Genetics and Molecular Biology, 31, 3, 704-710 (2008)
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www.sbg.org.br

Research Article

Developmental genetic analysis of fruit shape traits under different environmental conditions in sponge gourd (*Luffa cylindrical* (L) Roem. Violales, Cucurbitaceae)

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Abstract

Analysis of genetic main effects and genotype × environment (GE) interaction effects for the fruit shape traits fruit length and fruit circumference in the sponge gourd (*Luffa cylindrical* (L) Roem. Violales, Cucurbitaceae) was conducted for diallel cross data from two planting seasons. A genetic model including fruit direct effects and maternal effects and unconditional and conditional variances analysis was used to evaluate the development of the fruit at four maturation stages. The variance analysis results indicated that fruit length and circumference were simultaneously affected by fruit direct genetic effects and maternal effects as well as GE interaction effects. Fruit direct genetic effects were relatively more important for both fruit shape traits during the whole developmental period. Gene activation was mostly due to additive effects at the first maturation stage and dominance effects were mainly active during the other three stages. The fruit shape trait correlation coefficients due to different genetic effects and the phenotypic correlation coefficients varied significantly for the various maturation stages. The results indicate that it is relatively easy to improve the two fruit shape traits for market purposes by carefully selecting the parents at the first maturation stage 3 days after flowering instead of at fruit economic maturation.

Key words: fruit shape traits, genetic analysis, genetic variances, *Luffa cylindrical* (L) Roem.

Received: March 20, 2007; Accepted: September 27, 2007.

Introduction

The sponge gourd (*Luffa cylindrical* (L) Roem.) is one of the less popular vegetables in many parts of the world but is commonly grown in China and other Asia countries, and further research is needed on the unique properties of this plant. In China, sponge gourds are used for food at about 12 days after flowering when they are still physiologically immature, at what is called `economic maturity', and for industrial purposes at about 63 days after flowering when physiologically mature (Zhang *et al.*, 2007). Although it is well known that fruit shape affects the marketability of the sponge gourd as a vegetable, characteristics related to market acceptability have not been defined nor have their developmental modes of inheritance been understood. It is, therefore, important to select appropriate parent plants and develop the most appropriate strategy in breeding edible sponge gourds, with the length and circumference of the fruits being two of the important quantitative traits closely related to the exterior quality of sponge gourds.

Most agronomic and fruit quality traits are complex and controlled by several genes expressed throughout developmental stages (Beyer *et al.*, 2002; Jordaan and Krüger, 2005) and developmental genetics theory affirms that genes are selectively expressed at different growth stages (Shi *et al.*, 2001). Inheritance of fruit quality traits has been reported for several species (Lavi *et al.*, 1998; Umaharan *et al.*, 1997) but few studies have investigated maternal plant effects in relation to sponge gourds. However, in a previous study we reported that fruit shape traits of sponge gourd are also controlled by a maternal plant gene, or genes (Zhang *et al.*, 2007). Furthermore, since plant growth in the field is affected by environmental conditions such as climate, soil and cultivation and management methods (Wang, 2001; Rouphael and Colla, 2005) genotype × environment (GE) interactions may also affect fruit shape traits. It therefore follows that when studying the genetic improvement of fruit shape traits in sponge gourds there is a need to investigate the influence of the genetic main effects and GE interaction effects on the dynamic performance of fruit shape traits under different environmental conditions and at various stages of maturation.

The objectives of the study reported in this paper were to clarify the developmental behavior of gene expres-

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sion for fruit shape traits in sponge gourds at various stages of maturity. We used a correlation coefficients and a genetic model which included fruit direct effects, maternal effects and genotype × environment (GE) effects to investigate the genetic control of fruit length and circumference in sponge gourds at various stages of maturation from flowering to economic maturity under different environmental conditions.

Materials and Methods

Materials and experiments

The experiments were conducted in 2004 and 2005. The mating design used in this experiment was a 7 × 7 diallel cross and *Luffa cylindrical* (L) Roem. cultivars using the parent cultivars Wuyexiang (P_1), Lifeng (P_2), Tianhong (P_3), Jinke (P_4), Fengyuan (P_5), Jiutouniao (P_6), and Sanjiang 1 (P_7). The original seeds for these cultivars were provided by Hangzhou seed company. The seeds of the seven parent cultivars and their F_1 offspring were obtained by crossing males to females at flowering during the same growing season in the summer of 2004. Seedlings of the parent plants and the F_1 offspring were planted on the farm of Zhejiang University (Hangzhou, China) in the autumn of 2004 and the spring of 2005, the different years being considered to constitute different environments. For each planting season, 30 days after germination 10 seedlings were individually transplanted to 50 cm 180 cm plots using a randomized complete block design with two replicates and 150 cm between plots,. A trellis about 200 cm high was used to support the climbing vine and five well-grown plants in each parent plot and F_1 plot were marked for the determination of fruit shape traits. The length and circumference of four fruits from each of the five marked plants were measured at four post-flowering maturation stages at 3, 6, 9 and 12 days.

