Genetic Basis for Productivity in *Anthurium andraeanum* Hort.

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Abstract. *Anthurium andraeanum* Hort. is an important tropical ornamental crop regarded as second only to orchids in its commercial importance. The genetic basis for productivity in anthurium was studied using parent–offspring regression analysis. Sixteen parental genotypes (4 years old) and 14 biparental progeny families (60 plants each, 4 years old) derived from the parents were used in the study. Yield expressed as number of cut flowers per plant per year (CFPY) was significant both between parental genotypes ($P < 0.001$) and between progeny families ($P < 0.05$). Mean CFPY of the parent genotypes was normally distributed and ranged from 4.8 in ‘Local Mina Red’ to 9.8 in ‘Kalapana’ with a mean of 7.5. CFPY in Year 1 was strongly correlated to that in Year 2 (Pearson’s $r = 0.96$; Spearman’s $r = 0.93$) and the broad sense heritability (H^2) was high (87.6%) under controlled shadehouse conditions. CFPY in the progeny families varied from four to 14 with progeny means ranging from 5.7 in ‘Honduras/Local Mina Red’ to 7.2 in ‘Mirjam/Kalapana’. Progeny of seven and 10 crosses possessed mean CFPY greater than that of the more productive parent and the midparent values, respectively. The frequency distribution for productivity of the 840 progeny plants was skewed to the right with a modal class of six to seven. The correlation coefficient between progeny CFPY and midparent CFPY was large and significant ($r = 0.90$, $P < 0.001$). The regression of mean progeny CFPY on mean midparental CFPY was strong ($y = 0.51x + 2.56$; $R^2 = 0.81$) with an estimated narrow sense heritability (h^2) of 51.0%. A breeding strategy for improving per plant productivity based on the results is discussed.

Anthurium is a neotropical genus (Croat, 1988) belonging to the monocotyledonous family *Araceae*, which includes more than 100 genera and ≈ 1500 species (Croat, 1988; Higaki et al., 1994). Native species of *Anthurium* occur from Mexico through Central America and the Caribbean to Brazil (Kamemoto and Kuehnle, 1996). Cultivated anthuriums belong to two (*Calomystrium* and *Porphyrochitonium*) of 18 sections outlined by Kamemoto and Kuehnle (1996). Interspecific hybridization between species of *Anthurium* belonging to the section *Calomystrium* has resulted in an *Anthurium* species complex, referred to as *Anthurium andraeanum* Hort.

Anthurium is cultivated primarily for its showy cut flowers and glossy leaves that are exported or sold locally. The important horticultural features of the cut flower are its color, size, texture, shape and showiness of the spathe, spadix length and carriage, straightness of the peduncle and peduncle length, overall symmetry of the cut flower, and productivity (Kamemoto et al., 1986; Kamemoto and Kuehnle, 1996). Productivity is particularly important because it determines the profitability of an anthurium farm and hence is an important selection criterion in anthurium

breeding (Elibox and Umaharan, 2012; van Herk et al., 1998). On average, a single growing axis produces only five or six cut flowers per year, and consequently a difference of one cut flower per plant per year may translate into large economic differences on a hectare basis (Kamemoto and Kuehnle, 1996). Generally, in the Caribbean (Elibox, 2005; Elibox and Umaharan, 2012) and worldwide (Kamemoto and Kuehnle, 1996; Kamemoto and Nakasone, 1963), an average of six cut flowers per plant per year is considered critical for a profitable anthurium industry.

Although Trinidad and Tobago experiences two seasons (a dry and a wet season) per year, it has been found that seasonal difference in anthurium genotype productivity under shadehouse conditions, where shade regime, potting medium and watering, and fertilization regimes were controlled, was not significant (Campbell, 2006). Furthermore, anthurium productivity does not peak until after 3 years of field planting for either tissue-cultured plants or seedlings (Holder, 2005) and remains stable for at least 5 years thereafter. There has been very little progress with regard to productivity improvement in anthurium worldwide because there is no information on the heritability of productivity or its genetic basis, both of which are required in developing a breeding strategy to improve productivity in anthurium. The objective of this research is to determine the genetic basis for productivity in *Anthurium andraeanum* Hort.

