL	LL
Gomphrena globosa	NL	NL	NL, Mt	NL	NL
Nicotiana glutinosa	—	—	Mt	Mt	Mt
N. tabacum 'Burley 21'	—	—	M, YS	M	M
N. tabacum 'Van-Hicks'	—	—	M	M	RS
N. tabacum 'Havana 425'	—	—	YS	YS	YS
N. debneyi	Mt	Mt	Mt	Mt, M	Mt
N. rustica	—	—	—	—	—
N. benthamiana	—	—	Mt	Mt	M
Phaseolus vulgaris	—	—	M, Mt	M	—
Cucumis sativus 'Pixie'	—	M	M	M	M
Datura stramonium	—	—	—	—	—
Petunia hybrida	—	—	VC	VC	VC
Lycopersicum esculentum 'TN1'	M	—	M	M	M

*LL : local lesion. NL : necrotic lesion. Mt : mottling. M : mosaic. YS : yellow spot. VC : vein clearing. — : none

媒介傳染[1,7,10,17]。

血清反應測定：

以上述葡萄黃斑病之5個分離株與四種抗血清（GFLV, TmRSV, GBLV, GCMV）之ELISA血清反應試驗結果如表2。

表2. 葡萄病毒各病毒分離株及健全植物材料與GFLV, TmRSV, GBLV及GCMV抗血清之ELISA反應。

Table 2. ELISA reaction of virus isolates of grape yellow mottle to antisera against GFLV, TmRSV, GBLV and GCMV.

Preparations	Antisera*			
	GFLV	TmRSV	GBLV	GCMV
G608	—**	—	—	—
G612	—	—	—	—
G614	—	+	—	—
G615	—	+	—	—
G675	—	—	—	—
Healthy				
Cucumis sativus	—	—	—	—
Nicotiana debneyi	—	—	—	—
N. glutinosa	—	—	—	—

* Antisera against grape fanleaf virus (GFLV), tomato ringspot virus (TmRSV), grape Bulgarian latent virus (GBLV) and grape chrome mosaic virus (GCMV).
**— ; negative reaction. + : positive reaction

依上述結果，供試5個病毒分離株中之G614及G615與TmRSV抗血清有正反應（表2），可知該兩個病毒分離株與TmRSV有關[5,6,8,11,17]。上述G614病毒分離株，業經以 *N. benthamiana* 大量繁殖，供爲該病毒之純化材料，並已純化該病毒。以該純化之病毒爲抗原，已製成G614分離株之抗血清。又其他三個病毒分離株尚待檢定探討。

電子顯微鏡觀察：

供試5個病毒分離株，接種在草本檢定植物所得局部斑點及系統性病徵葉片，分別經陰染法及超薄切片法之電子顯微鏡觀察結果，皆觀察到分散或成堆集狀之球型病毒顆粒，直徑爲 26—30nm。此項結果與已報告之葡萄汁液傳播性病毒型態近似[3,5,6,7,8,9,10,11]。上述材料中G614及G615分離株之病毒型態及大小（圖H及I）與已報告之 TmRSV 相近似[17]。

耐稀釋度測定：

供試葡萄5個病毒分離株病葉粗汁液之耐稀釋度，測定結果如表3。

表3. 葡萄黃斑病毒之耐稀釋度測定

Table 3. Dilution end-point assay of different virus isolates of grape yellow mottle.

preparation dilution	Virus isolates				
	G608	G612	G614	G615	G675
10^{-1}	+*	+	+	+	+
10^{-2}	+	+	+	+	+
10^{-3}	+	+	−	+	−
10^{-4}	+	+	−	−	−
10^{-5}	+	+	−	−	−
10^{-6}	−	−	−	−	−

*Infectivity of several preparations.

依上述結果，供試5個病毒分離株之耐稀釋度有差異，其中 G614及G615之耐稀釋度分別爲10^{-2}～10^{-3}與10^{-3}～10^{-4}，而與已報告之TmRSV相近似[17]。

由上述各項試驗結果顯示，本省田間葡萄黃斑病爲汁液傳播性葡萄病毒所引起。經分離得到5個病毒分離株，其中之2個分離株（G614及G615）爲與TmRSV有關之葡萄病毒系統[5,6,8,13,16,17]。另其餘3個病毒分離株，究屬何種類型之葡萄病毒，尚待研究證實。本報告首次證實本省汁液傳播性葡萄病毒之存在[2]。葡萄病毒種類甚多，因隱避病徵之潛伏病毒、各國間之引種、無性繁殖之插枝、嫁接及土壤線蟲之傳播，導致病毒之擴散與複合感染，有些迄未確定其病原，又多數需經葡萄屬檢定品種嫁接檢定，致費時且效果不明確[2,3,4,5,7,9,11,13,15,18,19]。本省葡萄病毒之檢定與研究歷史甚短，年來由國外引進多量苗木，爲防止病毒之蔓延，對檢疫制度之建立、檢定研究工作之强化及病毒抗血清之製作等，有待有關單位之合作與加速進行。

誌　謝

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圖 版 說 明：

Explanation of plates：

圖A. 巨峰葡萄田病株葉片呈現黃斑病徵。
Fig. A. Yellow mottling symptoms in grape leaf found in Kyoho vineyards.

圖B. 葡萄黃斑病之汁液接種，在紅藜呈現局部斑點病徵。
Fig. B. Local lesions symptoms in *Ch. amaranticolor* caused by virus of grape yellow mottle with sap inoculation.

圖C. 白藜呈現之局部斑點病徵。
Fig. C. Local lesons symptoms in *Ch. quinoa.*

圖D. *N. glutinosa*呈現斑紋與嵌紋病徵。
Fig. D. Mottling and pattern mosaic symptoms in *N. glutinosa.*

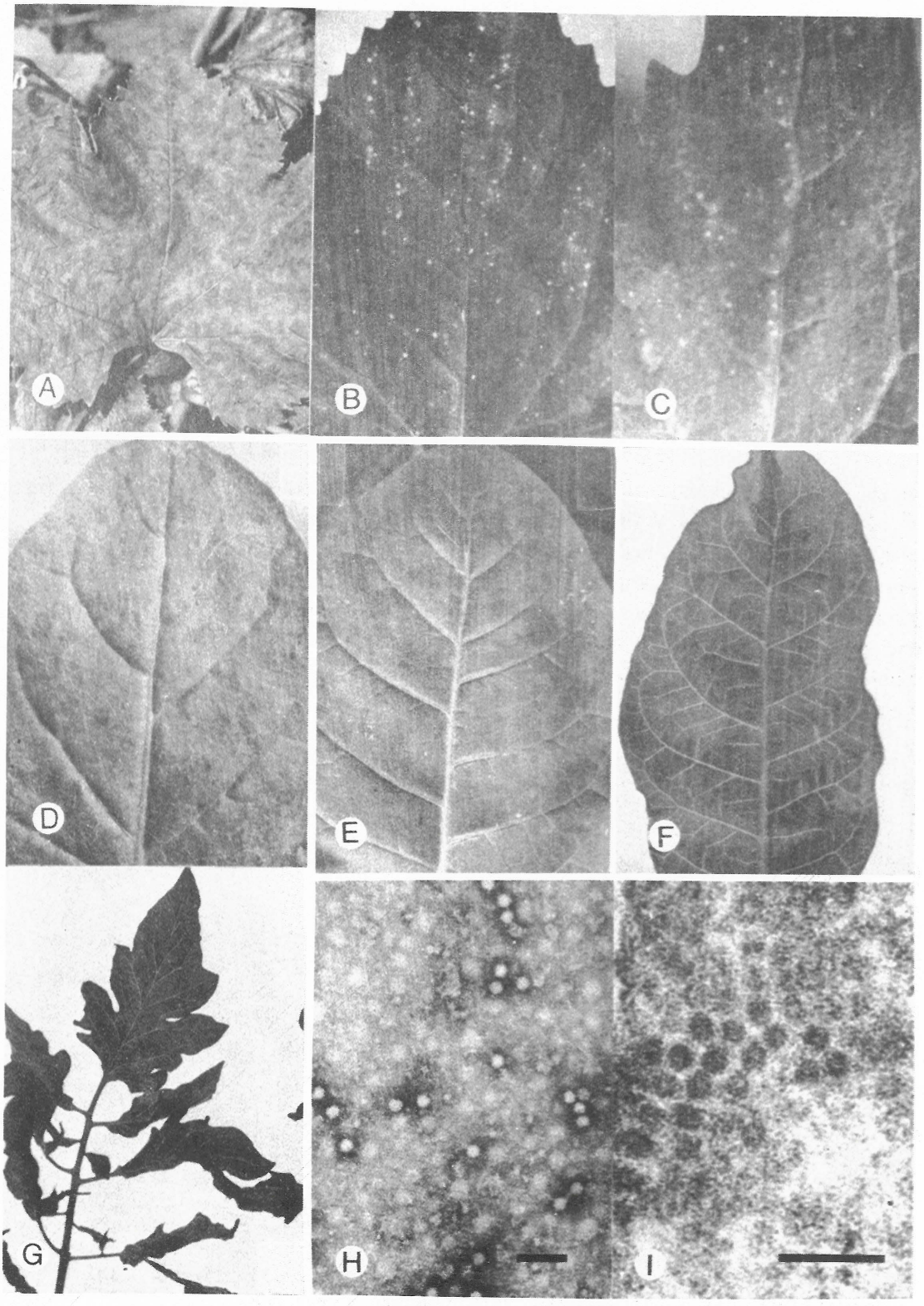
圖E. *N. tabacum* 'Burley 21'呈現斑紋與黃斑病徵。
Fig. E. Mottling and yellow spot symptoms in *N. tabacum* 'Burley 21'.

圖F. *N. debneyi*呈現斑紋與脈斑病徵。
Fig. F. Mottling and pattern veinbanding symptoms in *N. debneyi.*

圖G. 番茄（臺農1號）呈現嵌紋及扇葉病徵。
Fig. G. Mosaic and fanleaf symptoms in *Lycopersicum esculentum* 'TN1'.

圖H. 紅藜局部斑點病斑之陰染法電子顯微鏡觀察到病毒顆粒。
Fig. H. Negatively stained virus particles from the local lesions of *Ch. amaranticolor*. Bar represents 100nm.

圖I. *N. tabacum* 'Burley 21'黃斑之超薄切片法電子顯微鏡觀察到病毒顆粒。
Fig. I. Virus particles in the cytoplasm of infecetd *N. tabacum* 'Burley 21' cell. Bar repressents 100nm.


A
B
C
D
E
F
G
H
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Sap-transmissible Viruses Associated with Grapevine Yellow Mottle Disease in Taiwan[1]

I-lang Yang, Ting-ching Deng[2] and Moh-jih Chen[3]

Summary

Some virus-like disorder showing yellow mottle or yellow vein or mosaic symptoms were found in some vineyards in Taichung areas in 1982. These diseases were transmitted to 13 species of herbaceous plants by sap inoculation, and showed either local lesion or yellow spot or mosaic symptoms. Five virus isolates were isolated from different single lesions according to different host reactions and symptomatology. Back inoculation to healthy grape seedlings were succeeded by mechanical transmission. Graft indexings were succeeded by use of healthy *Vitis* indicators, and were also confirmed as a soil-borne virus disease. Two isolates showed positive reaction to antiserum against tomato ringspot virus. Electron microscopy found spherical virus particles, 26 to 30nm in diameter in either infected leaf extract or tissue section. Accordingly, two virus isolates of these grape yellow mottle were confirmed as relative to one strain of tomato ringspot virus.

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中華農業研究（Jour. Agric. Res. China）35(4)：511～520（1986）

香菇段木美髮網菌之發生及其生活史之觀察[1]

廖 英 明[2]

摘要：由本省香菇栽培區之土庫及埔里所採得之粘菌，依其孢子囊、子囊孢子、變形體、變形膜等特性鑑定爲 *Stemonitis splendens* Rost.。調查本菌孢子囊在香菇栽培場發生情形發現其在4～10月間發生較多，尤其在7月達到高峰，出現率爲1～14%。若以樹種而言，則硬質木材比軟質木材較不易被感染，且感染率隨著栽培時間而增加，在所有調查的一年半以上段木中以黃槿受感染率爲30%爲最多。當以七種不同培養液來培養子囊孢子時，發現20%木汁中的發芽率最高，可達85%，而在黑暗下較有利發芽，發芽所需時間爲48～72小時。段木經本菌孢子接種後，若有傷口處理則感染率爲86%，在無傷口處理時爲4%，而接種後所產生之子實體以光學顯微鏡觀察時發現其特性與原先採得者一致。由田間觀察及室內試驗結果可將本菌作成一生活史圖。本菌在香菇段木上完成其生活史所需時間爲120天，但會受環境因子如溫度、濕度等之影響而改變。

香菇（*Lentinus edodes*（Berk.）Sing, Shiitake）爲本省新興菇類，因其味道鮮美，頗受國人喜愛，其生產量及栽培面積均有逐年增加的趨勢[1,2]。在香菇栽培過程中除了受綠黴菌（*Trichoderma* spp.）嚴重之威脅外[3,4]，近年來發現粘菌之危害非常普遍而且頗嚴重，段木受感染後幾無收成。本省之香菇栽培已擴展到中低海拔地區，這些地區均爲高溫多濕，頗適合粘菌之生存，因此粘菌之爲害益形嚴重，也是亟待研究防治方法的重要病害。粘菌之研究始於1854年 De Bary 發現 *Hemitrichia vesparium* 等之孢子可產生具有鞭毛之游動細胞（Swarm cell），而與高等眞菌完全不同，因此將這一類眞菌自行分類成粘菌綱[12]。在本省過去的研究中僅記錄發現美髮網菌（*Stemonitis splendens*）存在於新竹、南投、臺北、臺中、宜蘭等地之硬樹皮或腐木上[23,31]，以它來當作病害之報告尚無。

粘菌之生活史中，子囊孢子的發芽是極重要的一環，也是決定是否可以感染香菇段木的重要因子，過去有關孢子發芽的研究也很多[5,6,16,18,28]。當孢子發芽後，可產生具有鞭毛之游動細胞，二個游動細胞會融合成粘變形體（myxoamoeba），而後再發育成變形體（plasmodium）[7]，雖然游動細胞的鞭毛可有一支以上[9,17]，但一般仍認爲單鞭毛才是正常[16]。在室內培養時也可完成粘菌之生活史[11,22,24,29,30]。

粘菌在香菇栽培過程中其孢子如何傳播是病害發生的重要因子，目前已知粘菌孢子可經由空氣、昆蟲、風、雨、節肢動物等來傳播[15,21]。在日本，香菇是重要之經濟作物，但粘菌之研究極少，大概與其低溫性地區有關，濱島[8]調查發現夏季高溫時以 *Stemonitis* sp. 及 *Arcyria* sp. 發生較多。本省地處高溫多濕，依筆者多年觀察發現本省所發生之粘菌以 *Stemonitis* spp. 危害較大，其中又以可產生美麗子實體之 *Stemonitis splendens* 爲甚，因此本研究將以 *S. splendens* 作爲對象，來調查其發生情形，並探討其孢子發芽及生活史，俾作爲日後研究防治方法之依據。

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材料及方法

一、粘菌發生情形調查：在中部之埔里及南部之土庫各調查一處香菇段木栽培場，隨機調查 500 支段木，調查時間爲一年，由73年12月到74年11月止，每個月調查一次，記錄孢子囊出現情形，當子實體出現時以「正」表示，否則爲「負」。