Statistical methods

A genetic model including maternal effects, additive and dominance effects (Zhu *et al.*, 1993) and their GE interaction effects (Zhu, 1996; Wu *et al.*, 2004) was employed to study the developmental inheritance of fruit shape traits in sponge gourd under different environmental conditions. According to the model, unconditional genetic analysis was conducted based on phenotypic values at time t ($y_{(t)}$), which can be partitioned as:

$$y_{(t)} = \mu_{(t)} + E_{(t)} + A_{(t)} + D_{(t)} + M_{(t)} + AE_{(t)} + DE_{(t)} + ME_{(t)} + B_{(t)} + e_{(t)}$$

where $\mu_{(t)}$ = population mean, $E_{(t)}$ = environment effect, $A_{(t)} \sim N(0, V_A)$ = fruit direct additive effect, $D_{(t)} \sim N(0, V_D)$ = fruit direct dominance effect, $M_{(t)} \sim N(0, V_M)$ = maternal plant effect, $AE_{(t)} \sim N(0, V_{AE})$ = fruit direct additive effect × environment interaction effect, $DE_{(t)} \sim N(0, V_{DE})$ = fruit direct dominance effect × environment interaction effect, $ME_{(t)} \sim N(0, V_{ME})$ = maternal plant effect × environment interaction effect, $B_{(t)} \sim N(0, V_B)$ = block effect, $e_{(t)} \sim N(0, V_e)$ = residual effect. All of the genetic effects in the model were random effects.

The phenotypic values at time t conditional on phenotypic values measured at time t-1 can be partitioned as (Zhu, 1995):

$$y_{(t|t\text{-}1)} = \mu_{(t|t\text{-}1)} + E_{(t|t\text{-}1)} + A_{(t|t\text{-}1)} + D_{(t|t\text{-}1)} + M_{(t|t\text{-}1)} + AE_{(t|t\text{-}1)} + DE_{(t|t\text{-}1)} + ME_{(t|t\text{-}1)} + B_{(t|t\text{-}1)} + e_{(t|t\text{-}1)}$$

where all parameters defined as the unconditional effects.

For conditional analysis, $t|t$-1 represents the measure at t given the trait measured at t -1 (Shi *et al.*, 2001). In this study, the genetic effects estimated by unconditional analysis were defined as the total accumulated genetic effects of genes expressed from the initial time (at flowering) to time t of the maturation stage ($0 \rightarrow t$), while the genetic effects estimated using conditional analysis represented the net genetic effects from genes expressed in the special maturating period from time t-1 to time t ($t|t$-1).

Different correlation coefficients between various maturating stages were calculated for the phenotypic correlation coefficient (r_P), correlation coefficients due to fruit genetic main effects (r_A = fruit direct additive correlation coefficient, r_D = fruit direct dominance correlation coefficient, r_M = maternal correlation coefficient) and the corresponding GE interaction correlation coefficients (r_{AE}, r_{DE}, r_{ME}).

To test the response of genotypes to fruit shape traits we performed analysis of variance (ANOVA) using the Statistical Analysis System (SAS) software release 6.11. (SAS Institute Inc, 1996). Both unconditional and conditional variances were estimated by the MINQUE(1) method (Zhu, 1992; Zhu and Weir, 1994). The jackknife method was applied to estimate standard errors of estimated fruit genetic variances and correlation coefficients (Miller, 1974; Zhu and Weir, 1994). A t-test following jackknifing was employed for testing the significance of genetic parameters.

The genetic effects of the seven parents (Wuyexiang = P_1, Lifeng = P_2, Tianhong = P_3, Jinke = P_4, Fengyuan = P_5, Jiutouniao = P_6 and Sanjiang 1 = P_7) were predicted using the adjusted unbiased prediction (AUP) method (Zhu, 1993; Zhu and Weir, 1996; Wu *et al.*, 2006).

Results and Discussion

Analysis of variance

The analysis of variance of parental and F_1 generation fruit length and circumference are summarized in Table 1. The results show that there was large variation between parents regarding the four maturation stages. The phenotypic values of both the shape traits (length and circumference) differed significantly among the seven cultivars over two maturation stages, suggesting that variation of these

Table 1 - Analysis of variance (ANOVA) of the mean square diallel analysis of sponge gourd (*Luffa cylindrical* (L) Roem.) fruit length and circumference at different stages of maturation.