Location. The study was conducted in a commercial anthurium farm, Kairi Blooms Ltd., situated in Arima, Trinidad and Tobago. The location experiences two seasons: a dry season (January to May) and a wet season (June to December). The average relative humidity, temperature, and light intensity at the location are 83%, 27.7 °C, and 57 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively.

Cultural conditions. The study was conducted in a shadehouse covered with clear plastic on top and Saran netting (75% shade) below. The plants were grown in plastic pots (21 cm diameter and 22 cm deep) containing peatmoss (Premier Horticulture Ltd., Quebec, Canada) at the center and coconut husk around. The plants were hand-watered once daily on an individual plant basis to prevent splashing and fertilized (1.5 g) on a monthly basis with either triple superphosphate (Chemcos GmbH, Regenstauf, Germany) or 12N–11P–13K (Norsk Hydro Olje AB, NYBRO, Sweden). The pH of the growing medium was maintained at 5.5 by continuous monitoring and applying calcium carbonate (limestone; TRINCARB, Trinidad) as necessary. The nematicide Temik (Aldicarb, Shandong, China) was applied once to prevent nematode infestation.

Measurements in the parental genotypes (Expt. 1). Four-year-old plants of 16 anthurium genotypes (Table 1) representing the range of variation for productivity were evaluated for productivity over a 2-year period (Kamemoto and Nakasone, 1963) in the shadehouse. The plants were originally derived from tissue culture. The experiment was set out in a randomized complete block design with three replications and with five plants per replicate. The plants were arranged on a plant stand (0.61 m high) made of wire mesh and spaced out, 60 cm $\times$ 60 cm.

Three-quarter ripe cut flowers (true flowers are open along three-fourths of the length of the spadix) were harvested on a daily basis from Monday to Friday between 0700 and 1100 hr over 2 years. Each plant was tagged with a white plastic tag that was ticked using a permanent marker every time a new cut flower was harvested. From the cut flowers harvested from each replicate, average number of CFPY for each genotype was calculated for each year separately.

Hybridization and aftercare of progeny. Fourteen random crosses were made involving the 16 parental genotypes without reciprocals. Crossing was as described by Higaki et al. (1994). Six months after pollination, the ripe berries from each cross were collected, seeds squeezed out, and planted in a labeled (name of cross, sowing date) seedling tray containing peatmoss in a nursery shadehouse (75% shade). The seedlings were watered every day for 10 s at 15-min intervals between 0900 and 1600 hr using a mist irrigation system. A 20N–20P–20K foliar fertilizer, Nutrex (Marman USA Inc., Tampa, FL), was spray-applied twice a week at a concentration of 1.5 g·L⁻¹ of water, and micronutrients

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Table 1. Productivity data, measured as number of cut flowers per plant per year (CFPY) and cv_{within} obtained for 16 genotypes of *Anthurium andraeanum* Hort. in Expt. 1 and Expt. 2.

Genotype	Productivity (number of CFPY)			
	Expt. 1		Expt. 2	
	Mean	cv within percent	Mean	cv within percent
Acropolis	5.8	9.1	6.0	11.3
Champagne	7.2	7.3	7.8	8.4
Cross 3962	6.3	6.2	6.0	7.6
Cuba	8.5	6.9	8.9	5.8
Hawaii	8.5	8.4	8.1	9.3
Honduras	8.7	8.8	9.1	11.0
Ibara	6.2	9.4	6.6	7.5
Kalapana	9.8	7.4	10.0	9.6
Local Mina Red	4.8	8.2	4.5	7.9
Local Orange	7.0	9.3	7.4	9.5
Lydia	8.8	11.3	9.1	9.8
Mirjam	9.2	11.1	8.8	10.5
Pierrot	7.0	11.3	7.5	12.2
Senator	8.2	8.6	7.1	8.6
Venus	7.4	10.8	7.6	11.7
Victoria	7.1	7.4	6.5	9.5
Significance ($P <$)	0.001	—	0.001	—
Mean	7.5	—	7.6	—
SEM	0.32	—	0.50	—
Least significant difference	0.77	—	1.20	—
cv within percent	8.8	—	9.4	—
Genotypic cv %	18.2	—	18.9	—

(Biolchim S.p.A, Italy) were applied by foliar application as necessary at a rate of $9 \text{ mL} \cdot \text{L}^{-1}$ of water. Six months after germination, the seedlings were transplanted into labeled (cross, seedling number) $8 \text{ cm} \times 8 \text{ cm} \times 8\text{-cm}$ pots and after another 1.5 years, they were transferred to larger pots (21 cm diameter and 22 cm deep), like for the parental genotypes. The pots were clearly labeled and potted plants were grown for another 2 years before evaluating them for productivity.

