Review

Ethylene Production and Petal Wilting during Senescence of Cut Carnation (Dianthus caryophyllus) Flowers and Prolonging Their Vase Life by Genetic Transformation

Shigeru Satoh1,2

1 Laboratory of Genetic Engineering, Graduate School of Life and Environmental Sciences, Kyoto Prefectural University, Kyoto 606-8522, Japan
2 Basic Research Division, Kyoto Prefectural Institute of Agricultural Biotechnology, Seika-cho 619-0244, Kyoto Prefecture, Japan

Senescence of carnation flowers is characterized by autocatalytic ethylene production from petals and subsequent wilting of the petals. Recent studies on the regulation of ethylene production and wilting in senescing carnation petals revealed that (1) petal senescence is triggered by ethylene evolved from the gynoecium during natural senescence, (2) ethylene production in the gynoecium is induced by a factor(s) other than pollination signals in carnation flowers lacking anthers, (3) there are two subsets of ethylene responses in the petals, one responsible for autocatalytic ethylene production and the other for wilting, (4) expression of genes involved in the execution of petal withering is differently regulated between ethylene-dependent or -independent senescence. Furthermore, it was revealed that the generation of transgenic carnation without detectable ethylene production is useful to prolong the vase life of cut carnation flowers.

Key Words: carnation, ethylene, genetic transformation, senescence mechanism, vase life.

Introduction

Senescence of carnation flowers is characterized by autocatalytic ethylene production from petals and the subsequent wilting of the petals. Many studies have been carried out to elucidate the regulation mechanism of autocatalytic ethylene production and wilting of petals for more than several decades (Abeles et al., 1992; Borochov and Woodson, 1989; Reid and Wu, 1992; Shibuya and Ichimura, 2010). A large amount of ethylene is synthesized several days after full opening of the flower during natural senescence (Woodson et al., 1992), or several hours after compatible pollination (Larsen et al., 1995; Nichols, 1977; Nichols et al., 1983) or treatment with exogenous ethylene (ten Have and Woltering, 1997; Wang and Woodson, 1989). A substantial portion of ethylene comes from flower petals. The increased ethylene production accelerates the inrolling of petals, resulting in flower wilting.

The gynoecium has been suggested to play a role in the induction of petal senescence, i.e., ethylene evolved from the gynoecium acts as a diffusible signal that is perceived by the petals and induces the onset of senescence in the petals (Jones and Woodson, 1997; Nichols, 1977; ten Have and Woltering, 1997; Woodson et al., 1992); however, this proposal remains a matter of dispute because petal senescence in the cut carnation flower was not delayed by removal of the gynoecium (Mor et al., 1980; Sacalis and Lee, 1987; Woodson and Brandt, 1991).

Several studies have dealt with pollination-induced ethylene production in the carnation gynoecium (Nichols, 1977; Jones and Woodson, 1997); however, many carnation cultivars do not have anthers, and cannot be pollinated by their own pollen. They nonetheless show an increase in ethylene production in the gynoecium, which must be induced by factors other than pollination. The mechanism of ethylene production in the gynoecium without pollination has thus far received little attention; however, it has been established that the increase in ethylene production in unpollinated flowers starts in the ovary (part of the gynoecium), whereas in pollination-induced senescence it starts in the style of the gynoecium. It is important to uncover the factors that induce ethylene production in the gynoecium of unpollinated carnation flowers.

The wilting of carnation petals is probably caused by
the degradation of cell components, which leads to cell
death during petal senescence, mediated by hydrolytic
enzymes such as cysteine proteinase (DcCP1) (Jones et
al., 1995), lipase (Hong et al., 2000) and so on.

Autocatalytic ethylene production and wilting occur
simultaneously during petal senescence (Abeles et al.,
1992; Borochov and Woodson, 1989; Reid and Wu,
1992). It has been believed that autocatalytic ethylene
production and petal wilting are regulated in concert and
cannot be separated, since they occur in close parallel.
There have been no studies on how these two phenomena
are regulated in terms of the gene expressions involved
in these events.

Much remains to be elucidated about the precise
mechanism of autocatalytic ethylene production from
petals and the subsequent wilting of the petals in
carnation flowers. This review outlines the results of our
recent study, which was conducted to address these
questions.

