J. Amer. Soc. Hort. Sci. 131(1):122–126. 2006.

Genetic Variation in Ethylene Responsiveness of Regal Pelargonium

Hye-Ji Kim[1], Richard Craig, and Kathleen M. Brown[2]
Department of Horticulture, Pennsylvania State University, University Park, PA 16802

Additional index words. abscission, postharvest, ethylene responsiveness, ethylene production, Martha Washington geranium, *Pelargonium* ×*domesticum*

Abstract. Ethylene induces significant petal abscission in regal pelargonium (*Pelargonium* ×*domesticum* L.H. Bailey). Three genotypes, 'Elegance Silver' and its progeny, 00-43-1 and 00-43-2, were developed with exceptional production and postproduction characteristics. These genotypes had significantly enhanced individual floret longevity and whole plant longevity, and displayed more than twice as many florets as commercial cultivars. Dose response analysis demonstrated that 'Elegance Silver' has reduced ethylene responsiveness throughout floret development, shown by lower petal abscission than other cultivars over a range of ethylene concentrations. Floret longevity was strongly correlated with ethylene responsiveness as indicated by S_{50} (ethylene concentration for 50% petal abscission), but not with ethylene production. These results suggest that reduced ethylene responsiveness is an important determinant of enhanced postproduction performance in the superior genotypes of regal pelargonium.

Floral life of many species is terminated by ethylene-induced floral senescence or abscission (Abeles et al., 1992). Flowers of the Geraniaceae are particularly sensitive to ethylene, and species within this family consistently demonstrated petal abscission in response to applied ethylene (van Doorn, 2001; Woltering and van Doorn, 1988). The postproduction quality of regal pelargonium, a flowering potted plant with extraordinary aesthetic characteristics, is limited by rapid petal abscission within 1 to 2.5 h after treatment with as little as 1 $\mu L \cdot L^{-1}$ ethylene (Deneke et al., 1990; Olson and Evensen, 1990). In the absence of exogenous ethylene treatment, petal abscission results from a combination of ethylene synthesis by floral parts and increasing ethylene responsiveness during flower development (Deneke et al., 1990; Evensen, 1991). In diploid zonal geraniums (*P.* ×*hortorum* L.H. Bailey) with single florets, pollination-induced ethylene production resulted in petal abscission within 4 h of pollination (Clark et al., 1997). However, in regal pelargonium, the abscission rate after intentional pollination was low, and petal abscission did not appear to be related to the rate of accidental pollination during shipping (unpublished data). We therefore speculated that the most important aspects of shipping quality for regal pelargonium are ethylene production, ethylene exposure (from endogenous or other sources) and ethylene responsiveness.

Through the breeding program of the Pennsylvania State Univ. (PSU), a genotype of regal pelargonium, 'Elegance Silver', has been developed with exceptional production and postproduction characteristics (Fig. 1A). Two progeny of 'Elegance Silver', 00-43-1 (Fig. 1B), and 00-43-2 (Fig. 1C), also exhibited enhanced postproduction quality compared to current commercial genotypes. In the present study, these PSU genotypes were compared with commercial genotypes in order to investigate the role of ethylene in explaining the variation in longevity and postproduction quality among regal pelargoniums. Preliminary work (Kim et al., 2005) indicated that ethylene production and responsiveness varies among cultivars and that this variation could explain the differences in postproduction characteristics.

Materials and Methods

Plant material. Rooted cuttings from culture-virus-indexed propagative stock of commercial regal pelargoniums were obtained from Oglevee Ltd., Connellsville, Pa. Cuttings of PSU genotypes 'Elegance Silver', 00-43-1, and 00-43-2 were taken from stock plants maintained in the PSU Horticulture Department greenhouses and rooted for 4 weeks in a greenhouse equipped with bottom heat and intermittent mist. Rooted cuttings were placed under natural light supplemented with 110 ± 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from high-intensity-discharge metal halide lamps (Sylvania GTE, Manchester, N.H.) for 4 weeks to stimulate floral initiation. Photosynthetically active radiation varied throughout the day with a maximum of 1400 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Temperatures in the greenhouse during the experimental period were 21 °C day/16 ºC night with an 18-h photoperiod. The plants were potted in 15-cm (1.5 L) azalea pots with Aggregate Plus Media-Sunshine Mix-4 (SUN GRO Horticulture, Bellevue, Wash.) and placed under the same light scheme as described above. The plants were alternately fertilized during irrigation with Peters Professional Foliar Feed 27N–6.6P–10K and Miracle-Gro Professional Excel 15N–2.2P–12.5K CAL-MAG (Scotts-Sierra, Marysville, Ohio). Foliar sprays of insecticidal soap were used before anthesis to control whitefly populations.

