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STRESS-INDUCED ETHYLENE PRODUCTION IN FLOWER PARTS OF CUT CARNATION FLOWERS CV. LIGHT PINK TASMAN

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Summary. Ethylene is a plant hormone with endogenous production associated with the process of senescence for a number of cut flowers. Different stressogenic factors, including signals such as pollination, exogenous ethylene and auxins have been found to be associated with the increase in ethylene emission and a specific tissue response has been documented. The present study was undertaken with the aim to investigate the role of external stress stimuli such as wounding and desiccation and the effect of IAA, NAA and 2,4-D and ethylene treatments on ethylene evolution of separated carnation flower parts. The experiments were conducted with cut carnation flowers (*Dianthus caryophyllus* L.) cv. Light Pink Tasman harvested in commercial maturity. Two groups of flowers were used: "A" – STS and non-STS pretreated. The flower heads were excised and dissembled to petals, ovaries and styles and young leaves from cuttings were taken. Ethylene production was measured by GC. The results showed that the reaction of component flower parts differed depending on the treatment used: wounding and desiccation accelerated the ethylene production in ovaries and styles; ethylene exposure resulted in enchanced ethylene emission of petals and auxin induced remarkable amount of ethylene released from leaves.

Key words: auxin, carnation, desiccation, ethylene, wounding

Abbreviations: ACC – 1-aminocyclopropane-1-carboxylic acid, ACC oxidase – oxidase of 1-aminocyclopropane-1-carboxylic acid, ACC synthase –

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synthase of 1-aminocyclopropane-1-carboxylic acid, 2,4-D – dichlorophenoxyacetic acid, FW – fresh weight, IAA – 3-indolylacetic acid, MACC – malonyl- aminocyclopropane-1-carboxylic acid, NAA-1-naphtaleneacetic acid, STS – silver thiosulphate

Introduction

Ethylene is a plant hormone the endogenous production of which is associated with the process of senescence (Abeles,1973; Lieberman,1979; Woodson et al., 1993) and a dramatic increase of the amount released has been well established in accordance with the wilting of a number of cut flowers (Nichols, 1980; Halevy and Mayak, 1981; Woltering and van Doorn, 1988). The biosynthetic rate changes depending on the stage of development and the hormonal status of tissues (Yang and Hoffman, 1984). Ethylene is involved in the response of flowers and fruits to different stresses leading to a significant rise of the production (Mattoo and Suttle, 1991). Induced increase of the level of endogenous ethylene has been observed to be caused by stressogenic factors: mechanical wounding (Hanson and Kende, 1976; Nichols, 1977; Boller and Kende, 1980; Yu and Yang, 1980; Hyodo et al., 1983), extreme temperatures, water loss, drought, chemical treatments, diseases, radiation (Woodson et al., 1992). Other factors such as pollination, exogenous ethylene and auxin treatments have been found to be associated with the increase in ethylene emission and a specific tissue response has been documented (Yoshii and Imaseki, 1981). An acceleration of ethylene evolution of isolated carnation petals has been shown to appear as a reaction to treatments with ethylene and ACC (Overbeek and Woltering, 1990). In contrast to petals, ethylene has been observed to suppress ethylene production in leaves while auxins induce it in vegetative tissues (Yang and Hoffmann, 1984). Ethylene production of carnation petals (Nichols, 1980; Sacalis and Nichols, 1980; Wulster et al., 1982) and orchid ovary development (O'Neill et al., 1993; Zhang and O'Neill, 1993) have been documented to be stimulated by auxins – exogenously applied IAA, 2,4-D and NAA or transferred by the pollen through the styles following the pollination of orchids.

According to the model of Larsen et al. (1993) ethylene production is regulated by different inducers in each flower organ. The growth of the pollen tube is a sort of physical wounding of stylar tissue and it has been supposed that mechanical damage could act in a manner similar to pollination (Hoekstra and Weges, 1986). As pollen tube penetration is a wounding factor, wound-induced ethylene might be one of the early events after pollination (Gilissen and Hoekstra, 1984).

