

# The Genetic Interaction on the Quantitative Traits of Prescutellar Bristles in Melon Fly, *Bactrocera (Zeugodacus) cucurbitae* (Coquillett)

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## Abstract

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The genetics of prescutellar bristles (prsc) in the melon fly, *Bactrocera (Zeugodacus) cucurbitae* (Coquillett) is polygenic with a quantitative trait of 1 to 20 prsc or more. The field population is polymorphic in regard of prsc and harbors 95% 2prsc phenotype (the major wild type) and 5% 4prsc phenotype (the minor wild type). Several laboratory strains with different numbers of prsc were established for genetic study. When the 2prsc (2P) strain crosses with other phenotypes, instead of blending into the continuous prsc traits, the 2prsc phenotype (2PHT) frequency surged in the F<sub>2</sub> progeny. The reappearing of the parental phenotype in F<sub>2</sub> progeny is unusual in a quantitative genetic event, and is examined by comparing the 2P strain and the multiple prsc (MB) strain in two serial step-up phenotype crosses. All six 2P serial crosses resulted in the 2PHT surge, demonstrating that the 2P strain is the genetic source of the surge. The surge only happened in the F<sub>2</sub> progeny at 22.5% ± 4.0% but not in the F<sub>1</sub> progeny. For the MB strain, the serial crosses with other phenotypes showed no trace of phenotypic surge, and the results of all five MB serial crosses followed the quantitative genetic principle in continuous traits accordingly. The comparative study suggests that the quantitative genetics of prsc can be modified by other genetic factors, although the 2PHT surge mechanism still remains to be investigated. In population genetics, the 2PHT surge is considered to be a contributing factor in the dominance of 2PHT as the major wild type in the field population.

**Key words:** Quantitative genetics, Prescutellar bristles, *Bactrocera (Zeugodacus) cucurbitae*, Mono-phenotype surge.

## INTRODUCTION

The insect specimen identification is essential in both the agricultural pest control program and the international trade quarantine. For the taxonomy of economic important fruit

fly of Tephritidae family, the notal bristles are important morphological characters (White & Elson-Harris 1992; Drew & Hancock 1994), with special attention that certain species are polymorphic in either the number or the loca-

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tion of bristles (White 2001). The melon fly, *Bactrocera (Zeugodacus) cucurbitae* (Coquillett) is polymorphic in regard of prescutellar bristle (prsc) with 95% 2prsc-phenotype (2PHT) and 5% 4prsc-phenotype (4PHT) in field (Cheng *et al.* 2014). This prsc polymorphism has not been investigated in both genetics and developmental biology. In other dipterans species, for examples, the variation of bristles in *Drosophila melanogaster* and several *cyclorapha dipterans*, including *Ceratitis capitata* (Mediterranean fruit fly) have been well studied for the interest of both quantitative genetics (Mackay 1995) and developmental biology (Ghysen & Dambly-Chaudière 1988; Simpson *et al.* 1999; Simpson & Marcellini 2006). In particular, the *achaete-scute* regulation on the notum of *Drosophila* has been related to the evolution of thorax development in dipterans (Alonso & Cabrera 1988; Garcia-Garcia *et al.* 1999; Wulbeck & Simpson 2000; Pistillo *et al.* 2002; Skaer *et al.* 2002). There are limited knowledge on prsc morphology of melon fly, and as a part of fruit fly control program, Taiwan Agricultural Research Institute (TARI) started investigating the possible cause of prsc polymorphism. The genetic analysis has confirmed the prsc polymorphism is a polygenic nature or a quantitative genetic controlled (Cheng *et al.* 2014). However, it is noticed that there is an unusual frequency surge of 2PHT in the  $F_2$  progeny of the 2P strain (the wild type) cross with other phenotypes. The unusual increase of a single phenotype frequency not only disrupts the continuous prsc

trait but also signaling the possibility of genetic interaction in quantitative genetics. The extra 2PHT progeny produced in this surge may also contribute to the field dominance of 2PHT in population genetics. The current study is tried to confirm the event, estimate the frequency, and locate its genetic source.

## MATERIALS AND METHODS

### Insect rearing

The melon fly rearing, phenotype separation and the definition of notum bristles following White & Elson-Harris (1992) were the same as described in the previous report (Cheng *et al.* 2014). The prsc phenotype characters of strains are described as follows: (1) the 2prsc phenotype (2P) strain: the mean =  $2.0 \pm 0.2$  prsc and ranged 1–5 (Fig. 1A); (2) the 4prsc phenotype (4P) strain: the mean =  $4.0 \pm 0.4$  prsc and ranged 1–8 (Fig. 1B); and (3) the multiple prsc (MB) strain: the mean =  $12.3 \pm 2.0$  prsc and ranged 8–19 (Fig. 1C).