Floret longevity, defined as the number of days between anthesis and senescence (petal abscission), was evaluated using florets on intact plants in the greenhouse. Florets were labeled at the day

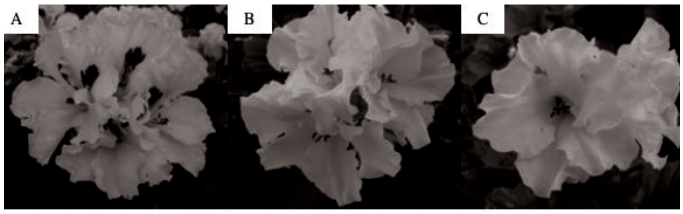

Fig. 1. Inflorescences of regal pelargonium: Pennsylvania State Univ. genotypes (**A**) 'Elegance Silver', (**B**) 00-43-1, and (**C**) 00-43-2.

Received for publication 3 May 2005. Accepted for publication 10 Sept. 2005. This research was supported by the Fred C. Gloeckner Foundation. We thank Kenneth Myers, Erwei Dong, and Messina Hodson for technical assistance. This research is part of a PhD dissertation submitted by Hye-Ji Kim.
[1]Current address: Dept. of Horticulture, 134A Plant Science Building, Cornell Univ., Ithaca, NY 14853-5904.
[2]To whom reprint requests should be addressed. E-mail address: kbe@psu.edu.

of anthesis with small paper tags to record the date. The date of floral senescence was recorded when 50% or more petals were abscised in response to a gentle touch.

For the evaluation of whole plant longevity, we used plants of the same age that had begun to flower ≈2 weeks previously. At that time, all open florets were removed from each plant to allow tracking of floret ages. When new florets began to open, the florets were labeled with paper tags recording the date of anthesis until the plant bore a population of 0- to 10-d-old florets. The plants were then moved to a simulated consumer environment to evaluate postproduction longevity as described below.

Evaluation of ethylene responsiveness. Individual florets of known ages were harvested from plants grown in the greenhouse, and placed in a plastic rack inside a plastic container with the pedicels in distilled water. The water level was adjusted to produce a standard container gas volume, and the container was sealed with a tight-fitting lid fitted with a septum. Ethylene gas was injected into the chamber to provide the desired concentration, and the container was kept at 22.5 ± 0.1 ºC for 90 min. Ethylene concentrations were analyzed by sampling with 1-mL syringes from the headspace of the sealed container, and determining ethylene concentration with a gas chromatograph (model 6890; Hewlett-Packard, Palo Alto, Calif.) fitted with a flame ionization detector and an activated alumina column. The detection limit was 0.013 $\mu L \cdot L^{-1}$. The lid was opened and petal abscission was evaluated 1 h after completion of ethylene treatment. Abscission rate was calculated based on the proportion of total petals shed when the florets were shaken lightly. The first set of experiments were conducted from February to March (season 1), and the second set of experiments from December to January (season 2). Each treatment included at least six florets of each age per genotype.

Ethylene production measurement. Ethylene production of florets was measured by enclosing each floret with petals attached and rolled gently in a 5-mL vial. After 1-h incubation at 22.5 ± 0.1 ºC, ethylene was sampled with 1-cm^3 syringes from the head space of the sealed vials and the concentration was determined by gas chromatography as described. Ethylene production ($nL \cdot g^{-1}$ FW per hour) was calculated on a fresh weight basis for each sample. Sample fresh weight was recorded before the ethylene measurement.

Evaluation of postproduction longevity. To evaluate whole plant longevity, plants bearing various ages of florets were moved to a simulated consumer environment (SCE). The SCE was maintained at 22.5 ± 0.1 °C, 50% ± 15% relative humidity, and 40 ± 0.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ provided by cool-white fluorescent lamps from 0800 to 2000 hr daily. Temperature, relative humidity and photosynthetic photon flux were measured at mid-shoot height and recorded by the HOBO data logger (Onset Computer Corp., Bourne, Mass.). Plants were irrigated as needed with distilled water.