二、粘菌在不同樹種上發生情形調查：如上之方法，調查同一栽培場之不同樹種受粘菌爲害情形，每樹種調查40支段木，調查時間爲74年 7 月，調查對象爲一年內及一年以上之段木，記錄時以累積數目爲準，並僅記錄子實體出現者。

三、子實體形態之觀察：粘菌子實體由孢子囊及囊孢子所組成，孢子囊具軸柱及細毛體。首先在段木上觀察其生長情形及發生環境，並採取子實體在光學顯微鏡下觀察其孢子囊 (sporangium)，子囊孢子 (sporangiospore)，軸柱 (columella) 及細毛體 (capillitium) 等，並加以記錄及照像。

四、孢子發芽該驗：採取段木上所產生之粘菌子實體，並取得子囊孢子，子囊孢子以無菌水稀釋。當採取子囊孢子時係在無菌箱中進行，首先用經殺菌之移殖針輕拍孢子囊，使孢子自然落下於經殺菌之培養皿中，得到成熟之子囊孢子，並以無菌水稀釋而後培養於下列水溶液中：（1）蒸餾水，（2）2％葡萄糖 (W/V)，（3）0.2％蔗糖 (W/V)，（4）20％木汁 (W/V)，（5）10％木汁 (W/V)，（6）2％蛋白腺 (W/V) 及（7）1％澱粉 (W/V)。其中木汁係爲楓樹木片加上蒸餾水以不同重量比混合後之煎煮30分鐘之過濾液。各種溶液以 1N NaOH 及 0.1N HCl 調整其 pH 值爲6.5，並置於 20°C 之恆溫箱培養。培養時係將 20ml 之培養液加於 6cm 直徑之培養皿中，再將已置於無菌水中之浸潤孢子 (5,000～8,000個孢子/ml) 移入 0.1ml 之量於培養皿中。處理方式分爲光照及黑暗處理二種，光照係在 20°C 之恆溫箱中 2000 lux 之光照下進行，黑暗處理則爲同一條件，唯培養皿先用黑色塑膠布包裹。

五、游動細胞鞭毛之觀察：依 Elliott (1949) 之報告，利用 Loeffler's method 來作鞭毛染色，即取上項已經發芽之孢子懸浮液，滴在玻片上，並加入染料，經水洗，陰乾後，再觀察其鞭毛著生情形。

六、接種試驗：將由子實體採得之新鮮子囊孢子製作成懸浮液，濃度調整爲 7,500～10,000 個孢子/ml，而後以兩種方式進行接種，一爲自然接種，即以噴霧方式將孢子懸浮液噴灑於楓樹段木上，而段木爲已接種香菇菌絲一星期之段木，每支段木接種量爲 100ml，共接種40支段木。另一種方法爲先將已接種香菇菌絲一星期之楓樹段木用刀砍傷，傷口深 0.5 公分，長度 5 公分，間隔與距離爲20×10公分，每支段木約20個傷口，而後以相同濃度及用量之孢子懸浮液噴灑，同樣接種40支段木，在自然栽培狀況下觀察粘菌子實體之生長情形。

七、美髮網菌在香菇段木栽培中之生活史：在眞菌學研究方面，楊氏 [29] 曾在室內以人工培養報導 *Stemonitis splendens* 之生活史，但在香菇段木上的情形則未有人研究。本研究參考楊氏 [29] 及湯淺氏 [9] 在室內生活史之部分過程，再配合接種及自然狀況下發生之過程改由病理學觀點來推定本菌在香菇段木上之生活史。首先由已發病之香菇段木上採得本菌之子實體，經人工接種後（如上項），觀察其子實體生長過程，並將其形態繪製成完整之生活史。

結果與討論

一、美髮網菌 (*S. splendens*) 在香菇栽培場發生季節之變化：調查不同地區一年生之段木其出現孢子囊之比率變化甚大，從 0 ％到14％，依月份區分以四～十月發生較多；若依地區分，平地土庫因爲氣溫較高所以發生比中溫地區之埔里爲高，土庫七月發生最高，達14％（圖 1）。在低溫期之十二月也可看到子實體，僅在一～二月無法看到，因此可推斷本省一年之中絕大多數時間均受

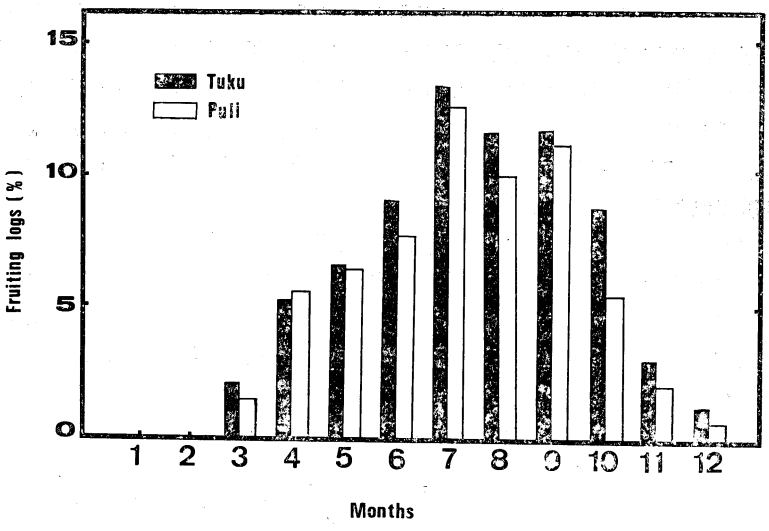


圖1. *S. splendens* 在土庫及埔里兩處香菇栽培場中出現之季節變化。

Fig. 1. Seasonal fluctuations of fruiting bodies of *S. splendens* on the logs at Tuku and Puli.

粘菌爲害。本菌在七月發生最多，此和氣象條件有關，即高溫多濕情形下發生嚴重。在日本，粘菌也發生於高溫期 (10)，濱島 (8) 發現粘菌在七～八月間出現頻度最高。而本省在一～二月間無法看到子實體，是由於溫度太低，到四、五月間子實體出現率突然增高可能與梅雨有關。由於下雨而提供了粘菌子實體形成與發育所需濕度，因此由四月開始到十月間之六個月內粘菌發生嚴重

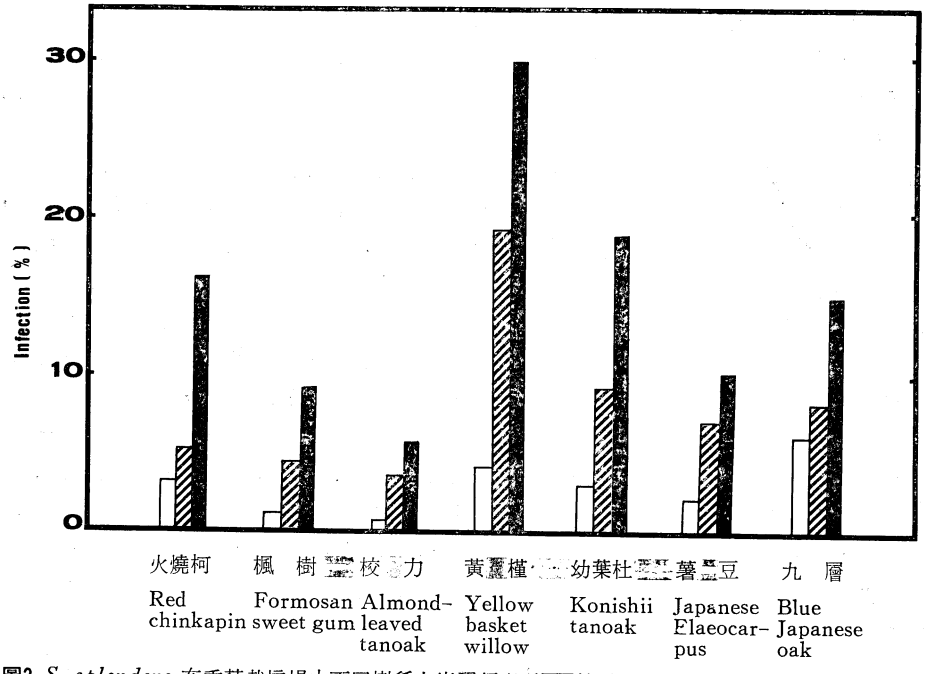


圖2. *S. splendens* 在香菇栽培場中不同樹種之出現頻度（□接種香菇六個月後；▨一年；■一年以上）。

Fig. 2. Infection percentage of various ages of logs by *S. splendens* (Six months □; one year ▨; and longer than one year ■ after inoculation of *Lentinus edodes*)

，實爲本省香菇栽培上應注意的地方。在不同樹種方面，一般習慣將樹種分爲硬質及軟質二種[3]，當以硬質木材作爲材料時，則感染率較低，如校力；而軟質木材如黃槿，九層、火燒柯等則受害較大。受害率也隨著栽培時間而增加，有累積受害結果，即表示一旦段木受害則無法回復（圖2），而且在接種六個月內即可被爲害。黃槿等樹種因樹皮薄且易於剝裂（圖版8）或受傷，易受粘菌感染，而另一原因可能爲此種樹種其含水量少，必須補水，無形中增加了段木表面的濕度，也提供了粘菌孢子發芽的良好條件。

二、本菌之外形觀察：（一）楓樹段木上之形態：以肉眼觀察本菌子實體，可見子實體由變形膜長出，呈紫褐色，變形體爲白色，變形膜爲銀色，子實體具有黑色光澤之短柄，簇生在一起，產生褐色粉末狀之子囊孢子，極易飛散，孢子囊長度爲15～22mm。㈡光學顯微鏡觀察：本菌之孢子囊爲圓柱形，頂端鈍圓，紫褐色，有柄，柄具光澤，黑色，細長約長1～3.8mm，軸柱可達到頂端，具細毛體（圖版1），其分枝形成一網狀，孢子淡赤褐色（圖版2），在高倍下可看到細小之突起，直徑 8.5×8.7μm。觀察本菌之孢子囊，子囊孢子，變形體及變形膜等特性，並與楊氏[29]，劉氏[23]等之敍述比較而可判定本菌爲 *Stemonitis splendens* Rost.。

三、子囊孢子發芽試驗：孢子經培養48小時後開始發芽（圖版3），發芽後產生具有鞭毛可游動之游動細胞。在供試之七種水溶液中，以20%木汁之發芽最好，但無菌水也可發芽，所有的供試溶液其發芽率在光照下（2—46%）都比黑暗下（10—85%）爲低。若檢查鞭毛分佈情形，則發現雙鞭毛與單鞭毛的比例在不同供試溶液中也不同，以在木汁中者爲最高，約爲⅓，而在澱粉中爲最低，只有$^1/_{12}$（表1）。鞭毛長度爲 32～39μm，若爲雙鞭毛，則二支鞭毛幾乎等長（圖版4.5）。當觀察超過72小時後，並未發現發芽率增加，且部分發芽者已轉變成阿米巴狀之粘變形體，且此時鞭毛消失。以前許多學者曾經研究過粘菌孢子之發芽，例如 Smith[28] 發現粘菌孢子可存活4—32年之久，且孢子年齡不是發芽的主要條件，而發芽率與 pH 值有關，但後來的研究發現孢子是否成熟爲決定發芽的重要因素，在 32°C 以上不發芽，適合發芽溫度爲 22～30°C，且 pH值在4.5—7.0時及在黑暗下較易發芽（6，16）。基於此，本試驗即採取成熟之孢子來作爲材料，並將培養液調整爲 pH 6.5。但 Cook[14] 指出 28°C 比 18°C 之發芽率低，加熱會使發芽數目減少，醣類（carbohydrates）及蛋白質（proteins）有助於發芽。由本試驗可看出在 20°C 之培養時發芽率可達85%，此與 Cook 報告相近。在本試驗中所有供試七種培養液以20%木汁之發芽率最高（表1），此也與安部[5]的報告相符。安部（5，6）曾用蒸餾水，有機化合物，無機化合物，植物抽出液及細菌體來培養粘菌孢子，發現 *S. splendens* 之發芽比例偏低，但其中以木汁或落葉浸出液之發芽率最高，一般發芽率在1—5%。但是 Gilbert[18] 報告本菌培養2—7日後發芽率可達 90—100%，或許是安部之觀察未達到適合發芽之時間所致。楊氏[29]用 Weak medium 培養本菌時發芽率僅達13%，可能與培養基質有關。觀察本菌孢子之鞭毛時發現具有二支鞭毛情形，且二支鞭毛幾乎等長。Elliott[16] 將鞭毛區分爲三種型式，即 Type I，二支鞭毛之其中一支長度爲另一支的一半以下者；Type II，二支鞭毛之其中一支爲另一支之一半以上者；Type III，二支鞭毛爲等長者。根據 Elliott 報告 *S. splendens* 絕大部分屬於 Type III，而其中極少數介於 Type II 與 Type III 之間，本試驗結果也與之吻合。在澱粉（starch）中培養孢子時，雙鞭毛出現比例特別少（表1），其原因不明，仍需作進一步研究。在黑暗中發芽比在光照中爲宜，此與安部之觀察報告相同，因此可知粘菌在發芽時期較適合在光線較少的環境下完成，但孢子囊之形成則需有光線[19]。

四、接種試驗：傷口接種時其感染率達86%，無傷口接種則爲4%，由此可知粘菌侵入樹皮內時若有傷口則可迅速擴展，無傷口則擴展速度大爲降低。從接種到發生子實體的時間爲120—140天（表2），即在段木中至少需有四個月的潛伏時間。傷口既是感染的重要因素，因此在選擇段木時若能淘汰破皮，裂縫或有蟲口之段木，則可預防粘菌感染的機會。若是遇有破皮現象，也可將患部

切除，並塗以殺菌劑，再用香菇臘封埋(3)，如此可減少粘菌孢子附著及發芽的機會。根據安部(5)報告粘菌在 18～22°C 發芽最好，而 15～30°C 均可發芽，而本省在此種溫度條件下的時間相當長，在一年之中幾乎大部分時間均可被本菌感染。接種後在 28°C 開始出現子實體，表示其較適合在高溫下形成子實體，而接種後需有120—140天的潛伏期，表示粘菌的發生並非驟發性，必需依賴段木上存在之微生物來提供其食物來源，若段木處理得當，則微生物愈少，而愈不利於粘菌繁殖。而接種後產生的子實體在外形上與光學顯微鏡觀察時均與原來一致（圖版 6,7），因此也符合了柯霍氏之接種原則（Koch's postulate），在未接種粘菌之段木其生長良好且可產生正常子實體（圖版 9）。

表1. 不同培養液對 *S. splendens* 子囊孢子發芽之影響

Table 1. The effect of various liquid media on germination of sporangiospores of *S. splendens*

培養基 Medium	發芽率 Germination (%)		發芽所需時間 Hours for germination	游動細胞，雙鞭毛/單鞭毛 Swarm cell, bi-flagellate/mono-flagellate
	光照 light	黑暗 darkness		
2%葡萄糖 glucose	22	68	72	1/10
0.2%蔗糖 sucrose	2	10	48	1/8
20%木汁 wood extract	46	85	48	1/3
10%木汁 wood extract	32	60	48	3/4
2%蛋白腖 Peptone	20	48	60	3/5
1% 澱粉 Starch	4	15	48	1/12
蒸餾水 Dist. water	5	10	72	1/10

表2. *S. splendens* 在楓樹段木上之接種感染率及子實體形成情形

Table 2. Infection Percentage and formation of fruiting bodies of *S. splendens* on the *Lentinus edodes* grown maple logs.

