Morphophysiological Characteristics Associated with Vase Life of Cut Flowers of Anthurium

Winston Elibox and Pathmanathan Umaharan¹

Department of Life Sciences, Faculty of Science and Agriculture, The University of the West Indies, St. Augustine Campus, College Road, St. Augustine, Republic of Trinidad and Tobago

Additional index words. anthocyanin, carotenoids, flavonoids, hydathodes, spathe discoloration, bluing

Abstract. The vase life of 26 anthurium (*Anthurium andraeanum* Hort.) cultivars was evaluated in three separate trials. In the first trial, the influence of 12 morphophysiological characteristics of the cut flower on vase life was investigated. Of these, only spathe color and abaxial stomatal density were able to accurately predict vase life. A vase life prediction equation based on abaxial stomatal density, green/not green and white/not white was able to explain the cultivar variation in vase life in two separate trials conducted over two seasons. The equation was further validated using a different set of anthurium cultivars. Although vase life varied over seasons, the relative ranking of cultivars was similar as indicated by joint regression analysis. Changes in vase life over season were mediated through changes in stomatal density. Time to spadix necrosis was the only senescence indicator that occurred in all cultivars and was highly correlated to vase life determined by a complex criterion in all trials. Time to spadix necrosis is therefore suggested as a simplified criterion for vase life assessment. The possible mechanism for vase life deterioration and an approach to improving vase life in anthurium is discussed.

Anthurium andraeanum (Hort.) (Kamemoto and Kuehnle, 1996) is an important tropical ornamental crop, second only to orchids, based on global trade volume. It is grown for its showy cut flower, which comprises a spadix with over 300 spirally arranged minute flowers subtended by a brightly colored modified leaf, the spathe (Croat, 1988). The size, shape, texture, color, and patterns on the spathe determine the commercial value of the cut flower; whereas its vase life determines its marketability (Paull et al., 1985).

Halevy and Mayak (1979) defined vase life as the useful longevity of the floral product at the final consumer's home. Commercially, a vase life of at least 3 weeks (Kamemoto and Kuehnle, 1996) is required to market anthurium cut flowers. Anthurium cut flowers are known for their relatively long vase life that ranges from 1 week to several months. An understanding of the morphophysiological characteristics associated with such a wide variation in vase life will allow breeders to develop varieties with long vase

lives. There are no such studies in the literature.

Paull and Goo (1985) ascribed the symptoms of cut flower senescence in anthurium, that is, loss of spathe glossiness, spathe and spadix browning, and spathe wilting, to water stress. Another symptom, spathe blueing, is attributed to an increase in pH from 5.2 to 5.6 caused by an increase in ammonium ions resulting from the breakdown of proteins (Paull et al., 1985).

There is no agreed set of criteria for determining vase life in anthurium, because what is deemed unsalable by a wholesaler or retailer is different from what a consumer is prepared to discard (Paull, 1982). Shirakawa et al. (1964) used spathe wilting or spathe or spadix darkening as indications of vase life termination. Paull (1982), in addition, used loss of spathe glossiness and spathe blueing. Vase life is therefore determined by a complex criterion based on whichever of these symptoms appears first.

The objective of this study was to determine the morphophysiological basis for cultivar differences in vase life toward developing a prediction equation for vase life and to ascertain the validity of the prediction equation over seasons and a different set of cultivars. We also propose a simplified criterion for assessing vase life in anthurium.

Materials and Methods

Season and location. Vase life was investigated in three trials, Trial 1 (Mar. 2001; dry season), Trial 2 (Sept. 2001; wet season), and

Trial 3 (Oct. 2001; wet season), at the laboratories of the University of the West Indies, St. Augustine, Trinidad. The cut flowers were harvested from a commercial farm, Kairi Blooms Ltd., in Arima, Trinidad. The average rainfall, temperature, and relative humidity for the months Mar., Sept., and Oct. 2001 in Arima were 34.3 mm, 25.7 °C, 77%; 202.5 mm, 26.5 °C, 84%; and 199.3 mm, 26.4 °C, 85%, respectively.

Cultivars and cultural practices. The 26 cultivars selected for the study were 3 to 4 years old and included various spathe shapes, textures, sizes, and colors. The cultivars were grown under shade houses (80% shade) on beds (23 m × 1.2 m) made of coconut husk and planted at a spacing of 0.45 m × 0.4 m. The beds were fertilized with either triple superphosphate (Chemos GmBH, Regensburg, Germany) or 12N–11P–13K (Norsk Hydro Olje AB, NYBRO, Sweden) every month at a rate of 0.45 kg per bed. Urea (National Agro, Trinidad) and diammonium phosphate (Brenntag, Dominican Republic) were applied as necessary at a rate of 0.23 kg per bed. The plants were irrigated once daily for 15 min by overhead sprinkler irrigation. The pH of the beds was maintained at 5.6 by regular liming (Limestone; Trincarb, Trinidad).

Harvesting and transport of cut flowers. Overall, 26 anthurium cultivars were used in three experiments. Cut flowers with no scratches, no deformities, and straight peduncles were harvested at the three-fourths mature stage of the spadix (Kamemoto, 1962). The cut flowers were cut with a sharp, sterile knife, packed in boxes containing wet shredded paper, and transported to the university laboratory in an air-conditioned vehicle. Cut flowers were harvested from along the length of the bed for each cultivar to ensure a uniform representation of the variation within each cultivar. Experiments were set up on the day of harvesting.