	Diallel analysis values at different stages of maturation (d)							
	Fruit length				Fruit circumference			
Source	3d	6d	9d	12d	3d	6d	9d	12d
Parent								
Variety	61.971**	206.172**	535.703**	813.801**	7.790**	12.964**	17.916**	28.978**
Year	126.479**	654.476**	2023.245**	3212.424**	16.497**	63.380**	213.413**	446.754**
Variety Year	10.401**	40.508**	97.566**	138.736**	0.798**	2.767**	5.711**	9.030**
Block	0.035	0.490	0.154	0.634	0.235	1.380*	4.626*	4.310
$F_{1:}$								
Variety	39.421**	112.654**	227.396**	311.867**	1.595**	3.386**	5.986**	9.577**
Year	748.167**	3783.543**	11509.768**	21022.470**	43.861**	184.28**	650.146**	1519.972**
Variety Year	7.460**	23.820**	49.128**	67.603**	0.528**	1.451**	2.726**	4.516**
Block	0.022	2.652	13.453	43.378*	0.001	0.026	3.025*	7.627**

*Significant at p = 0.05, **significant at p = 0.01.

traits in sponge gourd might be influenced by genotypic and maternal effects at various maturation stages. Both the effects of year and variety × year were significant at p = 0.01% and the mean square of the year parameter was very large, suggesting that the two fruit shape traits were influenced by the environment. The ANOVA results for the F_1 generation were similar to those of the parents (Table 1), suggesting that there could be a certain degree of heterosis in the F_1 seeds and that environment effects might also affect the length and circumference traits at various stages of maturation.

Unconditional variance component analysis

The ratios of unconditional variances for fruit length and circumference at four stages of maturation are summarized in Table 2. Our results show that the genetic variance components (V_A, V_D, V_M, V_{AE}, V_{DE}, and V_{ME}) for fruit length at 3, 6, 9 and 12 days post-flowering maturating stages were significant, except for V_{AE} at the 3 day post-flowering stage, while for fruit circumference only V_A, V_M, and V_{DE} were significant at all maturating stages. The performance of fruit shape traits at different developmental stages was, therefore, controlled by genetic effects of fruit direct genes and maternal plant genes, which could also be affected by environmental variation.

Fruit length and circumference at various maturating stages were subject to not only genetic main effects but also by GE interaction effects which were part of the genetic effects inherited by the generations along with the genetic main effects and were the main reason for the variation in fruit length and circumference at the different stages of maturation under different environmental conditions.

Table 2 - Estimation of unconditional variance components of sponge gourd (*Luffa cylindrical* (L) Roem.) fruit length and circumference at different stages of maturation.

	Unconditional variance component values at different stages of maturation (d)							
	Fruit length				Fruit circumference			
Ratio	3d	6d	9d	12d	3d	6d	9d	12d
V_A/V_P	0.455** ± 0.018	0.490** ± 0.018	0.495** ± 0.018	0.426** ± 0.018	0.544** ± 0.020	0.492** ± 0.018	0.443** ± 0.017	0.503** ± 0.017
V_D/V_P	0.161** ± 0.017	0.116** ± 0.015	0.122** ± 0.014	0.164** ± 0.014	0.100** ± 0.014	0.028* ± 0.014	0.000 ± 0.000	0.000 ± 0.000
V_M/V_P	0.064** ± 0.009	0.073** ± 0.008	0.059** ± 0.008	0.049** ± 0.005	0.035** ± 0.006	0.036** ± 0.006	0.046** ± 0.006	0.028** ± 0.004
V_{AE}/V_P	0.000 ± 0.000	0.026* ± 0.012	0.023* ± 0.012	0.032** ± 0.012	0.061** ± 0.015	0.093** ± 0.014	0.007 ± 0.012	0.009 ± 0.011
V_{DE}/V_P	0.243** ± 0.019	0.213** ± 0.020	0.211** ± 0.020	0.247** ± 0.020	0.146** ± 0.020	0.227** ± 0.019	0.390** ± 0.024	0.346** ± 0.022
V_{ME}/V_P	0.023** ± 0.008	0.015* ± 0.008	0.019* ± 0.009	0.019** ± 0.008	0.015* ± 0.007	0.003 ± 0.006	0.000 ± 0.001	0.011^{+} ± 0.007
V_e/V_P	0.054** ± 0.007	0.067** ± 0.009	0.073** ± 0.009	0.063** ± 0.008	0.099** ± 0.009	0.122** ± 0.010	0.113** ± 0.010	0.103** ± 0.009

$^{+}$Significant at p = 0.10; *significant at p = 0.05; **significant at p = 0.01.

