Autocatalytic Ethylene Production by *Dendrobium* Flowers
during Senescence Induced by Exogenous Ethylene

L. Lerslerwong and S. Ketsa*

Department of Horticulture, Kasetsart University, Bangkok 10900, Thailand

*Corresponding author. Email: agrsck@ku.ac.th

Abstract

Exogenous ethylene induced premature senescence of *Dendrobium* ‘Khao Sanan’ flowers. The visible symptoms of senescence developed completely within 5 days after C$_2$H$_4$ treatment and caused an increase in ethylene production. The burst in ethylene production of ethylene-treated columns was higher than that of the ethylene-treated perianth. AOA treatment delayed senescence of *Dendrobium* ‘Khao Sanan’ with ethylene treatment for 4 days. Furthermore, AOA decreased ethylene production of flowers with and without ethylene treatment. The transcripts of *Den-ETR1, Den-ACS* and *Den-ACO* gene were highly expressed in ethylene-treated flowers. AOA pretreatment in flowers with and without ethylene, the expression of *Den-ETR1* decreased in both perianth and column. *Den-ACS* transcripts were inhibited in perianth and decreased in column. The transcription of *Den-ACO* also decreased in perianth but it was still to express in column. Moreover, these three genes in ethylene-treated treatments were more expressed than that in only AOA treatment. It is concluded that exogenous ethylene regulated the autocatalytic ethylene production system while endogenous ethylene acted through signal transduction pathway and thus regulated the transcription of senescence-associated genes.

**Keywords:** aminooxyacetic acid (AOA), endogenous ethylene, ethylene biosynthetic gene, ethylene receptor, gene expression

Introduction

Orchid is the most important cut flower exported from Thailand. The main genus is *Dendrobium*. *Dendrobium* flowers are sensitive to ethylene (Ketsa and Rugkong, 2000). During transportation, ethylene may accumulate inside the cardboard boxes containing *Dendrobium* inflorescences (Uthaichay et al., 2007). Ethylene produced by inappropriate postharvest handling, exhaust gas from vehicles, long storage and shipping, can induce premature senescence of orchid flowers resulting in a short vase life and low quality. Up to now, there is a fair amount of information on pollination-induced senescence in orchid flowers, however, we know little about the senescence of unpollinated *Dendrobium* orchid flowers treated with exogenous ethylene.

Ethylene has been shown to play an important role in the regulation of flower senescence, including *Dendrobium* orchid flowers. Ethylene production has been found to increase during senescence (Ketsa and Rugkong, 2000). Ethylene action was investigated after the discovery of the Yang Cycle in ethylene biosynthesis. Exogenous ethylene and ethylene inhibitors were applied to study physiological and biochemical changes. Biotechnology tools are now being used to find out how plants, including flowers respond to ethylene.

Regulation of plant senescence begins before visible symptoms are evident (Buchanan-Wollaston, 1997). Relevant genes control senescence. Since many genes regulate senescence, the study of gene expression during senescence is necessary to understand better the process (Lim et al., 2003). The
rapid progress in plant molecular biology can contribute to the breeding of better ornamental plants, especially through recombinant DNA technology (Chandler, 2003). However, published information on the molecular biology of ethylene biosynthesis in *Dendrobium* is limited. Research reported in this paper was undertaken to study changes in ethylene production and the expression of ethylene receptor and biosynthetic genes of *Dendrobium* flowers during senescence induced by exogenous ethylene, so as to provide basic information for future strategies to increase flower longevity and quality.

**Materials and Methods**

**Plant Materials**

Inflorescences of *Dendrobium* ‘Khao Sanan’ without pretreatment were obtained from a commercial grower near Bangkok. Export-grade inflorescences, with 5-10 open flowers and 5-7 flower buds were selected for freshness and uniformity. They were harvested in the morning and were wet-packed in carton boxes and brought to the laboratory within 2 h after harvest. The second, third, and fourth of fully open flowers from the individual stem end were excised at the distal end of pedicels with a sharp razor blade and placed immediately in 10-mL vials containing distilled water. All flowers were held in a room with natural light (~12 h per day; ~15 µmol photons m⁻² s⁻¹). The temperature and relative humidity of the air-conditioned room were the average of 25°C and 80%, respectively.