Morphophysiological characterization. Seventeen cultivars were assessed for 12 morphophysiological characteristics using nine cut flowers per cultivar in Mar. 2001. Peduncle length was measured as the distance from the point of attachment of the peduncle to the spathe down to the cut end using a measuring tape. Peduncle diameter was measured using a pair of calipers (ENKAY Vernier Caliper 5-inch scale, Lo. 430-C ENKAY, Brooklyn, NY) at a distance of 15 cm from the spathe. Surface area of the spathe was obtained by tracing the spathe outline onto brown paper and measuring it with a ΔT Area Meter MK2 model (Delta-T Devices, Burwell Cambridge, UK) and multiplying the value obtained by two. Spathe color was recorded as described by Kamemoto et al. (1988). Spadix length was measured as the distance from the point of attachment of the inflorescence at the peduncle to the tip (Dai and Paull, 1990).

Stomatal density, stomatal size, and hydathode density were determined on three randomly selected spathes per cultivar. Four 1.5 × 0.5-cm pieces were cut from each

Received for publication 15 Aug. 2007. Accepted for publication 12 Feb. 2008.

This study was funded by the EUFORUM/CARIFORUM under the Caribbean Agricultural Technology Fund (CARTF) programme.

We thank the management and staff of Kairi Blooms Farm for providing the facilities for the research.

¹To whom reprint requests should be addressed; e-mail pumaharan@fsa.uwi.tt.

spathe and placed in a clearing solution in a petri dish to remove pigments. The clearing solution was prepared by adding 15 g of NaOH pellets to 500 mL of water and 500 mL of 95% ethanol and was replaced routinely as it became pigmented or dried up. Cleared sections were mounted on slides, stained with toluidine blue, and warmed for 2 min on a slide warmer at 40 °C. Stomatal density and hydathode density were enumerated for each section based on four views on the lower and four views on the upper spathe surface at $\times 100$ magnification using a light microscope (Euromex, Arnhem, Holland). From this, the mean number of stomata and hydathodes/mm on the abaxial and adaxial spathe surfaces of each cultivar were calculated. Stomatal size of each cultivar was measured under $\times 400$ magnification using a calibrated eyepiece micrometer (Pyser-SGI Ltd., Kent, UK). The length and width of 10 randomly selected stomata each from the four views per section were measured and mean stomatal length and width calculated. The length and width of stoma plus guard cell were also measured. From these data, the area of each stoma was calculated using the following formula: $\text{area} = \pi r_1 r_2$ where r_1 is half the length and r_2 is half the width, because the stomata were elliptical in shape.

Spathe thickness was recorded on three spathes per cultivar using three 1.5×0.5 -cm segments along the midrib per spathe. The nine spathe segments per cultivar were mounted in wax, sectioned transversely using a microtome (20 μm thicknesses), and fixed on slides (Johansen, 1940; O'Brien and McCully, 1981). Slides were viewed under a light microscope at $\times 100$ magnification and the mean thickness of each spathe was calculated from an average of five measurements per segment on each of the three spathe segments using a calibrated eyepiece micrometer as done previously.

To determine epicuticular wax, three whole spathes were first traced on brown paper and then placed in phenol–chloroform until all the wax had been removed (≈ 40 s). The wax was dried in a rotovac (Haake Buchler Instruments Inc., Saddle Brook, NJ) and weighed using an electronic balance (Acculab; AL-104, Mountville, PA) to 0.0001 g accuracy. The traced surface area of the spathes was measured using the “leaf area meter” and the average wax ($\text{mg}\cdot\text{m}^{-2}$) was calculated.

Only abaxial stomatal density and spathe color were measured in Trials 2 and 3 as described previously. Preliminary studies had shown that the other morphological characteristics were unaffected by seasonal differences.

Vase life determination. Cut flowers of the 17 cultivars used in the previous study were assessed for their vase life in sterile, 250-mL measuring cylinders in a laboratory setting (11 h white fluorescent light : 13 h dark; 24 °C; 75% relative humidity) (Trial 1). The cultivars were arranged in a completely randomized design with three to eight repli-

cations per cultivar and with three cut flowers per replicate. Cultivars ‘Pierrot’, ‘Mirjam’, and ‘Fla Range’ had five replications each; ‘Venus’ had four replications, ‘Spirit’ had seven replications, ‘Midori’ had eight replications, and the others had three replications each. Each cylinder contained 210 mL of sterile distilled water, which was maintained throughout the study period. Before placing the cut flowers into the cylinder, the outline of each spathe was traced on brown paper to determine the spathe area and the base of the peduncles were cut under water at an angle of 45° using a sterile scalpel.

The following variables were recorded daily: peduncle base browning, spadix browning/necrosis, spathe floppiness, spathe browning/necrosis, spathe discoloration, and loss of lustre/glossiness in the spathes. The experiment was continued for 70 d until all the cultivars began to show signs of spathe or spadix deterioration.

The vase life experiment was repeated using 16 of the 17 cultivars (except ‘Spirit’) used in Trial 1 under similar laboratory conditions (Trial 2). The experiment was arranged in a completely randomized design with three replications with three cut flowers per replicate. Vase life determination was done as before. The stomatal densities in the adaxial and abaxial surfaces were measured as previously described. Vase life was determined for an independent set of nine cultivars under similar conditions as before (Trial 3). The experimental design and data collection were the same as for Trial 2.