V_A, fruit direct additive variance; V_D, fruit dominance variance; V_M, maternal variance; V_{AE}, fruit additive interaction variance; V_{DE}, fruit dominance interaction variance; V_{ME}, maternal interaction variance; $V_{e,}$ residual variance; and V_P, phenotype variance.

Compared with the genetic main effects ($V_G = V_A + V_D + V_M$) and GE interaction effects ($V_{GE} = V_{AE} + V_{DE} + V_{ME}$), the performance of the fruit length and circumference traits at various maturating stages were principally affected by the genetic main effects ($V_G/(V_G + V_{GE}) = 0.531 \sim 0.681$) except for fruit circumference ($V_G/(V_G + V_{GE}) = 0.490$) at 9 days (Table 2). For the genetic main effects among different genetic systems, fruit direct effects ($(V_A + V_D)/V_G = 0.892 \sim 0.948$) were more important at different stages of maturation for both fruit length and circumference. For the GE interaction effects, the results of unconditional variance analysis indicated that the expression of fruit direct effects ($(V_{AE} + V_{DE})/V_{GE} = 0.914 \sim 0.999$) were also more important at different stages of maturation. Therefore, fruit shape traits were mainly controlled by the fruit direct nuclear genes, while maternal nuclear genes were also important for fruit shape traits at different developmental stages. The larger additive main variances ($V_A/V_G = 0.666 \sim 0.947$) for fruit shape traits at different stages of maturation suggests that the additive effects were more important than the other genetic effects and that, therefore, better improving effects could be expected by selection for fruit length and circumference in early generations. However, for GE the interaction effects, V_{DE} were the most important effects for fruit length and circumference at these developmental stages ($V_{DE}/V_{GE} = 0.657 \sim 0.981$).

We observed higher unconditional residual variances of conventionally cultivated sponge gourd fruit length and circumference at different stages of maturation as compared to those of flooded-field crops such as paddy rice (Shi *et al.*, 2002). However, the relatively small unconditional residual variances for our sponge gourd data indicated that the genetic effects were the predominant source of variation and that the performance of fruit shape traits at different stages of maturation was also influenced by sampling errors or environmental effects.

Conditional variance component analysis

From the unconditional variance analysis we concluded that expression of sponge gourd genes for fruit length and circumference might differ for the different stages of maturation. The conditional genetic variances of gene expression for the fruit shape traits at any particular period were then estimated using the conditional variance analysis, the estimated ratio of conditional variance components being listed in Table 3.

Our results indicated that the conditional fruit dominance variances ($V_{D(t|t-1)}$), conditional maternal variance ($V_{M(t|t-1)}$) and the conditional dominance interaction variance ($V_{DE(t|t-1)}$) of fruit length and circumference at various stages of maturation were significant except for the conditional dominance variance ($V_{D(t|t-1)}$) of fruit circumference for the last maturation stage at 10 to 12 days (Table 3). These results indicate that in the sponge gourd there were fruit dominance, maternal and dominance interaction effects caused by the new expression of genes at most stages of maturation. For fruit length, significant conditional additive variance ($V_{A(t|t-1)}$) and conditional maternal interaction variance ($V_{ME(t|t-1)}$) were also found at most stages of maturation except for the conditional additive variance ($V_{A(t|t-1)}$) at the third maturation stage at 7 to 9 days or the conditional maternal interaction variance ($V_{ME(t|t-1)}$) at the last maturation stage at 10 to 12 days, suggesting that there was new gene expression activated by additive and maternal interaction effects for the fruit length trait at most stages of maturation. Therefore, it appears that quantitative genes were gradually activated during the maturation stages and there were some differences in the magnitude or type of genetic effects during the different maturation stages of fruit shape traits.

Development is a dynamic process and gene expression is not always the same for all developmental quantitative traits. For example, in the sponge gourd new additive

Table 3 - Estimation of conditional variance components of sponge gourd (*Luffa cylindrical* (L) Roem.) fruit length and circumference at different stages of maturation.

