MARDI Res. Bull. (1986) 14 (1), 23–27

DIFFERENTIAL COMPATIBILITY IN A DIALLEL CROSS INVOLVING THREE GROUPS OF PINEAPPLE [*ANANAS COMOSUS* L. (MERR.)]

Y.K. CHAN*

Keywords: Ananas comosus L. (Merr.), Pineapple, Incompatibility, Varieties, Hybridization, Seeds.

RINGKASAN

Satu kacukan diallel yang lengkap melibatkan Cayenne, Spanish, Queen dan satu pemilihan F_1 daripada kacukan antara Spanish dan Cayenne (Hybrid 1) telah dijalankan untuk menentukan perbezaan pembentukan biji benih dan darjah ketidakserasian antara kacukan.

Kesemua genotip didapati tidak serasi sesama sendiri sementara kacukan-kacukan menunjukkan perbezaan-perbezaan set biji benih yang dipengaruhi oleh sumber-sumber betina dan jantan dan interaksi antara keduanya. Bergantung kepada jenis kacukan, bilangan biji benih yang dibentuk ialah di antara enam hingga 478 biji/kg buah. Perbezaan di dalam ketidakserasian bagi kacukan salingan telah didapati untuk dua set kacukan yang melibatkan Hybrid 1.

Penggunaan hasil-hasil percubaan ini daripada segi pemilihan induk-induk jantan dan betina yang sesuai untuk pengacukan nanas serta bahayanya penanaman bercampur antara varieti-varieti yang sangat serasi yang boleh menghasilkan buah-buah yang banyak biji telah dibincangkan.

INTRODUCTION

The three groups of pineapple [*Ananas comosus* L. (Merr.)] of commercial importance are Cayenne, Queen and Spanish. Cayenne is the most widely cultivated and is the principal variety in major pineapple growing countries like the Philippines, Hawaii, Queensland, Kenya and Taiwan. The Queen group is grown to a lesser extent, mainly for dessert fruit while the Spanish has, for a long time, been the noted canning variety extensively cultivated on peat soils in Malaysia.

It is well accepted that pineapple is self-incompatible (SI) but set seeds readily when crosses occur between varieties from different groups. It is believed that a single S locus with multiple alleles acting gametophytically, controls the incompatibility system. In gametophytic incompatibility, the alleles in both the pollen and style act independently and incompatibility results if the pollen has the same S allele as either one or both that are present in the diploid style.

For Cayenne, SI was found to be governed by two S alleles in the heterozygous state denoted S_1S_2 by BREWBAKER and GORREZ (1967). They also determined that the site of inhibition of pollen tube growth was located in the style. More recently, BHOWMIK (1982) established that SI of the Queen group was controlled by a different set of S alleles present in the homozygous state assigned S_bS_b. The genetics of SI for the Spanish group have not, hitherto, been established probably because the varieties in this group are of little economic importance elsewhere.

Differential seed set in crosses among the major groups of pineapple is of interest, at least to breeders involved in hybridization work on this crop. Information on differences in seed set in crosses and reciprocals between the groups is important in the planning of the hybridization programme particularly in ascertaining the direction of a cross, *i.e.*, choosing, between two varieties, the male or female parent. It also gives a guide in estimating the number

*Fruit Research Division, MARDI, Serdang, Selangor, Malaysia.

of crosses to be made to obtain the desired number of F_1 seeds and progenies for evaluation and selection.

MATERIALS AND METHODS

The three groups *i.e.*, Cayenne, Spanish, Queen and a selected F_1 hybrid between Spanish and Cayenne (called Hybrid 1) were planted at MARDI, Serdang on 13 August 1982. The experimental area was divided into two plots (female and male) and each plot consisted of 320 plants comprising the four genotypes.

The plants were grown at a distance of 0.3 m apart within a row, 0.6 m between rows and 1.2 m between the double-rowed beds. Cultural practices followed the recommendation of TAY (1979).

A complete diallel between the four genotypes was carried out and each of the 16 possible crosses was represented by pollinating all the flowers of 20 inflorescences in the female plot. Crosses were made daily on anthesis of the first flower in the inflorescence and continued for about two weeks until the whole inflorescence was pollinated. Fresh pollen was collected from flowers in the male plot and dusted gently onto the stigma of flowers at anthesis in the female plot to effect pollination.

Fruits from the female plot were harvested at 'two-eye riped' stage and their shell peeled to expose the seeds embedded in the fruitlets or 'eyes'. Bold seeds from each fruit were extracted, counted and expressed as number per kilogramme fruit weight to standardize the variation in seed number due to differences in fruit size.

The effects of female and male sources and their interactions on seed development (compatibility) were analysed by the Generalized Linear Model Procedure in SAS.