接種方法 Inoculated method	感染率 (%) Infection	子實體之形成 Fruiting body formation	
		接種後天數 Days after inoculation	開始形成溫度 (°C) Initiation
傷口 wounded	86	120	28
無傷口 Un-wounded	4	140	30

五、*S. splendens* 在香菇段木上生活史之模式：本試驗之調查及觀察結果可整理得其生活史如圖 3，即當段木接種香菇菌絲後，由外界如風，水、昆蟲及人體或動物所引入之子囊孢子附著在段木

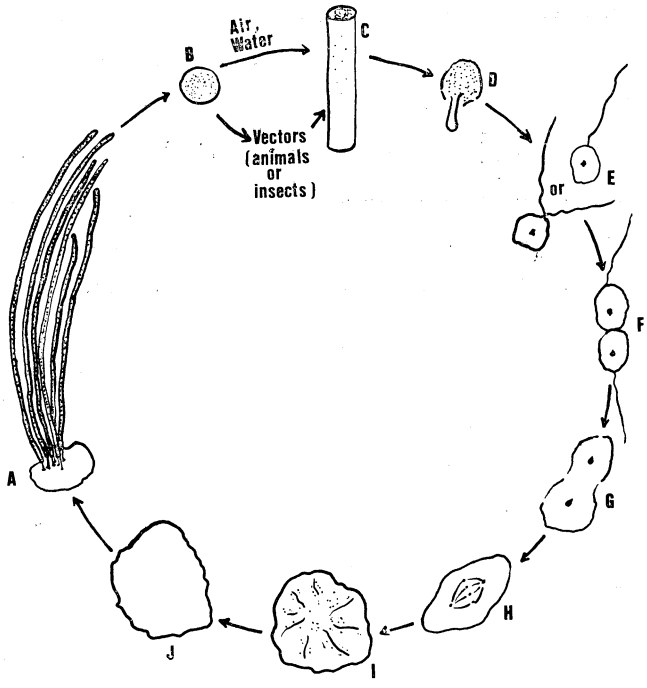


圖3. *Stemonitis splendens* Rost. 在香菇段木上之生活史。

Fig. 3. The life cycle of *Stemonitis splendens* Rost. On the logs of shiitake

說明：A. 孢子囊 B. 子囊孢子 C. 感染段木 D. 發芽 E. 游動細胞 F. 結合 G. 核融合 H. 核分裂 I. 變形體 J. 變形膜。

Illustration : A. Sporangia B. Sporangiospore C. attacked the log D. germination E. swarm cell F. conjugation G. fusion H. meiosis I. plasmodium J. hypothallus.

上，再由段木上之木液或藉洒水而提供了足够發芽之水份，即可發芽產生游動細胞。二個游動細胞可結合成粘變形體或結合體，而在段木上存在之細菌，酵母菌可作爲粘變形體養份之來源(11, 13,20,24) 粘變形體再進行核融合，核分裂等過程（9 ,26,27），最後形成變形體，變形體爲白色。此時突破樹皮，在段木上可見散落之白色變形體（圖版 6），而香菇菌絲在此部分均不可見，接著變形體消失，形成變形膜(25)。變形膜沿著樹皮與樹幹木質部之接縫處伸長，若遇陽光則停止生長，當環境適合時，突破較脆弱部分之樹皮而形成子實體（圖版 7）。子實體爲由一簇孢子囊所組成之結合體，孢子囊上生有軸柱及細毛體，子囊孢子在細毛體上形成，成熟時即脫離飛散，再感染其他新的段木，此時可經由風、水、及媒介如動物或昆蟲來傳播，如此完成一生活史，整個生活史可在 120 天完成。本菌在整個生活史中，均可在香菇段木上完成，而由孢子發芽後到變形體形成之過程係參考湯淺氏(9)與楊氏(29)之結果。唯楊氏係在人工培養基上進行觀察，與自然發生情形不同，如在人工培養基上僅產生少數子囊，不若在段木上可形成大量且正常之實子體，人工培養時整個生活史在24天可完成，但在香菇段木上則需 120 天，可能是培養條件不同所致。由本菌之生活史可知要撲滅本菌，可採下列方式，一爲阻礙其孢子發芽（圖 3 、 C→D ），一爲阻礙其子實體之形成（圖 3 、 J→A ）。前者可藉化學藥劑殺滅本菌孢子或採用消極方法，如段木先用藥劑處理，使段木表面之微生物減少，以減少粘菌之食物來源。後者則爲加强檢視段木，若在段木上看到已產生白色變形體則應予燒毀，以減少因產生子實體所形成之大量孢子再飛散而感染其他健全段木。本省地處高溫多濕 ， 極合適則菌之生長，若未加以注意 ，一旦擴展將不可

收拾。由於粘菌可存活的時間相當長，飛散又快，是一種應當重視的病害，尤其在舊栽培場，此菌益形重要。不僅段木如此，在太空包栽培方面，近年來也發現受粘菌爲害，但尚不嚴重，或許粘菌日後也是太空包栽培之重要病害。

本文爲本省香菇栽培之粘菌病害首次報告，除了敍述其爲害情形，發生季節外，也提出了粘菌在段木上之生活史，可作爲日後研究或病害防治之依據。

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Occurrence and Life Cycle of *Stemonitis splendens* on the Logs of Shiitake[1]

Ying-ming Liao[2]

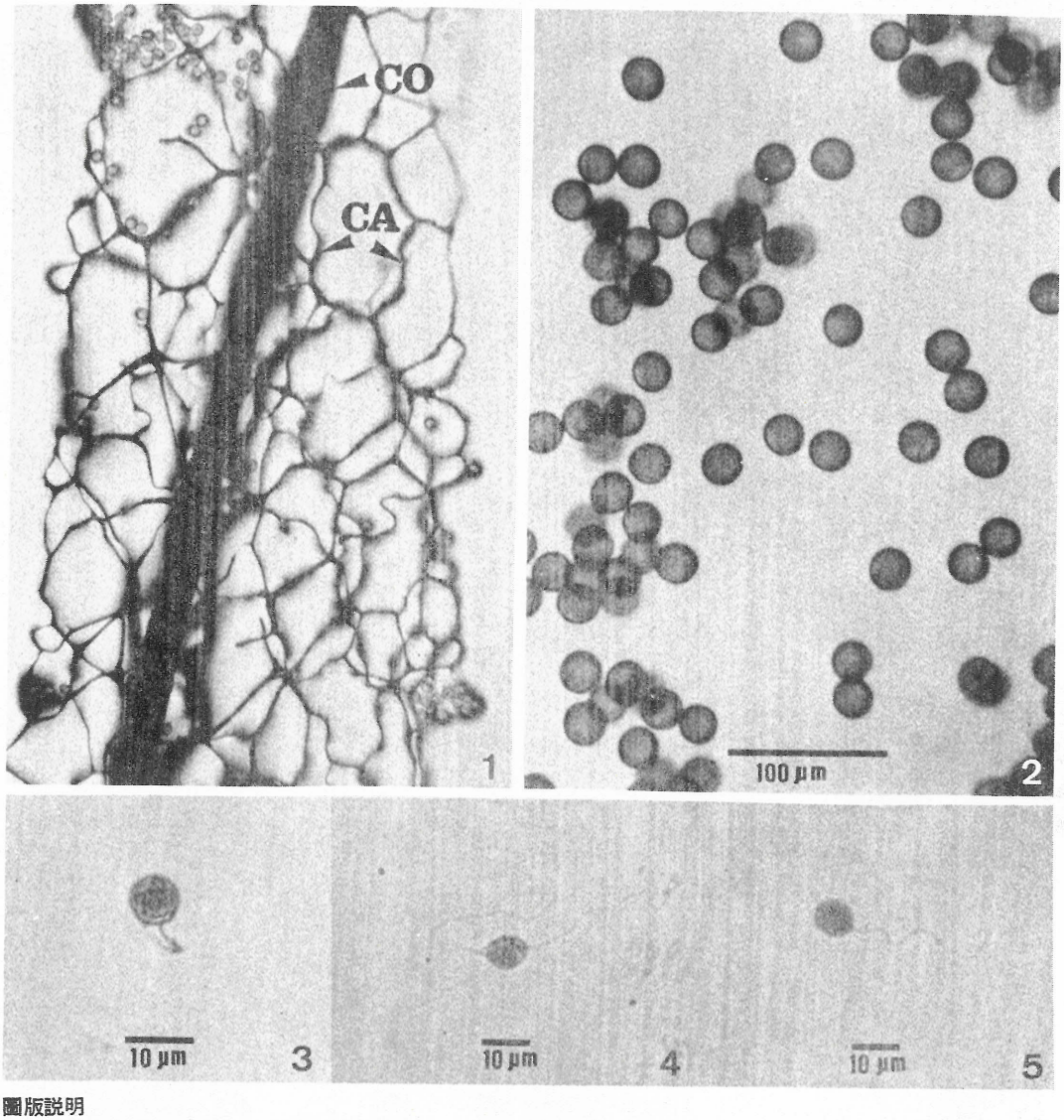
Summary

Depending on the morphological characteristics of sporangia, sporangiospores and hypothallus, the slime mould collected from the logs of shiitake at Tuku and Puli were identified as *Stemonitis splendens* Rost.. During the year, more fruiting bodies of the fungus were observed from April to October, with a maximum of occurrence in July, and the infection percentage on logs were between 1% and 14%. The soft-wood logs were more easily attacked than hard-wood logs by the fungus, and the infection percentage increase with the log ages. The highest infection, i. e, about 30%, was observed in the logs of yellow basket willow (*Engelhardtia roxburghiana*) after 1.5 years or longer of cultivation.

Sporangiospores germinated best in 20% wood-extract among the seven liquid media tested, and darkness was found more suitable for germination than under light conditions. Eight-five percent, which is the highest, of sporangiospores germinated in 2 to 3 days.

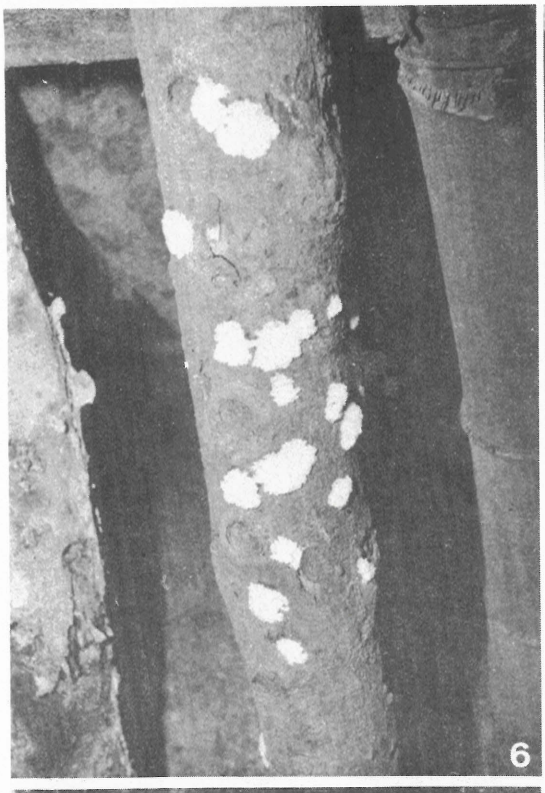
Inoculation of wounded and un-wounded logs of shiitake with sporangiospores of *S. splendens* resulted in 86% and 4% infection, respectively. No difference in morphological characteristics was observed between the fruiting bodies produced on the inoculated logs and those produced in nature. According to the results of laboratory studies and observation in nature, a complete scheme of the life cycle of *S. splendens* on the logs of shiitake was drawn. The fungus takes about 120 days to complete its life cycle. However, it is influenced by the environmental factors such as humidity, temperature ect..

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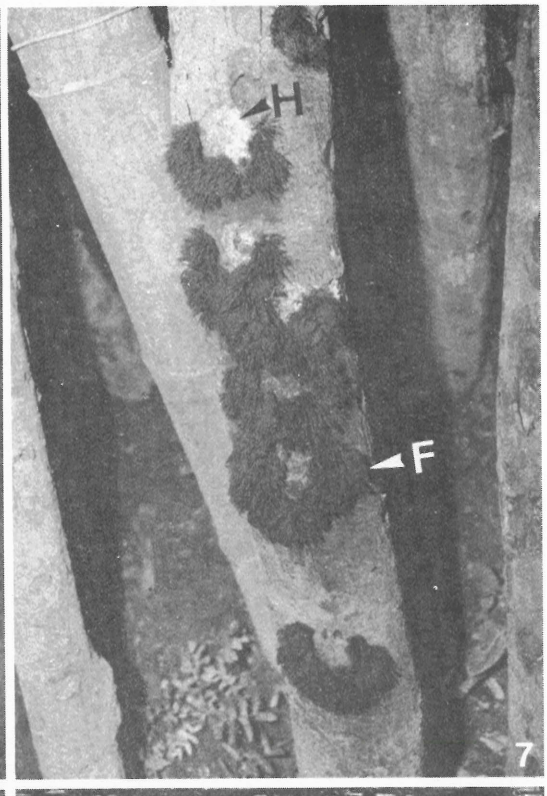


圖版說明

1.子囊具有軸柱（CO）及細毛體（CA）
Columella (CO) and capillitium (CA) of a sporangium.
2.淡紫褐色之子囊孢子。
Lilaceous brown sporangiospores.
3.子囊孢子發芽情形。
A germinating sporangiospore.
4.具有二支鞭毛之游動細胞。
A swarm cell with two flagella
5.僅有一支鞭毛之游動細胞。
A swarm cell with one flagellum
6.受害段木產生白色變形體（初期）。
White plasmodia produced on the infected log (early stage)
7.由變形膜（H）產生子實體（F）（後期）。
Production of fruititg bodies (F) form hypothallus (H) (later stage)
8.楓樹段木受感染後樹皮脫落。
The bark of a infected maple log disappeared.
9.若爲健全段木可產生正常子實體。
Health logs with fruiting bodies of shiitake.