Dates of floret anthesis and senescence of each floret were recorded on paper tags before, during and after simulated transport to determine individual floret longevity. Florets were considered senescent if they wilted or if ≥50% of the petals had abscised. Whole plant longevity was defined as the number of days from placement in the SCE until five or fewer healthy florets remained on the plant. Number of open florets was recorded at each week. At least four plants of each genotype were evaluated for individual floret longevity and whole plant longevity.

Statistical analysis. Analysis of variance (ANOVA) and mean separations (Fisher's protected least significant difference test) were conducted using StatView (SAS Institute, Cary, N.C.) and were considered significant at $P < 0.05$. The curve describing ethylene responsiveness (ethylene concentration vs. abscission) was fitted by SigmaPlot (SigmaPlot 8.0; SPSS, Chicago) with regression analysis.

Results

Longevity of individual florets. When the plants were grown in the greenhouse, the PSU genotypes 'Elegance Silver' and 00-43-2 displayed about twice the average floret longevity of other genotypes (Fig. 2). The floret longevity of 00-43-1 was also higher than that of other genotypes, while 'Maiden Lilac' displayed the shortest floret longevity among the evaluated genotypes. Individual floret longevity on intact plants was strongly correlated with whole plant longevity and floral display (number of florets at 2 weeks in the SCE) (Fig. 3). The PSU genotypes had greater whole plant longevity compared to other genotypes and retained a higher number of florets in the SCE compared to other genotypes (Fig. 3).

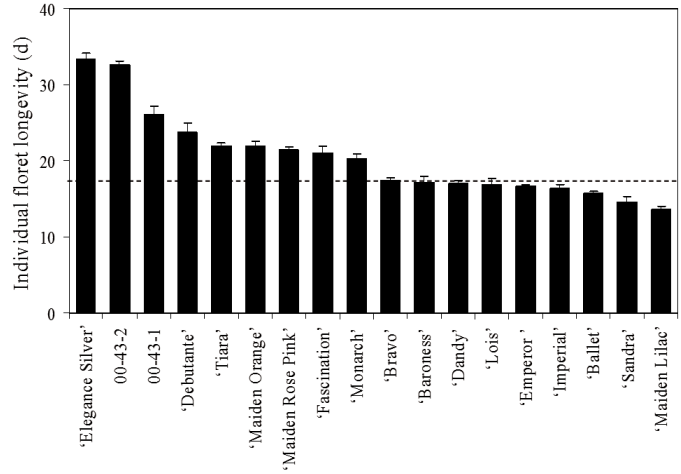

Fig. 2. Floral longevity of 18 regal pelargonium genotypes evaluated on intact plants in the greenhouse. The dotted horizontal line indicates the average floret longevity of the commercial genotypes. Data shown are means ±se of at least 10 florets.

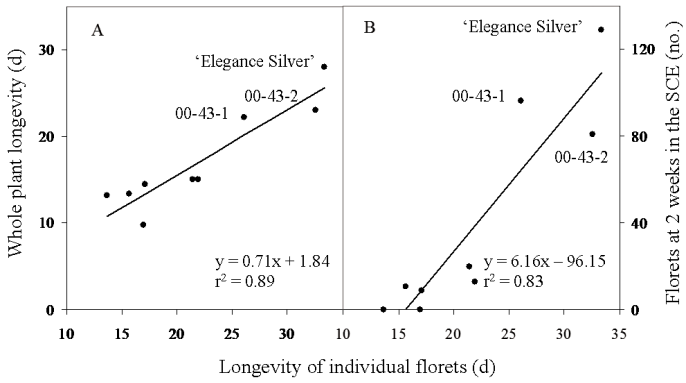

Fig. 3. Correlation between (**A**) longevity of individual florets on intact plants and whole plant longevity in the simulated consumer environment (SCE), (**B**) longevity of individual florets on intact plants and floret number of whole plants after 2 weeks in the SCE. Genotypes included in this data are 'Elegance Silver', 00-43-1, 00-43-2, 'Maiden Rose Pink', 'Maiden Orange', 'Maiden Lilac', 'Dandy', 'Ballet', and 'Baroness'. Unlabeled points on the lower end of the trend line represent the commercial genotypes.