The petal senescence rate in cut flowers is strongly dependant on temperature and on environmental water parameters (Halevy and Mayak, 1981). Exposure of flowers to drought leads to an earlier appearance of senescence symptoms (Borochov and Woodson, 1989). In carnations water stress is accompanied by accumulation of ACC

(Borochov et al., 1982). There are still relatively limited data concerning the ethylene production of component flower parts in accordance to desiccation and the mechanism in which the water loss affects directly the ethylene production of petals, ovaries, styles and leaves is not yet well known.

The present study was undertaken with the aim to assess the role of external stress stimuli such as wounding and desiccation and the effect of auxin and ethylene treatments on ethylene evolution of separated carnation flower parts. Specific tissue behaviour of petal, ovary, style and leave response to the factors applied is discussed.

Material and Methods

Material and treatments

The experiments were conducted at the Agrotechnological Research Institute, Wageningen, The Netherlands. Carnation flowers (*Dianthus caryophyllus* L.) cv. Light Pink Tasman were harvested in commercial maturity. The flower stems were recut to 40 cm length and the leaves on the lowest positions removed. Two groups of flowers, simultaneously harvested, were used for the experiments: "A" – placed in distilled water overnight, and "B" – pre-treated with 0.2 mM STS for 16 hours and than transferred into water for another 24 hours. The flowers were kept at controlled environmental conditions in Qualitron – temperature 20 °C, RH 60% and 12 hours white light (15 $\mu mol.m^{-2}.s^{-1}$). STS-pre-treatment was provided to suppress the autocatalytically induced ethylene production. STS solution was prepared as described by Veen (1979).

The flower heads were excised and dissembled to petals (from the outer whorls), ovaries and styles and second pair of leaves from cuttings were taken. Flower parts were collected from 160 flowers and average samples were treated as described below. All the experiments were conducted twice with two flower parts per every individual sample in the treatment in four replicates each. The data presented are means from one of the replicated experiments or mean value of 8 flower parts. Data were processed statistically using Genstat computer packaging and the significance was evaluated by LSD at $p \leq 0.05$.

Wounding

Petals, ovaries, styles and leaves were damaged by crushing and placed in $33.10^{-6}\,m^{-3}$ vials, containing 0.5 ml distilled water. The amount of water was considered as optimal for preventing desiccation and for avoiding an extra leakage of electrolytes from wounded tissues. After 1, 2.5, 4, 5.5, 7 and 18 hours the ethylene production was measured.

Desiccation

For desiccation the separated flower parts were left in Petry dishes on the table in the laboratory at temperature 21–22 °C and 26–34% RH of the air for a certain period of time (1, 2, 4, 6, and 18 hours). The effect of desiccation on fresh weight was registered by measuring the weight of flower parts immediately before and after the exposure for desiccation and expressed in percentage loss of the weight to the initial one.

Auxin treatment

The natural auxin IAA and two synthetic homologues NAA and 2,4-D were applied. Ovaries and styles were soaked and cut ends of petals and leaves placed in solution of IAA in concentration 5.10^{-4} M, 5.10^{-5} M and 5.10^{-6} M; 5.10^{-4} M NAA and 5.10^{-4} M 2,4-D for 1, 2, 3 and 19 hours respectively and also at 4, 22 and 46 hours intervals. Auxin solutions were prepared by desolving auxins first in 0.5 ml 70% ethanol and than diluted to final volume. Control flower parts were held in distilled water containing an amount of ethanol equal to the auxin solution.

Ethylene treatment

The effect of ethylene was examined by treating the excised and placed in water flower parts in 70 l stainless containers with 10 µl/l ethylene at 21 °C in darkness for 2, 10, 14, 18 and 24 hours incubation. Parallel controls were enclosed in an empty container with Ethysorb (aluminium oxide coated with $KMnO_4$). To discard the ethylene desolved in the water or collected in intracellular spaces of ovaries during ethylene treatment after its completion, the flower parts were transferred into vials with clean water and left open for 40 min before closing for 1 hour. In this case only non-STS pre-treated flowers were analysed.