Productivity of progeny generations (Expt. 2). Three replicates each of the parental genotypes (4 years old; five plants per replicate) and three replicates each of the 14 progeny families (4 years old) were arranged in a completely randomized design and evaluated for productivity over a period of 1 year as described before. Each replicate of the progeny family consisted of 20 randomly chosen progeny plants from the specific cross. The plants were spaced at $60 \text{ cm} \times 60 \text{ cm}$ as before. Aftercare and data collection were as described before.

Data analysis. With respect to Expt. 1, mean CFPY for each parent genotype per replicate (averaged over the 2 years) was calculated and a one-way analysis of variance (ANOVA) (NCSS, 2007) was performed to determine the significance of genotypic differences for CFPY. The cv for each genotype (NCSS, 2007), the average cv within genotypes ($cv_{within} = \text{square root of the error mean square from ANOVA/grand mean}$), and the genotypic cv ($cv_{between} = \text{SD between the mean of the genotypes/grand mean}$) were calculated. A two-way ANOVA was performed to determine the significance of year-to-year differences and the presence of genotype $\times$ year interactions. Pearson's product moment correlation and Spearman's rank correlation (NCSS, 2007) were performed to determine

the association between parent genotype productivity over the 2 years. Shapiro-Wilk W test (NCSS, 2007) was conducted to test whether the distribution of mean CFPY for the parent genotypes over the 2 years was normally distributed. H^2 for parent productivity was calculated according to Dabholkar (1999).

Correlation coefficients were calculated as before between mean genotype productivity in Expt. 1 and Expt. 2. In Expt. 2, mean CFPY and range for each progeny family were determined and the significance of differences between progeny family mean CFPY was tested using a one-way ANOVA (NCSS, 2007). Pearson's product moment correlation was carried out (NCSS, 2007) separately between mean progeny CFPY and that for male parent, female parent, and midparent values from Expt. 2. cv within each individual family and average cv within and between progeny families were determined as described before. The frequency histogram of productivity values for the 840 progeny plants evaluated was tested for normality using the Shapiro-Wilk W test (NCSS, 2007). The number of progeny plants that possessed productivity values larger than the more productive parent and midparent values were determined for each progeny family. Parent-offspring regressions were performed between progeny CFPY and those for male parent, female parent, and midparent values to determine the nature of the relationships; and the h^2 for CFPY was estimated as the slope of the midparent-offspring regression according to Lush (1943).

Results

Productivity of the parent genotypes. There were significant differences in productivity

(CFPY) among the parent genotypes in Expt. 1 ($P < 0.001$) (Table 1). The year-to-year differences and genotype $\times$ year interactions were not significant ($P > 0.05$). The correlation between mean CFPY values between the 2 years was large (Pearson's $r = 0.96$; Spearman's $r = 0.93$) and significant ($P < 0.001$). Mean productivity values for the 16 parent genotypes ranged from 4.8 CFPY in 'Local Mina Red' to 9.8 CFPY in 'Kalapana' with a mean of 7.5 CFPY. The average cv within parent genotypes was small (8.8%) but the genotypic cv was 2-fold larger (18.2%). The distribution of productivity values for the parental genotypes was normal (Shapiro-Wilk W test probability = 0.88, $P > 0.05$) with a high H^2 (87.6%).

In Expt. 2, productivity of parents ranged from 4.5 CFPY in 'Local Mina Red' to 10 CFPY in 'Kalapana' with a mean of 7.6 CFPY. The cv between the parent genotypes (18.9%) was 2-fold larger than the average cv within genotypes (9.4%). The correlation between mean parent genotype productivity in Expt. 1 and Expt. 2 (Table 1) was large (Pearson's $r = 0.94$; Spearman's $r = 0.91$) and significant ($P < 0.001$) and showed that productivity values for the parent genotypes were repeatable over 2 years.