1. Role of the gynoecium in natural senescence of
carnation flowers

Although the petals contribute substantially to the
ethylene that is produced during natural or pollination-
induced senescence in carnation flowers, the
gynoecium produces a significant amount of ethylene
before the onset of production of the gas by the
petals (Nichols, 1977; ten Have and Woltering, 1997;
Woodson et al., 1992). During natural senescence, 1-
aminocyclopropane-1-carboxylate (ACC) content and
ethylene production increase in the gynoecium earlier
than in the petals (Hsieh and Sacalis, 1986; Nichols,
1977; Veen and Kwakkenbos, 1984). The expression of
ACC synthase and ACC oxidase genes (and ethylene
production) first started in the ovary followed by the
style and petals in naturally senescing carnation flowers.
When the petals were detached from the flowers at the
presenescent stage, they showed no ethylene production
and exhibited delayed withering (ten Have and
Woltering, 1997). These findings suggested a role of the
gynoecium in controlling the senescence of petals in
carnation flowers; however, removal of the gynoecium
did not delay the petal senescence of cut carnation
flowers in previous reports (Mor et al., 1980; Sacalis
and Lee, 1987; Woodson and Brandt, 1991). These
results are in apparent conflict with the proposed role
of the gynoecium in controlling petal senescence. In
contrast to these previous investigations where the
gynoecium was removed by forceps or scissors, Shibuya
et al. (2000) carefully snapped them off by hand. This
treatment prevented the increase in ethylene production
and markedly prolonged flower life (Fig. 1). This
experiment showed the decisive role of the gynoecium
in controlling the natural senescence of carnation
flowers. Treatment with exogenous ethylene induced
autocatalytic ethylene production and petal wilting in
flowers with gynoecia removed. By contrast, abscisic

acid (ABA) and indole-3-acetic acid, which induced
ethylene production and accelerated petal senescence in
carnation flowers, did not stimulate ethylene production
in flowers with gynoecia removed (Shibuya et al., 2000).
These results strongly indicated that ethylene is initially
produced in the gynoecium in response to some internal
stimuli, including plant hormones, which in turn trigger
the onset of ethylene production in the petals, resulting
in petal wilting in carnation flowers.

2. Repressed ethylene production in long-lasting
flowers is due to the absence of ethylene
production in the gynoecium of the flowers

To obtain further evidence of the role of ethylene
production from the gynoecium in carnation flower
senescence, ethylene production and the expression of
genes for ethylene biosynthetic enzymes were investi-
gated with flowers of the ‘White Candle (WC)’ cultivar,
which has long-lasting flowers, in comparison with that
of the conventional cultivar ‘Light Pink Barbara (LPB)’
(Nukui et al., 2004). Ethylene production of whole ‘WC’
flowers was below the limit of detection throughout the
19-day study period. When petals and gynoecia were
detached from the whole flowers and ethylene production
by respective tissues was measured, their ethylene
production rates were also mostly below the detection limit. By contrast, whole ‘LPB’ flowers produced ethylene in a significant amount with the maximal production rate of 2.7 nmol·g$^{-1}$·h$^{-1}$ on day 5.

Since three genes for ACC synthase (DcACS1, DcACS2 and DcACS3) and one gene for ACC oxidase (DcACO1) have been identified in carnation (Henskens et al., 1994; Jones and Woodson, 1999; Park et al., 1992; Wang and Woodson, 1991), the accumulation of transcripts of these genes were determined in the gynoecium and petals of unpollinated ‘WC’ and ‘LPB’ flowers (Fig. 2).

In the gynoecium of ‘LPB’ flowers, the DcACS3 transcript accumulated on day 3 through day 9, the DcACS1 transcript on days 5 and 6, and the DcACS2 transcript, although in a small amount, on day 5. On the other hand, in the gynoecium of ‘WC’ flowers, DcACS1 and DcACS2 transcripts were not detected throughout the experiment, although DcACS3 transcript accumulated in a small amount on day 9 through day 15. The DcACO1 transcript was already present in a small amount on day 0 and its amount increased, with the peak on day 6 in the gynoecium of ‘LPB’ flowers. By contrast, the DcACO1 transcript was not detected on day 0, accumulated on day 6 and decreased thereafter in the gynoecium of ‘WC’ flowers.

The accumulation of DcACO1 and DcACS1 transcripts on day 6 through day 9 was obvious in the petals of ‘LPB’ flowers. The DcACS1 transcript was not detected in the petals of ‘WC’ flowers during the senescing period of 21 days, although the DcACO1 transcript was present on day 9 through day 21, except for day 15.