**Ethylene and AOA treatment**

Detached flowers held in 10-mL vials containing 8 mL of distilled water were placed in an airtight plastic chamber (37×47×35 cm). Ethylene was applied by introducing an appropriate volume through an injection port, and brought to a final concentration of 0.4 µL L⁻¹. Flowers were exposed to ethylene for 24 h. For AOA pretreatment, pedicels of detached flowers were placed in 10-mL vials containing 0.5 mM of AOA solution and left for 18 h. Distilled water was used for the control treatment. In the AOA + ethylene treatment, detached flowers were treated once with AOA prior to ethylene treatment. Senescence symptoms and ethylene production were recorded.

**Senescence Symptoms**

Visible symptoms such as wilting, venation, yellowing and water soaking were scored daily. Wilting and venation were scored as symptom percentage of perianth based on the following: a score of 0, 1, 2, 3, 4 and 5 was used to define 0% (no visible senescence symptom), 10%, 11-25%, 26-50%, 51-75%, 76-100% of senescence symptoms, respectively. Wilting is scored as a drooping flowers. Veneration is when veins of vascular bundles can be seen clearly on the surface area of perianth organs (2 petals, 3 sepals, and lip). Yellowing is when white parts change to yellow. Water soaking is indicative of bruising on flower tissue at very late senescence (when more than 75% wilting and venation). The time to senescence of flowers was considered terminated when 50% of all symptoms occurred.

**Ethylene Production**

Ethylene production of detached flowers, isolated perianth organs and isolated columns were measured. Detached flowers were placed in 10-mL vials containing 8 mL of distilled water and then placed into 320 mL plastic bottles. The basal end of isolated perianth organs (2 petals, 3 sepals and 1 lip) was placed in plastic dishes containing 8 mL of distilled water, whereas the basal end of pedicels with excised column was placed in 10-mL vials containing 8 mL of distilled water. Isolated perianth organs held in plastic dishes containing distilled water were placed into 260 mL plastic bottles fitted with gas sampling ports. For excised column, the vials were closed with serum caps. Measurements were taken from three replicate plastic bottles. A one-mL gas sample was withdrawn from the sampling port after 1 h closure for ethylene determination. Composition of the headspace gas was measured with a gas chromatograph (Shimadzu GC 8A, Kyoto, Japan), equipped with a flame ionization detector and a 2.1-m stainless steel column with an inner diameter of 4 mm containing activated alumina of 80/100 mesh. The column temperature was 80°C. Injector and detector temperatures were 150°C. Serum caps were opened after gas sampling. The value of the three gas samples at a measuring point were averaged and expressed per gram fresh weight of the plant material.
RNA Extraction

Isolated perianths and columns were harvested at before pretreatment (day 0; D0) and after each treatment at day 1 (D1), day 2 (D2) and day 5 (D5). Total RNA was isolated from one gram of frozen tissue using CTAB method (Chang et al., 1993). Before reverse transcription reaction, contaminated DNA in total RNA of various stages of flower senescence was eliminated using deoxyribonuclease I (DNasel, RNase-free, Fermentus, Canada). For reverse transcription reaction, first strand cDNA was reverse transcribed from DNase-treated RNA of *Dendrobium* using M-MLV reverse Transcription System Kit (Promega, USA). The first strand cDNA was further used as a template in the PCR reaction or stored at -20°C until further use.

Cloning of Partial cDNA Fragment Encoding for Den-ETR1 and Den-ACS Genes

A pair of forward and reverse primers of ethylene receptor gene (ETR1) was designed from the sequence of 623 bp of *Dendrobium* hybrid cultivar (GenBank Accession number: AY746972). ACC synthase gene was designed from the sequence of 1678 bp of *Dendrobium crumenatum* (GenBank Accession number: DCU64031). The products from PCR reaction of Den-ETR1 and Den-ACS cDNA fragments were 212 and 197 bp, respectively. After cloning and sequencing, their sequences were blasted in NCBI and it was found that these nucleotide sequences were cDNA fragment encoding for ethylene receptor and ACC synthase. A new pair of specific primers for the gene encoded for ethylene receptor and ACC synthase genes of *Dendrobium* ‘Khao Sanan’ Den-ETR1 (accession number EU152212), Den-ACS (accession number EU152213) were designed. While Den-ACO primer was obtained from Ms. Bhunchot (BIOTEC, Thailand). A pair of forward and reverse primers of these three genes were used for semi-quantitative RT-PCR are described as Table 1.