Ethylene measurement

For the purpose of measuring ethylene production after the relevant duration of the treatment, two petals, ovaries, styles or leaves were enclosed in 33.10^{-6} m^{-3} glass vials for 1 hour and 3 ml gas sample from the head space was withdrawn for analysing. The amount of ethylene was determined by gas chromatography: gas chromatograph, Intersmat, Pavillion du Bois, France equipped with a stainless steel column filled with Aluminia GC (Chompack, Middelburg, The Netherlands) and a flame ionisation detector. Apparently, the ethylene production of IAA, NAA and 2,4-D continuously treated leaves was measured by GC flow through-system within 46 hours period.

Results

Flowers used in experiments were harvested at pre-senescent phase of development. The level of ethylene at zero time – immediately after the excision of the flower parts was low 0–5 nl ethylene per gram FW for styles and ovaries and no ethylene production was found in petals and leaves. An exception was registered for unwounded ovary controls. They produced a rise of ethylene released following the same tendency as that of wounded ovaries (Fig. 1). Almost the same rate of ethylene production was found in 2 and 4 hours desiccated ovaries (Fig. 3). No significant difference was observed between petal, ovary, style and leave controls kept in water and in water containing small amount of ethanol in auxin experiments which gave us a reason to exclude the effect of ethanol on ethylene production in further discussion of the results.

Wounding of ovaries and styles resulted in obvious increase in ethylene production 1 hour after the treatment. Well pronounced response was registered after 2.5 hours for both ovaries (Fig. 1) and styles (Fig. 2) and the styles showed a peak of the production that appeared earlier than that in ovaries. Maximum ethylene emission was monitored in ovaries after 5.5 hours. Following the peaks ethylene level stayed high by the 7th hour and evident decrease was observed 18 hours after crushing. No detectable effect of wounding on ethylene evolution of petals was measured. Slight ethylene production was registered in STS pre-treated and wounded leaves while unwounded STS leaves did not show such a response.

The relationship between ethylene production and desiccation was studied by separate measurements at intervals within 19 hours. The desiccation enhanced ethylene production of ovaries and styles. The rate of ethylene appeared to be lower of STS

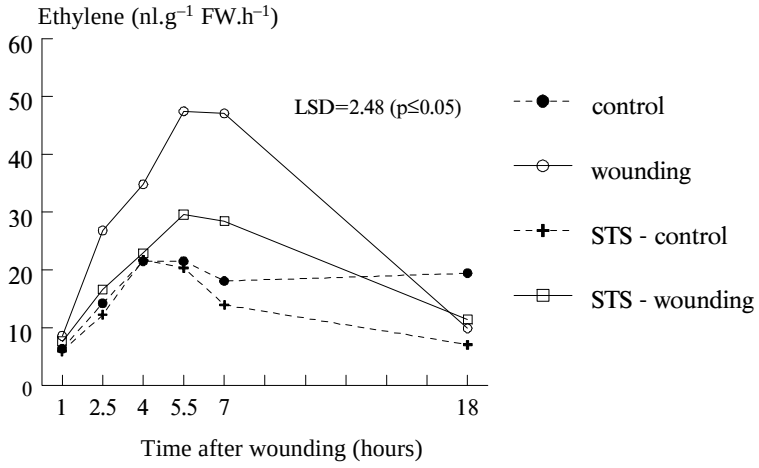

Fig. 1. Wound-induced ethylene production in isolated ovaries of cut carnation (*D. caryophyllus* L.) flowers, cv. Light Pink Tasman