Close relationships between the transcription levels of ACC synthase genes and ACC synthase activity and ethylene production rates have been reported in carnation petal senescence (Iwazaki et al., 2004; Kosugi et al., 2000, 2002; ten Have and Woltering, 1997; Woodson et al., 1992). It is assumed, therefore, that undetectable levels of DcACS1 transcripts in the petals of ‘WC’ could contribute to the absence of ethylene production in this cultivar. Expression of the DcACS1 and DcACO1 genes in the petals of carnation flowers is induced by ethylene from the gynoecium (Shibuya et al., 2000). It is possible that the absence of the DcACS1 transcript and the presence of the DcACO1 transcript in the petals of ‘WC’ flowers was due to very low ethylene production in the

**Fig. 2.** Changes in transcript levels of ACC synthase genes (DcACS1, DcACS2, and DcACS3) and an ACC oxidase gene (DcACO1) in the gynoecium (Top) and the petals (Bottom) of ‘White Candle (WC)’ and ‘Light Pink Barbara (LPB)’ flowers. The petals and gynoecium (ovary plus styles) were collected from 3 flowers, combined to make respective samples, and used for isolation of total RNA. The level of ACC synthase and ACC oxidase transcripts in total RNA fractions were determined by amplification by RT-PCR. An actin fragment (DcACT1) was amplified to check PCR operation and the amount of template RNA.
gynoecium, insufficient to induce the expression of the \textit{DcACS1} gene but sufficient to induce the \textit{DcACO1} gene. By contrast, in ‘LPB’ flowers, the amount of ethylene produced in the gynoecium was high enough to induce the expression of both \textit{DcACO1} and \textit{DcACS1} in the petals.

Accumulation of the \textit{DcACO1} transcript in the gynoecium of both ‘WC’ and ‘LPB’ flowers indicated that the expression of the \textit{DcACO1} gene did not play a causal role in determining ethylene production ability in the gynoecium of ‘WC’ and ‘LPB’ flowers. Transcripts of \textit{DcACS3} and \textit{DcACS1} accumulated in a significant amount in the gynoecium of ‘LPB’ flowers, whereas only the \textit{DcACS3} transcript was detected in a small amount on day 9 through day 12 in the gynoecium of ‘WC’ flowers. The repressed accumulation of ACC synthase transcripts, especially \textit{DcACS1} transcript, was probably responsible for the low ethylene production in the gynoecium of ‘WC’ flowers. These findings further supported the primary role of gynoecium in ethylene production from senescing carnation flowers.

3. Factors responsible for inducing ethylene production in the gynoecium during natural senescence of carnation flowers

As described in the Introduction, several studies have dealt with pollination-induced ethylene production in the carnation gynoecium (Jones and Woodson, 1997; Nichols, 1977); however, many carnation cultivars do not have anthers and cannot be pollinated by their own pollen. They nonetheless show increased ethylene production in the gynoecium, which must be induced by factors other than pollination. The mechanism of gynoecium ethylene production without pollination has thus far received little attention.

Regarding the possible factors involved in the onset of ethylene production in unpollinated senescing carnation flowers, Onoue et al. (2000) reported that ABA concentration in the gynoecium increased transiently, before the rise of ethylene production. 1,1-dimethyl-4-(phenylsulfonyl)semicarbazide (DPSS), a potent preservative of carnation flowers (Midoh et al., 1996), inhibited the transient increase in the ABA concentration, resulting in the suppression of petal ethylene production. Application of ABA to carnation flowers accelerates petal senescence through the induction of ethylene synthesis in the gynoecium (Shibuya et al., 2000). These observations suggest the causal role of ABA in the initiation of ethylene production in the unpollinated gynoecium.

Preliminary studies on water relationships in cut carnation flowers revealed that, in the control ‘LPB’ flower, the water balance, i.e., the net amount of water taken up into the cut flowers, decreased rapidly from the beginning of incubation (day 0), whereas this decrease in water balance occurred much later in ‘LPB’ flowers treated with DPSS, as well as in untreated ‘WC’ flowers (Satoh et al., 2005a). This rapid decrease in the water balance is indicative of low water potential, i.e., drought stress, which may result in the accumulation of ABA. Taking these data together, it could be hypothesized that unpollinated cut ‘LPB’ flowers suffer from drought stress, which is accompanied by ABA accumulation. This in turn results in induction of the expression of ethylene biosynthetic genes in the gynoecium. Such an event apparently does not occur or is delayed in cut ‘WC’ flowers.