Data analysis. One-way analysis of variance was conducted (NCSS, 2001) to determine the significance of cultivar differences for the morphophysiological characteristics studied in Trial 1 and vase life as determined by the time taken to deterioration. The association between morphophysiological characteristics and vase life was assessed using Pearson’s product moment correlation (NCSS, 2001). Multiple regression analysis (NCSS, 2001) and forward and backward model selections were performed to identify a minimal subset of characteristics that best predicted vase life and time to spadix necrosis. For these purposes, spathe color was coded as follows: red/not red, orange/not orange, white/not white, and green/not green as described by Kamemoto et al. (1988). Boolean numbers 0 (absence of color) and 1 (presence of color) were used to describe categories.

Pearson’s product moment correlations (NCSS, 2001) were carried out in Trial 2 to determine the association between the morphophysiological characteristics measured. Comparison of regression lines (COLR program, Version 1, 1974; CARDI, 1974) between average vase life and vase life in Trial 1 or Trial 2 was performed to determine the stability of vase life over trials. The same was done for abaxial stomatal density, time to spadix, and spathe necrosis.

The regression equations developed in Trial 1 to predict vase life and time to spadix necrosis were validated in Trial 2 using the

same set of 16 cultivars and in Trial 3 using a different set of nine cultivars.

Results

Cultivar differences in cut flower morphophysiology. There were significant cultivar differences ($P < 0.05$) for all characteristics except adaxial spathe hydathode density (Table 1). Cultivar differences for adaxial and abaxial stomatal density as well as abaxial hydathode density were particularly large as indicated by their large genotypic coefficient of variation (83% to 108%).

Abaxial stomatal density ranged from 1.8 per mm^{-2} (‘Fla Range’) to 25.7 per mm^{-2} (‘Evergreen’) with a mean of 6.2 per mm^{-2} . Adaxial stomata were generally very low in number or absent in the cultivars studied. Area of stomatal openings showed a twofold variation (209 μm^2 in ‘Midori’) to 442 μm^2 in ‘Success’; mean, 331 μm^2 .

The abaxial stomatal densities were on average 60-fold higher than abaxial hydathode densities and varied between 1.8 in ‘Fla Range’ to 25.7 per mm^{-2} in ‘Evergreen’. Adaxial hydathode densities were very small with 53% of cultivars having no adaxial hydathodes. The large se for hydathode density supports the uneven distribution noted in observations under the microscope.

Spathe epicuticular wax content showed a 3.5-fold variation among cultivars, from 50 $\text{mg}\cdot\text{m}^{-2}$ in ‘Spirit’ to 170 $\text{mg}\cdot\text{m}^{-2}$ in ‘Mirjam’.

The spathe size varied from 190 cm^2 in cultivar ‘Fla Range’ to 804 cm^2 in ‘Evergreen’; whereas spadix length varied from 53 mm in ‘Mirjam’ to 84 mm in ‘Cuba’ with a general mean of 69.5 mm. ‘Spirit’ and ‘Acropolis’ had the narrowest spadix (8 mm), whereas ‘Terra’ and ‘Evergreen’ had the widest.

‘Evergreen’ had the widest peduncle diameter, whereas the cultivar ‘Acropolis’ had the narrowest. ‘Acropolis’ also had the shortest peduncle, whereas ‘Local Pink’ had the longest.

Cut flower senescence. There were highly significant ($P < 0.001$) differences in vase life among cultivars, varying from 14 to 49 d (Table 2). ‘Evergreen’, ‘Spirit’, and ‘Venus’ had short vase lives (14 to 15 d), whereas ‘Cuba’ and ‘Honduras’ had extremely long vase-lives (greater than 45 d).

Vase life was determined by the time to first evidence of cut flower deterioration. Some signs of deterioration such as peduncle base browning and spadix necrosis were common to all cultivars, whereas others (spathe floppiness, loss of lustre, and discoloration) were specific to only certain cultivars. Spathe necrosis was evident in all cultivars except ‘Cuba’. Photo bleaching/lightening and blueing were the most common forms of spathe discoloration with blueing being evident in all red-spathed cultivars.

Peduncle base browning was the first sign of senescence and occurred between 8 and 15 d in the various cultivars with approximately half showing browning in 8 to 10 d.

Table 1. Morphophysiological characteristics of cut flowers of 17 cultivars of *Anthurium andraeanum* (Hort.).