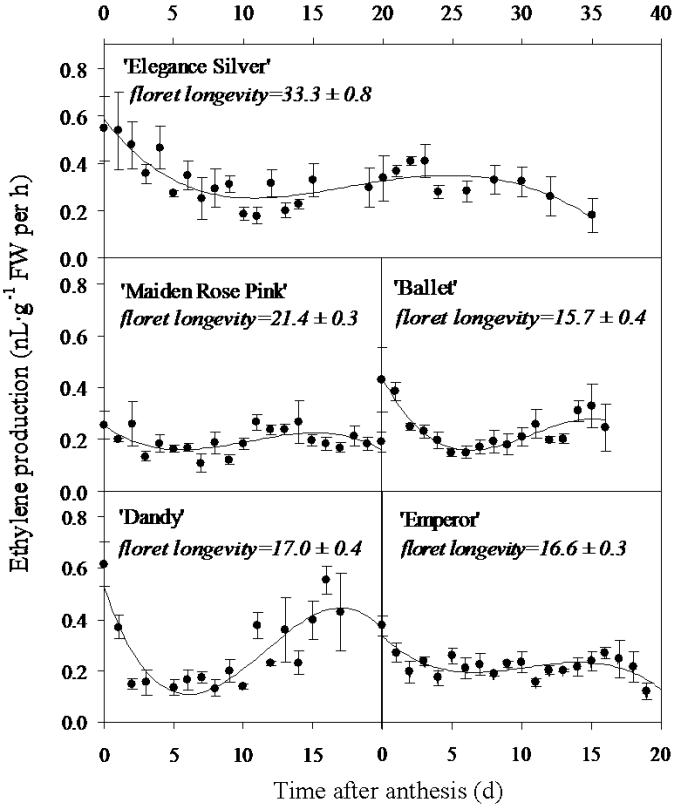

Fig. 4. Relationship between floret age and ethylene production by freshly excised florets of five genotypes of regal pelargonium. Data shown are means ±SE of at least four florets. Note variation in scale of x-axis reflecting differences in floret longevity.

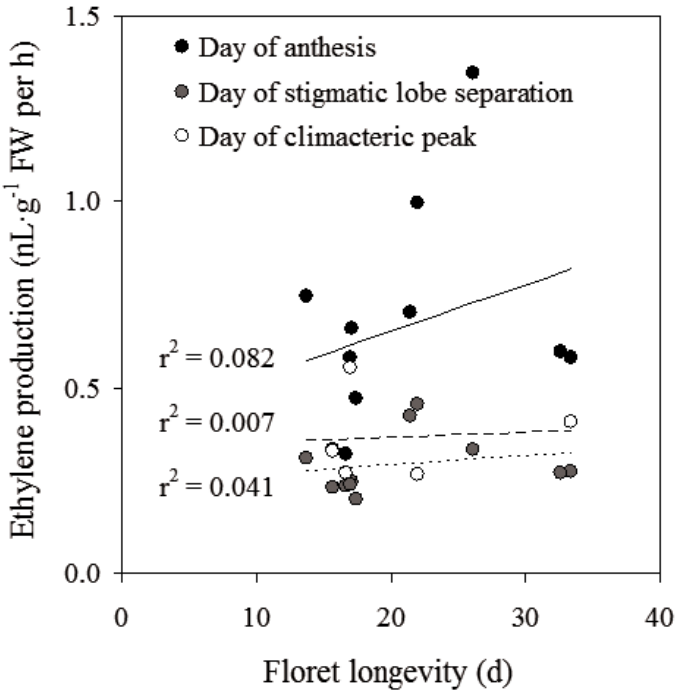

Fig. 5. There was no significant relationship between individual floret longevity and ethylene production of regal pelargonium. The ethylene production of excised florets harvested on the day of anthesis, when stigmatic lobes had separated, or at the climacteric peak was plotted against floret longevity on the intact plant. All the genotypes shown in Fig. 4 were included in this figure. The regression equations for the lines were: day of anthesis: y = 0.012x + 0.404; day of stigmatic lobe separation: y = 0.001x + 0.337; day of climacteric peak: y = 0.002x + 0.241.

Endogenous ethylene production. Ethylene production rates of excised florets of regal pelargonium were quite low, ranging from 0.1 to 1.4 nL·g^{-1} FW per hour (Fig. 4). Regardless of genotype, ethylene production was highest on the day of anthesis, decreased within 1 week, and then demonstrated a climacteric-like pattern as the floret aged (Fig. 4). In addition to the genotypes shown in Fig. 4, ethylene production was evaluated during the first 6 d after anthesis for 00-43-1, 00-43-2, 'Maiden Orange', 'Maiden Lilac', 'Bravo', 'Baroness', and 'Ballet' (data not shown). Freshly opened florets of 00-43-1 produced significantly higher ethylene on the day of anthesis (1.35 nL·g^{-1} FW per hour) than other genotypes (not shown). 'Ballet' and 'Emperor', which display relatively short floret life (Fig. 2), produced the lowest rate of ethylene on the day of anthesis and the ethylene production rate remained low (Fig. 4). There was no correlation between ethylene production rates and individual floret longevity on intact plants either on the day of anthesis or 3 d after anthesis, when stigmatic lobes begin to separate (Fig. 5).