### The comparative study of the continuous prsc traits in 2P and MB strains

The occurrence of 2PHT surge is compared in two series of step-up phenotype crosses. (1) The 2PHT is chosen as the representing phenotype of the 2P strain to cross with the 4, 6 and 8PHT of 4P strain, and the 10, 12 and 14PHT of MB strain. (2) The 12PHT is chosen as the representing phenotype of the MB strain to cross with the 4, 6 and 8PHT of 4P strain, and the 10 and 12PHT of MB strain. Each cross



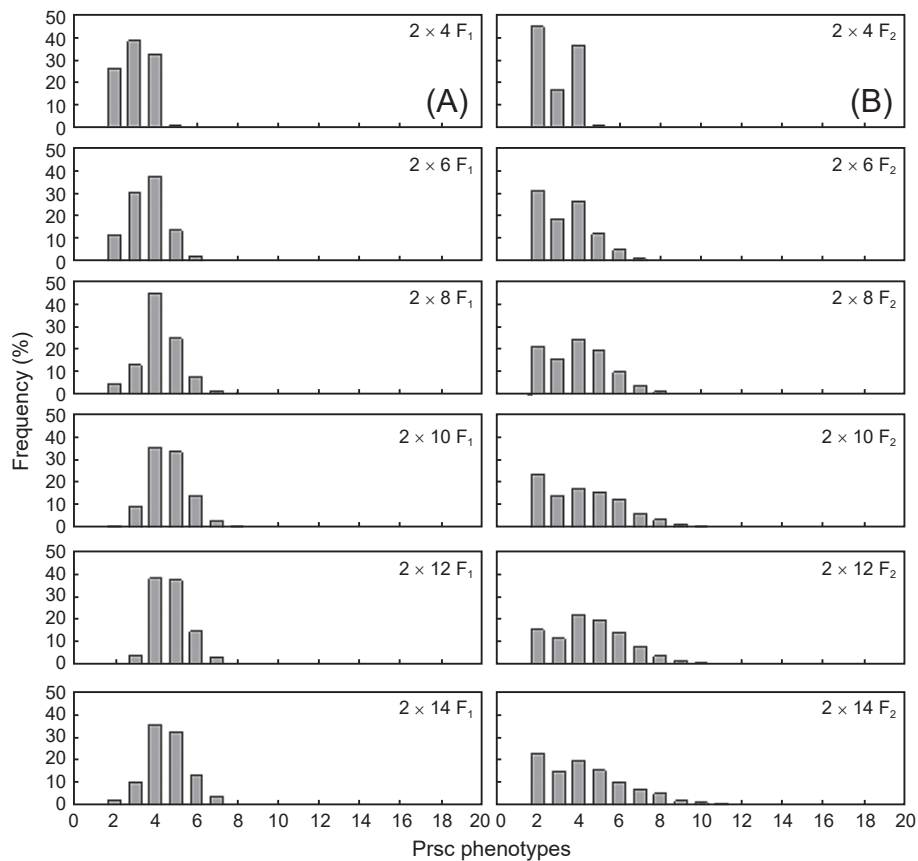
**Fig. 1.** The comparison of prsc. (A) the 2PHT of the 2P strain; (B) the 4PHT of the 4P strain; (C) the 12PHT of the MB strain. PHT: prsc-phenotype.

contains 4–6 replicates with males and females from both parental phenotypes alternatively to average out the possible variables, even it has been determined that prsc genetics is not sex related (Cheng *et al.* 2014). The  $F_1$  offspring was self-crossed for the  $F_2$  generation. Due to the spread out quantitative trait, on average of 1,000  $F_1$  and 2,000  $F_2$  offspring were inspected for their prsc PFDs (phenotype frequency distribution).