Semi-Quantitative RT-PCR

Gene expression of senescence-related genes by semi-quantitative RT-PCR method was performed. The 159, 151 and 820 bp cDNA fragments encoding ETR1, ACS, and ACO genes, respectively were amplified. The PCR condition was set as follows: preheated at 94°C for 2 min, followed by 40 cycles for ETR1 and ACS and 30 cycles for ACO, a denaturing temperature set at 94°C for 30 sec (but 45 sec for ACO primers), annealing temperature at 55, 58 and 53°C for ETR1, ACS and ACO, respectively. The reaction was terminated with a final extension at 72°C for 10 min. The PCR machine was operating at 100 volts for 25 min. After finishing electrophoresis, the gel was stained in 2.5 µg mL-1 ethidium bromide (EtBr) solution for 15 min. The RNA bands were visualized under UV transilluminator and photographed by SYNGENE BIO IMAGINE Gel Documentation. For 18S rRNA used as control, the PCR conditions was set as followed: preheated at 94°C for 2 min, followed by 24 cycles of denaturing temperature at 94°C for 30 sec, annealing temperature of 18S rRNA primers at 55°C for 30 sec and extension temperature at 72°C for 30 sec.

Statistical Analysis

The experiment of time to senescence and senescence scoring after treatment were conducted at 10 replications. Three replicates were used per treatment in the measurement of ethylene production. Where possible, the means between treatments were compared after calculating the LSD. All experiments were repeated at least once at a later date, with very similar results.

Table 1 Oligonucleotide primers of *Dendrobium* flowers.

<table>
<thead>
<tr>
<th>Name</th>
<th>Oligonucleotide primer</th>
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<tr>
<td><strong>Den-ETR1</strong></td>
<td>Forward 5’&gt;TGTGCCATCGGAGATGAGAA&lt;3’</td>
</tr>
<tr>
<td></td>
<td>Reverse 5’TGGGATGGGGTAGAACTCTGG&lt;3’</td>
</tr>
<tr>
<td><strong>Den-ACS</strong></td>
<td>Forward 5’&gt;CAACCTGTTCAGAACAAGCAC&lt;3’</td>
</tr>
<tr>
<td></td>
<td>Reverse 5’&gt;GGGAAGCTTGAGATTGTCG&lt;3’</td>
</tr>
<tr>
<td><strong>Den-ACO</strong></td>
<td>Forward 5’&gt;ATGGAGCTTCTTGGTAGG&lt;3’</td>
</tr>
<tr>
<td></td>
<td>Reverse 5’&gt;TCAAGCAGTAGGAGATCGCGT&lt;3’</td>
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Results

Visible Symptoms during Flower Senescence after Ethylene and AOA Treatment

Intact flowers of *Dendrobium* ‘Khao Sanan’ were treated with- and without AOA solution to compare senescence symptoms treated- and untreated-ethylene. It was found that the score of senescence symptoms of all treatments increased when the time advanced, especially in flowers treated with ethylene alone. The suitable concentration, 0.5 mM of AOA was chosen from the preliminary experiment to study effect on ethylene synthesis and four treatments comprised untreated, 0.4 mL L⁻¹ C₂H₄, 0.5 mM AOA and 0.5 mM AOA + 0.4 mL L⁻¹ C₂H₄ (data not shown). Vase life of the control flowers was 13 days while vase life of flowers treated with AOA and AOA plus ethylene was about 9 days (Table 2). Flowers senesced 5 days after ethylene treatment while senescence scores of untreated flowers, AOA alone or AOA plus ethylene treatment were about 2, 2 and 3 scores, respectively (Figure 1).

The Effect of Ethylene and AOA Treatment on Ethylene Production

Ethylene production by intact flowers increased rapidly after ethylene treatment as monitored over 5 days (1.8 nL C₂H₄ g⁻¹ h⁻¹) while there was no significant difference in ethylene production among other treatments (Figure 2A). Changes in ethylene production in all treatments of isolated perianths fluctuated but they were no significant differences (Figure 2B). Ethylene production by isolated columns after ethylene treatment peaked on day 3 (32.7 nL C₂H₄ g⁻¹ h⁻¹, Figure 2C) while ethylene production of control column occurred later and reached a maximum on day 4 (12.2 nL C₂H₄ g⁻¹ h⁻¹, Figure 2C).