Ethylene responsiveness. We previously showed that petal abscission in response to ethylene exposure (0.015 μL·L^{-1} ethylene for 90 min) varied with genotype and floret age (Kim et al., 2005). Florets up to 6-d-old of 'Elegance Silver' and 00-43-2 were unresponsive to this concentration of exogenous ethylene, and 00-42-1 demonstrated an intermediate response. The other genotypes responded to ethylene with a high rate of petal abscission, sometimes even in freshly opened florets.

In season 2, 3-d-old florets of each genotype were treated with a range of ethylene concentrations to generate dose-response curves. Petal abscission sharply increased over a narrow ethylene concentration range in most genotypes, and ethylene responsiveness was highest in 'Maiden Lilac' and 'Maiden Orange' (Fig. 6). Three-day-old florets of 'Elegance Silver', 00-43-2, and 00-43-1 did not respond to ethylene concentrations lower than 0.4 μL·L^{-1} for 90 min (Fig. 6).

The responsiveness coefficients (Nissen, 1985) were used to analyze ethylene responsiveness of various genotypes in two different seasons. PSU genotypes had higher values of S_{10}, S_{50}, and S_{90} (the ethylene concentration for 10%, 50%, and 90% abscission, respectively) relative to other genotypes, reflecting their lower ethylene responsiveness (Table 1). These values varied between seasons but the ranking of genotypes remained almost the same (Table 1). Floret longevity was correlated with the S_{50} of 3-d-old florets, which was higher in season 2 (Fig. 7). The responsiveness coefficient, S_{90}/S_{10}, tended to be lower in PSU genotypes than in commercial genotypes (Table 1), reflecting the smaller slopes of the dose-response curves (Fig. 6). However, these values were not consistent between seasons, indicating that the range of ethylene concentration to proceed from a small to a large response varied with season as well as genotype.

Discussion

'Elegance Silver' and its progeny, 00-43-2, displayed superior postproduction performance in comparison with other genotypes. Our results demonstrate that postproduction quality of regal pelargonium varies significantly among genotypes. The genetic differences in postproduction quality were consistent between seasons, indicating stable genetic effects for the characteristic.

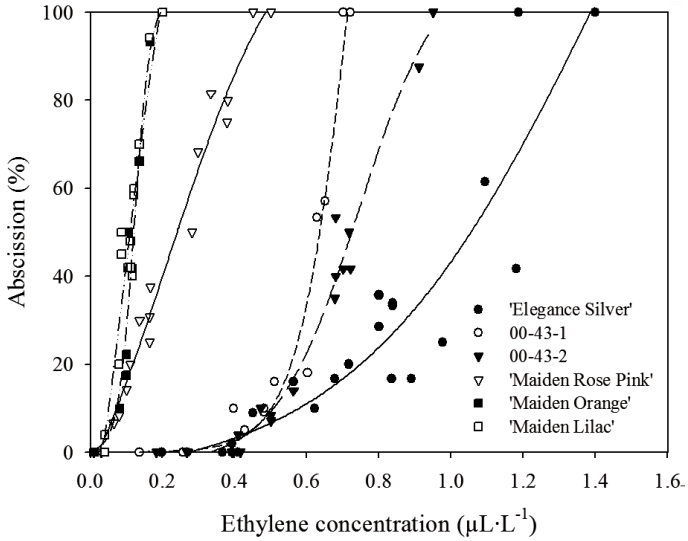

Fig. 6. The effect of ethylene concentration on petal abscission for 3-d-old florets of six different genotypes of regal pelargonium (Season 2). Each point represents the percent abscission of at least eight florets in a single experiment. The variables cultivar and ethylene concentration significantly affected petal abscission at $P < 0.001$.