4. Separation of autocatalytic ethylene production and wilting in senescing carnation petals

Autocatalytic ethylene production and wilting occur simultaneously in senescing carnation petals (Abeles et al., 1992; Borochov and Woodson, 1989; Reid and Wu, 1992). It has been believed that ethylene production and wilting are regulated in concert and cannot be separated, since the two events occur in close parallel in senescing carnation petals. Kosugi et al. (2000) challenged this problem by using an ACC oxidase-suppressed transgenic carnation line, sACO-1, harboring an \textit{sACO} transgene, i.e., \textit{DcACO1} cDNA in sense orientation under the control of a strong constitutive promoter, CaMV35S promoter, with additional enhancer sequences (Mitsuhara et al., 1996). Cut flowers of the sACO-1 line produced only a trace amount of ethylene during the senescence period, and had a vase life about 2-fold longer than the flowers of the parent ‘Nora’ carnation.

We further examined the responses of petals of the transgenic carnation line to exogenous ethylene with regard to the induction of in-rolling, ethylene production and genes involved in these events, and found that the gene expressions of ACC synthase (\textit{DcACS1}), ACC oxidase (\textit{DcACO1}), and cysteine proteinase (\textit{DcCP1}) are separately regulated in carnation petals. \textit{DcCP1} is probably one of the enzymes responsible for hydrolytic degradation of cell components leading to cell death during petal senescence (Panavas et al., 1998, 1999).

\begin{figure}[h]
\centering
\includegraphics[width=0.8\textwidth]{figure3.png}
\caption{Accumulation of transcripts of \textit{DcACO1}, \textit{DcACS1}, and \textit{DcCP1} in petals of non-transformed ‘Nora’ carnation and the sACO-1 transgenic line after treatment with ethylene at 10 µL·L\textsuperscript{-1} for 18 h.}
\end{figure}
Interestingly, treatment with ethylene of petals detached from sACO-1 flowers caused the accumulation of mRNA for DcCP1 and petal wilting, but not the accumulation of mRNA for DcACS1 and DcACO1 and ethylene production (Fig. 3). These findings indicated that the exogenous ethylene-induced expression of DcACS1 and DcACO1 genes, leading to autocatalytic ethylene production, and that of the DcCP1 gene, leading to petal wilting, were regulated separately in the petals of sACO-1 flowers. It is reasonable to speculate that ethylene production and wilting are separately regulated in the petals of other carnation cultivars.

Although further investigation is required to uncover the mechanisms by which autoctalytic expression of DcACS1 is suppressed in the sACO-1 line, the findings described above propose the presence of two subsets of ethylene responses, leading to the expression of the respective genes in carnation petals. One subset leads to the expression of DcACS1 and DcACO1 genes and autocatalytic ethylene production, whereas the other leads to the expression of the DcCP1 gene and probably other genes for enzymes for hydrolytic degradation and petal wilting (Satoh et al., 2005b) (Fig. 4).

5. Mechanism executing the degradation of cell constituents leading to petal wilting

During the senescence of carnation flowers, petals induce autocatalytic ethylene production, and the ethylene evolved causes subsequent petal wilting, which is probably caused by the degradation of cell components, which leads to cell death during petal senescence, mediated by hydrolytic enzymes including cysteine proteinase (DcCP1, Jones et al., 1995).

Carnation plants have a gene for the cysteine proteinase inhibitor (DcCPIn) (Kim et al., 1999; Sugawara et al., 2002), which is thought to act as a suppressor of cysteine proteinase (DcCP1) and to play a role in the regulation of petal wilting in senescing carnation flowers (Sugawara et al., 2002).

Researchers have noticed another type of senescence, which proceeds differently from the above-described ethylene-dependent senescence. This type of senescence occurs independently of ethylene in carnation flowers treated with inhibitors of ethylene production and perception such as DPSS (Onoue et al., 2000) and silver thiosulfate anionic complex (STS; Veen, 1979), respectively, and in flowers with their gynoecia removed in the presenescent stage, flowers of transgenic non-ethylene-producing carnation (Kosugi et al., 2002) and flowers of long-lasting cultivars (Nukui et al., 2004) (Fig. 5).