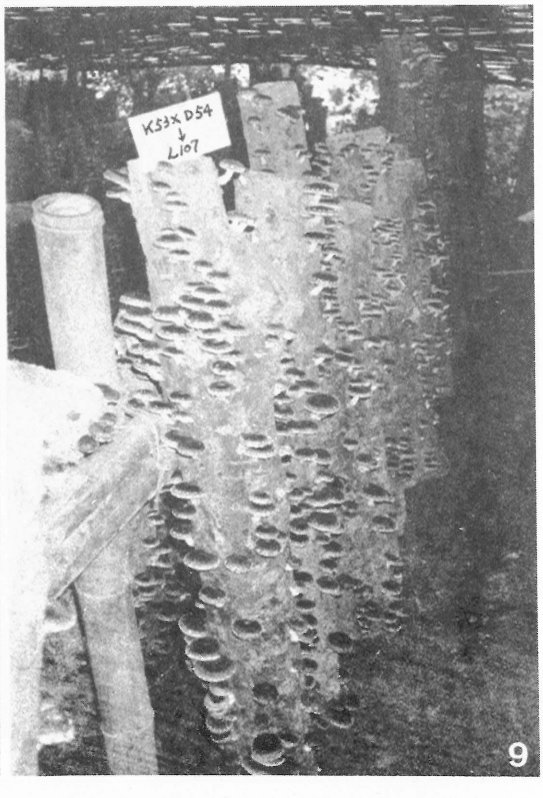
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中華農業研究（Jour. Agric. Res. China）35(4)：521～529（1986）

小菜蛾性誘劑之田間誘效試驗[1]

1. 性費洛蒙添加物之誘雄效果與性誘劑誘雄距離之探測

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摘要：本試驗目的爲探明小菜蛾（*Plutella xylostella*）性費洛蒙（Z11-16：Ald+Z11-16：Ac）添加其類似物（Z11-16：OH 或 Z9-14：Ac）是否影響其田間誘雄效果，並探測該劑之誘雄距離。試驗結果得知性費洛蒙在冬季若以1：1：0.02與1：1：0.001之比例添加 Z11-16：OH 與 Z9-14：Ac，劑量爲 10μg 時，其誘力均增强，分別約爲未添加者之 1.5 與1.7-4.3 倍。若在夏季添加則無增效作用。又兩種性誘劑 Z11-16：Ald+Z11-16：Ac+Z11-16：OH(1：1：0.02) 與Z11-16：Ald+Z11-16：Ac+Z9-14：Ac (1：1：0.001)，劑量爲 10 或 100 μg，與對照組（5 隻活處女蛾）在其下風處 0.5、1.0、1.5 及 3.0m 釋放標記雄蛾，各處理之誘雄力均無顯著差異。性誘劑在田間之誘雄有效距離爲1.0m。

小菜蛾（*Plutella xylostella*）屬鱗翅目、菜蛾科（Plutellidae），乃本省十字花科蔬菜之重要害蟲，在本省氣候下繁殖迅速，每年發生 19 至 21 代[1]。其幼蟲之爲害可使蔬菜減產，品質降低，影響市售價格。該蟲歷年使用化學藥劑防治，因抗藥性品系之產生，使藥劑防治頗難收效。試驗人員除遴選有效藥劑供防治外，更加强其天敵之利用研究[3,4]。本所自民國 62 年開始即與中央研究院合作進行其性誘劑之利用研究[9]，期能開發該蟲之防治新途徑。

小菜蛾性費洛蒙首先經 Tamaki 氏鑑定爲 Z11-hexadecenal（Z11-16：Ald）與 Zll-hexadecenyl acetate（Z11-16：Ac）之1：1混合物[12]。但周等與 Koshihara 等氏均認爲其在田間之誘雄力不如小菜蛾處女蛾，因而推測其雌蛾所散發出之性費洛除上述兩種化合物外，可能尙含有1種或多種之未知物質[2,10,11]。Ando 等與 Chisholm 等氏用觸角電析法（electroantennogram method）探測其雄蛾觸角對性費洛蒙類似物如 10-18 個碳之飽和脂肪、與含醇類（alcohols）、醛類（aldehydes）及醋酸（acetates）之單不飽和脂肪等之反應，結果顯示雄蛾觸角對Z11-16：Ald 與 Z11-16：Ac 均有極强烈之反應，對 Z11-16：OH、E11-16：Ac、E11-16：Ald、E12-16：Ald、Z11-14：Ald、Z11-14：Ac、及 Z9-14：Ac 等亦呈中度反應[7,8]。Ando 等與腰原及山田亦證實 Z11-hexadecenol（Z11-16：OH）在日本田間使用時對誘集該蛾有很强之協力作用[6,7]。

本試驗旨在探測小菜蛾性費洛蒙（Z11-16：Ald+Z11-16：Ac）在本省田間環境下添加 Z11-16：OH、Z9-tetradecenly acetate（Z9-14：Ac）及 Z9-hexadecenyl propionate（Z9-16：P）等是否有協力效果，同時探明該劑對田間小菜蛾之有效誘雄距離。

1.臺灣省農業試驗所　研究報告 1309 號。本試驗承行政院農委會補助經費，71農建-4.1-產-56（II）；試驗期間蒙中央研究院動物研究所所長周延鑫博士提供性誘劑及寶貴意見，文復蒙斧正，蘇淑芬小姐協助飼蟲，謹此誌謝。

2.本所應用動物系助理研究員、研究員。臺灣省　臺中縣　霧峰鄉。

材料與方法

性費洛蒙添加增效劑之誘雄效果

民國67年11月至69年7月在臺中萬豐本所0.14 ha面積之不施藥甘藍田進行小菜蛾性費洛蒙添加物對誘集小菜蛾雄蛾之增效試驗，共4次。第一、二次試驗分別在67年11月20日至12月20日與68年3月6日至4月2日進行。用劑量10μg，1：1之性費洛蒙(Z11-16：Ald+Z11-16：Ac)分別添加100、10、1、0.1、0.01、0.001及0.0001等不同比例之 Z9-14：Ac 與 Z9-16：P。誘集桶之間距爲 6m，共3重複。第三、四次試驗於69年1月12日至2月12日與6月10日至7月10日分別進行。用劑量 10μg，1：1之性費洛蒙 (Z11-16：Ald+Z11-16：Ac)分別添加 0.02之 Z11-16：OH 及 0.001 之 Z9-14：Ac。誘集桶之間距爲 8m，共5重複。完全逢機設計。4次試驗均於隔日記錄落入誘集桶內之雄蛾數，連續記錄1個月。桶內裝肥皂水每10天更換1次。資料以鄧肯氏多變域法分析，5%顯著基準比較。

各處理組之誘蟲裝置因當時試驗進行時本省尚無適當之性誘器可供使用，乃以深藍色塑膠桶代之。其內徑23cm，高26cm，容量8ℓ，裝水4ℓ溶入2g之肥皂粉。先將桶之提柄豎起，再將裝有誘劑之塑膠小管（polyethylene cap, 2×1cm）用細鐵絲紮上，小管距水面約4cm，桶上覆以直徑約 40cm 之竹笠。對照組之誘集桶與各處理組之裝置相同，但不加裝誘劑。供試驗之性誘劑係由中央研究院動物所周延鑫所長提供。

性誘劑誘雄距離之探測

1.釋放標記雄性小菜蛾探測性誘劑之誘雄距離

小菜蛾之飼育：在溫室內用33×25cm 塑膠盤播種油菜種子 6g，幼苗長出即供40對小菜蛾成蛾產卵，孵化出之第一、二齡幼蟲取食菜苗，菜苗將被食盡時，改用甘藍葉片餵食，此時小菜蛾幼蟲已發育至第二至四齡。待其結繭化蛹後，移至7°C恆溫箱冷存，每次供應試驗蛹約15,000個。

雄蛾之標記：小菜蛾成蛾羽化後，立將雌、雄蛾分開，以50隻雄蛾爲1組，裝入 300cc 三角瓶，餵水1至3天後，予以標記。標記時用CO_2使之昏迷，再用紅、藍、黑等色萬能筆分別在其前翅做1記號。

雄蛾之釋放：在本所農場面積0.3ha 之試驗田種植初秋甘藍，於其生長全期，每隔7天噴25.3%美文松（mevinphos，500倍）1次。試驗時兩種供試之性誘劑 Z11-16：Ald+Z11-16：Ac+Z11-16：OH（1：1：0.02）與 Z11-16：Ald+Z11-16：Ac+Z9-14：Ac（1：1：0.001），劑量分別爲10與 100μg，對照組係用5隻活處女蛾。誘蟲盒採用甲富公司出品厚硬紙製成，上下合蓋式，下層塗黏膠。誘劑按定量注入 PE細管，並用膠帶黏於誘蟲盒上層之內面。誘蟲盒放置高度約距畦面0.4m。另將裝有標記雄蛾之玻瓶於釋放日之下午4時放置在誘蟲盒下風向之 0.5、1.0、1.5及 3.0m 處。於下午5時釋放。次晨8時檢查各誘蟲盒誘得之有標記雄蛾數，計算其回收率。逢機完全區集設計，3重複。資料經轉角校正後以變方分析F值測定其顯著程度。同時記錄試驗期間之田間氣象因子。該試驗自 70 年11月10日至 71 年2月4日共進行4次。用室內飼育之第三、四、五及六世代雄蛾供試。

2.誘劑放置距離不同之誘效測定。在本所面積 0.072 與 0.5 ha 之二處試驗田種植初秋甘藍，並進行下述2次試驗。

第一次試驗：試驗期間爲 69年11月17日至 70年1月20日。甘藍種植後每隔7天噴25.3%美文松（500倍）1次，共 4 次以保護菜株之生長。隨後不再施藥，任由小菜蛾發生爲害。試驗田劃分3小區，每小區面積爲 240m^2，分別放置有性誘劑之誘集桶，各桶之間距爲 4、7及10m 等處理，即每小區放置15、6及2支劑量均爲 100μg 之誘劑，Z11-16：Ald+Z11-16：Ac+Z11-16：OH(1：1：0.02)。

第二次試驗：試驗期間爲71年9月22日至12月22日。甘藍種植後於9月29日、10月6日、及11月5日各施用25.3%美文松（500倍）與50%比加普(pirimor，2,000倍)1次，共4次。每小區面積爲100m²，放置誘蟲盒之間距爲2.2、3.6、5.6及 11.0m等4種處理。即各區內分別放置裝有誘劑之誘蟲盒25、9、4及1個。對照組放置無誘劑之誘蟲盒1個。各小區間隔10m，間隔區不種作物。誘蟲盒放置高度距畦面 0.4m。誘劑爲 Z11-16：Ald+Z11-16：Ac+Z11-16：OH（1：1：0.02），劑量50μg。添加1,000μg之 BHT 抗氧化劑。每2週更換誘蟲盒1次，每4週更換誘劑1次。逢機完全區集設計，3重複。

於69年12月17日至70年1月20日及71年11月10日至12月22日之誘蟲期間，每天上午9時記錄誘集桶或誘蟲盒內之雄蛾數與氣象資料。試驗資料用鄧肯氏多變域法分析，5%顯著水準比較。

結　果

性費洛蒙加用增效劑之誘雄效果

本試驗係於67年11至12月與69年1至2月在臺中地區甘藍田使用劑量 10μg 之性誘劑（Z11-16：Ald+Z11-16：Ac）添加7種不同比例之 Z9-14：Ac 或 Z11-16：OH ，結果比例爲（1：1）：0.001 或（1：1）：0.02 時，其對小菜蛾雄蛾之誘集均具有增效作用（表1、2）。同樣比例之添加方式在69年夏季之6至7月試驗時，並無增效作用(表2)。又性費洛蒙分別用7種比例添加 Z9-16：P，結果用（1：1）：1與（1：1）：0.0001 比例所誘得之雄蛾數較未添加者爲多，但經分析後，其差異並不顯著（表1）。

表1. 小菜蛾性費洛蒙添加第三種化合物之田間使用比例測定

Table 1. Field test of male DBM captured using 10μg per trap of Z11-16 : Ald, Z11-16 : Ac and the 3rd compounds (Z9-14 : Ac or Z9-16 : P)

Ald : Ac : 3rd compound	No. males captured/trap[1]	
	Z9-14 : Ac	Z9-16 : P
	Nov.-Dec. 1978	Mar.-Apr. 1979
1 : 1 : 100	14.3 b	292.9 a
1 : 1 : 10	14.7 b	432.7 a
1 : 1 : 1	28.0 b	699.0 a
1 : 1 : 0.1	111.0 ab	369.0 a
1 : 1 : 0.01	110.0 ab	460.7 a
1 : 1 : 0.001	186.3 a	436.3 a
1 : 1 : 0.0001	40.7 b	555.3 a
1 : 1 : 0	43.3 b	364.7 a

1. Data shown in table are mean of 3 replications.
Means followed by the same letter are not significantly different at 5% level by Duncan's multiple range test.

表2. 小菜蛾性費洛蒙添加第三種化合物之田間誘雄效果

Table 2. Field capture of male DBM using 10μg per trap of synthetic sex pheromone

Treatment	No. males captured/trap[1]	
	Jan.-Feb. 1980	Jun.-Jul. 1980
Z11-16 : Ald+Z11-16 : Ac+ Z11-16 : OH (1 : 1 : 0.02)	832.8 ab	45.5 a
Z11-16 : Ald+Z11-16 : Ac+ Z9-14 : Ac (1 : 1 : 0.001)	944.4 a	37.5 a
Z11-16 : Ald+Z11-16 : Ac	546.2 b	44.0 a
None	123.4 c	1.5 b

1. Data shown in table are mean of 5 replications.
Means followed by the same letter are not significantly different at 5% level by Duncan's multiple range test.

性誘劑不同配方與不同劑量之誘雄效果

爲避免田間自然發生之雄性小菜蛾干擾及性誘劑之誘效，本試驗將室內飼育之雄蛾加以標記，然後在試驗田以不同距離釋放之，並觀察其回收率，以瞭解不同配方與不同劑量性誘劑之誘雄效果。結果發現2種性誘劑 Z11-16 : Ald+Z11-16 : Ac+Z11-16 : OH (1 : 1 : 0.02) 與 Z11-16 : Ald+Z11-16 : Ac+Z9-14 : Ac (1 : 1 : 0.001)，在70年 11月至71年2月不論其劑量爲 10或100μg，與5隻活處女蛾之對照組誘得之雄蛾數比較，結果經變方分析後差異均不顯著（表3）。

表3. 小菜蛾性誘劑之配方與田間放置距離之變方分析

Table 3. Analysis of variance of field capture of male DBM using synthetic sex pheromone

Source of variation	DF	MS	F	P>F
Replication	3	424.3940	3.0063	0.0719
Pheromone[1]	4	165.9458	1.1755	0.3703
Error (A)	12	141.1666		
Distance[2]	(3)	513.3299	12.4424	0.0000
Linear	1	1167.3052	28.2940	0.0000
Quadratic	1	366.8710	8.8925	0.0046
Cubic	1	5.8068	0.1407	0.7103
Pheromone×Distance	12	13.1451	0.3186	0.9818
Error (B)	45	41.2563		

1. Pheromone : Z11-16 : Ald+Z11-16 : Ac+Z11-16 : OH (1 : 1 : 0.002), 10 and 100μg. Z11-16 : Ald +Z11-16 : Ac+Z9-14 : Ac (1 : 1 : 0.001), 10 and 100μg. CK (5♀♀)
2. Distance : 0.5、1.0、1.5 and 3.0m.