The PSU genotypes displayed exceptional postproduction performance when compared to commercial cultivars. They had dramatically prolonged whole-plant longevity and maintained higher number of florets in the SCE (Fig. 3). In the season 1 experiment, the PSU genotypes had much higher number of florets even at the commencement of the experiment (data not shown), although all the genotypes reached first anthesis at about the same time. The increased whole plant longevity of these genotypes is attributable to greater individual floret longevity and the development of more florets per plant (Fig. 3).

Significantly reduced ethylene responsiveness contributes to the superior postproduction performance of PSU genotypes. Regal pelargonium is classified as one of the ornamental species most sensitive to ethylene (Deneke et al., 1990; Woltering, 1987). All of the regal pelargonium genotypes that we examined responded to ethylene, however, ethylene responsiveness varied significantly among genotypes. Commercial genotypes displayed significant petal abscission in response to ethylene treatment at concentrations as low as 0.01 $\mu L \cdot L^{-1}$ (Fig. 6) (Kim et al., 2005). This concentration is extremely low compared to concentrations used to survey floriculture crop responsiveness to ethylene (van Doorn, 2001; Woltering, 1987; Woltering and van Doorn, 1988) and demonstrates the reason for the poor shipping performance of regal pelargonium. Commercial genotypes could easily abscise petals even in the presence of very small amounts of ethylene resulting from stresses imposed during shipping or handling, or in response to even minor sources of exogenous ethylene.

Ethylene responsiveness was higher in season 1 than in season 2 for all genotypes except 'Elegance Silver' (lower S_{50} values, Table 1), indicating that ethylene responsiveness was altered by the growth environment. We previously showed that higher forcing temperature increased ethylene responsiveness in two other cultivars of regal pelargonium (Evensen and Olson, 1992). Although greenhouse set-point temperatures were the same for all our experiments, it is possible that there were more sunny days during season 1, driving daytime temperatures above the setpoint and increasing ethylene responsiveness.

To investigate the cause of the superior postproduction quality of 'Elegance Silver', we measured endogenous ethylene production and ethylene responsiveness of florets at different ages. There was no clear relationship between the cumulative amount of ethylene production in excised florets and the longevity of florets on intact plants (Fig. 5). The timing of a climacteric-like rise in ethylene production preceded petal abscission, reflecting differences in floret longevity of the evaluated genotypes (Fig. 4).

Dose response data indicated that 'Elegance Silver' was significantly less sensitive to ethylene than any other genotype evaluated (Fig. 6). Even with 1 $\mu L \cdot L^{-1}$ ethylene exposure, petal abscission of 3-d-old 'Elegance Silver' florets remained <50% (Fig. 6). The differences in ethylene responsiveness among the genotypes can explain most of the genetic variation in postproduction quality in regal pelargoniums. 'Elegance Silver' and its progeny 00-43-2 displayed extended floret longevity, which was strongly associated with reduced ethylene responsiveness (Fig. 7). Therefore, our results clearly demonstrate that ethylene responsiveness plays a critical role in regulating petal abscission and floral longevity in regal pelargoniums, and that the PSU genotypes have significantly prolonged floral longevity because of lower ethylene responsiveness.

Quantification of ethylene responsiveness indicated that the PSU genotypes, like commercial cultivars, are classified ultra-responsive despite their significantly reduced ethylene responsiveness. The S_{10}, S_{50}, and S_{90} values allow direct comparison of ethylene responsiveness among genotypes and indicate the absolute values of ethylene concentration to which these plants respond, while the responsiveness coefficient (S_{90}/S_{10}) reflects the slope of the main part of the response curve, indicating the narrowness of the range over which responses change. The PSU genotypes, in every case but one (S_{10} for 00-43-1, season 1), had higher S_{10}, S_{50}, and S_{90} values than commercial cultivars. However, the responsiveness coefficients were not associated with long floret life. In practice, the absolute amount of ethylene resulting in a response is more important, since it is exposure to endogenous or exogenous ethylene that results in undesirable petal abscission during the postproduction period.

Table.1. Effect of genotype and season on ethylene responsiveness of regal pelargonium florets. Excised florets were treated with various concentrations of ethylene for 90 min. S_{10}, S_{50}, and S_{90} are ethylene concentrations for 10%, 50%, and 90% abscission, respectively. S_{90}/S_{10} is a measure of the slope of the dose-response curve.