	Spathe								Spadix		Peduncle	
	Stomata			Hydathode		Cuticle Wax (mg·m ⁻²)	Surf.* area (cm ²)	Thickness (mm)	Leng. ^w (mm)	Dia. ^v (mm)	Leng. (cm)	Dia. (mm)
	Adax. ^z (no./mm ²)	Abax. ^y (no./mm ²)	size (µm ²)	Adax.	Abax.							
Spirit	0.1	9.6	266	0	0.1	50	302	0.39	70	8	49.6	5.3
Lydia	0	2.8	325	0	0	130	306	0.41	74	9	56	5.7
Local Pink	0.1	2.2	381	0.04	0.1	160	213	0.47	69	9	63.7	6.1
Fantasia	0	16.4	221	0.02	0.2	80	270	0.46	73	10	45.3	6.7
Cuba	0	1.9	376	0.02	0	70	301	0.49	84	10	47	5.7
Pierrot	0.2	5	442	0.02	0	60	272	0.47	80	9	56.4	6.1
Acropolis	0	11	210	0.02	0.1	150	211	0.41	77	8	35.9	4.9
Tropical	0.1	3.3	352	0	0	90	323	0.43	67	10	52.6	6.2
Honduras	0.1	4.2	403	0	0	140	286	0.39	60	10	48.8	5.7
Success	0	2.6	448	0	0	100	251	0.54	78	10	45.4	6
Mirjam	0.2	6.6	248	0.04	0.1	170	222	0.48	53	10	48.3	5.1
Midori	0	5.9	209	0.02	0.1	120	373	0.47	59	9	54.3	5.7
Tequila	0.1	4.1	256	0	0	100	261	0.52	64	10	56.8	6
Venus	0.1	5.3	358	0	0.2	70	328	0.53	69	9	42.7	5.3
Fla Range	0.1	1.8	399	0	0.3	120	190	0.56	67	9	54.1	5.9
Terra	0.2	5.1	399	0.04	0	90	300	0.44	68	11	52.5	5.8
Evergreen	0	25.7	329	0	0.4	70	804	0.34	69	11	40.5	7
Sig. ^u ($P \leq$)	0.001	0.001	0.001	NS	0.05	0.05	0.001	0.001	0.001	0.001	0.001	0.001
Mean	0.07	6.7	331	0.01	0.1	104.1	306.6	0.459	69.5	9.5	50	5.8
SEM	0.04	1.05	28.3	0.02	0.08	0.02	24.4	0.02	2.4	0.4	2.58	0.25
LSD (0.05)	0.1	3.01	78.6	—	0.23	0.07	69.34	0.06	5.52	0.93	7.32	0.71
Genotypic cv (%)	83.1	92.7	24.4	—	108.2	35.1	44.6	13	11.4	9.2	13.8	9.1

^zAdaxial. ^yAbaxial. ^xSurface. ^wDiameter. ^vLength. ^uSignificance.^{ns}Nonsignificant.Table 2. Mean time (days) to cut flower senescence of 17 *Anthurium andraeanum* (Hort.) cultivars during Trial 1 and the symptoms associated with loss of vase life.

Cultivar	Spathe color	Days to						Vaselife (days)
		Peduncle base browning	Spathe floppiness	Loss of spathe luster	Spathe discoloration	Spathe necrosis	Spadix necrosis	
Spirit	Pink	8	15	18	—	31	19	15
Lydia	Pink	9	—	—	—	26	26	26
Local Pink	Dark pink	8	—	20	20 (L) ^z	30	17	17
Fantasia	White/pink veins	14	—	20	20 (L)	22	19	19
Cuba	White	8	—	—	54 (G) ^y	—	49	49
Pierrot	White	15	—	—	—	52	37	37
Acropolis	White	10	23	—	—	24	18	18
Tropical	Red	12	—	—	26 (B) ^x	27	24	24
Honduras	Red/green	8	—	—	56 (B)	61	45	45
Success	Red	9	27	25	29 (B)	33	16	16
Mirjam	Red	12	—	18	19 (B)	23	18	18
Midori	Green	12	—	—	40 (L)	54	34	34
Tequila	Green	8	—	—	34 (Bl) ^w	38	33	33
Venus	Coral	12	—	15	16 (Bl)	26	23	15
Fla Range	Orange	12	—	—	39 (Bl)	45	33	33
Terra	Green/orange	15	—	42	42 (P) ^v	47	40	40
Evergreen	Green/white	8	14	—	—	19	18	14
Sig. ^u (<i>P</i> ≤)		0.001				0.001	0.001	0
Mean		10				34.9	27.6	26.6
SEM		0.62				2.7	2.2	2.19
Least significant difference (0.05)		1.47				6.32	5.3	5.21
Genotypic coefficient of variation (%)		24				37	39	43

^zLightening. ^yGreen color development. ^xBlue color development. ^wBleaching. ^yPink color development. ^uSignificance.

This was usually followed by spadix necrosis in all cultivars, although some cultivars (e.g., ‘Spirit’, ‘Venus’, and ‘Evergreen’) showed spathe floppiness or loss of lustre a few days earlier. Spadix necrosis was often followed by spathe discoloration and necrosis. The time course for these senescence symptoms, however, varied with the cultivars.

Although there were significant differences ($P < 0.001$) between cultivars for peduncle base browning, this did not correlate significantly with vase life. Spadix necro-

sis was the first symptom of deterioration on the showy part of the cut flower in all but three cultivars. Even in these three cultivars, the other signs of deterioration were earlier than spadix necrosis by only a few days and were not larger than the least significant difference ($LSD_{0.05}$) for vase life data. As a result, days to spadix necrosis were highly correlated ($r = 0.98$; $P < 0.001$; $df = 16$) to vase life determined by a combined criterion. There was also a strong and significant correlation between time to spadix necrosis

and spathe necrosis ($r = 0.88$; $P < 0.001$; $df = 15$) and time to spadix necrosis and time to spathe discoloration ($r = 0.91$; $P < 0.001$; $df = 11$). These results together suggest that spadix necrosis is a generally acceptable criterion to measure vase life of anthurium.

Morphophysiological characteristics associated with vase life. Correlations between vase life and morphophysiological parameters (Table 3) of cut flower investigated were not significant ($P > 0.05$). However, there was a strong, significant, and

Table 3. Correlation coefficients between vase life and cut flower morphophysiological characteristics in 17 *Anthurium andraeanum* (Hort.) cultivars in Trinidad (Trial 1).