Expression of Ethylene Receptor and Ethylene Biosynthesis Genes in Ethylene-Induced Senescence of *Dendrobium* Flowers

Figure 3A shows the transcription of mRNA in perianth organs. The transcript of *Den-ETR1* gene expressed in all treatments but the higher expression was found in ethylene treatment. Expression of *Den-ACS* gene was found only in ethylene treatment while there had no expression of *Den-ACS* in control.

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**Figure 1** Effect of ethylene and AOA on senescence symptoms (scores) of *Dendrobium* ‘Khao Sanan’ flowers. Flowers were treated with dH₂O (●), 0.4 mL L⁻¹ ethylene (○), 0.5 mM AOA (▲), 0.5 mM AOA + 0.4 mL L⁻¹ ethylene (Δ). Means are the average of 3 replications.

**Figure 2** Effect of exogenous ethylene and AOA on ethylene production of *Dendrobium* ‘Khao Sanan’ of intact flowers (A), isolated perianth (B), and isolated column (C). Flowers were treated with dH₂O (●), 0.4 mL L⁻¹ ethylene (○), 0.5 mM AOA (▲), and 0.5 mM AOA + 0.4 mL L⁻¹ ethylene (Δ). Means are the average of 3 replications.
Table 2 Effect of ethylene and AOA on time to senescence of Dendrobium ‘Khao Sanan’ flowers. Results are means of 10 replicates ± se.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Time to senescence (day)</th>
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<tbody>
<tr>
<td>Distilled water</td>
<td>13.4 ± 0.3</td>
</tr>
<tr>
<td>0.4 µL L⁻¹ Ethylene</td>
<td>5.0 ± 0.4</td>
</tr>
<tr>
<td>0.5 mM AOA</td>
<td>9.6 ± 0.5</td>
</tr>
<tr>
<td>0.5 mM AOA + 0.4 µL L⁻¹ ethylene</td>
<td>9.2 ± 0.5</td>
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AOA and AOA+ethylene treatment. The Den-ACO mRNA of ethylene treatment expressed throughout experimentation and a maximum transcription occurred on day 5. Den-ACO of control and AOA treatment had no expression while Den-ACO of AOA+ethylene treatment occurred on day 2 and day 5.

Gene expression in columns is shown in Figure 3B. Den-ETR1 gene in ethylene-treated column expressed throughout 5 days while the expression only occurred at the end in control. Moreover, the little abundance of Den-ETR1 expression of AOA and AOA+ethylene occurred on day 2. The expression of Den-ACS of ethylene, AOA and AOA prior ethylene treatment was found at the end of experiment that the mRNA transcript in ethylene treatment was higher than other treatments. There was no expression of Den-ACS in untreated columns. The transcription of Den-ACO was found in ethylene-treated column on day 2 and 5 while the low amount of Den-ACO expression of AOA and AOA prior to ethylene treatment was found on day 5.

Figure 3 Expression of Den-ETR1 (30 cycles), Den-ACS (40 cycles) and Den-ACO (30 cycles) of Dendribium ‘Khao Sanan’ flowers. Semi-quantitative RT-PCR analysis was performed in perianths (A) and columns (B). Total RNA extracted from petals and columns after treatment of control (lane 1-4), 0.4 µL L⁻¹ ethylene (lane 5-7), 0.5 mM AOA (lane 8-10), or 0.5 mM AOA prior 0.4 µL L⁻¹ ethylene (lane 11-13) on day 0, day 1, day 2 and day 5 for controls and day 1,2 and 5 for the rest.
Discussion

Ethylene treatment induced premature senescence of *Dendrobium* ‘Khao Sanan’ flowers. Orchid flowers exhibited visible symptoms including venation, wilting, drooping, yellowing, water soaking (Figure 1) and burst of ethylene production (Figure 2) following ethylene treatment. This indicates that *Dendrobium* ‘Khao Sanan’ is sensitive to ethylene similar to other cultivars of *Dendrobium* flowers (Ketsa et al., 2006) and other flowers including carnation (Nukui et al., 2004), Phalaenopsis (O’Neil, 1998), Cymbidium (Woltering, 1990), daffodil (Hunter et al., 2004), and petunia (Holden et al., 2003). It was our interest to find out whether endogenous or exogenous ethylene plays an important role in inducing senescence of *Dendrobium* ‘Khao Sanan’ flowers.