Generally, the ethylene-dependent and -independent senescence of carnation flowers is distinguished by observing ethylene production and morphological changes of flower petals during senescence. The former is characterized by in-rolling of the petal margin followed by rapid wilting of the whole petals, while the latter is by desiccation, discoloration and necrosis of the petal margins, which gradually spread to the remaining petal portions. These two types of senescence in carnation flowers are morphologically designated as wilting and fading, respectively. So far, however, no or little study has been conducted on the molecular mechanism of the ethylene-independent senescence of carnation flowers. Elucidation of the molecular events in ethylene-independent senescence will foster better understanding of the process of the ethylene-dependent senescence of carnation petals.

The differences in ethylene production, appearance of flowers and expression of senescence-related genes between ethylene-dependent and -independent senescence were investigated using ‘LPB’ carnation flowers treated with or without DPSS, respectively (Otsu et al., 2007a). Changes in the levels of transcripts for senescence-related genes were examined by northern blot analysis with probes made from the corresponding cDNAs. Total RNA for analysis was isolated from the petals of carnation flowers, which were left for 10 days for ethylene-dependent senescence, but 20 days for ethylene-independent senescence. Some genes related to
petal senescence were regulated similarly, aside from the time of their expression, in the petals of both ethylene-dependent and -independent (DPSS-treated) flowers (Otsu et al., 2007a), whereas others were regulated differently between the two types of flowers (Otsu et al., 2007b).

Genes which were regulated similarly in both ethylene-dependent and -independent senescence were those for cysteine proteinase (DcCP1), cysteine proteinase inhibitor (DcCPIn), and glutathione-S-transferase (DcGST, corresponding to the previously reported carnation SR8; Lawton et al., 1989). In the control flowers, transcripts decreased for DcCPIn and accumulated for DcCP1 and DcGST, coinciding with ethylene production in flowers and petal wilting. Moreover, delayed changes in the transcript levels of these genes in DPSS-pretreated ‘LPB’ flowers coincided with delayed senescence in the petals of these flowers.

The transcript of the β-glucosidase gene (DcbGlc, corresponding to carnation SR5; Lawton et al., 1989) was present abundantly in non-senescing petals. Its transcript rapidly diminished during wilting, whereas its level decreased slowly before the onset of fading and recovered to its original level at the culmination of fading (Otsu et al., 2007a). A marked difference was observed in the change of the transcript of the β-galactosidase gene (DcbGal, corresponding to carnation SR12; Lawton et al., 1989). Its transcripts accumulated in a large amount in the petals of control flowers, coinciding with the onset of wilting, whereas its level showed only a little change in the petals of DPSS-treated flowers throughout the incubation period of 20 days (Otsu et al., 2007b). The involvement of β-galactosidase in cell wall modification associated with fruit development and softening has been reported (reviewed by Tateishi, 2008). Tateishi et al. (2001) reported that in Japanese pear (Pyrus pyrifolia) fruit the β-galactosidase gene (JP-GAL) was specifically expressed during fruit ripening, and its possible translate β-galactosidase III was responsible for fruit softening. In spite of the apparent difference between petal wilting in carnation flowers and fruit softening in Japanese pears, there may be a common mechanism between these two phenomena since both events involve the degradation of cell walls.

### 6. Generation of transgenic carnation deficient in ethylene production and perception

In cut ornamental flowers susceptible to ethylene, preservatives containing silver thiosulfate anionic complex ion (STS) (Veen, 1979) are currently being used to prolong their vase life; however, STS is harmful to the environment and may be banned in the near future. Thus, transgenic ornamentals with suppressed production or action of ethylene are excellent alternatives for the preservation of flower longevity. So far, transformation with transgenes related to the biosynthesis and action of ethylene has been successfully used to down-regulate ethylene production or responsiveness to ethylene in petunia (Wilkinson et al., 1997), torenia (Aida et al., 1998), and carnation (Bovy et al., 1999; Savin et al., 1995). Cut flowers of these transgenic plants have a prolonged vase life compared with non-transgenic plants.

As described above, Kosugi et al. (2000, 2002) generated a transgenic carnation line (sACO-1) transformed with DcACO1 cDNA in sense orientation (sACO transgene) using ‘Nora’ carnation. The transfor-
mation vector was constructed using pMLH2113-GUS, and the transgene was driven by CaMV35S promoter (Mitsuhara et al., 1996). Transformation was conducted using the Agrobacterium-mediated gene transfer technique. The transformed carnation plants obtained were grown in a containment greenhouse until they flowered.