	Conditional variance component values at different stages of maturation (d)							
	Fruit length				Fruit circumference			
Ratio	3d|initial	6d|3d	9d|6d	12d|9d	3d|initial	6d|3d	9d|6d	12d|9d
V_A/V_P	$0.455^{**} \pm 0.018$	$0.030^{**} \pm 0.009$	0.000 ± 0.000	$0.025^{**} \pm 0.009$	$0.544^{**} \pm 0.020$	$0.132^{**} \pm 0.014$	0.000 ± 0.000	0.010 ± 0.009
V_D/V_P	$0.161^{**} \pm 0.017$	$0.164^{**} \pm 0.017$	$0.333^{**} \pm 0.020$	$0.027^{+} \pm 0.021$	$0.100^{**} \pm 0.014$	$0.255^{**} \pm 0.020$	$0.233^{**} \pm 0.023$	0.000 ± 0.000
V_M/V_P	$0.064^{**} \pm 0.009$	$0.063^{**} \pm 0.007$	$0.123^{**} \pm 0.011$	$0.087^{**} \pm 0.007$	$0.035^{**} \pm 0.006$	$0.072^{**} \pm 0.006$	$0.053^{**} \pm 0.008$	$0.020^{**} \pm 0.006$
V_{AE}/V_P	0.000 ± 0.000	0.005 ± 0.015	0.000 ± 0.000	0.000 ± 0.000	$0.061^{**} \pm 0.015$	$0.073^{**} \pm 0.014$	0.003 ± 0.013	0.000 ± 0.000
V_{DE}/V_P	$0.243^{**} \pm 0.019$	$0.454^{**} \pm 0.023$	$0.186^{**} \pm 0.025$	$0.672^{**} \pm 0.026$	$0.146^{**} \pm 0.020$	$0.224^{**} \pm 0.024$	$0.401^{**} \pm 0.025$	$0.797^{**} \pm 0.028$
V_{ME}/V_P	$0.023^{**} \pm 0.008$	$0.054^{**} \pm 0.008$	$0.114^{**} \pm 0.013$	0.009 ± 0.007	$0.015^{*} \pm 0.007$	0.000 ± 0.000	0.004 ± 0.008	0.000 ± 0.000
V_e/V_P	$0.054^{**} \pm 0.007$	$0.229^{**} \pm 0.012$	$0.244^{**} \pm 0.011$	$0.180^{**} \pm 0.011$	$0.099^{**} \pm 0.009$	$0.244^{**} \pm 0.012$	$0.306^{**} \pm 0.011$	$0.173^{**} \pm 0.011$

$^{+}$Significant at p = 0.10; *significant at p = 0.05; **significant at p = 0.01.

V_A, fruit direct additive variance; V_D, fruit dominance variance; V_M, maternal variance; V_{AE}, fruit additive interaction variance; V_{DE}, fruit dominance interaction variance; V_{ME}, maternal interaction variance; V_e, residual variance; and V_P, phenotype variance.

effects due to the expression of fruit genes could affect fruit length and circumference more during the first maturation stage from flowering to 3 days post-flowering than at the latter stages from 4 to 12 days after flowering. The dynamics of the genetic effects can be investigated by analyzing the conditional and unconditional data for the different developmental traits at specific stages of maturation. For example, we found that for sponge gourd fruit circumference there was no new gene effect during the third and last stages of development from 7 to 12 days (Table 3) but a relatively large fruit circumference V_A value was observed by unconditional analysis due to the accumulated results from earlier stages of maturation. Furthermore, our results for fruit circumference significant dominance variances ($V_{D(t|t-1)}$) at the third maturation stage (Table 3) revealed that the new genetic effects detected by conditional variance analysis could be earlier than those detected by unconditional variance analysis, since the latter could not find this effect at the corresponding stage (Table 2) in this experiment. Thus, conditional analysis could help to clarify the presence of genetic effects due to new gene expression that could not be detected by unconditional analysis. Significant conditional residual variances ($V_{e(t|t-1)}$) showed that the performance of fruit shape traits at different developmental stages were also influenced by sampling errors (Table 3).

Correlation coefficient analysis

The genetic variation in fruit shape traits analyzed using the statistical methodology described above could only provide insight into gene action during specific stages of maturation, so we also examined the correlation between different stages of maturation such as the fruit length genetic variation between 6 and 12 days ($r_{(6d)\&(9d)}$). Such analysis could facilitate understanding of the interaction between gene effects and whether the genetic association pattern could be altered by the expression of different genes for each trait at specific stages of maturation. Analysis of unconditional and conditional correlation coefficients indicated that the relationship between fruit shape traits varied considerably at different stages of maturation (Tables 4 and 5), suggesting that genetic effects during the later stages of maturation were not always the same as during earlier stages.