	Stoma		Hydathode		Stoma	Spathe			Peduncle		Spadix		Vaselife
	Abax. ^z	Adax. ^y	Abax.		Size	Wax	Surf. ^x area	Thickness	Dia. ^w	Len. ^v	Dia.	Len.	
Stoma adaxial	-0.14	0.42	-0.14		0.21	0.01	-0.18	0.00	-0.23	0.27	-0.38	0.11	0.09
Stoma abaxial		-0.07	0.73**		-0.42	-0.3	0.74**	-0.59*	0.44	-0.57*	-0.01	0.23	-0.45
Hydathode adaxial			-0.19		-0.12	0.38	-0.28	0.04	-0.16	0.21	-0.11	0.11	0.10
Hydathode abaxial					-0.15	-0.20	0.63	-0.17	0.44	-0.36	-0.14	0.17	-0.47
Stoma size						-0.20	-0.04	0.23	0.23	0.26	0.34	0.27	0.32
Spathe wax							-0.39	0.05	-0.36	0.17	-0.47	-0.13	-0.05
Spathe surface area								-0.56*	0.55*	-0.32	-0.03	0.44	-0.19
Spathe thickness									-0.14	0.24	0.05	-0.07	0.11
Peduncle diameter										0.16	0.15	0.58*	-0.02
Peduncle length											-0.20	-0.06	0.31
Spadix diameter												-0.17	0.06
Spadix length													0.24

^zAbaxial. ^yAdaxial. ^xSurface. ^wDiameter. ^vLength.

**Significant at $P < 0.05$ and 0.01 , respectively.

positive correlation coefficient ($P \leq 0.01$) between abaxial stomatal density and abaxial hydathode density ($r = 0.73$) and between abaxial stomatal density and spathe surface area ($r = 0.74$) (Table 3). Cultivars with larger abaxial stomatal density also tended to have smaller spathe thicknesses ($r = -0.59$; $P < 0.05$) and shorter peduncle lengths ($r = -0.57$; $P < 0.05$). There was a significant positive correlation ($P \leq 0.05$) between spathe surface area and peduncle diameter ($r = 0.55$) and a significant ($P < 0.05$) negative correlation between spathe surface area and spathe thickness ($r = -0.56$).

Nevertheless, a stepwise multiple regression analysis on the dependence of vase life on morphophysiological characteristics showed that the smallest subset that best predicted vase life was given by the following equation:

$$\begin{aligned} \text{Vase-life (days)} = & 29.1 - 1.99(\text{abaxial stomatal density}) \\ & + 18.3(\text{green/not green}) \\ & + 18.5(\text{white/not white}). \\ (R^2 = 0.802; P < 0.001; \text{Fig. 1}). \end{aligned}$$

Trial 2: stability of stomatal density and vase life. Cultivar differences for abaxial stomatal density were significant ($P \leq 0.001$) in Trial 2 (Table 4). The correlation coefficient between Trial 1 and Trial 2 for stomatal density was high ($r = 0.95$). A comparison of regression lines showed that genotype $\times$ trial interactions were not significant ($P > 0.05$) for stomatal density and that the stomatal numbers for the cultivars in Trial 1 and Trial 2 can be represented by parallel lines. Overall, abaxial stomatal density was greater by one stoma/mm² in Trial 2.

Vase life in Trial 2 ranged from 14 d in the cultivars 'Fantasia' and 'Tropical' to 49 d in 'Midori' with a mean of 24.3 d. The SE values obtained for vase life in Trial 2 (2.26) and Trial 1 (2.29) were essentially the same. There was a general correspondence between vase life of cultivars over the two trials ($r = 0.76$). A comparison of regression lines showed that there were no cultivar-trial interactions. Most cultivars (75%) showed a decrease in vase life in Trial 2, with vase life

Fig. 1. Comparison of actual vase life versus expected vase life based on the prediction equation [vase life (days) = 29.1 - 1.99 (abaxial stomatal density) + 18.3 (green/not green) + 18.5 (white/not white)] for 17 *Anthurium andraeanum* (Hort.) cultivars evaluated in Trial 1. Triangles = red and pink spathe cultivars; squares = orange and coral spathe cultivars; diamond = green spathe cultivars; circle = white spathe cultivars.

in Trial 1 on average being 3 d more than in Trial 2. Correspondingly, time to spathe necrosis and spathe necrosis in Trial 1 were significantly correlated ($P \leq 0.01$) to those in Trial 2 ($r = 0.78$ and 0.92 , respectively).

Again, as was observed in Trial 1, time to spathe necrosis correlated significantly with vase life ($r = 0.95$; $P \leq 0.001$), but vase life did not correlate with abaxial stomatal density (data not presented). Furthermore, the prediction equation developed from Trial 1 was able to predict vase life ($R^2 = 0.84$; Fig. 2) and spathe necrosis ($R^2 = 0.81$) of cultivars in Trial 2.

Trial 3: Validity of the prediction equation. The cultivar differences for abaxial stomatal density, time to spathe necrosis, and vase life in Trial 3 (Table 5) were significant

($P \leq 0.01$). The red-obake cultivar, 'Kalapana', had the most abaxial stomata, whereas the pink cultivar, 'Lunette', had the least. The cultivars 'Champagne' and 'Sweety' had the longest vase lives (21 d), whereas 'Ibara' and 'Kalapana' had the shortest (10 d).