The appearance of cut flowers during the senescence period (10 days) in the sACO-1 line significantly differed from that in non-transformed ‘Nora’ (Fig. 6). Flowers of the sACO-1 line remained turgid without petal in-rolling until about day 10, but began to show desiccation and discoloration of the rim of petals on day 11 or later. By contrast, flowers of the non-transformed ‘Nora’ remained turgid until day 5, showed in-rolling of petals on day 6, and completely wilted on day 9. Petal in-rolling at the onset of flower wilting is a well-known characteristic of ethylene-dependent senescence of carnation flowers. Flowers of non-transformed ‘Nora’ showed a climacteric rise in ethylene production, peaking on day 5, whereas flowers of the sACO-1 line produced a negligible amount of ethylene during the senescence period.

The suppressed ethylene production in the sACO-1 line was accompanied by no accumulation of mRNA of the DcACO1 gene in the gynoecia and mRNA for DcACO1 and DcACS1 genes in the petals. As described above, ethylene is produced first in the gynoecium, and the evolved ethylene acts on petals, as a diffusible signal, to induce the expression of DcACO1 and DcACS1 genes, resulting in autocatalytic ethylene production in the petals (Shibuya et al., 2000). The results indicate that the sACO transgene inhibits the expression of DcACO1, probably by cosuppression in the gynoecium, which eventually suppresses ethylene production in the whole flower of the sACO-1 line.

Iwazaki et al. (2004) generated 5 lines of ‘Nora’ carnation transformed with DcACS1 cDNA in sense and antisense orientation (sACS transgene and aACS transgene, respectively). Cut flowers of all the transgenic lines obtained, 2 lines transformed with sACS transgene and 3 lines with aACS transgene, showed suppressed ethylene production during natural senescence as compared with the flowers of non-transformed ‘Nora’ carnation. Among 5 transgenic lines, the sACS-1 line harboring sACS transgene had the most severe reduction in ethylene production in flowers, and the flowers completed their vase life by drying and discoloring of the rim of petals, which is the ethylene-independent deterioration of carnation flowers. These results confirmed that the generation of transgenic carnations, which lack ethylene production after full opening of their flower, is an excellent way to prolong the vase life of cut carnation flowers.

7. Concluding remarks and future study

Senescence of carnation flowers is characterized by autocatalytic ethylene production from petals and subsequent wilting of the petals, however, much remains to be elucidated to understand precisely the regulation mechanism of autocatalytic ethylene production from petals and subsequent wilting of the petals of carnation flowers. Our recent studies revealed several important features of the regulation of ethylene production and wilting in senescing carnation petals and confirmed the usefulness of generating transgenic carnation without ethylene production (and perception) to lengthen the vase life of cut carnation flowers. Some of the important features revealed are: (1) petal senescence is triggered by ethylene evolved from the gynoecium during natural senescence, (2) ethylene production in the gynoecium is induced by factor other than pollination signals in carnation flowers lacking anthers, (3) there are two subsets of ethylene responses in the petals; one responsible for autocatalytic ethylene production and the
other for wilting, (4) expressions of some genes involved in petal withering are differently regulated between ethylene-dependent and -independent senescence.

In the study of the possible factors inducing ethylene production in the gynoecium of carnation flowers in which pollination-induced ethylene production does not occur, ABA has been suggested. Elucidating these factors is an important future study to develop a novel method of regulating flower senescence. Cloning of the genes responsible for ABA biosynthesis from carnation plants and analysis of their expression are being conducted in our laboratory.

The vase life of cut ornamental flowers, including carnation, consists of periods spent in flower opening and senescence. It is necessary to slow down both processes to prolong the display time of the flowers. So far, few studies have been performed to elucidate the mechanism of flower opening (van Doorn and van Meeteren, 2003; Yamada et al., 2009) as compared with the mechanism of flower senescence. With more precise understanding of the mechanism of flower opening, it would be possible to develop new procedures to slow down the flowering process, lengthening the display time of the flowers. We have recently started a study on the molecular mechanism of flower opening using cut carnation flowers as a model ornamental (Harada et al., 2010). It is expected that some key findings will be obtained and used to develop novel technologies to retard the flower opening process.

**Literature Cited**


Otsu, S., S. Satoh and Y. Kosugi. 2007a. Expression of senescence related genes in carnation petals undergoing wilting and...