		Ethylene ($nL \cdot L^{-1}$) for proportion of response			Responsiveness coefficient
Season	Genotype	S_{10}	S_{50}	S_{90}	S_{90}/S_{10}
1	'Elegance Silver'	995	1316	1616	1.62
(February–	00-43-2	81	384	594	7.3
March)	00-43-1	11	114	272	23.95
	'Maiden Rose Pink'	14	50	103	7.36
	'Maiden Lilac'	5	15	28	5.28
	'Maiden Orange'	1	6	20	21.95
2	'Elegance Silver'	577	1054	1325	2.3
(December–	00-43-2	507	724	903	1.8
January)	00-43-1	561	636	683	1.2
	'Maiden Rose Pink'	73	240	422	5.8
	'Maiden Lilac'	51	111	175	3.4
	'Maiden Orange'	73	121	164	2.2

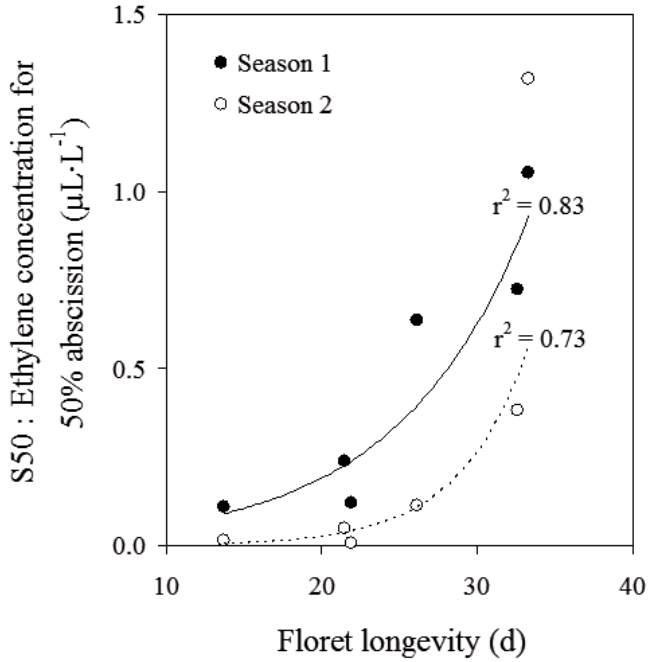

Fig. 7. The relationship between floret longevity and the ethylene concentration required for 50% petal abscission for 3-d-old florets of regal pelargonium. All the genotypes shown in Fig. 6 were included in this figure.

What accounts for the reduced ethylene responsiveness of 'Elegance Silver'? Florets of this genotype take 1 or 2 d longer than other genotypes to progress from anthesis to separation of stigmatic lobes. Separation of the stigmatic lobes signifies receptiveness to pollination and the development of ethylene responsiveness (Evensen, 1991). Delayed development of ethylene responsiveness could partly explain the reduced ethylene responsiveness of 'Elegance Silver.' However, even 6-d-old florets of 'Elegance Silver' were less ethylene responsive than 1- to 2-d-old florets of the commercial cultivars, so other factors must also play a role.

Another possibility is that 'Elegance Silver' and its progeny have modified concentrations or activity of ethylene signal transduction components. Ethylene signal transduction begins with ethylene binding to receptors, resulting in their inactivation and loss of CTR1-mediated repression of downstream components of the signal transduction pathway (Guo and Ecker, 2004). One way that ethylene responsiveness may be reduced is by increasing the abundance of ethylene receptors (Zhao and Schaller, 2004). A higher concentration of receptors would provide more binding sites to be filled by ethylene before the ethylene-receptor complex inactivates CTR1 and the ethylene response (petal abscission) can commence. Another candidate is EIN3, a transcription factor necessary for ethylene responses (Chao et al., 1997; Solano et al., 1998). In protoplasts from *Zea mays* L. and *Arabidopsis thaliana* (L.) Heynh. leaves, the stability of the EIN3 protein was enhanced by ethylene and reduced by glucose (Yanagisawa et al., 2003). A reduction in the concentration or stability of EIN3 in 'Elegance Silver' would result in reduced ethylene responsiveness. The seasonal differences in S-coefficients found in our experiments (Table 1) could result from variations in carbohydrate status impacting the stability of EIN3. Previous work with regal pelargonium plants grown under controlled light and temperature regimes implicated carbohydrate status in several aspects of postproduction quality, including ethylene responsiveness (Evensen and Olson, 1992). Research is needed to determine whether carbohydrate metabolism is linked with ethylene responsiveness via EIN3, and whether this can be exploited for improved flower crop quality.