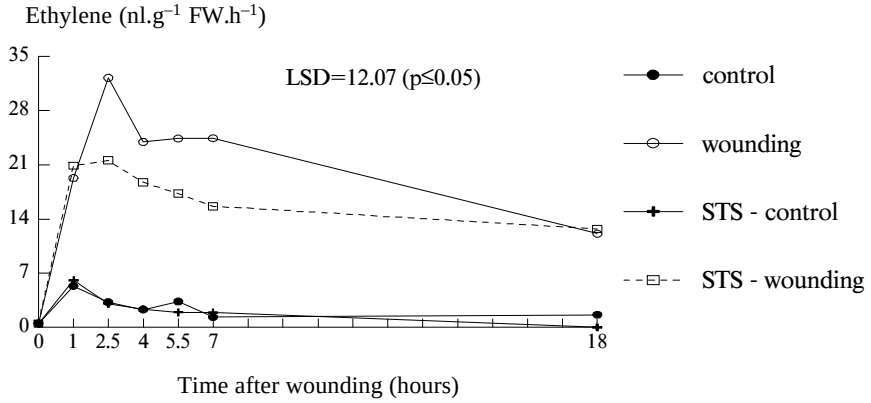

Fig. 2. Wound-induced ethylene production in isolated styles of cut carnation (*D. caryophyllus* L.) flowers, cv. Light Pink Tasman

ovaries and styles after 6 hours desiccation (Fig. 3, 4). Desiccated leaves did not react very clearly to desiccation. They released some level of ethylene but the effect was not well pronounced. Petals did not respond to desiccation. The measurements of percentage loss of water showed that the reduction in leave and petal fresh weight was less than that in styles and ovaries for the same duration of experiments. When the results of each individual ethylene measurements were compared to the percentage of weight loss the data showed a tendency of stimulated ethylene production in ovaries and styles concomitant to the rate of desiccation (Table 1).

Leaves were the only isolated part in which auxin treatment resulted in accelerated ethylene production within 46 hours treatment with IAA, NAA and 2,4-D. Rapid

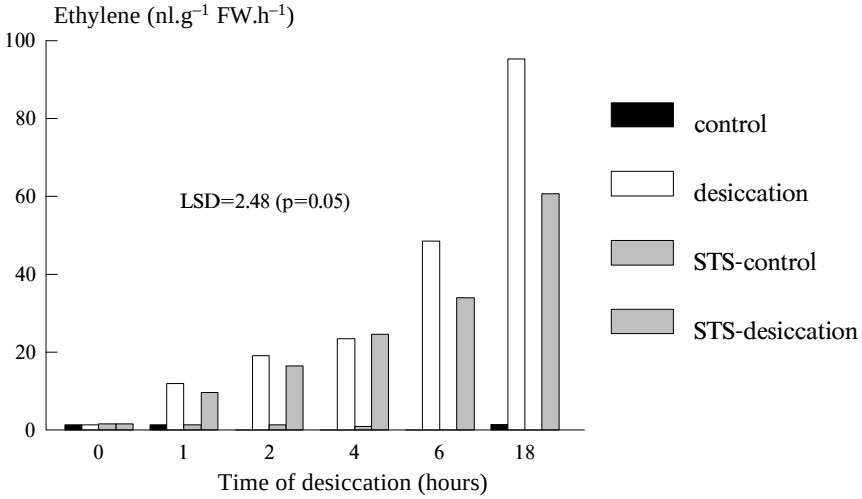

Fig. 3. Effect of desiccation on ethylene production in isolated ovaries of cut carnation (*D. caryophyllus* L.) flowers, cv. Light Pink Tasman