For fruit length, we found that there was a relatively large positive correlation between genetic effects during different stages of maturation and that this contributed most to the differences in performance between the various stages. However, the noticeable negative correlation detected by the conditional method indicated that additional genetic effects caused by the expression of new direct gene and maternal gene effects at a specific maturation stage had a negative effect on fruit length. The negative conditional r_P value was significant between the first and third ($r_{D(3d|initial)\&(9d|6d)}$ and $r_{ME(3d|initial)\&(9d|6d)}$) and the first and last stages ($r_{D(3d|initial)\&(12d|9d)}$ plus $r_{M(3d|initial)\&(12d|9d)}$ and $r_{DE(3d|initial)\&(12d|9d)}$) (Table 4). Although the positive unconditional $r_{AE(6d)\&(9d)}$, $r_{AE(6d)\&(12d)}$ and $r_{AE(9d)\&(12d)}$ values were relatively large, there was zero conditional correlation between the second and third and second and last plus third and last maturation stages, caused by the zero conditional V_{AE} value at the third and last maturation stages. The significant positive conditional $r_{D(6d|3d)\&(9d|6d)}$ and $r_{D(6d|3d)\&(12d|9d)}$ values indicated that genetic effects due to fruit dominance effects

Table 4 - Estimation of unconditional and conditional correlation coefficients for sponge gourd (*Luffa cylindrical* (L) Roem.) fruit length at four stages of maturation.

Stage 1	Stage 2	r_P	r_A	r_D	r_M	r_{AE}	r_{DE}	r_{ME}
Unconditional								
3d	6d	$0.970^{**} \pm 0.028$	$1.000^{**} \pm 0.030$	$0.967^{**} \pm 0.009$	$0.980^{**} \pm 0.013$	0.000 ± 0.000	$0.951^{**} \pm 0.014$	$0.946^{**} \pm 0.002$
	9d	$0.941^{**} \pm 0.028$	$1.000^{**} \pm 0.029$	$0.852^{**} \pm 0.010$	$0.962^{**} \pm 0.014$	0.000 ± 0.000	$0.933^{**} \pm 0.009$	$0.719^{**} \pm 0.001$
	12d	$0.911^{**} \pm 0.030$	$1.000^{**} \pm 0.027$	$0.827^{**} \pm 0.013$	$0.848^{**} \pm 0.017$	0.000 ± 0.000	$0.829^{**} \pm 0.008$	$0.808^{**} \pm 0.001$
6d	9d	$0.984^{**} \pm 0.026$	$1.000^{**} \pm 0.033$	$0.965^{**} \pm 0.006$	$0.975^{**} \pm 0.014$	$1.000^{**} \pm 0.000$	$0.989^{**} \pm 0.010$	$0.921^{**} \pm 0.003$
	12d	$0.961^{**} \pm 0.028$	$1.000^{**} \pm 0.031$	$0.971^{**} \pm 0.007$	$0.893^{**} \pm 0.018$	$1.000^{**} \pm 0.000$	$0.914^{**} \pm 0.010$	$0.997^{**} \pm 0.005$
9d	12d	$0.984^{**} \pm 0.029$	$1.000^{**} \pm 0.031$	$1.000^{**} \pm 0.008$	$0.970^{**} \pm 0.020$	$1.000^{**} \pm 0.000$	$0.957^{**} \pm 0.007$	$1.000^{**} \pm 0.000$
Conditional								
3d|initial	6d|3d	0.008 ± 0.0017	-0.003 ± 0.003	0.014 ± 0.010	-0.010 ± 0.013	0.000 ± 0.000	-0.045 ± 0.034	0.003 ± 0.007
	9d|6d	$-0.090^{**} \pm 0.0028$	0.000 ± 0.000	$-0.307^{**} \pm 0.033$	0.046 ± 0.032	0.000 ± 0.000	-0.065 ± 0.064	$-0.390^{**} \pm 0.006$
	12d|9d	$-0.067^{**} \pm 0.004$	$0.096^{+} \pm 0.054$	$-0.388^{**} \pm 0.002$	$-0.332^{**} \pm 0.009$	0.000 ± 0.000	$-0.125^{**} \pm 0.047$	$0.679^{**} \pm 0.001$
6d|3d	9d|6d	$0.342^{**} \pm 0.032$	0.000 ± 0.000	$1.000^{**} \pm 0.004$	$-0.136^{**} \pm 0.001$	0.000 ± 0.00	$0.165^{**} \pm 0.010$	$1.000^{**} \pm 0.001$
	12d|9d	$0.155^{**} \pm 0.007$	$0.499^{**} \pm 0.000$	$1.000^{**} \pm 0.004$	$0.584^{**} \pm 0.012$	0.000 ± 0.000	$0.242^{**} \pm 0.014$	$-0.763^{**} \pm 0.006$
9d|6d	12d|9d	$0.206^{**} \pm 0.0234$	0.000 ± 0.000	$0.060^{+} \pm 0.027$	$1.000^{**} \pm 0.012$	0.000 ± 0.00	$0.664^{**} \pm 0.004$	$-1.000^{**} \pm 0.005$

$^{+}$Significant at p = 0.10; *significant at p = 0.05; **significant at p = 0.01.

r_P, phenotype correlation; r_A, fruit additive correlation; r_D, fruit dominance correlation; r_M, maternal correlation; r_{AE}, fruit additive interaction correlation; r_{DE}, fruit dominance interaction correlation; and r_{ME}, maternal interaction correlation.