性誘劑誘雄距離之測定

按釋放標記雄蛾之回收率測定性誘劑（Z11-16：Ald+Z11-16：Ac+Z11-16：OH，或 Z11-16：Ald+Z11-16：Ac+Z9-14：Ac）在田間使用時之有效距離，得知雄蛾釋放距離爲 0.5、1.0、1.5及3.0m時，處理間差異顯著（表3）。當性誘劑設置點與釋放雄蛾點距離在1.5m範圍內時，其誘雄效果幾乎成直線關係，而且距離愈近，誘效愈佳，但兩者距離在1.5及3.0m 時，性誘劑之誘效差異不顯著（圖1）。試驗期間田間之溫度、風速及雨量之記錄見表4。

表4. 小菜蛾性誘劑田間試驗之氣象記錄

Table 4. Meteorologic data during 4pm to 8am in field

Factor	1981			1982
	Nov. 10	Dec. 3	Dec. 29	Feb. 4
Temperture (°C)	12.2—21.2	8.5—23.4	15.5—21.4	13.9—24.9
Wind velocity (m/s)	0.3— 1.5	3.4— 5.4	1.6— 3.3	1.6— 3.3
Precipitation (mm)	0	0	34.5	0

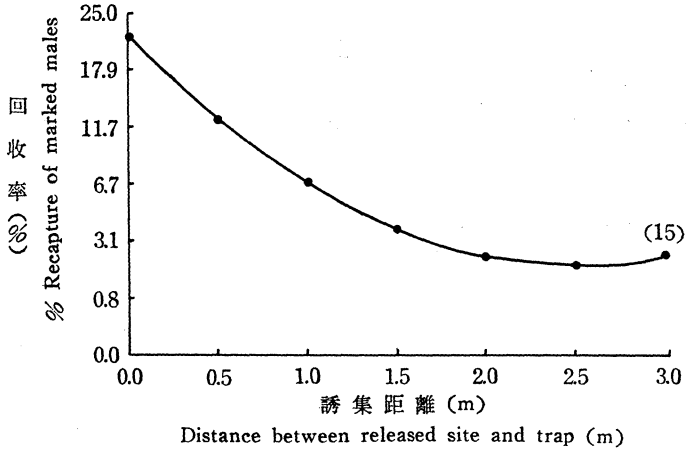


圖1. 小菜蛾性洛費蒙誘集試驗

Fig. 1. Field test on the active distance of the synthetic sex pheromone of DBM

在田間2次使用性誘劑誘雄試驗時，得知誘劑（Z11-16：Ald+Z11-16：Ac+Z11-16：OH）之間距爲 4、7及 10m，各處理間誘得之雄蛾數差異不顯著(表5)。但間距爲 2.2、3.6、5.6 及 11.0m時，各處理間之誘效差異顯著，即間距爲 2.2 與 3.6m 時，彼此間之誘雄數無顯著差異，但與間距5.6及 11.0m 之處理及無性誘劑之對照組，則差異顯著，而且距離愈近者誘得之雄蛾數愈多（表5）。此項試驗與前項標記雄蛾之回收率測得性誘劑在田間使用時有效距離小於 1.5m 之結果頗爲一致

表5. 小菜蛾性誘劑之田間放置距離試驗

Table 5. Using synthetic sex pheromone attracted male of DBM as affected by traps distance

Distance of traps	Mean no. males captured/7 days	
	Dec. 1980-Jan. 1981	Nov.-Dec. 1982
2.2	—	152.1 a
3.6	—	132.7 a
4.0	126.2 a	—
5.6	—	97.4 b
7.0	75.6 a	—
10.0	58.8 a	—
11.0	—	68.7 c
11.0 (w/o pheromone)	—	2.7 d

1. Means followed by the same letter are not significantly different at 5% level by Duncan's multiple range test.

討論與結論

添加 Z9-14：Ac 對小菜蛾性費洛蒙誘效之影響

Chow等氏認爲 **Z9-14：Ac** 乃小菜蛾性費洛蒙之類似物(parapheromone)[9]，在室內可以引起10%雄性小菜蛾之性反應，但在田間使用則無誘蟲效力[2]。Chisholm 等氏曾以觸角電析法探測小菜蛾雄蛾之觸角對 Z9-14：Ac 之反應得知其僅略次於 Z11-16：Ald 與 Z11-16：Ac。但3者若以1：1：1比例混合在田間使用時，對誘集雄蛾非但無增效作用，反而有抑制之效果[8]。本試驗在臺中地區11至2月用小菜蛾性費洛蒙，Z11-16：Ald＋Z11-16：Ac 以(1：1)：0.001比例添加 Z9-14：Ac，誘集雄蛾確有增效作用，但添加比例多或少於 1：1：0.001 均無效。又在高溫之6至7月，雖用 1：1：0.001 比例添加 Z9-14：Ac，或用1：1：0.02 比例添加 Z11-16：OH，對性誘劑均無增效作用。其原因或與誘劑成分在不同溫度之蒸散速率有關。本省冬季平均氣溫約 17.1°C (7.7-28.2°C)，夏季則高達 29.4°C (25-35°C)。而腰原與山田 (1980) 曾報導在日本仲夏時 (20°C) 小菜蛾性費洛蒙添加 Z11-16：OH (1：1：0.02) 對其誘雄數確有顯著協力效果[6]。

性誘劑之有效距離

小菜蛾性誘劑之田間使用，日本學者慣用之間距爲 5m[5]，加拿大爲 10-15m[8]。石井等氏報告該誘劑之有效距離爲 0.6-0.9m[5]。本試驗經釋放標記雄蛾之回收率與性誘劑在田間之誘得雄蛾數，均顯示該劑之有效距離約在 1m 左右。但筆者等發現此距離有時會受該蛾遷移活動之影響。如在每隔7天施藥1次之菜園，5隻活處女蛾與性誘劑於甘藍生長期中1夜間可誘得自然發生之平均雄蛾數分別爲10-469.3 與 6-232 隻，最多爲 723 與 241 隻（表6）。就此現象而言，性誘劑之誘蛾範圍顯然超出 1m 以上。其原因可能爲甘藍近收穫時，正逢小菜蛾成蛾發生期，而附近已收穫菜園中之小菜蛾亦大批遷來。故對該蛾夜間之活動範圍及其遷移距離可達多遠，尚待繼續探討。

表6. 小菜蛾性誘劑對田間自然發生小菜蛾雄蛾之誘集蟲數

Table 6. Attracted natural occurrence males DBM by using synthetic sex pheromone

Treatment	No. males captured/trap			
	1981			1982
	Nov. 10	Dec. 3	Dec. 29	Feb. 4
Z11-16 : Ald+Z11-16 : Ac+ Z11-16 : OH (1 : 1 : 0.02, 100μg)	14	25.0	24.7	232.0
Z11-16 : Ald+Z11-16 : Ac+ Z9-14 : Ac (1 : 1 : 0.001, 100μg)	6	8.3	12.3	57.0
5우우	10	10.7	15.7	469.3

小菜蛾近親繁殖對性誘劑與標記雄蛾回收率之影響

將室內繁殖小菜蛾之第三代雄蛾釋放於田間，當性誘劑放置距離爲 0.5m 時，其雄蛾之平均回收率爲 33.3-42.9%，5隻活處女蛾對照組之平均回收率爲 42.9%。若在室內繼續繁殖至第四、五及六代，各代雄蛾經釋放後，誘劑組其平均回收率爲1.7-15.0%，均較第三代雄蛾之回收率爲低（表 7）。又試驗顯示甘藍生長接近採收期時，田間小菜蛾密度升高，雖經噴布農藥亦無法予以抑制，此時第六代活處女蛾與性誘劑對田間自然發生之雄蛾誘力仍强，1夜之間分別平均可誘得雄蛾469.3與232.0-57.0隻（表 6），似可推測第四、五及六代雄蛾回收率之偏低，可能因供試之小菜蛾係連續數代之近親繁殖，其飛翔能力減弱或對性費洛蒙之感應較差所致，或可能還有其它原因存在，必須續加探討。

表7. 小菜蛾性誘劑對室內飼育小菜蛾標記雄蛾釋放田間之回收率

Table 7. Recapture percentage of continuous rearing male DBM by using synthetic sex pheromone

Treatment	Mean recapture (%)			
	generation			
	3rd	4th	5th	6th
Z11-16 : Ald+Z11-16 : Ac+ Z11-16 : OH (1 : 1 : 0.02, 100μg)	42.9	4.7	15.0	8.6
Z11-16 : Ald+Z11-16 : Ac+ Z9-14 : Ac (1 : 1 : 0.001, 100μg)	33.3	3.4	4.1	1.7
5우우	42.9	18.7	8.3	9.6

Fifty marked males were released 0.5m from the synthetic sex pheromone of DBM, 3 replications.

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Field Trapping of the Diamondback Moth by Using Synthetic Sex Pheromone

I. Tests on the Synergistic Effects of Sex Pheromone Analogues and the Effective Distance of Sex Pheromone Lure of Diamondback Moth in Field[1]

by

Ching-chin Chien and Shui-chen Chiu[2]

Summary

Three analogues, Z11- hexadecenol(Z11-16 : OH), Z9-tetradecenyl acetate(Z9-14 : Ac) and Z9-hexadecenyl propionate (Z9-16 : P), were individually added to the synthetic sex pheromone (Z11-16 : Ald+Z11-16 : Ac) of diamondback moth (*Plutella xylostella*, DBM) for testing its synergistic effects on the DBM males caught in field. In winter, the number of moths caught by a mixture of Z11-16 : Ald, Z11-16 : Ac and the 3rd compounds (Z11-16 : OH or Z9-14 : Ac) in the ratio of 1 : 1 : 0.02 or 1 : 1 : 0.001 showed 1.5 or 1.7 to 4.3 times respectively than the sythetic sex pheromone used alone. However, these two analogues did not show synergistic effect on DBM males caught. in summer

Marked adult males of DBM were released in cabbage field at 4 points located at 0.5, 1.0, 1.5 and 3.0m far from a pheromone trap. Five different kinds of lure sources were used in the traps e.g., Z11-16 : Ald+Z11-16 : Ac + Z11-16 : OH (1 : 1 : 0.02) and Z11-16 : Ald+Z11-16 : Ac+Z9-14 : Ac (1 : 1 : 0.001) in 10, and 100μg dosages respectively, and with 5 virgin females as check. The number of recaptured marked males indicated that the distance downwind of the active distance was 0.5 to 1.0m, but no difference were shown among the 5 treatments.

Z11-16 : Ald+Z11-16 : Ac+Z11-16 : OH (1 : 1 : 0.02) with 50, and 100μg dosages per trap were set up at distance of 2.2-11.0m indicated that the maximum active space between lure traps was 2.2-3.6m.

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甘藍主要害蟲在臺灣南部之發生消長[1]

李　錫　山[2]

摘要　在臺灣南部經3年連續調查甘藍主要害蟲，結果得知常見者有9種。（1）小菜蛾（*Plutella xylostella*）幾乎全年均有出現，其發生盛期由12月至次年3月，高峯都在2月。其每年發生豐量受氣象因子影響，差異頗鉅，夏季降雨雖可影響其發生，但在春季微量降雨反可助長發生。（2）白粉蝶（*Artogeia rapae crucivora*）亦幾乎全年都有出現。一年有兩次發生盛期，一在2—5月，最高峯多在4月或3月。另一次在9—12月，其次高峯在10月。每年發生豐量和各月之起伏，受晴、雨天之影響至鉅。因該成蟲多在晴朗的天氣出現。（3）大菜螟（*Crocidolomia binotalis*）亦全年均有出現。5—12月爲其發生盛期，高峯在9—11月。惟每年各異，其發生除受氣象因子影響外，和白粉蝶的族羣有此起彼落的現象。（4）斜紋夜盜（*Spodoptera litura*）亦全年出現，6—12月爲其發生盛期，高峯在11或12月。其發生情形和大菜螟頗相類似。（5）菜心螟（*Hellula undalis*）之發生盛期在4—9月，無明顯高峯，1—3月幾無發生。（6）擬尺蠖（*Trichoplusia ni*）於3—9月爲其發生盛期，因密度低無明顯高峯。（7）黃條葉蛬（*Phyllotreta striolata*）發生盛期因年而異，但以5—12月之蟲數較1—4爲高。（8）僞菜蚜（*Lipaphis erysimi*）每年9月至次年2月爲其發生盛期，高峯期受8月降雨量多寡之影響，而出現在9、10或次年1月。（9）桃蚜（*Myzus persicae*）發生盛期在1—4月，由前一年8月降雨量多寡，可推測次年1—3月桃蚜高峯期發生之遲早。

十字花科蔬菜爲國人所偏好，所以亦爲目前臺灣栽培最普遍，產量最多之蔬菜。尤其在春、秋、冬三季產量最豐。爲害該蔬菜之害蟲種類亦多[3,10]，影響其產量和品質至鉅。有關十字花科蔬菜害蟲在臺灣之發生消長，在此之前先後有張艮傳[8]，王雪香[1]在北部及陳秋男等[7]在中部之調查報告。但南部僅有李錫山[5]對黃條葉蛬（*Phyllotreta striolata*）之消長調查資料，至鱗翅類及蚜蟲類害蟲之資料則尚缺如。此類害蟲如小菜蛾（*Plutella xylostella*），白粉蝶（*Artogeia rapae crucivora*），大菜螟（*Crocidolomia binotalis*），斜紋夜盜（*Spodoptera litura*）；菜心螟（*Hellula undalis*），擬尺蠖（*Trichoplusia ni*），僞菜蚜（*Lipaphis erysimi*）及桃蚜（*Myzus persicae*）等爲目前在十字花科蔬菜發生最普遍之害蟲。復因臺灣之地形爲南北長而東西窄，南北之天候差異頗鉅，害蟲之發生亦隨氣象因子和生態環境之變遷而異。據張氏在臺北之調查，以小菜蛾、白粉蝶、大菜螟、斜紋夜盜、黃條葉蛬、僞菜蚜和桃蚜等發生最多。綠黥白粉蝶（*Pieris canidia sordida*）、菜心螟、擬尺蠖和白紋夜蛾（*Spodoptera exigua*）等發生較少。主要發生期因寄主之不同而異。小菜蛾在青梗白菜上之發生高峯分別在2和5月；在甘藍則在12至次年1月。僞菜蚜在青梗白菜之族羣密度高峯在3、4月；但同時期在甘藍之密度甚低。桃蚜族羣之高峯在青梗白菜分別於11和4月；在

1.臺灣省農業試驗所　研究報告1310號。本系溫宏治，蔡世雄、陳黨、劉少武諸先生協助調查及林明枝、張淑敏、林素美、趙永蘭、簡月美諸小姐整理資料，文成後承臺灣大學朱耀沂主任，農委會陳秋男博士斧正，及本分所呂鳳鳴、梁曉雲小姐協助統計、繪圖，並蒙行政院國科會七十二年度研究補助，謹此一併誌謝。

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甘藍則在12月。黃條葉蚤在青梗白菜上之高峯在8月；在甘藍，其高峯期在3、4月。所以害蟲之族羣動態，或因對寄主之偏好性及寄主間栽培季節之不同而有差異。陳氏在中部係調查包心白菜所發生之害蟲。其結果仍以小菜蛾、大菜螟、白粉蝶、僞菜蚜和桃蚜等數種害蟲之族羣密度較高；黃條葉蚤、斜紋夜盜次之；菜心螟、擬尺蠖和猿葉蟲等之密度不相上下。至各主要害蟲之消長，小菜蛾和白粉蝶之發生盛期都在11月至次年4月，大菜螟在7—11月，菜心螟在7—9月，斜紋夜盜全年均有出現，僞菜蚜之族羣密度於7—9月較桃蚜爲高，但桃蚜於9、10月起便超越僞菜蚜。爲瞭解上述害蟲在臺灣南部發生消長，特將三年調查結果報告如下。

材料與方法

每半月盆栽70株甘藍，定植後暫置於玻璃網室內半月，再將其中60株移置室外，經一週後即開始調查害蟲數。每週每批各固定調查40株，每批連續調查8週（次）。如此，每週乃調查不同生長期之甘藍4批共160株，使各種害蟲之族羣包括在不同生長期之甘藍均計算在內，以免因甘藍之生長期不同，害蟲之族羣密度各異而影響其代表性。調查時全株每葉均經檢查，分別記錄各種害蟲之蟲期及其棲息葉數。蚜蟲類則以各蟲期之蟲數分爲5級，換算其爲害度，各種害蟲復計算其爲害株及爲害葉百分率，以明瞭該蟲在植株間及植株內棲羣分佈情形。蚜蟲類之爲害度分級[30]（並加修正）及計算公式如下：1級＝1－5隻，2級＝6－20隻，3級＝21－50隻，4級＝51－100隻及5級＞100隻。

$$\text{爲害度}=\frac{\Sigma\,(\text{級距}\times\text{該級距被害葉數})}{5\times\text{調查葉數}}\times 100$$