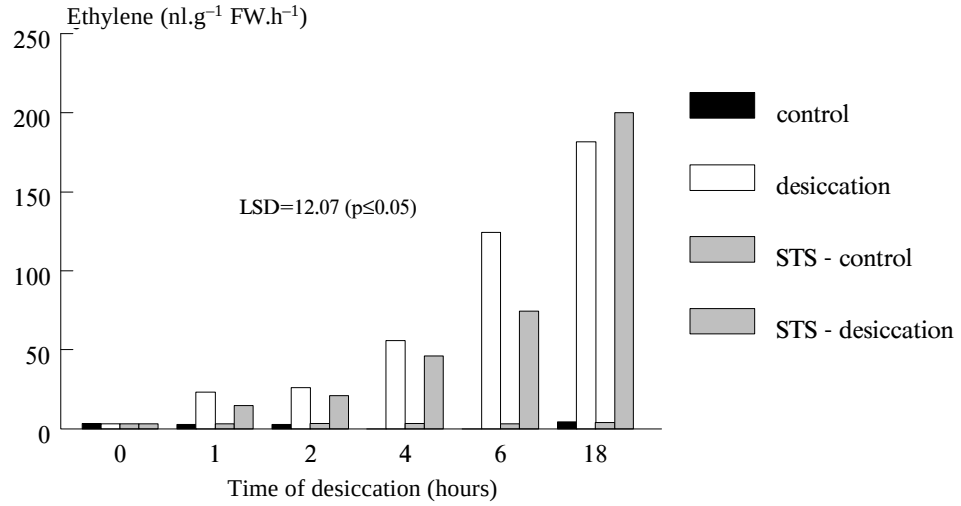

Fig. 4. Effect of desiccation on ethylene production in isolated styles of cut carnation (*D. caryophyllus* L.) flowers, cv. Light Pink Tasman

Table 1. Effect of desiccation on ethylene production in isolated styles and ovaries of cut carnation (*D. caryophyllus* L.) flowers, cv. Light Pink Tasman

Styles Loss of FW (%)	Ethylene (nl. g^{-1} FW. h^{-1})	Ovaries Loss of FW (%)	Ethylene (nl. g^{-1} FW. h^{-1})	Time of desiccation (hours)
0	3.2	0	1.5	0
11.2	18.6	8.7	13.5	1
11.7	30.1	9.6	14.0	1
12.1	21.5	10.6	11.7	1
15.3	25.3	14.2	19.7	2
16.4	30.8	14.8	12.5	2
16.5	23.4	15.5	24.6	2
18.2	35.1	16.3	19.4	3
19.2	28.7	17.0	16.2	3
19.9	30.0	18.4	19.9	3
23.6	67.0	20.2	25.4	4
24.2	51.3	23.0	17.4	4
28.0	55.2	24.5	32.9	4
38.8	148.9	37.6	33.1	6
45.4	149.2	37.7	24.7	6
52.8	134.6	49.8	68.7	6
56.2	260.1	60.0	98.6	18
64.4	133.6	60.0	111.7	18
66.0	152.0	62.5	82.8	18

Data of individual ethylene measurements are ploted as data points against the percentage of fresh weight loss

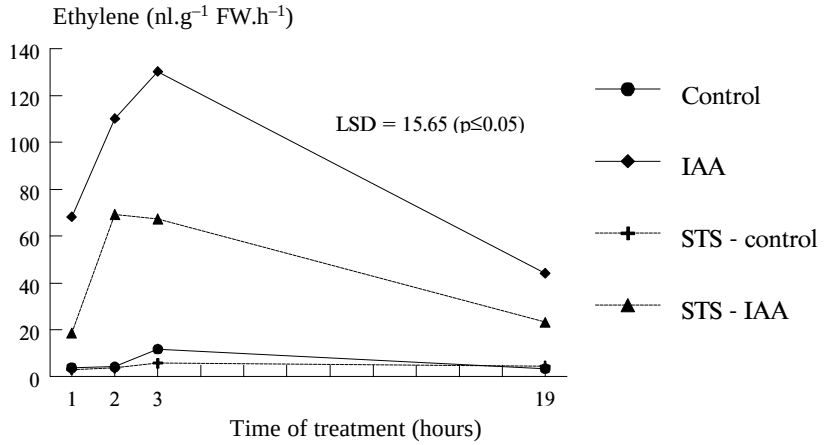

Fig. 5. Effect of 5.10^{-4} M IAA on ethylene production in excised leaves of cut carnation (*D. caryophyllus* L.), flowers, cv. Light Pink Tasman