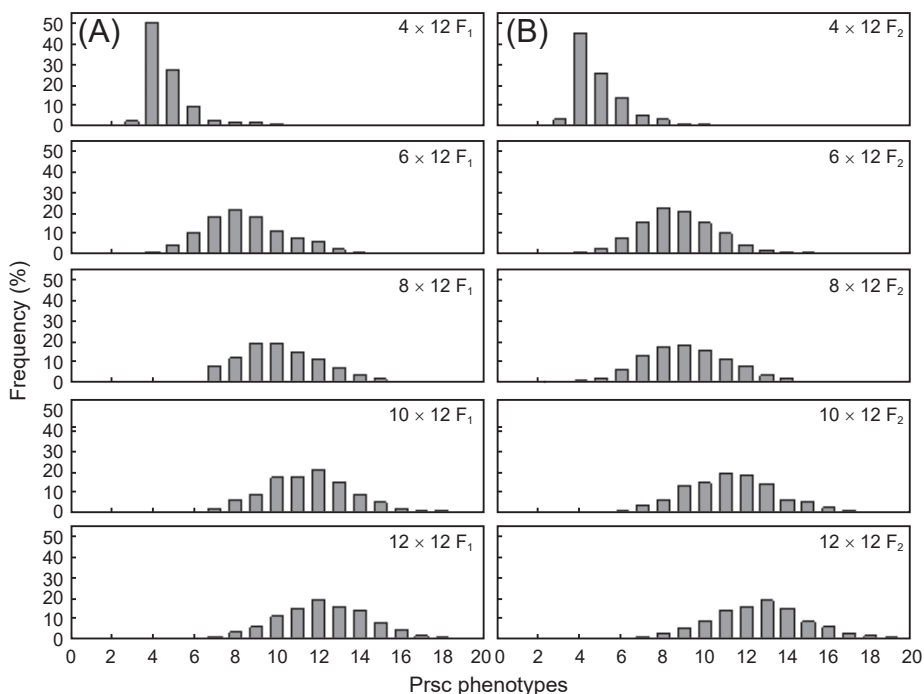
## RESULTS AND DISCUSSION

The purpose of this study is to clarify the unexpected finding of the 2prsc phenotype surge in our previous quantitative genetic report of the prescutellar bristle in melon fly (Cheng *et al.* 2014). The 2P strain, the major

wild type, was compared to an artificially selected MB strain in two serial crosses with step-up phenotypes. The PFDs of both  $F_1$  and  $F_2$  progeny were presented in Figs. 2 and 3 for 2P and MB serial crosses, respectively. The quantitative genetic nature of prsc traits has been demonstrated in progeny of both serial crosses, as all PFDs are continuously distributed (Emerson & East 1913; Russell 2005; Griffiths *et al.* 2008), except the 2PHT surge which appeared in the  $F_2$  progeny of all six 2P serial crosses. The test results confirmed that the previous observation of the parental 2P-phenotype reappeared in  $F_2$  at a significant frequency is not accidental (Cheng *et al.* 2014). When comparing the 2P serial result to the continuous PFD prsc trait of MB series, the on and off of the 2PHT surge indicates that the



**Fig. 2.** The phenotype frequency distributions (PFDs) of  $F_1$  (A) and  $F_2$  (B) generations of the 2P serial crosses, and the 2PHT frequency surged in  $F_2$  progeny.



**Fig. 3.** The phenotype frequency distributions (PFDs) of  $F_1$  (A) and  $F_2$  (B) generations of the MB serial crosses.

2P strain is the genetic source of the surge. In quantitative genetics, the cross of two different strains resulted in an intermediate trait in following generations, and the MB serial crosses follow this principle accordingly while the 2P serial crosses were not. The reappearing frequency of 2PHT in progeny of both 2P and MB serial crosses were compared in Tables 1 and 2, and the results indicated that the MB strain did not produce 2PHT in its progeny and can serve as the blank control in the cross test, hence by

grouping the three  $2P \times MB$  crosses, i.e.,  $2 \times 10$ ,  $2 \times 12$  and  $2 \times 14$  (total 13 replicates). It is possible to obtain the reappearing frequency of 2PHT in  $F_2$  progeny at  $22.5\% \pm 4.0\%$  with almost no 2PHT appeared at the frequency of  $1.7\% \pm 1.6\%$  in the  $F_1$  generation.

The 2PHT trait of 2P strain has blended with the prsc trait of MB strain in the  $F_1$  progeny but then surged in the  $F_2$  progeny, suggesting that the prsc quantitative genetics has been modified by other genetic mechanism or that

**Table 1.** The 2-prescutellar bristle phenotype frequencies (%) of  $F_1$  and  $F_2$  progeny in 2P-serial crosses, with the parental strains indicated.