Eighty-one percent of the variation in vase life (Fig. 3) and 77% of the variation in spathe necrosis of the nine cultivars (Trial 5) was explained by the prediction equation developed in Trial 1 indicating its validity over a different set of cultivars.

Discussion

The postharvest life of anthurium cut flowers is usually determined by the onset of one of a number of senescence symptoms: loss of spathe glossiness, blueing of spathe, spathe dehydration and necrosis, spathe wilting, browning of the peduncle base, or

Table 4. Abaxial stomatal density, time to spadix necrosis, spathe necrosis, and vase life of 16 *Anthurium andraeanum* (Hort.) cultivars evaluated in Trial 2.

Cultivar	Spathe abaxial stomatal number (mm ⁻²)	Days to necrosis		Vase life (days)
		Spadix	Spathe	
Acropolis	14.6	16	21.8	16
Cuba	2.6	41.4	48.7	41
Evergreen	24.5	21.4	21.7	21
Fantasia	16.2	14.2	14.4	14.2
Fla Range	2.8	22	30.7	22
Honduras	4.2	37.6	47.2	37.7
Local Pink	2.5	21	28.4	21
Lydia	4.3	15.3	16.6	15
Midori	6.2	48.7	49.4	48.7
Mirjam	6.9	15	24.1	15
Pierrot	6.5	34.3	42.2	34.3
Success	5.6	19	32.3	19
Tequila	11.2	21.5	28.8	21.5
Terra	6.6	30	39	30
Tropical	6.2	14.3	16.2	14
Venus	5.6	20.3	23.3	18
Significance (<i>P</i> ≤)	0.001	0.001	0.001	0.001
Mean	7.4	23.1	30.3	22.8
SEM	0.954	2.339	4.45	2.26
LSD (0.05)	2.27	5.56	10.6	5.37
Genotypic cv (%)	80.4	44.5	39	45.6

Fig. 2. Comparison of actual vase life versus expected vase life based on the prediction equation (developed in Trial 1) for 16 *Anthurium andraeanum* (Hort.) cultivars evaluated in Trial 2. Triangles = red and pink spathe cultivars; squares = orange and coral spathe cultivars; diamond = green spathe cultivars; circle = white spathe cultivars.

stem collapse (Paull, 1982; Paull et al., 1985; Shirakawa et al., 1964). Furthermore, the point of termination of vase life is determined at the first sign of senescence symptoms (Mayak and Dilley, 1976), fixed up to the point of 50% loss of cut flower quality (Paull and Goo, 1985), or extended until the total death of cut flowers (Salinger, 1975). This makes the measure of vase life complex, less precise and therefore not amenable for use in breeding programs.

This study for the first time investigated senescence symptoms in a wide range of anthurium cultivars. Although the cultivars showed a variety of symptoms, that is, peduncle base browning, loss of glossiness, spathe wilting (floppiness), spadix and spathe necrosis, and spathe discoloration, in conformity with previous studies (Paull et al., 1985), peduncle base browning, spadix necrosis, and spathe necrosis were the only signs of senescence that were common to all cultivars.

Peduncle base browning was the first senescence symptom to appear in anthurium cultivars, but it neither discriminated between the cultivars nor correlated with time to onset of spathe or spadix symptoms, and therefore was not considered a good measure of vase life. Spadix necrosis was usually the second symptom (14 to 49 d after initiation) to appear in anthurium cut flowers. This, apart from being discriminatory, correlated very well with vase life, the onset of spathe necrosis, and spathe discoloration, which, however, were either delayed in a cultivar-specific manner or did not occur at all. Importantly, the vase life of 82% of the cultivars was ended because of spadix necrosis.

The study demonstrated that time to spadix necrosis was the best measure of vase life in anthurium cut flowers for several reasons. It was the earliest occurring senescence symptom that is common to all anthurium cultivars and was highly correlated to all other important senescence symptoms. Furthermore, the study demonstrated that vase life determined by a more complex criterion correlated well with vase life determined by spadix necrosis and had a similar error estimate. It is recommended that vase life should therefore be based on the first sign of spadix necrosis.

Although vase life and time to spadix necrosis were found to be affected by the season, the relative ranking of cultivars was similar as indicated by the joint regression analysis. The study also showed that changes in vase life of cultivars over season were mediated through changes in stomatal density.

Of the 12 morphophysiological characteristics studied, only abaxial stomatal density and spathe color explained variation in vase life among the cultivars tested. The vase life prediction equation suggested that cultivars with a lower number of abaxial stomatal density and with green or white spathe colors were able to prolong their vase life. The prediction equation suggests that the relationship between stomatal density and vase life varied depending on whether the spathes had a color (red/orange) or not (white/greens). The prediction equation developed for vase life based on stomatal density, green/not green, and white/not white was robust and was able to predict vase life over trials (conducted in two different seasons) as well as in a different set of cultivars. The robustness of the equation suggests that it can be used in a wide range of situations for cultivars grown under standard management conditions.

The senescence rate of cut flowers is affected by many metabolic processes, the most studied being those related to carbohydrate metabolism, water relations, cell membrane properties, and ethylene production and sensitivity (Borochov and Woodson, 1989; Halevy and Mayak, 1979, 1981; Shvarts et al., 1997). Spathe color in anthurium is the result of carotenoids such as chlorophyll or colored flavonoids (anthocyanins) (Iwata

Table 5. Abaxial stomatal density, time to spadix necrosis and actual vase life of nine *Anthurium andraeanum* (Hort.) cultivars evaluated in Trial 3.