increase of ethylene production was observed 1 hour after placing the leaves in auxin solutions for both STS and non STS pre-treated leaves as the rate of ethylene production was almost twice lower for STS pre-treated leaves (Fig. 5). When treatments with 5.10^{-4} M, 5.10^{-5} M and 5.10^{-6} M IAA were applied a rise of ethylene production measured at intervals appeared after 4 hours. Less ethylene (2.5–4 times) was emitted after 22 hours in same solutions. A decrease was monitored after 45 hours. Similar dynamic was pronounced when leaves were held in 5.10^{-4} M 2,4-D. The treatments with 5.10^{-4} M NAA stimulated same level of ethylene after 4 and 22 hours and the ethylene production declined after 46 hours (Fig. 6).

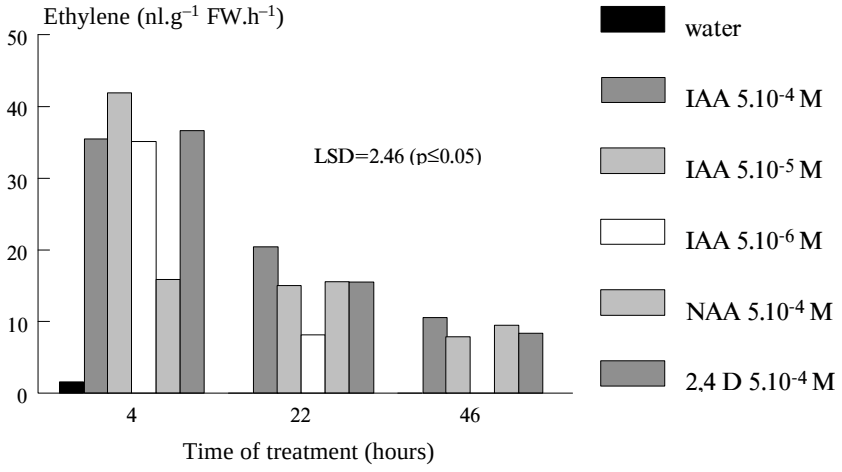

Fig. 6. Effect of auxins on ethylene production in excised leaves of cut carnation (*D. caryophyllus* L.) flowers, cv. Light Pink Tasman

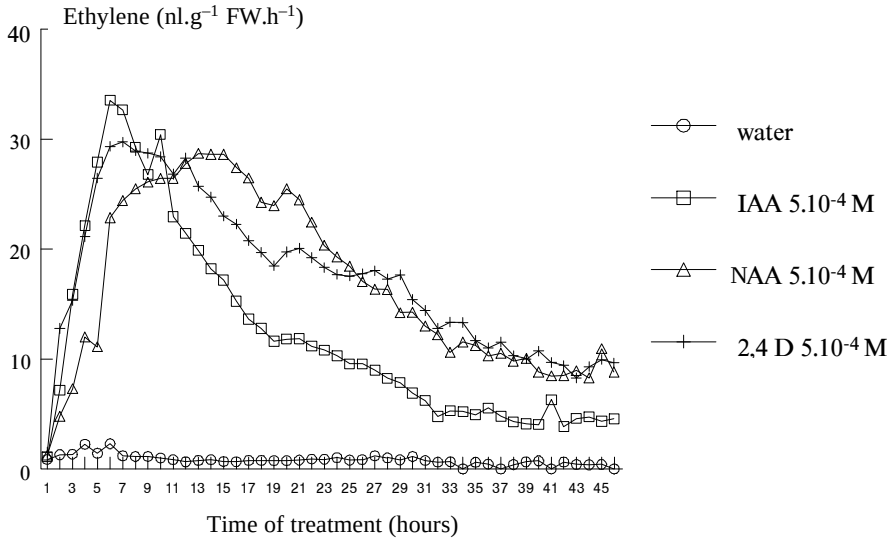

Fig. 7. Auxin-induced ethylene production in isolated leaves of cut carnation (*D. caryophyllus* L.) flowers, cv. Light Pink Tasman. The amount of ethylene was measured by GC flow-trough system