鱗翅目及黃條葉蚤諸害蟲之直線迴歸方程式圖中之蟲數均經以 $\sqrt{x+1}$ 換算後標示之。

結果與討論

自民國71（1982）年1月7日至民國73（1984）年12月28日三年共調查72批。雖預定每批甘藍調查8週，但因調查期間若逢害蟲發生高峯期，尤其是白粉蝶，或雨期受豪雨侵襲等之影響，有些甘藍經調查數週後，最少者僅3、4週，便告缺株。故每株之調查次數，每隨氣象、季節或害蟲發生密度不同而異。三年期中，分別在1982年調查6,285株（次），1983年調查4,975株（次），1984調查5,022株（次）；三年合計調查16,282株（次）。調查期中，在甘藍出現之主要害蟲包括鱗翅目之小菜蛾、白粉蝶、大菜螟、菜心螟、斜紋夜盜及擬尺蠖等；鞘翅目僅黃條葉蚤；蚜蟲類有僞菜蚜和桃蚜等。但在1982年10月8日調查時發現菜蚜（*Brevicoryne brassicae*）有翅成蟲一隻在甘藍葉背，以後便未見再出現。1984年3月曾發現菜潛蠅（*Liriomyza brassicae*（Riley）發生很嚴重，但關於該蟲之生態及發生消長，容後另篇詳述。茲將上述9種害蟲之三年發生消長分述如下：

（一）小菜蛾：該蟲在三年調查期中除1984年5月18日，7月13和27日等三次未見其幼蟲外，其餘各次調查都有。每年由12月至次年3月爲其發生盛期，三年之高峯都在2月（圖1、表1），其次高峯在9—10月間，而以6—8月最低。全年其族羣動態，依月別似有規律可循，尤其高峯期於三年中都發生在2月中旬。單株最高密度分別爲1982年2月12日232隻，1983年2月18日572隻，1984年2月17日165隻，前後三年僅相差6天。

小菜蛾每年其族羣之大小，受氣象因子之影響，差異很大。以2月之高峯期爲例，每10株甘藍上之小菜蛾平均蟲數爲1982年462.82隻，1983年967.11隻，1984年僅160.03隻。其族羣大小相差達6倍之多（表1）。此種現象，除直接受氣象因子影響外，其他如種間之競爭及寄主植物之生長發育狀態之良窳等影響至鉅[25,29]。如表1所示，1983年2月之降雨量爲三年中最高者，但小菜蛾之族羣亦在該月爲三年中最高者。雖降雨量多寡爲影響該蟲族羣之重要因素[1,9,18]，但若日平均降雨量低，可能反而有利於植物生長及小菜蛾之繁殖。例如臺灣北部冬、春微雨不斷，但小菜蛾之族羣密度仍在2

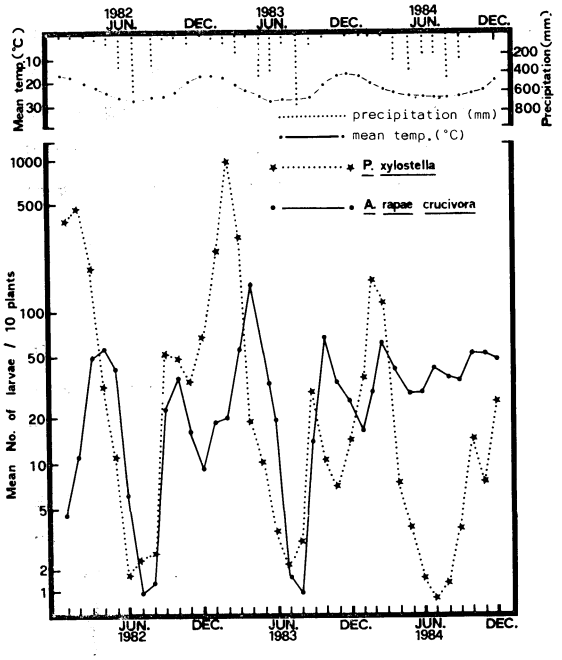


圖1.甘藍小菜蛾與白粉蝶幼蟲棲羣消長。

Fig. 1 Larval population of *Plutella xylostlla* and *Artogeia rapae cruclvore* on cabbaege.

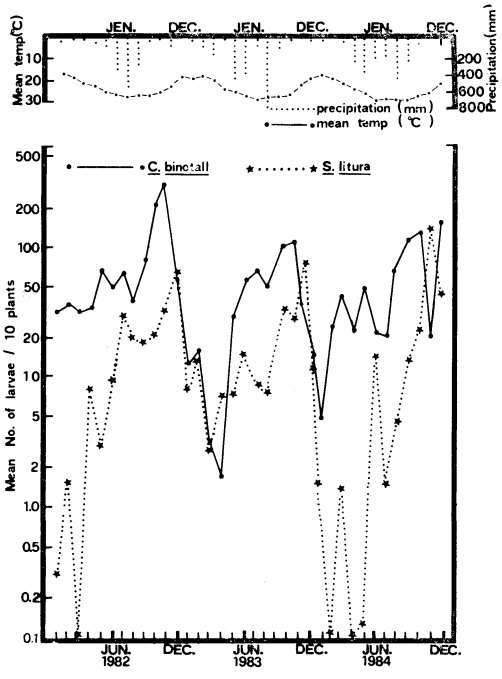


圖2.甘藍大菜螟與斜紋夜盜幼蟲棲羣消長。

Fig. 2 Larval population of *Crocidolomia binotalis* and *Spodotera litura* on cabbage.

表1.小菜蛾在 1 ～ 3 月（1982～1984）族羣之大小與氣溫及降雨量關係之比較

Table 1. Comparison of the populations of *Plutella xylostella* in relation to the temperature and precipitation from January to March during 1982-1984

Month		$\bar{X}$ density (larvae/10 plants)	$\bar{X}$ temp. (℃)	Monthly rainfall (mm)	Rainy days	Max. rainfall (mm/day)
	Jan.	370.41	17.58	0	0	0
1982	Feb.	462.83	19.53	17.0	2	10.0
	Mar.	182.75	22.27	0.8	2	0.5
	Jan.	239.11	19.21	34.0	7	12.6
1983	Feb.	967.11	18.36	91.5	10	31.5
	Mar.	312.83	20.60	177.8	13	60.0
	Jan.	31.50	17.11	6.4	1	6.4
1984	Feb.	160.03	18.02	0	0	0
	Mar.	113.33	21.63	5.5	3	4.3

—3月達高峯[1,9]。在芬蘭和蘇格蘭亦有此現象[18,24]。此外，冬、春二季氣溫低，小菜蛾之生殖力(Fecundity)較高溫時爲大。雌成蟲之產卵量在低溫季節，1—4月，較高溫之5—9月約增加52%左右；其卵之孵化率約增加16%。因其發育適溫爲 20—25°C[6,15]。所以小菜蛾之族羣密度在夏季較

低，除受驟雨有直接影響外，高溫造成生殖力降低亦爲主因。

至於2—4月影響小菜蛾族羣密度升降之間接因素，可能係受種間競爭之影響。如白粉蝶幼蟲多在蔬菜之生長初期出現（圖12），其食葉量爲小菜蛾之13倍[26,27]。故若在蔬菜之生長初期有白粉蝶幼蟲爲害，後期之其他害蟲便因食物缺乏而減少。由於白粉蝶多在晴天產卵；若逢陰雨，其產卵行爲受阻，可能造成其族羣降低，因而有利於小菜蛾之繁殖。例如，1984年2月之氣溫雖爲三年中最低者，但因無雨量（表1），故白粉蝶之族羣在該月爲三年中同月最高者（圖1）。反之，小菜蛾之族羣在該月爲三年中同月最低者（表1）。復甘藍之生長期適當的雨量，可使其發育良好，葉部組織幼嫩，葉數增多，而能容忍較多之小菜蛾爲害，故害蟲族羣密度亦豐。

小菜蛾幼蟲在株間之分佈，以爲害株率而論，三年中最高者達95%，月平均最高爲74—81%（圖6），年平均約41%。有時小菜蛾族羣密度雖增高，但爲害株率並不隨之增加（圖15）。如1982年1月小菜蛾幼蟲平均蟲數爲370.4隻／10株，其平均爲害株率爲80.94%，但1983年2月其平均蟲數爲967.1隻／10株，但其平均爲害株率却僅80.04%。兩相比較，蟲數雖增加2.6倍，但其平均爲害株率幾無差別。小菜蛾族羣在低密度時其爲害株率隨蟲數之小幅增加而大幅升高。如其爲害株率在60%時之族羣密度僅約62隻／10株，但當其爲害株率達70%時其族羣密度躍升爲283隻／10株，其間平均蟲數約增4.5倍之多。所以小菜蛾在低密度時其爲害株率偏高，至密度驟然升高時其爲害株率却緩慢增加。小菜蛾幼蟲在植株內之分佈，以受害葉觀之，三年中之最高者爲56.54%，月平均最高者由25—51%不等，此和其族羣密度高低有密切關係（圖1和9）。有關小菜蛾幼蟲數（x）和受害株率及受害葉率（y）之迴歸方程如圖15。由圖所示，小菜蛾族羣密度高低與受害葉率之關係較受害株率爲密切。

小菜蛾之族羣密度和其他鱗翅目害蟲比較，在1～3月都在首位（表2）。若以三年全年比較1982—1983都佔諸害蟲之首，但1984便落在大菜螟和白粉蝶之後。此乃因氣象因子影響及種間族羣競爭所致。

表2.六種鱗翅類幼蟲在甘藍每月發生平均百分比

Table 2. Percent composition of 6 species of lepidopterous larvae on cabbage each month during 1982-1984

Species	%												
	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.	Overall
Plutella xylostella	78.0	86.4	68.6	15.5	7.8	2.7	1.8	3.3	16.6	9.1	5.3	20.4	26.4
Artogeia rapae crucivora	12.2	5.9	20.3	58.7	38.1	23.1	21.9	12.6	13.3	23.5	15.6	19.4	22.0
Crocidolomia binotalis	7.0	7.0	10.0	20.0	42.1	54.6	63.4	65.9	56.4	56.1	38.2	35.6	38.0
Spodoptera litura	2.0	0.6	0.3	3.4	11.0	17.1	11.8	15.8	12.9	10.9	40.8	24.2	12.6
Hellula undalis	0	0	0.1	1.6	0.4	1.2	1.1	2.2	0.6	0.3	0.1	0.1	0.6
Trichoplusia ni	1.0	0.1	0.4	0.8	0.7	1.4	0	0.2	0.2	0.1	0	0.3	0.4

（二）白粉蝶：該蟲在1982年之6—8月各有1—2次和1983年之7—8月亦各有一次未見其幼蟲外，其餘各次調查均有出現。一年有兩次發生盛期。第一次在2—5月，其高峯有兩年在4月，1984年4月因降雨量爲三年中同月最高者，故白粉蝶發生較少，其高峯則出現在3月。第二次發生盛期爲9—12月，其高峯都在10月。全年兩次高峯之族羣密度比較，均以3—4月高於10月（圖1）。1982之6—8月和1983之7—8月爲該蟲發生之最低點。1984除1月之族羣密度最低外，5—6月亦

較低，其餘各月該蟲族羣之起伏除高峯外沒有很大差距。

白粉蝶族羣密度之高低受氣象因子如降雨量，降雨日數和氣溫高低等之影響至鉅。因其成蟲多在晴朗而和暖的天氣出而產卵，故其發生盛期多在高溫乾燥之月份。以1984年 7 — 8 月爲例，雖在濕季，但因降雨量爲三年中同期最少者，故其時之族羣密度較其餘兩年爲高。1984全年累積氣溫較其餘兩年爲高，故全年發生豐量亦爲三年中最高者。1983年 4 月之降雨量和降雨日數爲三年中同月最少者，故白粉蝶之族羣奇峰突起，爲三年中同月最高者（圖 1 ）。

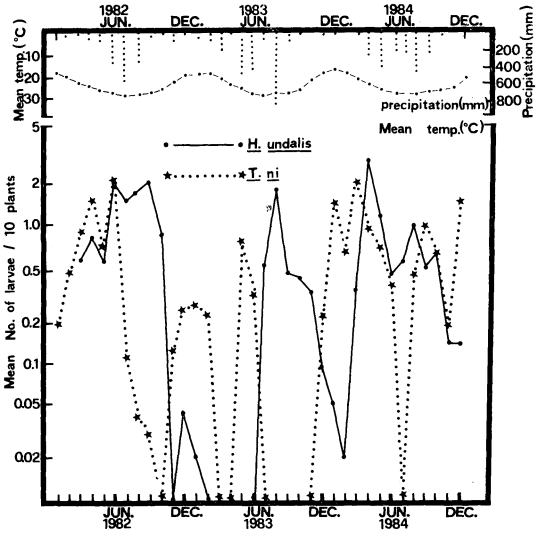


圖3.甘藍菜心螟與擬尺蠖幼蟲棲羣消長。

Fig. 3 Larval population of *Hellula undalis* and *Trichoplusia ni* on cabbage.

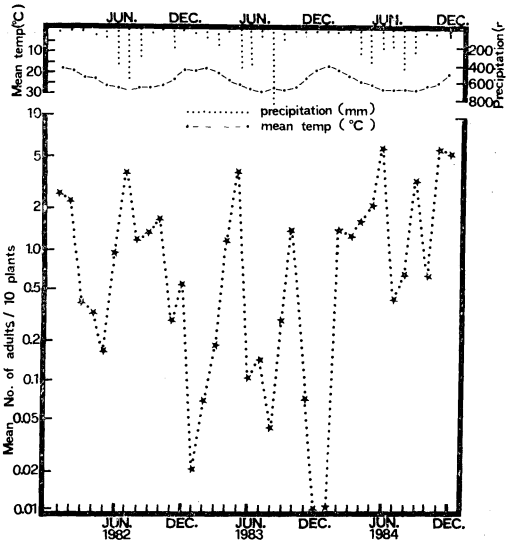


圖4.甘藍黃條葉蚤成蟲棲羣消長。

Fig. 4 Adult population of *Phyllotreta striolata* on cabbage.

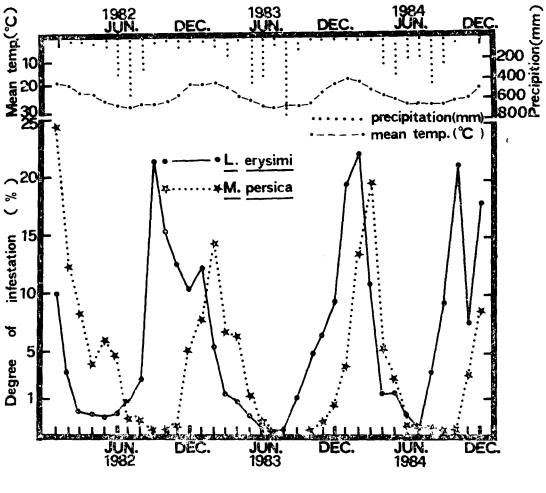


圖5.甘藍僞菜蚜與桃蚜爲害度之變遷。

Fig. 5 Degree infestation of *Lipaphis erysimi* and *Myzus persicae* on cabbage.