Productivity of the progenies in the crosses.

There were significant differences in productivity among the progeny families ($P < 0.05$). Family 'Mirjam/Kalapana' had the largest mean productivity value (7.2 CFPY) and 'Honduras/Local Mina Red' had the lowest CFPY (5.7) (Table 2). Progeny plants within 'Acropolis/Victoria' had the largest range in productivity (four to 14 CFPY) followed by 'Honduras/Cross 3962' (four to 12 CFPY). On the other end, four families had smaller ranges for CFPY ('Honduras/Local Mina Red', 'Champagne/Venus', 'Mirjam/Kalapana', and 'Senator/Hawaii').

The frequency distribution for progeny productivity values over all crosses was continuous and skewed to the right (Shapiro-Wilk test probability = 0.00; $P < 0.05$), i.e., toward low productivity (Fig. 1) with the modal class between six and seven CFPY. Among the progeny families, there was evidence of better parent heterosis in seven (50%) families ('Acropolis/Victoria', 'Acropolis/Cross 3962', 'Champagne/Ibara', 'Champagne/Venus', 'Honduras/Cross 3962', 'Local Orange/Cuba', and 'Pierrot/Local Orange'), but $\approx 71.4\%$ of the progeny families showed midparent heterosis (Table 2).

Parent-offspring regression. Correlation between mean progeny productivity values and mean female parent productivity values was very small and not significant ($r = 0.14$, $P > 0.05$), but the correlations between mean progeny productivity values and mean male parent productivity values ($r = 0.79$, $P < 0.01$) and between mean progeny productivity values and midparent productivity values ($r = 0.90$, $P < 0.001$) were significant. Regression of mean progeny productivity values against mean male parent productivity values was moderate ($R^2 = 0.63$) and can be represented by the equation $y = 0.2219x + 4.80$, whereas

Table 2. Mean progeny productivity (number of cut flowers per plant per year $\pm$ SD), CV_{within} each family, range of productivity, and percentage of progeny plants with productivity larger than the more productive parent, midparent for 14 crosses of *Anthurium andraeanum* Hort. evaluated in Expt. 2.

<i>Anthurium andraeanum</i> Hort. crosses	Mean progeny productivity ^z	cv within percent	Progeny productivity range	Percentage of progenies with productivity larger than the	
				More productive parent	Mid-parent value
Cross 3962/Lydia ^y	6.2	20.7	4–8	0	25
Acropolis/Victoria	6.0	43.6	4–14	20	20
Champagne/Cross 3962	5.9	20.5	4–8	10	10
Champagne/Ibara	6.2	25.4	4–8	35	35
Champagne/Venus	6.4	12.8	6–8	20	20
Champagne/Honduras	7.1	17.0	4–8	0	0
Honduras/Cross 3962	6.6	26.2	4–12	5	30
Honduras/Local Mina Red	5.7	12.9	4–6	0	0
Local Orange/Cuba	6.8	22.2	6–12	5	5
Local Orange/Honduras	6.8	16.9	4–8	0	0
Mirjam/Ibara	6.4	19.2	4–8	0	30
Mirjam/Kalapana	7.2	14.0	6–8	0	0
Pierrot/Local Orange	6.7	22.2	6–12	25	25
Senator/Hawaii	6.6	14.2	6–8	0	30
Significance ($P <$)	0.05	—	—	—	—
Mean	6.5	—	—	—	—
SEM	0.31	—	—	—	—
Least significant difference	0.72	—	—	—	—
cv within percent	21.7	—	—	—	—
Genotypic cv %	6.8	—	—	—	—

^zProductivity = number of cut flowers per plant per year.

^yFirst parent is the female parent and the second parent is the male parent. Each progeny family comprised 60 plants.

Fig. 1. Frequency distribution for productivity of 840 *Anthurium andraeanum* Hort. progeny plants derived from 14 crosses.