Cultivar	Abaxial stomatal density (mm ⁻²)	Time to spadix necrosis (days)	Vase life (days)
Champagne	11.1	21.0	21
Cheers	4.7	15.0	15
Gloria	5.0	16.3	16
Ibara	18.6	10.0	10
Kalapana	20.9	10.0	10
Lunette	2.6	19.0	19
Rosa	8.3	14.0	14
Senator	12.7	18.0	18
Sweetey	4.7	21.0	21
Significance ($P \leq$)	0.001	0.001	0.001
Mean	9.83	16.05	16
SEM	0.76	0.86	0.86
Least significant difference (0.05)	2.39	2.09	2.09
Genotypic coefficient of variation (%)	66.2	26.6	26.7

Fig. 3. Comparison of actual vase life versus expected vase life based on the prediction equation (developed in Trial 1) for nine *Anthurium andraeanum* (Hort.) cultivars evaluated in Trial 3. Triangles = red and pink spathe cultivars; squares = orange and coral spathe cultivars; circle = white spathe cultivars.

et al., 1979, 1985) or copigmentation of both carotenoids and flavonoids (Kamemoto and Kuehnle, 1996) as seen in the cultivars 'Honduras' and 'Terra'. The anthocyanin pigments are mainly pelargonidin 3-rutinoside and cyanidin 3-rutinoside and accumulate only in the hypodermal cells of both the upper and lower epidermis of anthurium spathes (Higaki et al., 1984; Watson and Shirakawa, 1967).

The inclusion of green/not green in the prediction equation for vase life may suggest a direct or indirect role for carbohydrates in the senescence process. The green-spathed cultivars performed better in vase life experiments than the reds (as also reported by Guo

et al., 2003), oranges, and pinks. The red cultivar 'Honduras', which has a green copigmentation, also performed well in vase life experiments. Because the senescence symptoms in anthurium cut flowers are largely the result of water stress, it may well be that carbohydrate status is involved in the regulation of stomatal function. Paull et al. (1985) noted that the water-soluble carbohydrate balance of the anthurium cut flowers remained constant through senescence with only a little change in total sugar content, which led them to conclude that carbohydrate and sugar levels may not influence vase life in anthurium. Their study, however, did not include any green-spathed cultivars. In a

subsequent study, Paull et al. (1992), found a strong relationship between preharvest temperature and vase life with higher temperatures resulting in lowered vase life, which suggested a role for carbohydrates. Cut flowers are usually known to last longer if harvested after a protracted period of photosynthesis (Sacalis, 1993).

Similarly, the variable, spathe white/non-white, was important in the prediction of anthurium vase life. The dominant pigments in white cultivars are flavones (Iwata et al., 1985), which have a strong and proven antioxidant capacity (Rice-Evans et al., 1997) and are excellent free radical scavengers. Furthermore, flavones are lipophilic (Gould et al., 2000) and may be involved in maintaining membrane integrity or they may have a role in protection from photoinhibition (Dodd et al., 1998; Gould et al., 1995).

The red group showed typical bluing of spathe during senescence in this study. Paull et al. (1985) showed that pH increases from 5.2 to 5.6 as spathe bluing begins, which is consistent with the findings of Chaparro de Barrera and Arenas (1999). Paull et al. (1985) also demonstrated that the increase in pH detected in spathe, spadix, and peduncle tissues may be the result of a simultaneous increase in tissue ammonium ion concentration caused by the breakdown of α -amino acids.

Paull et al. (1985) also showed that anthocyanin concentration increases on senescence, which also corresponds to an increase in total phenols. The phenols may account for the browning of spathes seen particularly in the white-spathed cultivars in this study.

The role of abaxial stomatal density in the vase life prediction equation suggests that loss of water from the spathe may contribute to loss of vase life. Cultivars that had a higher stomatal number had a shorter vase life compared with those with lower densities. Furthermore, abaxial stomatal density explained 84% of the variation (based on the vase life regression equation) over trials (cultivar spathe color remained constant over trials). Dufour and Guerin (2003) demonstrated that young cut flowers had more abaxial stomata than mature ones with a corresponding decrease in vase life. Hence, the equation could be applied with the proviso that cut flowers used in vase life assessment be obtained from cultivars grown under similar conditions and harvested using the same harvesting standard.

The prediction equation, presented here, eliminates the need for vase life experiments in selection programs, which require replications (Kamemoto and Kuehnle, 1996) and are time-consuming, requiring up to 3 months. The prediction equation contains terms that are relatively easy to assess. If the stomatal density can be assessed without the clearing solution step, it can further accelerate selection as well as reduce the cost of breeding programs.

The prediction equation does not discriminate reds from pinks and oranges from

corals. More importantly, the study shows a minimum acceptable vase life of 3 weeks (Kamemoto and Kuehnle, 1996) can be achieved in all the colors by selecting for lower abaxial stomatal density under standard conditions.