Phenotype (parental strains)	2PHT frequency (%)	
	$F_1$	$F_2$
2PHT (2P) $\times$ 4PHT (4P)	26.8	45.1
2PHT (2P) $\times$ 6PHT (4P)	12.5	31.9
2PHT (2P) $\times$ 8PHT (4P)	4.9	21.8
2PHT (2P) $\times$ 10PHT (MB)	0.9	24.2
2PHT (2P) $\times$ 12PHT (MB)	0.5	15.6
2PHT (2P) $\times$ 14PHT (MB)	1.3	22.8

**Table 2.** The 2-prescutellar bristle phenotype frequencies (%) of F<sub>1</sub> and F<sub>2</sub> progenies in MB-serial crosses, with the parental strains indicated.

Phenotype (parental strains)	2PHT frequency (%)	
	F <sub>1</sub>	F <sub>2</sub>
12PHT (MB) × 4PHT (4P)	0.2	0.1
12PHT (MB) × 6PHT (4P)	0.0	0.0
12PHT (MB) × 8PHT (4P)	0.0	0.0
12PHT (MB) × 10PHT (MB)	0.0	0.0
12PHT (MB) × 12PHT (MB)	0.0	0.0

the genetic interaction was involved, and the responsible factors are only being carried in the 2P strain but not in the MB strain. The 2P strain only harbors a portion of the polygenic prsc traits and why this portion can be activated and overrides the expression of other phenotypes remains unknown. The expression of 2PHT surge only in the F<sub>2</sub>, not in the F<sub>1</sub> progeny, coincides with the Mendelian segregation expression of a recessive gene, and can serve as a study lead in future. The 2PHT/F<sub>2</sub> frequency of 2P × MB cross is measured at 22.5% ± 4.0% in contrast to the theoretical 25% recessive homozygotes expression, and is worth to be noticed. The 2PHT is only a portion of prsc polygenic traits, and the mono-phenotype surge in a continuous trait suggests that other factor is involved.

In related subjects, the extra amount of 2PHT produced by the surge mechanism can actually be a contributing factor in population genetics for the dominance of 2PHT in field population. Besides, there is an interesting example in a closely related species, i.e., the oriental fruit fly, *Bactrocera dorsalis* (Hendel), which has fixed 2prsc morphology. It then raises the question as to why the 2PHT surge is just an intermediate step in the prsc evolution in Tephritidae.

## CONCLUSIONS

The study has concluded: (1) The prescutellar bristles of melon fly is quantitative genetic controlled, but the phenotype expression in field population is deviated from the contin-

uous trait, particular the dominance of 2PHT at 95%. It implies that other mechanism involvement is possible; (2) The genetic source of 2-phenotype surge is 2P strain; (3) The 2PHT surge expressed only in F<sub>2</sub> progeny with 22.5% ± 4.0% frequency; (4) The F<sub>1</sub> progeny of 2P strain cross is not affected by the 2PHT surge; and (5) The 2PHT surge may be a contributing factor for 2PHT to be the major wild type in the polymorphic population of melon fly.

## REFERENCES

- Alonso, M. C. and C. V. Cabrera. 1988. The achaete-scute gene complex of *Drosophila melanogaster* comprises four homologous genes. *EMBO J.* 7:2585–2591.
- Cheng, Y., C. H. Wang, Y. B. Huang, and M. Y. Chiang. 2014. The quantitative genetics of prescutellar bristles in melon fly, *Bactrocera cucurbitae* (Coquillett). *J. Taiwan Agric. Res.* 63:179–187.
- Drew, R. A. I. and D. L. Hancock. 1994. The *Bactrocera dorsalis* complex of fruit flies (Diptera: Tephritidae: Dacinae) in Asia. *Bull. Entomol. Res.* 2:1–68.
- Emerson, R. A. and E. M. East. 1913. The inheritance of quantitative characters in maize. *Nebr. Agric. Exp. Stn. Res. Bull.* 2:1–120.
- Garcia-Garcia, M. J., P. Ramain, P. Simpson, and J. Modolell. 1999. Different contributions of pannier and wingless to the patterning of the dorsal mesothorax of *Drosophila*. *Development* 126:3523–3532.
- Ghysen, A. and C. Dambly-Chaudière. 1988. From DNA to form: The *achaete-scute* complex. *Genes Dev.* 2:495–501.
- Griffiths, A. J. F., S. R. Wessler, R. C. Lewontinn, and S. B. Carroll. 2008. *Introduction to Genetic Analysis*. 9th ed. W. H. Freeman and Company. New York. 838 pp.