Measurement of ethylene amount by flow through system confirmed the dynamic established in previous experiments with separated measurements. Peaks of ethylene production of IAA treatment were observed on the 6th hour and on the 7th hour for 2,4-D which stayed high till the 12th hour. Induction of ethylene production by NAA appeared later – after 13 hours and the expressed duration of ethylene evolu-

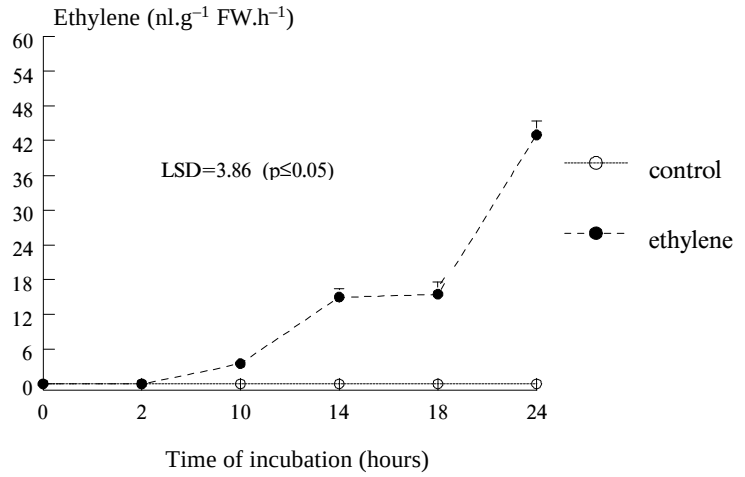

Fig. 8. Effect of exposure in 10 µl/l ethylene on ethylene production in excised petals of cut carnation flowers (*D. caryophyllus* L.), cv. Light Pink Tasman

tion lasted for about three further hours (Fig. 7). No response was exhibited by ovaries and styles to any of above auxins and concentrations applied. In contrast, petals did not react to auxin treatment with 5.10^{-4} M IAA but when IAA in concentrations 5.10^{-5} M and 5.10^{-6} M was used well detectable increase of ethylene production was registered 46 hours after placement in the solutions. Treatments with 5.10^{-4} M NAA and 5.10^{-4} M 2,4-D produced no effect on ethylene evolution of petals (data not presented).

The expectation that ethylene treatment would induce ethylene production in all flower parts was not confirmed in our experiments. Dramatic increase of ethylene amount was established only in petals (Fig. 8). They exhibited a rise starting 10 hours after the treatment with 10 µl/l ethylene. From 14 to 18 hours the level of ethylene production stayed almost constant. Remarkable stimulation of ethylene emission was measured after 24 hours in ethylene atmosphere. No response was observed in ethylene treated leaves, styles and ovaries.

Discussion

Significant experimental data and hypotheses have been reported by now but the mechanism of initiation the biosynthesis of stress ethylene in cut flowers is still insufficiently studied. Taken together the estimated facts have shown possibly different regulation of ethylene synthesis in the tissues of isolated flower parts resulting as an effect of different external stimuli. Looking for a clearance of mechanisms in which stress-factors such as wounding and desiccation and exogenous plant growth regulators (auxin and ethylene) influence the biosynthetic steps in ethylene pathway we investigated the response of separated carnation petals, ovaries, styles and leaves to the above factors on the level of ethylene production.