RESULTS AND DISCUSSION

The mean seed number of each of the 16 crosses or selfs expressed as seeds per kilogramme fruit weight is presented in *Table 1*. Because of the positive correlation between the mean and variance of the crosses (r = 0.92**), a logarithmic transformation was done to make the variances more homogeneous.

The analysis of variance on the transformed data set shown in *Table 2* indicates significance in male and female effects as well as their interactions on the development of seeds in the population studied. With significance of the interaction term, the superiority of either the female or male source in influencing development of seeds cannot be generalized. In fact, seed set would be dependent on specific combinations of female and male parents. Examining the data in *Table 1* more closely, it becomes clear that when Hybrid 1 was used as female, seed set was generally poor except in combination with Cayenne which gave an unusually high seed number (477.6 seeds). On the other hand, the reciprocal cross of the same two genotypes yielded low number of seeds (5.8 seeds).

A comparison of the log transformed means for seed number of the 16 combinations is presented in *Table 3*. In general, the ranking followed a definite pattern with Queen used as female falling in the 'high seed' category followed by Spanish and Cayenne. As for Hybrid 1, it was incompatible with Queen and Spanish pollen because the quantity of seeds formed from these crosses was not significantly different from that of selfed Hybrid 1 fruits. However, it was extremely compatible with Cayenne pollen and the unusually high seed set from this particular cross pushed up the otherwise low mean for Hybrid 1 fruits. Selfed fruits of the other groups were found to have negligible seed sets.

From the results of differential seed set obtained in the diallel cross, the genetics of incompatibility was examined. *Table 3* shows the crosses and their fertility. Two of the crosses involving Hybrid 1 female with Queen and Spanish and all selfs were considered incompatible. The one-way

Table 1. Seed number per kilogramme of fruit from a complete diallel of 4 genotypes

♀ \ ♂	Queen	Spanish	Cayenne	Hybrid 1 (SxC)	♀Mean
Queen	1.8 (1.78)*	182.5 (63.76)	162.5 (54.63)	227.5 (49.41)	143.6
Spanish	96.9 (35.48)	1.6 (1.47)	38.7 (49.58)	112.9 (46.28)	62.6
Cayenne	17.5 (47.75)	25.8 (47.88)	0.2 (0.56)	5.8 (3.92)	12.3
Hybrid 1 (SxC)	4.9 (3.65)	3.7 (4.08)	477.6 (164.83)	4.6 (3.49)	122.7
♂ Mean	30.3	53.4	169.8	87.7	85.3

*σ given in parentheses
r ($\bar{x}$ with σ) = 0.92**

Table 2. Analysis of variance of log (seed no.) in pineapple diallel cross

Source	d.f.	M.S.
Male	3	39.6557**
Female	3	93.6463**
Male and female	9	61.5173**
Error	260	0.6451
Total	275	

Table 3. Comparison of seed number means (log transformed) of crosses with the means of the incompatible self-pollination in each maternal group

Cross	Log mean
Q x H	5.4351b*
Q x S	5.1841bc
Q x C	4.8721bcd
Q x	0.7873hi
S x H	4.6254cd
S x Q	4.4857d
S x C	3.1182e
S x	0.6855ij
C x S	2.2509f
C x Q	1.9316fg
C x H	1.6638fg
C x	0.1505j
H x C	6.2026a
H x Q	1.6140g
H x S	1.3041gh
H x	1.5307g

*Values with same letter are not significantly different at P=0.01 according to Duncan's Multiple Range Test.
Q = Queen
S = Spanish
C = Cayenne
H = Hybrid 1

compatibility found in the crosses between Hybrid 1 and Queen as well as with Spanish may be explained if Queen and Spanish were both assumed to be homozygous in their S allele make up *i.e.*, S_4S_4 and S_3S_3 respectively. Hybrid 1 was assumed to be heterozygous carrying alleles of both Queen and Spanish *i.e.*, S_3S_4. In this way, when Hybrid 1 was used as female, neither Queen pollen (S_4) nor Spanish pollen (S_3) would be compatible with the Hybrid (S_3S_4), but in the reciprocal cross, S_3 pollen of Hybrid 1 will be compatible with the S_4S_4 diploid style of Queen as is the S_4 pollen with the S_3S_3 make up of Spanish. However, S alleles in the homozygous state assumed for both Queen and Spanish is highly unlikely because in the gametophytic system, all progenies arising from compatible crosses are, in fact, enforced heterozygotes.