The activity of ACC synthase, the rate-limiting step of ethylene biosynthesis, is markedly reduced by inhibitors of pyridoxal phosphate enzymes, such as aminooxyacetic acid or AOA (Reid and Wu, 1992). Therefore, we applied AOA in holding solution for 18 h prior to ethylene exposure. After treatment, AOA pretreatment delayed time to senescence of ethylene-treated flowers for 5 days (Table 1), this related to senescence symptoms of *Dendrobium* ‘Khao Sanan’ was inhibited by AOA in flowers with ethylene about 60%. While AOA alone did not delay senescence when compared with control flowers (Table 1). Similarly, Rattana-wisalanon et al. (2003) found that AOA pretreatment did not delay senescence in *Dendrobium* ‘Jew Yuay Tew’ flowers. They also reported that AOA either has no effect on the time to wilting, or is toxic and therefore hastens wilting. This present results clearly confirmed that AOA only delayed senescence in ethylene-treated *Dendrobium* flowers.

The effect on time to senescence may also relate to a reduction of ethylene synthesis by AOA, but if such an effect is present it only shows when AOA is treated prior to ethylene. In the present study we observed ethylene production in *Dendrobium* flowers after ethylene treatment. Ethylene production in the flowers and the perianth was detected at the basal levels and there was no significant difference among treatments (Figures 2A and 2B) while a large of ethylene production was found in the isolated column treated with 0.4 mL L⁻¹ C₂H₄ (Figure 3C). Interestingly, ethylene production in columns was much more than that in perianth after ethylene exposure. The burst of ethylene production in ethylene-treated column after day 2 was higher than that of the control and reached 300 folds. The column has been reported to be the primary source of ethylene induced premature senescence of orchid flowers (Arditti et al., 1973) as in the case of carnation flowers (Jones and Woodson, 1997). This increase in ethylene production was also prevented by treatment with AOA in both columns with and without ethylene, but there was no significant difference in ethylene production of control, AOA-treated and AOA+ethylene-treated columns. A large LSD (least significant difference) in Figure 2B may be due to the differences among a large ethylene production in ethylene treatment and the rest treatments. If we only mentions about those three treatments, the result may show the effect of AOA in both columns with and without ethylene on low ethylene production which differed from control treatment.

Endogenous ethylene has been reported to be a signal to induce senescence of flowers (O’Neil et al., 1993). It may be possible that exogenous ethylene induced autocatalytic ethylene production system in orchid flowers, which in turn, endogenous ethylene involved in premature floral senescence of ethylene-treated *Dendrobium* flowers. In the other word, both endogenous and exogenous ethylene regulate senescence of *Dendrobium* flowers. That exogenous ethylene induces autocatalytic ethylene production has been reported in carnation (Nukui et al., 2004) and petunia (Jones et al., 2005). In addition, autocatalytic ethylene production system of *Dendrobium* flowers was similar to climacteric fruits during ripening (Lelievre et al., 2002; Inaba, 2007). Woltering and van Doorn (1998) classified petal senescence of *Dendrobium* species into Type I, wilting apparently mediate by ethylene and Type I is generally accelerated by exogenous ethylene. While two systems of ethylene regulation have been proposed to operate in fruits (Inaba, 2002). However, ripening of climacteric fruit was classified into System 2 that ethylene is produced during climacteric fruit ripening and flower senescence, is the autocatalytic system or positive feedback, when the rate of ethylene production is greatly increased and can be further accelerated by exogenous ethylene.
(Chang et al., 2008). This indicated that exogenous ethylene induced premature senescence of orchid flowers mediated partially via endogenous ethylene.