In this study we found that the reaction of component flower parts differed depending on the treatment used. The results of measuring ethylene production assessed that wounding and desiccation accelerated ethylene production in ovary and style; ethylene exposure reflected in enchanced ethylene emission of petals and auxin induced remarkable amount of ethylene released from leaves. The rise in ethylene production in petals in response to auxin was observed to appear only in case when IAA in concentrations 5.10^{-5} M and 5.10^{-6} M was applied.

Increased ethylene production due to physical stress deteriorates the post-harvest quality and accelerates the senescence process of cut flowers (Yang and Hoffman, 1984). Very often desiccation also unfavourably affects storage life and diminishes ornamental value. It is well known that high concentrations of exogenous ethylene promote the synthesis of endogenous ethylene and trigger to an early senescence of cut carnations (Nichols, 1980; Halevy and Mayak, 1981; Overbeek and Woltering, 1990; Woodson et al., 1993; Henskens et al., 1994). The formation of endogenous

ethylene has been established to occur also in response to application of auxins (Burg and Burg, 1966; Nichols, 1971; Sacalis and Nichols, 1980; Wulster et al., 1982). Increased synthesis of ethylene in petals has been supposed to be due to action of auxin transferred from other floral organs (Bufler et al., 1980). Our results were concomitant with the findings that auxin enhances the ethylene production in leaves (Yu and Yang, 1979; Yang and Hoffman, 1984). The stimulation of ethylene evolution in ovary and style by wound- and water-stress (desiccation) and a lack of response in petals and leaves indicated that in this process an activation of different genes connected to ethylene biosynthesis might be involved. To examine where the action of these stressogenic factors took place concomitant analyses of the activity of ACC synthase and ACC oxidase and the amount of ACC and MACC were provided. These results will be presented and discussed in our further papers.

No effect on ethylene production of styles has been established following application of auxin to the stigma of carnation and petunia (Hoekstra and Wages, 1986; Reid et al., 1984). The model of Larsen et al. (1993) for interorgan communication in pollinated carnation flowers has predicted an increase of auxin content and ethylene concentration in ovary after pollination. In this study we have not assayed the endogenous level of auxins in dissected floral parts. Therefore it is difficult to discuss the lack of auxin effect in our case although if we compare the results for ethylene production in ovaries and styles in response to auxins to the results for petals it is also possible another lower concentration of IAA to be able of inducing the ethylene synthesis. The treatment of whole carnation flowers with ethylene has been observed (Henskens et al., 1994) to induce a dramatic increase of ethylene production in petals. Despite the fact that in our experiments we used component flower parts the exposure to ethylene also resulted in acceleration of ethylene production in petals. The pre-incubation of carnation flowers in ethylene has been reported to trigger an acceleration of ethylene production (Overbeek and Woltering, 1990; Drory et al., 1993). In our case an interorgan and intertissue communication could be excluded and the reaction was considered only organ-specific since the transmission of substances and co-ordination between organs were eliminated by the dissection. The action of ethylene on petal ethylene rate in natural senescence is autocatalytic (Yang and Hoffman, 1984) when small amount of ethylene produced promotes its synthesis at a certain stage of development (Park et al., 1992). In this contest the treatment with ethylene was applied to mimic a similar effect. The data available in the present study pointed that ovaries and styles did not express the same way of response to exogenous ethylene as petals. The floral parts were isolated from pre-senescent flowers therefore possibly ovaries and styles needed to reach another latter stage of becoming sensitive, different of that for petals. A specificity of cultivar behaviour could be suggested too since a different reaction of carnation cultivars concerning ethylene sensitivity has been described earlier (Woltering et al., 1993).

Further investigations should focus the attention on the abundance of mRNA transcripts for ACC synthase and ACC oxidase in dissembled carnation flower parts and the identification of relevant cDNA sequence the expression of which takes place in conditions of wound- and water-stress or in case of auxin and ethylene incubation. Inhibition of the expression of certain senescence-responsible genes is a future way for extending vase-life of cut flowers and for avoiding the effect of external stress-factors leading to diminished keepability and deteriorating the fresh appearance.

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