Our results demonstrate a large variation in ethylene responsiveness that explains the differences in postproduction performance of PSU genotypes compared with commercial cultivars. These genotypes were developed in a conventional breeding program for improved disease and insect resistance, continued flowering under high temperature, and improved postproduction quality. This work shows that genotypes with improved postproduction quality could be identified by selection for reduced ethylene responsiveness of florets. In seed-propagated geraniums (*P.* ×*hortorum*), seedlings were screened for impaired triple-response to ethylene, which was shown to correlate with reduced petal abscission (Clark et al., 2001). However, regal pelargonium plants are propagated by rooted cuttings. The majority of these plants are putative tetraploids, and seedling production is not presently feasible due to low seed numbers and germination rates (Craig, 1982). Screening of genotypes for individual floret responses to ethylene can therefore be used to identify genotypes with good postproduction characteristics.

Literature Cited

Abeles, F.B., P.W. Morgan, and M.E. Saltveit. 1992. Ethylene in plant biology. Academic, San Diego, Calif.

Chao, Q.M., M. Rothenberg, R. Solano, G. Roman, W. Terzeghi, and J.R. Ecker. 1997. Activation of the ethylene gas response pathway in arabidopsis by the nuclear protein ETHYLENE–INSENSITIVE3 and related proteins. Cell 89:1133–1144.

Clark, D.G., C. Dervinis, J.E. Barrett, and T.A. Nell. 2001. Using a seedling hypocotyl elongation assay as a genetic screen for ethylene sensitivity of seedling geranium cultivars. HortTechnology 11:297–302.

Clark, D.G., C. Richards, Z. Hilioti, S. LindIversen, and K. Brown. 1997. Effect of pollination on accumulation of ACC synthase and ACC oxidase transcripts, ethylene production and flower petal abscission in geranium (*Pelargonium* ×*hortorum* L.H. Bailey). Plant Mol. Biol. 34:855–865.

Craig, R. 1982. Chromosomes, genes, and cultivar improvement, p. 380–411. In: J.W. Mastalerz and E.J. Holcomb (eds.). Geraniums. Pennsylvania Flower Growers, University Park, Pa.

Deneke, C., K. Evensen, and R. Craig. 1990. Regulation of petal abscission in *Pelargonium* ×*domesticum*. HortScience 25:937–940.

Evensen, K. 1991. Ethylene responsiveness changes in *Pelargonium* ×*domesticum* florets. Physiol. Plant. 82:409–412.

Evensen, K. and K. Olson. 1992. Forcing temperature affects postproduction quality, dark respiration rate, and ethylene responsiveness of *Pelargonium* ×*domesticum*. J. Amer. Soc. Hort. Sci. 117:596–599.

Guo, H.W. and J.R. Ecker. 2004. The ethylene signaling pathway: New insights. Current Opinion Plant Biol. 7:40–49.

Kim, H., R. Craig, and K. Brown. 2005. Genetically enhanced postproduction quality of regal pelargonium. Acta Hort. 669:135–141.

Nissen, P. 1985. Dose responses of auxins. Physiol. Plant. 65:357–374.

Olson, K.M. and K.B. Evensen. 1990. The influence of irradiance on ethylene sensitivity and postproduction quality of *Pelargonium* ×*domesticum*. Acta Hort. 272:341–346.

Solano, R., A. Stepanova, Q.M. Chao, and J.R. Ecker. 1998. Nuclear events in ethylene signaling: A transcriptional cascade mediated by ETHYLENE–INSENSITIVE3 and ETHYLENE–RESPONSE–FACTOR1. Genes Dev. 12:3703–3714.

van Doorn, W.G. 2001. Categories of petal senescence and abscission: A re-evaluation. Ann. Bot. 87:447–456.

Woltering, E.J. 1987. Effects of ethylene on ornamental pot plants: A classification. Scientia Hort. 31:283–294.

Woltering, E.J. and W.G. van Doorn. 1988. Role of ethylene in senescence of petals—Morphological and taxonomical relationships. J. Expt. Bot. 39:1605–1616.

Yanagisawa, S., S.D. Yoo, and J. Sheen. 2003. Differential regulation of EIN3 stability by glucose and ethylene signaling in plants. Nature 425:521–525.

Zhao, X.C. and G.E. Schaller. 2004. Effect of salt and osmotic stress upon expression of the ethylene receptor ETR1 in *Arabidopsis thaliana*. FEBS Lett. 562:189–192.