Fig. 2. Midparent–offspring regression for 14 crosses of *A. andraeanum* Hort. used in the productivity experiment.

regression of progeny mean productivity values on mean midparent productivity values (Fig. 2) was much stronger ($R^2 = 0.81$) and can be represented by the equation: $y = 0.5101x +$

2.56. This strongly suggests that inheritance for productivity in anthurium is biparental with an estimated h^2 (breeding value) of 51.0%.

Discussion

Maintaining high productivity is essential for the commercial viability of the anthurium cut flower industry. Much of the work in the past (Campbell, 2006; Kobayashi et al., 2006; Nakasone and Kamemoto, 1962) has focused mainly on improving the agronomy toward improving productivity. This is the first study investigating the genetic variation and heritability of productivity in *Anthurium* with the view to improving productivity through breeding.

The study showed that there were differences between the parent genotypes and progenies with respect to productivity, which is in agreement with observations made in Hawaii by Kamemoto and Nakasone (1963). Furthermore, the productivity of the parent genotypes was consistent between the 2 years tested as evidenced by lack of year-to-year variation and lack of a significant genotype $\times$ year interaction based on ANOVA, a strong and significant positive correlation between mean genotypic values across trials, and a high H^2 estimate of 87.6%. Earlier work in Trinidad has also shown that under controlled shadehouse conditions, where the important environmental factors such as shade, growing medium, water, and nutrients are regulated, anthurium productivity is unaffected greatly by seasonal variation (Campbell, 2006). These results together suggest that under the uniform environmental conditions that prevail within the shadehouse setting, productivity levels can be ascertained with minimal environmental influences.

The frequency distribution for parent genotype productivity was found to be normal in this study with only ‘Local Mina Red’ possessing productivity values (mean of 4.7) below the accepted level of six to seven cut flowers per plant per year that is required for

commercial success (Kamemoto and Kuehnle, 1996). The superiority of performance of parents used in this study may be because they were selected from commercially successful genotypes grown locally. The small CV within parental genotypes of 8.8% and 9.4%, respectively, for Expt. 1 and Expt. 2 suggests that productivity was consistent among the clonal propagules of each genotype. The genotypic CV was 2-fold larger, suggesting that there exists a wide variation in productivity among locally adapted anthurium genotypes grown in Trinidad, which augurs well for future breeding efforts to improve productivity. A previous study (Elibox and Umaharan, 2012) reported that productivity was not associated with any other horticulturally important traits of anthurium and hence can be improved without affecting any other trait.

Mean productivity of progeny families across all crosses ranged from four to 14 cut flowers per plant per year. The CV_{within} progeny families was 3-fold that of $CV_{between}$ families indicating that considerable variation was created through hybridization. This was especially evident in the cross 'Acropolis/Victoria', which had a within family CV of 43.6%.

The frequency distribution of progeny productivity showed a skewed distribution with a mode of six to seven CFPY, which was just about the average required for a farm to be commercially viable (Elibox and Umaharan, 2012; Kamemoto and Kuehnle, 1996). The lack of transgressive segregation in four (28.6%) crosses viz. 'Champagne/Honduras', 'Honduras/Local Mina Red', 'Local Orange/Honduras', 'Mirjam/Kalapana' (Table 2), and the observation of transgressive segregation in 10 crosses (71.4%) suggest that both non-additive genetic effects (dominance and epistasis) and additive genetic effects (Falconer, 1981; Simmonds, 1979) are important in the inheritance of productivity in anthurium. The observation of better parent heterosis in only 50.0% of the families suggests that careful selection of parent combinations would be important in anthurium breeding to improve productivity. Generally, better parent heterosis (Kearsey and Pooni, 1996) is the most useful because it results in progeny plants that can markedly increase the number of CFPY. An increase of one cut flower per plant per year translates into a significant economic benefit to the farmer, because anthurium is cultivated at high plant densities (Kamemoto and Kuehnle, 1996). Although seven crosses (50%) did not possess any better parent heterosis, the other seven crosses showed better parent heterosis ranging from 8.3% to 58.3% of the progenies (Table 2).

The h^2 (the proportion of the phenotypic variability that is the result of the additive genetic effects) for productivity was moderate (51%). The moderate h^2 and relatively high H^2 (the proportion of the phenotypic variability that is the result of the genetic variation) of 87.6% suggests an important role for non-additive genetic effects (accounting for 36.6% of the phenotypic variability) in the inheritance of productivity (Simmonds, 1979).