Another explanation which appears more likely is based on heterozygosity of S alleles for all the groups of pineapple and that none of them have the same genotype *(Table 4)*. This means that all were cross compatible in all combinations, including that for Hybrid 1 female with Queen or Spanish. However, the insignificant seed set in the latter mentioned crosses suggests that while pollen tube entry is perhaps not inhibited in these two crosses, there may be maternal inhibition factors in Hybrid 1 that affect zygote formation and subsequent seed development in crosses involving Queen and Spanish. From *Table 4*, the zygotes formed from these crosses had similar genotypes *i.e.*, S_2S_4 and S_3S_4 and development of zygotes with these allelic constitutions was perhaps inhibited by the effects of Hybrid 1

Table 4. Genetics of incompatibility system of 3 pineapple groups and 1 F_1 Hybrid

♀ \ ♂	Queen S_2S_4	Spanish S_3S_4	Cayenne S_1S_2	Hybrid (SxC) S_2S_3
Queen S_2S_4	I	S_2S_3 S_3S_4	S_1S_2 S_1S_4	S_2S_3 S_3S_4
Spanish S_3S_4	S_2S_3 S_2S_4	I	S_1S_3 S_1S_4 S_2S_3 S_2S_4	S_2S_3 S_2S_4
Cayenne S_1S_2	S_1S_4 S_2S_4	S_1S_3 S_1S_4 S_2S_3 S_2S_4	I	S_1S_3 S_2S_3
Hybrid (SxC) S_2S_3	S_2S_4 S_3S_4 I*	S_2S_4 S_3S_4 I*	S_1S_2 S_1S_3	I

I = Incompatible
I* = No viable seed development possibly due to inhibition of zygote development by Hybrid (SxC) maternal tissues.

maternal tissues. Other zygotes with different genotypes *e.g.*, those formed from crosses with Cayenne (S_1S_2 and S_1S_3) were not inhibited by the Hybrid 1 maternal tissues and subsequently formed viable seeds. The present scope of this experiment is insufficient in providing data to support this explanation and further research is required to develop a better understanding in this area.

Moving back to the primary purpose of this study, the practical application of the results from this experiment can be viewed from the point of hybridization work which, in the consensus of pineapple breeders, is probably the most effective method in improvement of present day cultivars. The results obtained in this experiment give valuable guide in the choice of female and male parents for the crosses. As examples, in the backcrossing programme involving the Hybrid 1 with Spanish, the former should not be used as female parent because the cross was incompatible while the reciprocal cross was fertile. Similarly, on the assumption that no cytoplasmic inheritance is present, the Hybrid 1 female should be used for crossing with Cayenne since the reciprocal cross yielded very low number of seeds.

The other aspect that has to be further investigated is the extent of seed set of the Hybrid 1 when intercropped with the Cayenne varieties. From *Table 1*, the seed set of supposedly incompatible crosses involving Hybrid 1 female as well as their selfed fruits showed fairly high seed set (about eight to ten seeds for a normal 2-kg fruit). This was probably because of natural pollination from the Cayenne which was highly compatible with the Hybrid 1. In smallholders' farms with a mixture of these two genotypes grown close by each other and with the presence of natural pollinating agents, the seed number in Hybrid 1 fruits can be expected to be alarmingly high.

Hybrid 1 is a recent release by MARDI and it is expected to be quite widely cultivated especially by smallholders in the near future. It is opportune, therefore, to warn farmers of the danger in cultivating the mixture of these two types, a practice which is expected to be fairly widespread. In situations where the mixture is desired, some form of isolation between the two genotypes or staggering the flower induction to prevent synchronized flowering should be practised.

ACKNOWLEDGEMENTS

The author expresses his sincere thanks to Mr. W.K. Toh for assistance in the hybridization work and also to Dr. T.C. Yap, Dr. C.S. Lee, Dr. B.H. Chew, Miss S.L. Tan and Dr. N.T. Arasu for critical comments on the manuscript.

ABSTRACT

A complete diallel involving the Cayenne, Spanish, Queen and an F_1 selection from a hybrid between Spanish and Cayenne, was carried out to study the differential seed set and compatibility between the crosses.

All genotypes were self-incompatible while the crosses showed differential seed set influenced by female and male sources and their interaction. Depending on the cross, seed set ranged from six seeds to 478 seeds/kg of fruit. Further, one-way compatibility was found for two sets of crosses involving the Hybrid female with Queen and with Spanish.

Application of the results from this experiment in terms of ascertaining the direction of cross between two parents in pineapple hybridization as well as the danger of mixed cropping of highly compatible varieties which may produce seedy fruits were discussed.

REFERENCES

BHOWMIK, G. (1982). Self-incompatibility in pineapple. *Indian J. Genet.* ***42***, 345–7.

BREWBAKER, J.J. and GORREZ, D.D. (1967). Genetics of self-incompatibility in the genera Ananas (pineapple) and Gasteria. *Am. J. Bot.* ***44***, 611–6.

TAY, T.H. (1979). A guide to cultivation of pineapple. *MARDI Siri Maklumat Penyelidikan.* 7 pp.

Accepted for publication on 15 January 1986

First Published 1986.

Dicetak oleh Unit Percetakan MARDI, Serdang, Selangor.