Table 5 - Estimation of unconditional and conditional correlation coefficients for sponge gourd (*Luffa cylindrical* (L) Roem.) fruit circumference at four stages of maturation.

Stage 1	Stage 2	r_P	r_A	r_D	r_M	r_{AE}	r_{DE}	r_{ME}
Unconditional								
3d	6d	$0.916^{**} \pm 0.023$	$0.981^{**} \pm 0.016$	$0.698^{**} \pm 0.005$	$0.832^{**} \pm 0.013$	$0.936^{**} \pm 0.017$	$0.942^{**} \pm 0.002$	$1.000^{**} \pm 0.004$
	9d	$0.824^{**} \pm 0.022$	$0.951^{**} \pm 0.017$	0.000 ± 0.000	$0.580^{**} \pm 0.017$	$1.000^{**} \pm 0.008$	$0.847^{**} \pm 0.004$	$1.000^{**} \pm 0.001$
	12d	$0.802^{**} \pm 0.022$	$0.954^{**} \pm 0.017$	0.000 ± 0.000	$0.390^{**} \pm 0.022$	$1.000^{**} \pm 0.007$	$0.615^{**} \pm 0.003$	$1.000^{**} \pm 0.003$
6d	9d	$0.945^{**} \pm 0.022$	$1.000^{**} \pm 0.014$	0.000 ± 0.000	$0.971^{**} \pm 0.008$	$1.000^{**} \pm 0.006$	$0.987^{**} \pm 0.007$	$1.000^{**} \pm 0.000$
	12d	$0.913^{**} \pm 0.020$	$1.000^{**} \pm 0.004$	0.000 ± 0.000	$0.943^{**} \pm 0.004$	$1.000^{**} \pm 0.008$	$0.785^{**} \pm 0.003$	$0.891^{**} \pm 0.001$
9d	12d	$0.945^{**} \pm 0.023$	$1.000^{**} \pm 0.017$	0.000 ± 0.000	$0.997^{**} \pm 0.009$	$1.000^{**} \pm 0.006$	$0.920^{**} \pm 0.003$	$1.000^{**} \pm 0.002$
Conditional								
3d|initial	6d|3d	0.002 ± 0.004	-0.007 ± 0.044	0.014 ± 0.062	0.006 ± 0.059	-0.069 ± 0.069	0.033 ± 0.020	0.000 ± 0.000
	9d|6d	$-0.145^{**} \pm 0.047$	0.000 ± 0.000	$-0.463^{**} \pm 0.007$	$-0.933^{**} \pm 0.010$	$1.000^{**} \pm 0.002$	$-0.258^{**} \pm 0.004$	$1.000^{**} \pm 0.002$
	12d|9d	-0.026 ± 0.06	$0.457^{**} \pm 0.009$	0.000 ± 0.000	$-0.201^{**} \pm 0.038$	0.000 ± 0.000	$-0.426^{**} \pm 0.018$	0.000 ± 0.000
6d|3d	9d|6d	$0.340^{**} \pm 0.030$	0.000 ± 0.000	$0.390^{**} \pm 0.001$	$1.000^{**} \pm 0.007$	$-1.000^{**} \pm 0.002$	$0.755^{**} \pm 0.002$	0.000 ± 0.000
	12d|9d	$0.076^{**} \pm 0.023$	$-0.583^{**} \pm 0.001$	0.000 ± 0.000	$0.691^{**} \pm 0.010$	0.000 ± 0.000	0.031 ± 0.068	0.000 ± 0.000
9d|6d	12d|9d	$0.227^{**} \pm 0.051$	0.000 ± 0.000	0.000 ± 0.000	$0.522^{**} \pm 0.006$	0.000 ± 0.000	$0.905^{**} \pm 0.007$	0.000 ± 0.000

**Significant at $p = 0.01$.

r_P, phenotype correlation; r_A, fruit additive correlation; r_D, fruit dominance correlation; r_M, maternal correlation; r_{AE}, fruit additive interaction correlation; r_{DE}, fruit dominance interaction correlation; and r_{ME}, maternal interaction correlation.

during the second maturation stage could ultimately affect the performance of fruit length at the final maturation stage and could intimately influence the fruit dominance effects of fruit length this final stage of development.