Literature Cited

- Borochoy, A. and W.R. Woodson. 1989. Physiology and biochemistry of flower petal senescence. Hort. Rev. (Amer. Soc. Hort. Sci.) 11:15–43.
- CARDI. 1974. COLR programme, version 1. Caribbean Agricultural Research and Development Institute, St. Augustine, Trinidad.
- Chaparro de Barrera, A. and G. Arenas. 1999. Cutting-time effect during harvest cycle on post harvest behaviour of three *Gypsophila paniculata* cv. *Perfecta* clones. Acta Hort. 148:71–76.
- Croat, T.B. 1988. Ecology and life forms of *Araceae*. Aroideana 11:4–55.
- Dai, J. and R.E. Paull. 1990. The role of leaf development on anthurium flower growth. J. Amer. Soc. Hort. Sci. 115:901–905.
- Dodd, I.C., C. Critchley, G.S. Woodall, and G.R. Stewart. 1998. Photoinhibition in differently colored juvenile leaves of *Syzygium* species. J. Expt. Bot. 49:1437–1445.
- Dufour, L. and V. Guerin. 2003. Growth, developmental features and flower production of *Anthurium andraeanum* Lind. in tropical regions. Scientia Hort. 98:25–35.
- Gould, K.S., D.N. Kuhn, D.W. Lee, and S.F. Oberbauer. 1995. Why leaves are sometimes red. Nature 378:241–242.
- Gould, K.S., K.R. Markham, R.H. Smith, and J.J. Goris. 2000. Functional role of anthocyanins in the leaves of *Quintinia serrata* A. Cunn. J. Exp. Bot. 51:1107–1115.
- Guo, Z., L. Xiao, Y. Zou, Y. Hong, and R. Wang. 2003. Comparison of fresh-keeping age of different cultivars of *Anthurium* cut flowers. J. Hunan Agr. Univ. 29:485–487.
- Halevy, A.H. and S. Mayak. 1979. Senescence and postharvest physiology of cut flowers Part 1. Hort. Rev. (Amer. Soc. Hort. Sci.) 1:204–236.
- Halevy, A.H. and S. Mayak. 1981. Senescence and postharvest physiology of cut flowers Part 2. Hort. Rev. (Amer. Soc. Hort. Sci.) 3:59–143.
- Higaki, T., H.P. Rasmusen, and W.J. Carpenter. 1984. A study of some morphological and anatomical aspects of *Anthurium andraeanum* Lind. University of Hawaii: HITAH Res. Ser. 030:1–12.
- Iwata, R.Y., C.S. Tang, and H. Kamemoto. 1979. Anthocyanins of *Anthurium andraeanum* Lind. J. Amer. Soc. Hort. Sci. 104:464–466.
- Iwata, R.Y., C.S. Tang, and H. Kamemoto. 1985. Concentration of anthocyanins affecting spathe color in anthuriums. J. Amer. Soc. Hort. Sci. 110:383–385.
- Johansen, D.A. 1940. Plant microtechnique. McGraw Hill Book Company Inc., London, UK.
- Kamemoto, H. 1962. Some factors affecting the keeping quality of anthurium flowers. Hawaii Farm Sci. 11:2–4.
- Kamemoto, H., R.Y. Iwata, and M. Marutani. 1988. Genetics of the major spathe colors in anthuriums. HITAH Res. Ser. 056:8–88.
- Kamemoto, H. and A.R. Kuehnle. 1996. Breeding anthuriums in Hawaii. Univ. of Hawaii Press, Honolulu, HI.
- Mayak, S. and D.R. Dilley. 1976. Effects of sucrose in the response of cut carnations to kinetin, ethylene and abscisic acid. J. Amer. Soc. Hort. Sci. 101:583–585.
- NCSS. 2001. Number crunching statistical system. NCSS, Kaysville, UT.
- O'Brien, T.P. and M.E. McCully. 1981. The study of plant structure, principles and selected methods. Termarcaphi Pty. Ltd., Melbourne, Australia.
- Paull, R.E. 1982. *Anthurium* (*Anthurium andraeanum* André) vase life evaluation criteria. Hort-Science 17:606–607.
- Paull, R.E., N.J. Chen, and J. Deputy. 1985. Physiological changes associated with senescence of cut anthurium flowers. J. Amer. Soc. Hort. Sci. 110:156–162.
- Paull, R.E. and T.T.C. Goo. 1985. Ethylene and water stress in the senescence of cut anthurium flowers. J. Amer. Soc. Hort. Sci. 110:84–88.
- Paull, R.E., T. Higaki, and J.S. Imamura. 1992. Season and fertilizer affect the post-harvest flower life of anthurium. Scientia Hort. 49:125–134.
- Rice-Evans, C.A., N.J. Miller, and G. Paganga. 1997. Antioxidant properties of phenolic compounds. Trends Plant Sci. 2:152–159.
- Sacalis, J.N. 1993. Cut flowers: Prolonging freshness. Ball Publishing, Batavia, IL.
- Salinger, J.P. 1975. Criteria for the evaluation of post-harvest senescence of cut flowers. Acta Hort. 41:207–216.
- Shirakawa, T., R.D. Edolph, and D.P. Watson. 1964. N-6-Benzyladenine effects on chilling injury, respiration and keeping quality of *Anthurium andraeanum*. Proc. Amer. Soc. Hort. Sci. 85:642–646.
- Shvarts, M., A. Borochoy, and D. Weiss. 1997. Low temperature enhances petunia flower pigmentation and induces chalcone synthase gene expression. Acta Physiol. Plant. 99:67–72.
- Watson, D.P. and T. Shirakawa. 1967. Gross morphology related to shelf-life of anthurium flowers. Hawaii Farm Sci. 16:1–3.