The continuous but skewed distribution for progeny productivity also suggests that inheritance of productivity is polygenic (Falconer, 1981; Mather, 1943) with a moderate non-additive component. Productivity has been shown to be polygenically determined in ornamentals such as gerbera (Harding et al., 1981) and sunflower (Leon et al., 2001). Anthurium plants produce one cut flower per leaf axil during the sympodial phase of growth (Dai and Paull, 1990; Dufour and Guerin, 2003; Kamemoto and Nakasone, 1963), and hence productivity is affected by genotype vigor (rate of leaf production), which affects its production potential. Furthermore, the productivity of anthurium plants is affected by light intensity (Henny et al., 1991), temperature, insects, diseases, water, and nutrition (Kamemoto and Kuehnle, 1996). Therefore, superior producing hybrids must be grown under the conditions that they were selected for to realize their full genetic potential.

We suggest that the lack of progress in breeding for increased productivity in anthurium may be attributed to variable field conditions in which selection was carried out and the moderate h^2 estimates obtained for productivity even under controlled environmental conditions such as those in this study. First, the study shows that under controlled shadehouse conditions such as those used in this study, the environmental effects can be minimized and repeatable results can be obtained. Second, understanding the genetic basis for productivity allows the breeder to use modifications to the selection strategy, which can greatly improve genetic gain. The moderate h^2 for productivity suggests that breeding for high productivity may require progeny testing before selecting the parents. As was evident in this study, the superior parents did not necessarily provide the most productive families or the largest better parent heterosis. Progeny testing, however, will increase the cost of breeding. Alternatively, molecular markers that correlate with productivity can be researched and marker-assisted selection (Han et al., 2002; Mohan et al., 1997) can be practiced on the seedlings to determine the progeny plants that possess the quantitative trait loci for high productivity. This method has the ability to reduce the length and cost of breeding and quickly accumulate genes for productivity.

We also suggest a clonal breeding program with recurrent mass selection or marker-assisted selection be instituted to improve *Anthurium*. In this method, a large number of parents will be crossed and evaluated for progeny family performance and the top performing progeny from the best families will be clonally multiplied and distributed to anthurium growers. Based on the farmer testing, the top contenders could be used as parents in the second breeding cycle. Over several cycles, important genes for productivity will be accumulated.

Twenty-one progeny plants of the 840 evaluated possessed productivity values of 11 or greater. Such high productivity levels have never been observed in anthurium genotypes grown in Trinidad. The results suggest that anthurium breeding for productivity has the

potential to double the yield per unit area of cultivation. Although not shown, some of the progeny plants possessed novel spathe colors that have never been reported before in anthurium, but the spathe sizes and shapes were in the range reported by Elibox and Umaharan (2012).

In summary, the study shows considerable variability for productivity in *Anthurium* among genotypes and progenies derived from crosses between them in Trinidad that augurs well for breeding. The high level of repeatability for productivity and the lack of genotype $\times$ environmental influences under shadehouse conditions suggest that significant improvements in productivity through selection can be obtained under this environment. All crosses produce some progenies with productivity of at least six CFPY (the minimum acceptable productivity for an anthurium genotype grown in the Caribbean) and all crosses except for 'Honduras/Local Mina Red' resulted in families with a proportion of the progenies with at least eight CFPY. The genetic study suggests that inheritance of productivity is polygenic and governed by both additive and non-additive genetic effects. Clonal breeding with recurrent selection strategies to harness both the additive and non-additive genetic effects should be instituted to accumulate genes for productivity. Special interventions such as progeny selection or line selection or marker-assisted selection are needed to exploit the non-additive genetic effects. Horticulturally acceptable genotypes from these crosses have the ability to markedly increase the revenue of farmers. However, these genotypes have to be evaluated for other important traits such as disease resistance. Four crosses, 'Acropolis/Victoria', 'Honduras/Cross 3962', 'Local Orange/Cuba', and 'Pierrot/Local Orange', possessed progenies with productivities larger than the current most productive genotype, 'Kalapana'.

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