For fruit circumference, the unconditional correlation coefficient r_A, r_{AE} and r_{ME} values were the most important, with most of the unconditional phenotypic and genotypic correlation coefficients between the first and second maturation stages being significant. However, nearly every conditional correlation coefficient between the first and second maturation stages was not significantly different from zero, indicating that the effects of new gene expression during the first maturation stage had no relationship with those at the second stage (Table 5). No significant direct dominance unconditional correlation (r_D) were observed between the various maturation stages except for $r_{D(3d)\&(6d)}$, while the significant conditional $r_{D(3d|initial)\&(9d|6d)}$ and $r_{D(6d|3d)\&(9d|6d)}$ values indicated that net genetic dominance effects occurred during the first three stages. All unconditional r_{ME} values were positive between the various maturation stages, while conditional analysis revealed that the only positively correlated extra maternal effects were those between the first maturation stage, which occurred from flowering to 3 days post-flowing, and the third maturation stage at 6 to 9 days post-flowing.

Discussion

The performance of fruit shape quantitative traits appears to be controlled by gene expression and regulation during the different stages of maturation, although the genetic mechanisms controlling the performance of quantitative traits may vary during different developmental stages. This is supported by Ye *et al.* (2003) in their study of upland cotton (*Gossypum hirsutum* L.) where they found correlations due to different genetic effects in different stages of development. In a paper concerning intra-cultivar heterosis in crops, Zhu *et al.* (1993) proposed a genetic model for quantitative traits controlled by direct genes and maternal plant genes. By using this model, fruit length and circumference of fruit shape traits influenced by maternal effects were found in the previous (Zhang *et al.*, 2007) and present research. Thus, the maternal plant genes as well as fruit direct genes were also important for the performance of fruit shape traits in sponge gourd. Therefore, the maternal plant gene also should be considered in the future research of fruit quality traits in other horticultural plant.

The results of our variance analysis indicated that in the sponge gourd fruit length and circumference were simultaneously controlled by the effects of fruit direct nuclear and maternal plant genes. Our research also showed the dynamic expression of sponge gourd fruit length and circumference quantitative genes and the dynamic genetic effects and net genetic effects expressed at specific developmental stages under different environments. We further showed that fruit genetic effects ($V_A + V_D$ and $V_{AE} + V_{DE}$) were the main cause of the genetic variation for both of the fruit shape traits during whole developmental period and that fruit length and fruit circumference could be improved more efficiently by selecting individual fruits. Since the main genetic effects for the fruit shape traits studied were fruit additive effects, selection in early generations could be used for improving fruit shape breeding. The correlation coefficients due to different genetic effects and the phenotypic correlation coefficients for fruit shape traits varied significantly between the various maturation stages, with the results of the correlation coefficient analysis confirming the results of the variance analysis.

In our study we also found that gene activation during the first maturation stage was mostly due to additive effects ($V_A + V_{AE}$), while dominance effects were mainly active during the other three stages ($V_D + V_{DE}$). Therefore, the selection of fruit length and circumference in the sponge gourd might be best carried out during the first maturation stage 3 days after flowering instead at economic maturation. To further confirm this result, the genetic effects of the seven parents (Wuyexiang = P_1, Lifeng = P_2, Tianhong = P_3, Jinke = P_4, Fengyuan = P_5, Jiutouniao = P_6 and Sanjiang 1 = P_7) were predicted using the adjusted unbiased prediction (AUP) method (Zhu, 1993; Zhu and Weir, 1996; Wu *et al.*, 2006). The results showed that at the three later maturation stages the net genetic effect of new fruit gene expression was subject to relatively small positive or negative effects. For example, for fruit length at the first maturation stage at 3 days the predicted additive effect value was $A1_{(3d)}$ = -1.181 for the Wuyexiang cultivar (P_1), $A2_{(3d)}$ = 3.895 for the Lifeng cultivar (P_2) and $A5_{(3d)}$ = -1.055 for the Fengyuan cultivar (P_5), while at the second maturation stage at 4 to 6 days $A1_{(6d|3d)}$ = 0.205, $A2_{(6d|3d)}$ = 0.171 and $A5_{(6d|3d)}$ = -0.079, with at the last maturation stage from 10 to 12 days $A1_{(12d|9d)}$ = 0.188, $A2_{(12d|9d)}$ = 0.086 and $A5_{(12d|9d)}$ = -0.275.

The results indicate that it is relatively easy to improve the two fruit shape traits for market purposes by carefully selecting the parents at the first maturation stage 3 days after flowering instead of at fruit maturation. These results provide a useful insight into sponge gourd genetics and may be useful in breeding and management programs as well as basic research on this interesting plant species.

Acknowledgments

The research was supported by the National Nature Science Foundation of China under grant number 30370911 and the Science and Technology Department of Zhejiang Province under grant number 2005C32001.

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Senior Editor: Ernesto Paterniani