Since, ethylene directly causes the senescence of ethylene-sensitive flowers, most study of gene expression focus on ethylene receptor and biosynthetic genes. From the results, Den-ETR1 gene in perianths was expressed in all treatments but was most highly expressed after ethylene treatment (Figure 3A). Expression of Den-ETR1 in ethylene-treated columns occurred throughout 5 days but was only expressed on day 5 in control columns (Figure 3B). In Delphinium flowers, ethylene exposure differently regulated the transcription of ethylene receptor genes during senescence (Tanase and Ichimura, 2005). Exogenous ethylene increased transcript levels of DI-ERS-1-3 and DI-ERS2 in sepal, but not in gynoeica and receptacles, which produced ethylene (Tanase and Ichimura, 2005). These genes are responsible for ethylene perception (Arora, 2005). The result confirmed that endogenous ethylene up-regulated Den-ETR1 gene expression in senescence of Dendrobium flowers (Figure 3). Lawton et al. (1989) reported that AOA virtually eliminates the accumulation of at least two classes of mRNAs are expressed at higher levels during senescence of carnation petals. Our result showed that AOA pretreatment delayed senescence and also inhibited the transcription of Den-ETR1. However, no experiments were done with AOA treatment on the expression of ethylene receptor gene(s) in floral senescence. Even though AOA is an inhibitor of ethylene biosynthesis, but we expected that AOA may inhibit autocatalytic ethylene production through reduction of ACS activity resulted in less endogenous ethylene to induce premature senescence. However, blocking ethylene effects at the receptor level is more effective as it will protect against both endogenous and exogenous ethylene (Serek and Reid, 1993).

Based on the results of gene expression, Den-ACS in column and Den-ACO in both organs showed to be positively regulated by endogenous and exogenous ethylene (Figure 3B). Similarly, in carnations, autocatalytic ethylene production was regulated by the expression of DC-ACS and DC-ACO and which also induced in-rolling of petals (Jones and Woodson, 1999; Kosugi et al., 2000; Sugawara et al., 2002). The expression of Den-ACS gene in petals was only found in ethylene treatment and less expression in AOA + ethylene treatment while there had no expression in the rest of treatments. This expression accompanied with ethylene production and senescence of flowers. So we concluded that Den-ACS and Den-ACO involved in autocatalytic system of flower senescence of Dendrobium.

AOA delayed time to senescence in flowers induced premature senescence by exogenous ethylene. It was found that the time to senescence of flower treated with AOA alone was not longer than untreated flowers (Table 1). This may be explained by molecular level. Even though AOA had an effect to decrease the expression of ethylene biosynthetic genes, but Den-ACS gene in column and Den-ACO in both organs were also expressed on day 5 (Figure 3B). Normally, the accumulation of senescence-related mRNAs in presenescent flowers that have been exposed to ethylene occurred before the development of any visible symptoms of senescence (Buchanan-Wollaston, 1997). In addition, this time to senescence of flowers was not delayed to the expected level with respect to suppression of the expression of the ACC synthase and ACC oxidase genes, suggesting an involvement of a negatively regulated gene(s) in ethylene biosynthesis in Dendrobium flowers. After AOA + ethylene treatment, however, Den-ACS in columns and Den-ACO in both organs (AOA would decrease ACS and possibly ACO transcripts if it is an effective C2H4 inhibitor) were also expressed. This expression may explain by the hypothesis described as Den-ACS and Den-ACO genes responded to AOA as negative feedback. The pattern of ethylene-sensitive flowers response to ethylene consisted of positive (as described before) or negative feedback. For negative feedback or system1, is functional during normal vegetative growth and rate of ethylene production is low and is inhibited by exogenous ethylene. In ethylene-treated flowers, ethylene biosynthesis is regulated (positive feedback), which in turn inhibited ethylene production itself (negative feedback) (Nakatsuka et al. 1998). Using MCP, an ethylene action inhibitor, Nakatsuka et al. (1998) previously demonstrated that the expression of the LE-ACS genes in ripening tomato fruits is highly regulated through a positive feedback mechanism. They suggested that possible existence of a gene(s) under negative feedback
regulation, because the inhibitory effects of MCP on the expression of genes were not correlated with those on ethylene biosynthesis. Therefore, in a case for Dendrobium flowers, the three genes that response to ethylene may be expressed later as negative feedback, even though the flowers treated with an inhibitor of ethylene biosynthesis and result in flower senescence finally.

Conclusions

Exogenous ethylene induced premature senescence of Dendrobium flowers. The burst of ethylene production after ethylene treatment related to the transcription of genes in ethylene signaling and biosynthesis. AOA pretreatment delayed senescence and inhibited the transcription of Den-ETR1, Den-ACS and Den-ACO genes of Dendrobium ‘Khao Sanan’ with- and without ethylene treatment. It is concluded that endogenous ethylene induced system of autocatalytic ethylene production resulting in premature senescence in Dendrobium flowers.

Acknowledgments

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References


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