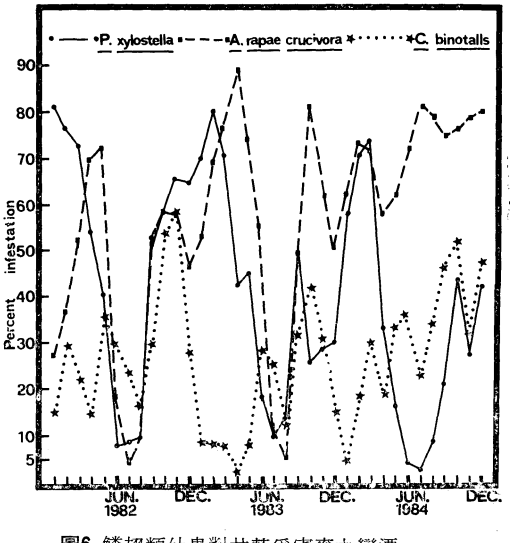


圖6.鱗翅類幼蟲對甘藍爲害率之變遷。

Fig. 6 Percentage of cabbage plants infested by the species of lepidopterous larvae,

白粉蝶幼蟲在甘藍生長期中之族羣密度以調查時之第三週最高（圖12）。因其幼蟲食葉量大，此時甘藍葉片已被嚴重食害，殘存葉片不足以維持更多蟲數，故在第四週以後其密度便急劇下降。該蟲之株間分佈較小菜蛾爲廣，其爲害株率三年中最高者達 100%，月平均最高由 73—89%（圖 6），年平均 54.78 %，爲鱗翅目害蟲中最高者。白粉蝶和小菜蛾兩者在族羣密度高時之分佈模式略有差異。前者族羣密度較小，故和株間之分佈略成比例增高，後者之族羣密度較大，故當其密度驟增時，其在

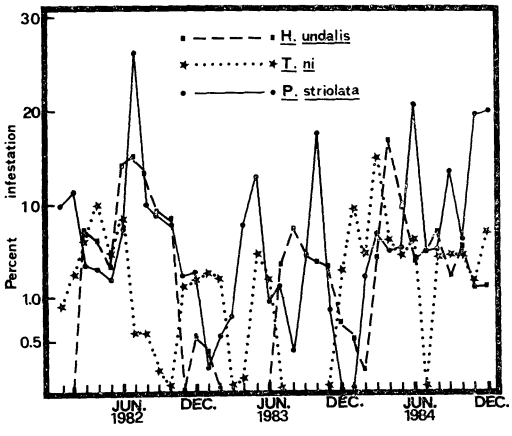


圖7.鱗翅類與黃條葉蚤對甘藍爲害率之變遷。

Fig. 7 Percentage of cabbage plants infested by the species of lepidopterous larvae and the adults of stripped flea beetle.

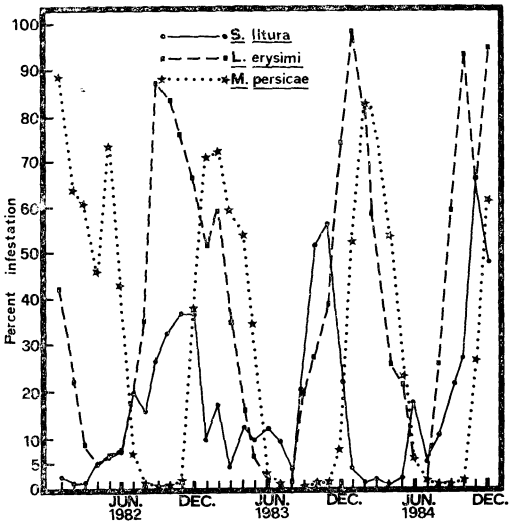


圖8.斜紋夜盜與兩種蚜蟲對甘藍爲害率之變遷。

Fig. 8 Percentage of cabbage plants infested yb the larvae of tobacco cutworm and two species of aphids.

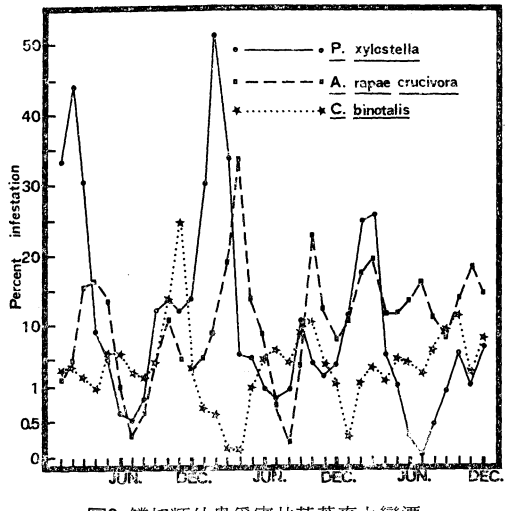


圖9.鱗翅類幼蟲爲害甘藍葉率之變遷。

Fig. 9 Percentage of cabbage leaves infeseted by the species of lepidopterous larvae.

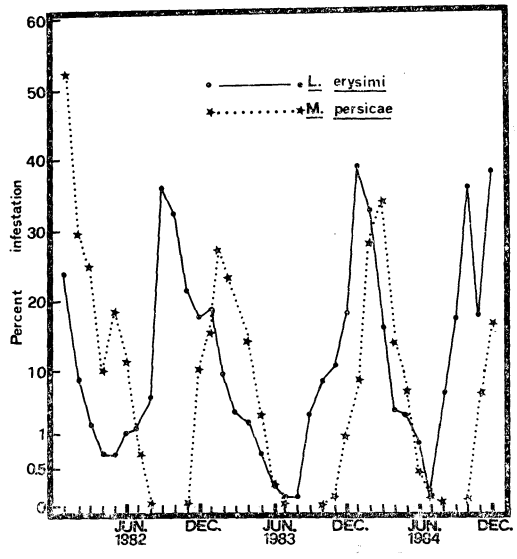


圖10.僞菜蚜和桃蚜爲害甘藍葉率之變遷。

Fig. 10 Percentage of cabbage leaves infested by the species of *Lipaphis erysimi* and *Myzus persicae*.

株間之分佈却徐緩而升。該蟲幼蟲在植株內之分佈，以受害葉率示之，三年中最高者達 54.17 %，月平均最高由16—33%（圖 9），較小菜蛾低。雖白粉蝶之族羣密度較小菜蛾和大菜螟爲低，但其在田間之分佈却較其他兩種害蟲爲廣，食葉量亦較大，同時亦有左右此兩種害蟲族羣變動之趨向，實爲十字花科蔬菜之首要害蟲。該蟲之幼蟲數（x）與受害株率和受害葉率（y）之迴歸方程式如圖 16。由圖所示，白粉蝶族羣密度之高低和受害葉率之關係較爲密切。該蟲之幼蟲數，全年各月和其他鱗翅目害蟲比較，其所佔百分比在 4 月爲諸害蟲中最高者（表 2）。

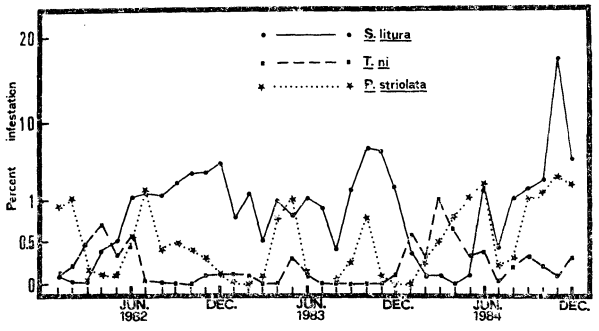


圖11.斜紋夜盜擬尺蠖和黃條葉蚤爲害甘藍葉率之變遷。

Fig. 11 Percentage of cabbage leaves infested by *Spodoptera litura*, *Trichoplusia ni* and *Phyllotreta striolata*.

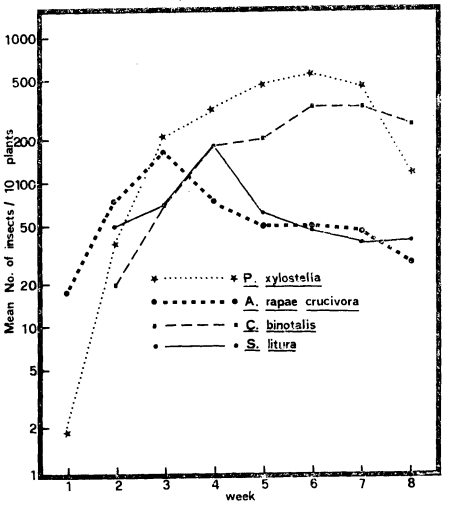


圖12.四種害蟲在甘藍上棲羣高峯期之增長比較

Fig. 12 Population development of the insect pests on cabbage during their peak period.

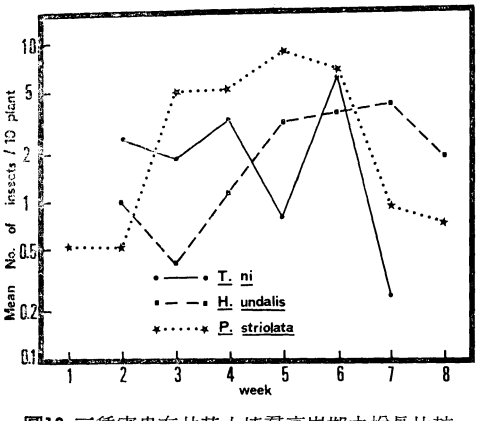


圖13 三種害蟲在甘藍上棲羣高峯期之增長比較

Fig. 13 Population development of the insect pests on cabbage during their peak period.

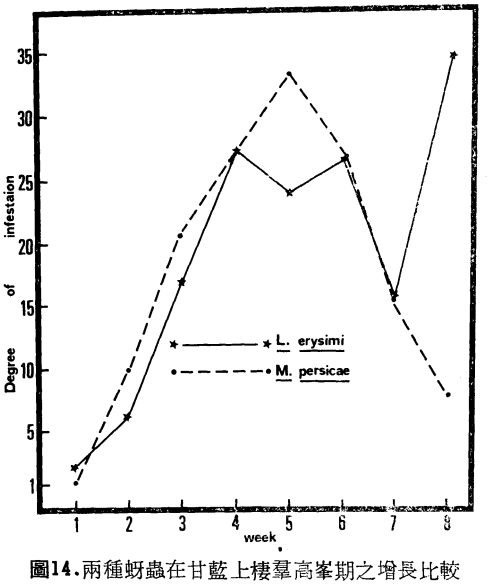


圖14.兩種蚜蟲在甘藍上棲羣高峯期之增長比較

Fig. 14 Population development of the aphids on cabbage during their peak period.

（三）大菜螟：該蟲在三年調查期中，僅1983年4月29和5月6日兩次未見其幼蟲。該蟲全年除1—4月發生較少外，5—12月爲該蟲發生盛期，其高峯在9—11月間。該蟲多發生在高溫之月份，降雨量之多寡則影響不大。例如降雨量多之6—8月，其族羣密度顯較其他鱗翅目害蟲爲高（表2）

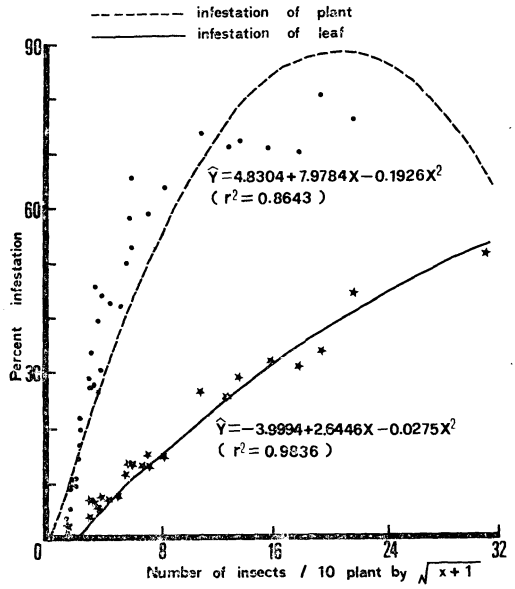


圖15.小菜蛾幼蟲數與甘藍受害株率和受害葉率之迴歸方程。

Fig. 15 Regression between the insect number of *Pluella xylostella* and the infested plant and leaf of cabbage.

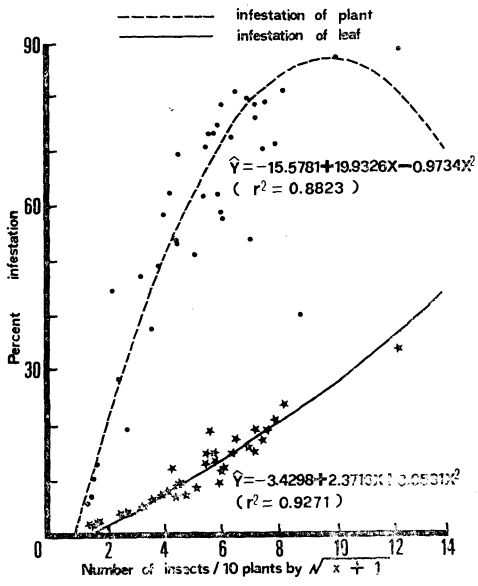


圖16.白粉蝶幼蟲數與甘藍受害株率和受害葉率之迴歸方程。

Fig. 16 Regression between the insec number of *Artogeia rapae crucivora* and the infested plant and leaf of cabbage.

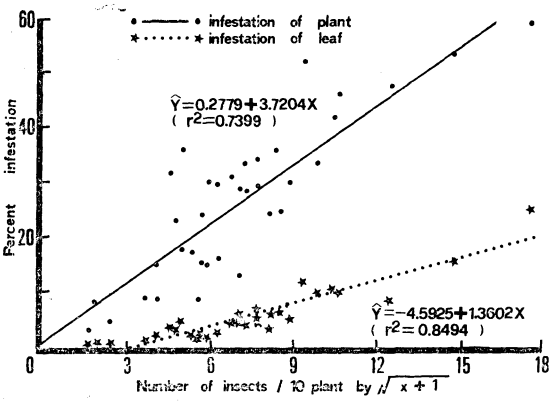


圖17.大菜螟幼蟲數與甘藍受害株率和受害葉率之迴歸方程

Fig. 17 Regression between the insect number of *Crocidolomia binotalis* and the infested plant and leaf of cabbage.

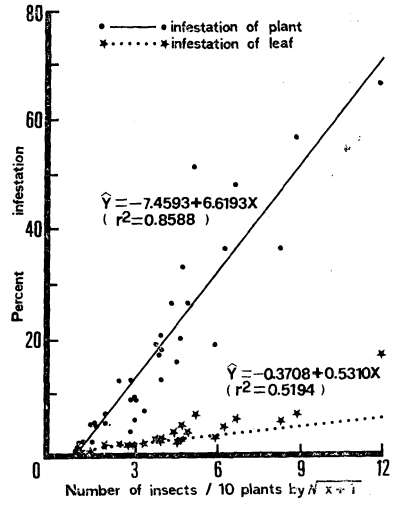


圖18.斜紋夜盜幼蟲數與甘藍受害株率和受害葉率之迴歸方程。

Fig. 18 Regression between the insect number of *Spodoptera litura* and the infested plant and leaf of cabbage.