- Mackay, T. F. C. 1995. The genetic basis of quantitative variation: Numbers of sensory bristles of *Drosophila melanogaster* as a model system. *Trends Genet.* 11:464–470.
- Pistillo, D., N. Skaer, and P. Simpson. 2002. *scute* expression in *Calliphora vicina* reveals an ancestral pattern of longitudinal stripes on the thorax of higher Diptera. *Development* 129:563–572.
- Russell, P. J. 2005. *iGenetics: A Mendelian Approach*. Benjamin Cummings. San Francisco, CA. 842 pp.
- Simpson, P., R. Woehl, and K. Usui. 1999. The development and evolution of bristle patterns in Diptera. *Development* 126:1349–1364.
- Simpson, P. and S. Marcellini. 2006. The origin and evolution of stereotyped patterns of macrochaetes on the nota of cyclorhaphous Diptera. *Heredity* 97:148–156.
- Skaer, N., D. Pistillo, and P. Simpson. 2002. Transcriptional heterochrony of *scute* and changes in bristle pattern between two closely related species of blowfly. *Dev. Biol.* 252:31–45.
- White, I. M. 2001. Morphological features of the tribe Dacini (Dacinae): Their significance to behavior and classification. p.505–533. *in: Fruit Flies (Tephritidae): Phylogeny and Evolution of Behavior.* (Aluja M. and A. L. Norrbom, eds.) CRC Press. Boca Raton, FL. 984 pp.
- White, I. M. and M. M. Elson-Harris. 1992. *Fruit Flies of Economic Significance: Their Identification and Bionomics*. CAB International. Wallingford, UK. 601 pp.
- Wulbeck, C. and P. Simpson. 2000. Expression of *achaete-scute* homologues in discrete proneural clusters on the developing notum of the medfly *Ceratitis capitata*, suggests a common origin for the stereotyped bristle patterns of higher Diptera. *Development* 127:1411–1420.

# 瓜實蠅 [*Bactrocera (Zeugodacus) cucurbitae* (Coquillett)]

## 中胸背板剛毛數量性狀之遺傳交互作用

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### 摘要

鄭允、王志賢、黃毓斌、江明耀、呂秀英、吳東鴻、楊崇民、粘君琪。2018。瓜實蠅 [*Bactrocera (Zeugodacus) cucurbitae* (Coquillett)] 中胸背板剛毛數量性狀之遺傳交互作用。台灣農業研究 67(1):9-15。

前期研究中已針對瓜實蠅 *Bactrocera cucurbitae* (Coquillett) 中胸背板之 prescutellar bristles (prsc) 數目屬數量遺傳 (quantitative genetics) 機制控制，惟在研究中發現野生型 (wild type) 之 2PHT (2prsc phenotype; 2P-strain) 與多剛毛品系 (multiple prsc phenotypes; MB-strain) 雜交時，F<sub>1</sub> 子代遵循數量遺傳法則，但 F<sub>2</sub> 之頻度分布 (phenotype frequency distribution) 中，2PHT 卻有異常增加之現象，可能有「非屬數量遺傳」之其他機制介入，因此本研究一方面確認前述觀察之確實性，另一方面則藉此探討其原因。本研究係以 2P 品系及 MB 品系分別與 MB 品系之各表現型 (phenotypes) 進行兩系列之雜交試驗，並比對 F<sub>1</sub> 與 F<sub>2</sub> 之表現型頻度分布，以分析其異同。結果發現凡以 2P 品系進行之雜交試驗，F<sub>1</sub> 均依照數量遺傳法則表現，但 F<sub>2</sub> 均出現 2PHT 表現型增多之情形，平均幅度為 22.5% ± 4%，因此 2PHT 之增加極有可能來自於專限於 2PHT 之其他因子表現。以 MB 品系之 12PHT 與其他表現型之雜交，無論 F<sub>1</sub> 或 F<sub>2</sub> 則依數量遺傳法則表現，並無任何一種 prsc 表現型突然增加頻度之現象。研究結果顯示瓜實蠅之中胸背板剛毛數確實依「數量遺傳」之機制控制。但田間族群之表現卻以 2PHT 占 95% 之野生型，並未依數量遺傳之連續型 (continuous traits) 表現，因此，其他遺傳因素之介入，至為明顯。而本研究發現之「2PHT 突增」(2PHT surge) 現象可能為介入遺傳因素之一，而此現象也的確有提升 2PHT 野生型表現頻率之效益。

**關鍵詞：**數量遺傳、小盾板前剛毛、瓜實蠅、隱性基因。

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