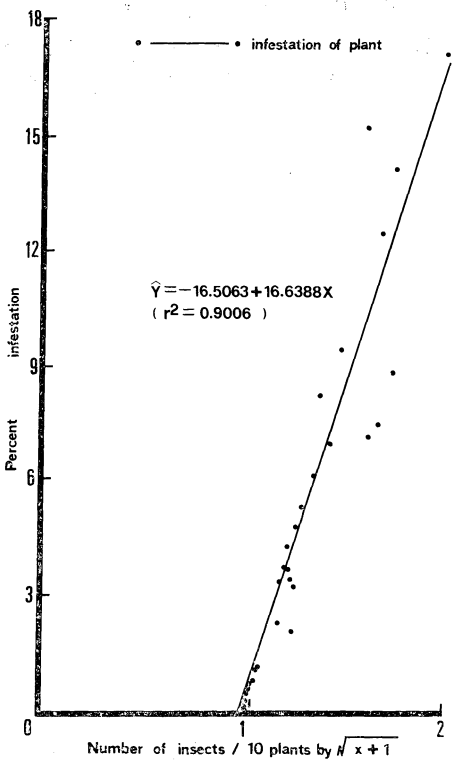


圖19.菜心螟幼蟲數與甘藍受害株率之迴歸方程。

Fig. 19 Regression between the insect number of *Hellula undalis* and the infested plant of cabbage.

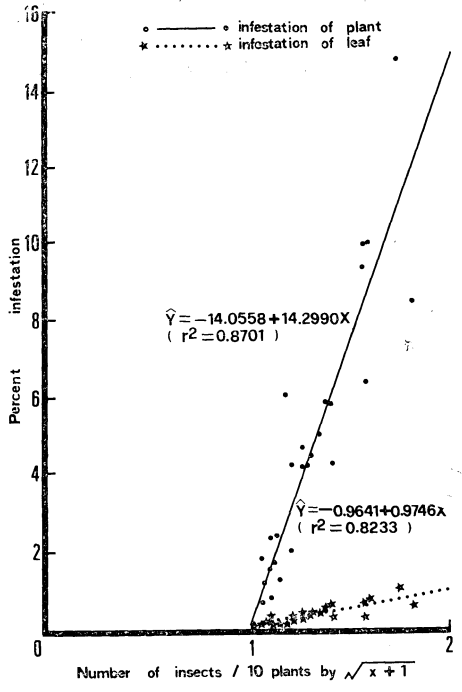


圖20.擬尺蠖幼蟲數與甘藍受害株率和受害葉率之迴歸方程

Fig. 20 Regression between the insect number of *Trichoplusia ni* and the infested plant and leaf of cabbage.

。因其爲害部位多在老葉背面或蛀入結球內，較不易受雨水之影響。1982年11月爲三年中該蟲之族羣最高者，考其原因，可能與降雨量和白粉蝶之發生有密切關係。因是年11月之降雨量（91.7公厘）爲三年中同月最高者，同時白粉蝶之族羣亦爲三年中最低者。反觀1984年11月之降雨量爲零，白粉蝶之族羣密度均比前兩年之同月爲高，但大菜螟在該月之族羣却爲三年中最低者。同樣的情況，該蟲在1—4月發生較少，亦因受小菜蛾和白粉蝶兩者之族羣所壓抑（圖1和2）。

大菜螟幼蟲喜羣集爲害，故在田間之分佈不若白粉蝶和小菜蛾之分散。三年中之爲害株率最高者90%，月平均由42—58%（圖6），年平均爲26.38%。該蟲之爲害葉率三年中最高者37.64%，月平均最高由10.26—24.68%（圖9），年平均爲4.95%。該蟲之幼蟲數（x）與受害株率及受害葉率（y）之迴歸方程式如圖17。其蟲數和受害葉率之關係較密切。

大菜螟之幼蟲數，全年各月和其他鱗翅目害蟲比較，其所佔百分比，在5—10月都甚高，多在高溫多濕之月份，尤以7—8月最高（表2）。全年發生密度僅次於小菜蛾，1982—83都佔第二位，1984躍居第一位。所以該蟲和小菜蛾及白粉蝶都屬十字花科蔬菜之主要害蟲。該蟲多發生在蔬菜生長之中後期，又其分佈，無論其爲害株和爲害葉率都不若前兩種害蟲分散，故其重要性較前兩種爲小。

（四）斜紋夜盜：該蟲在三年中之2—5月每月偶有1—2次未見其幼蟲，其餘各月每次調查均有出現。其發生密度除1—5月較低外，6—12月爲其盛期，11—12月爲高峯期，但以11月居多（圖2）。除高峯外，其發生盛期和大菜螟頗相似，都在氣溫較高之月份發生較多。該蟲和白粉蝶之種間競爭小，屬羣集型爲害。其族羣密度雖較大菜螟低（因其3、4齡以後幼蟲多潛入土中），但在田間分佈較大菜螟分散。三年中最高爲害株率有達100%者，月平均最高由36.8—66.5%（圖8），年平

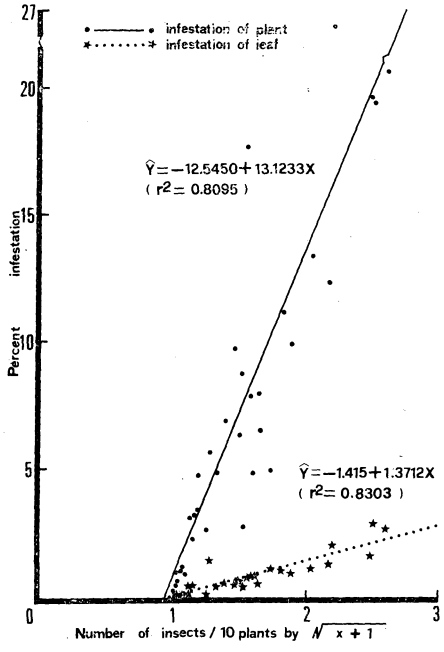


圖21.黃條葉蚤蟲數與甘藍受害株率和受害葉率之迴歸方程。

Fig. 21 Regression between the insect number of *Phyllotreta striolata* and the infested plant and leaf of cabbage.

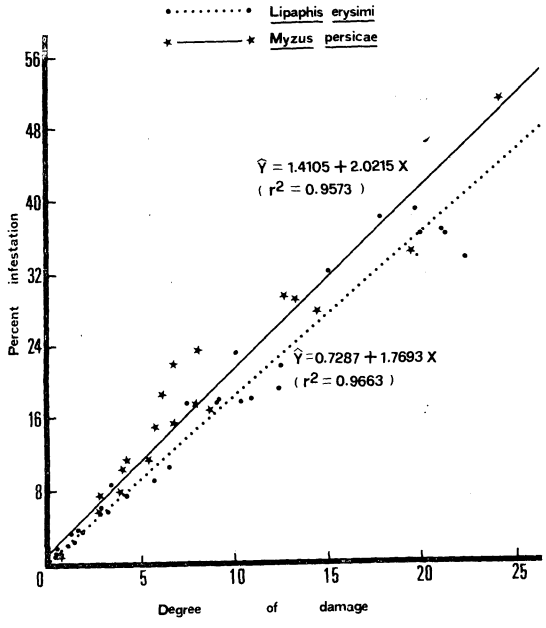


圖22.兩種蚜蟲爲害度與甘藍受害葉率之相關關係

Fig. 22 Relationship between the damage degree of aphid and percentage of infested leaf of cabbage.

均17.3%。其幼蟲最高爲害葉率有達46.77%，月平均最高由4.10—17.21%（圖11），年平均2.07%，較大菜螟爲低。初齡幼蟲多羣集葉背，三齡以後漸分散潛入土中或於心部包葉爲害，惟不若大菜螟之嚴重。其全年發生密度顯較前述三種鱗翅目害蟲爲低（表2）。其幼蟲數（x）與受害株率及受害葉率（y）之迴歸方程式如圖18。其蟲數與受害株率之關係較密切。

（五）菜心螟：該蟲多發生於蔬菜生長前期。其發生盛期在4～9月間，高峰分別在4、6、8月不定。發生盛期多在高溫多濕之雨季（圖3）。幼蟲之爲害部位多在心部，牽絲結葉隱蔽其中，雖降雨量多亦不受影響，和大菜螟類似。該蟲之密度很低，三年其月平均最高爲害株率僅7.48～17.02%（圖7），年平均4.24%。其幼蟲數和受害株率之直線迴歸方程式如圖19。其全年發生密度雖偏低，但仍爲夏季十字花科蔬菜主要害蟲。

（六）擬尺蠖：該蟲主要發生在3～9月，由於其密度低無明顯之高峯期，僅在氣溫較高之月份發生較多（圖3）。三年其月平均最高爲害株率爲4.19～14.71%（圖7），年平均3.13%。月平均最高爲害葉率爲0.32～0.98%(圖11)，年平均0.25%。其全年發生密度和其他鱗翅目害蟲比較，其比率

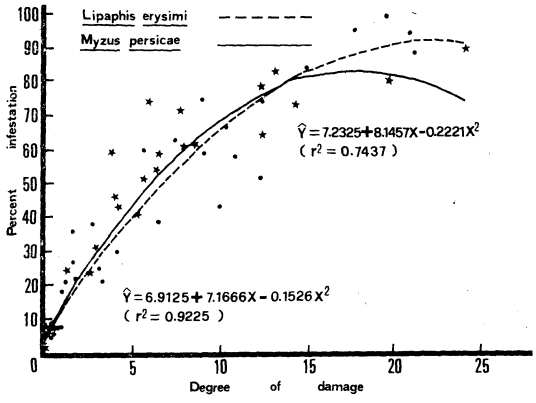


圖23.兩種蚜蟲爲害度與甘藍受害株率之相關關係

Fig. 23 Relationship between the damage degree of aphids and percentage of infested plant of cabbage.

係最低者之一（表2）。其幼蟲數（x）與受害株率及受害葉率（y）之迴歸方程式如圖20。蟲數和受害株率之關係較密切。

（七）黃條葉蚤：該蟲之發生盛期因年而異。1982其發生盛期在1、2月和7～10月。1983則在4、5月。1984在5、6和11、12月。其中1984年可能係高溫低濕，其發生密度最高。綜觀三年該蟲之發生盛期由5～12月之間除8月較低外，其餘都較1～4月之密度高（圖4）。但李氏[5]前在小白菜調查結果，該蟲之發生高峯期乃在1、2月。此可能由於寄主植物之不同及栽培期之差異和對寄主之偏好性而有遷移爲害之現象。該蟲三年之最高爲害株率爲43.57%，月平均最高爲害株率由17.67～26.42%（圖7），年平均6.85%。其最高爲害葉率爲 5.79%，月平均最高爲害葉率爲 1.22～2.78%（圖11），年平均爲0.66%。其成蟲數（x）和受害株率及受害葉率（y）之迴歸方程式如圖21。

（八）僞菜蚜：該蟲除因受雨季豪雨之影響發生較少外，全年各月幾均有出現。迨雨期結束後，每年由9至次年2月爲其發生盛期，受雨期長短及降雨量多寡之影響，其高峰期亦因年而異。所以三年該蟲發生之高峯分別在9、1及10月不定。但由三年8月降雨量之多寡，幾可推測該蟲高峯期發生之早晚。如 1982年8月之降雨量 311.9公厘，爲三年中最少者，該蟲之高峰提前在9月。1983年8月之降雨量825.4公厘，爲三年中最多者，其高峯便延至1984年1月。1984年8月之降雨量444公厘，高峯則發生在同年之10月（圖5）。

僞菜蚜之爲害度最高達 41.39%，三年月平均之最高爲害度由 22.26～21.38%。其最高爲害株率達100%。三年月平均最高爲害株率由74.16～98.23%（圖8），年平均39.59%。其株間之分佈亦較白粉蝶和小菜蛾爲廣。其發生期間及株間之分佈亦較桃蚜爲長且廣。其最高爲害葉率達 59.60%，月平均最高爲害葉率爲 19.01～38.97%（圖10），年平均爲害葉率爲 12.27%。其爲害度（x）與平均受害株率及受害葉率（y）之迴歸方程式如圖22和23。

（九）桃蚜：該蟲在7～10月因高溫及豪雨的影響，7、8兩月偶有發生，9、10兩月幾無踪跡。三年之中均在11月出現至次年1～4月爲其發生盛期，5、6月急劇下降。其高峯乃受前一年8月降雨多寡之影響而早晚不一。如1981年8月降雨量爲259.2公厘，其高峯在次年之1月。1982年8月之降雨量爲311.9公厘，其高峯在次年之2月。1983年8月之降雨量爲825.4公厘，其高峯在次年之3月（圖5）。顯而易見，8月之降雨量越多，便影響次年桃蚜之高峯期越往後移。該蟲在臺灣南部出現之期間較僞菜蚜短，此可能較不適於高溫多濕使然。冬、春二季爲其發生盛期，夏末和秋季則不發生。

桃蚜之最高爲害度爲 34.85%，較僞菜蚜低。其最高爲害株率達 99.38%，三年月平均最高由72.13～88.03%（圖8），年平均 30.80%。爲害葉率最高達 66.78%，較僞菜蚜高，月平均最高爲害葉率由 27.67～51.20%（圖10），年平均 12.74%。爲害度（x）與爲害株率和爲害葉率（y）之迴歸方程式如圖22及23。

上述數種害蟲當其高峯期在甘藍生長期中出現先後及其爲害盛期各異。其中白粉蝶在第一週之平均蟲數即達 17.38隻／10 株，爲鱗翅類諸害蟲中最高者，第三週達最高峯。小菜蛾在第一週之族羣密度僅次於白粉蝶，約其⅓，但第二週之增殖率便超越白粉蝶，第六週達最高峯。大菜螟在第二週方始出現，其密度逐漸增高，至第七週達最高峰。斜紋夜盜亦在第一週出現，但密度很低，第二週漸增，第四週達高峰；因其老熟幼蟲多潛入土中，故在後期之族羣密度反較大菜螟爲小（圖12）。擬尺蠖和菜心螟在第一週均無出現，分別至第六、七週達高峯。黃條葉蚤在第一週便出現，第五週達高峯（圖13）。僞菜蚜和桃蚜都在第一週出現，前者之高峯在第八週，後者之高峯在第五週（圖14）。由於在蔬菜生長期中害蟲族羣之高峯期出現之遲早，便可瞭解其爲害之嚴重程度如何。

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Seasonal Occurrence of the Important Insect Pests on Cabbage in Southern Taiwan[1]

Hsi-Shan Lee [2]

Summary

Seasonal occurrence of nine species of insect pests on cabbage was investigated in southern Taiwan during 1982 to 1984. *Plutella xylostella* was abundant from December to March of the next year with population peaks in February. *Artogeia rapae crucivora* appeared from March to May with a peak in April or March; and from September to December with a peak in October. *Crocidolomia binotalis* occurred almost year round but was numerous from May to December with a peak in November. *Spodoptera litura* also occurred in the warmer months from September to December with peaks in November or December. *Hellula undalis* occurred from April to October. Its population is very low. *Trichoplusia ni* occurred very often in the warmer months with no peak period. The looper was extremely low as compared to other species. *Phyllotreta striolata* occurred almost year round. *Lipaphis erysimi* occurred periodically during the dry seasons. Its population was drastically affected by rainfall. *Myzus persicae* also occurred periodically as that of the turnip aphid, but appeared several months later and almost constantly occurred in November during the three years. The population abundance was also greatly influenced by the rainfall during the spring.

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中華農業研究

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