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REVIEW

Ornamentals: A review of the role of ethylene in post-harvest flower senescence and abscission and methods to ameliorate ethylene effects

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1. SUMMARY

Senescence has been broadly defined as those processes that follow physiological or horticultural maturity (harvest stage) and lead to the death of the whole plant, organ, tissue or cell. In practical terms, post-harvest longevity is determined by the onset and rapidity of senescence and in many species this is regulated by the gaseous plant growth hormone, ethylene. The main effects of ethylene in accelerating the senescence of ornamental plants are to cause flower fading and wilting, to induce the abscission of flowers or flower parts (such as petals), to induce leaf abscission (leaf 'drop'), and to accelerate chlorophyll break-down leading to leaf yellowing.

Perhaps the most convincing evidence for a role of ethylene in regulating senescence is that the exposure of many species to ethylene in the air (exogenous ethylene) results in premature senescence with all of the symptoms associated with natural senescence, such as the typical in-rolling and wilting of the petals of carnation and *Kalanchoe*, the induction of anthocyanin pigments in *Cymbidium* orchid flowers and the abscission of flowers or petals in geranium. Response to exogenous ethylene is dosage dependent, and is a function of concentration and duration of exposure. Exogenous ethylene can stimulate the production of ethylene by the plant itself, and this phenomenon is known as autocatalysis.

Exogenous ethylene is a major source of problems during transport and marketing and levels as high as 1000 vpm (volumes per million) have been reported in airport terminals. The major sources of ethylene as a pollutant are internal combustion engines, fruit and vegetables which are transported with or displayed alongside ornamental plants and the flowers themselves. Hoyer (1989), in studying ethylene exposure during transport, has set the critical exposure for sensitive species at 0.05 vpm for 24 hours at a temperature of 15 - 18°C. In general, older flowers are more sensitive to the effects of ethylene than younger flowers and it follows from this that exposure to ethylene will have more deleterious effects on older flowers than on younger flowers.

Pollination of flowers results in very rapid ethylene-induced flower senescence in species such as carnation and petunia, and the trigger appears to be pollen tube growth rather than fertilisation itself. Pollination-induced flower senescence can be shown by species such as cyclamen which are otherwise little affected by exogenous ethylene. In such cases as cyclamen, it is not so much the effect of pollination in increasing ethylene production which gives rapid senescence, but rather the effect of pollination in conferring increased sensitivity of the flower to ethylene. Plant breeders have sought to overcome the problem of pollination-induced senescence by developing lines which are pollen sterile (e.g. triploids) or which lack sexual organs (e.g. 'double' flowers).

Ethylene production leading to premature senescence can be induced in plants by forms of environmental stress such as water deficit, flooding and low temperature. In addition, ethylene can be produced as a response to chemical stimuli such as herbicides, SO_2 and ozone, and to infection by pests, fungi, bacteria and viruses.

Some species are far more sensitive to ethylene than others, and strategies to combat ethylene and to promote increased longevity need to take this into account. Indeed, some of the major commercial ornamental species are insensitive to ethylene and these will neither show

premature senescence when exposed to ethylene as a contaminant, nor prolonged longevity following treatment with anti-ethylene agents. In practice, the sensitivity of a species to ethylene has generally been judged by the effects of exposing plants to controlled levels of ethylene gas for defined periods, or to sprays of the ethylene-releasing compound, ethephon. Tables are presented of the relative sensitivities of flowering and foliage pot plants (Tables 1 and 2) based on the studies of Woltering (1987) at the Sprenger Institute in Wageningen, and of the relative sensitivities of cut flower species (Table 3) based on the studies of Woltering & van Doorne (1988).

Leaf abscission was shown in about 30% of the flowering pot plants and about 50% of the foliage plants, with older leaves generally abscising first. Abscission of flowers, flower buds or whole inflorescences occurred in about 65% of the flowering plants tested. Species that exhibited abscission of leaves as well as flowers showed the latter at lower ethylene concentrations or after shorter exposure times. All fruit-bearing plants exhibited fruit drop. Some plants showed premature wilting of the flowers and this was sometimes accompanied by buds failing to open (bud blasting). Premature leaf wilting was never observed. Some species were totally unaffected by ethylene exposure

In the case of cut flowers, the commonest symptom of senescence was wilting of the flowers followed, at some later stage, by abscission More rarely, flowers abscised without prior wilting. High sensitivity to ethylene was found in many botanical families, but occurred in all *Campanulaceae, Caryophyllaceae, Geraniaceae, Labiatae, Malvaceae, Orchidaceae, Primulaceae, Ranunculaceae* and *Rosaceae* species investigated. Low sensitivity or insensitivity was shown by all the *Compositeae* and *Iridaceae* species investigated, and also by most of the *Amaryllidaceae* and *Liliaceae* species. In general, sensitivity was similar for species within a genus and for cultivars within a species. Species showing flower or petal abscission without prior wilting were generally sensitive to ethylene: *Geraniaceae, Labiatae, Primulaceae, Ranunculaceae, Rosaceae and Scrophulariaceae.* Wilting flowers with high sensitivity to ethylene were found only in: *Campanulaceae, Caryophyllaceae, Dipsacaceae, Malvaceae and Orchidaceae.* These family relationships ought to be useful pointers to the likely performance of other, untested species.

There are four levels of manipulation which can be used to regulate or suppress ethylene-mediated senescence responses: removal of ethylene as an aerial pollutant, inhibition of ethylene biosynthesis, inhibition of ethylene binding and genetic manipulation. Ethylene removal removes the threat posed by exogenous ethylene but does not delay natural senescence. Ethylene inhibitors can delay natural senescence in ethylene-free air, but cannot protect against exogenous ethylene. However, binding inhibitors have the potential both to protect against exogenous ethylene and delay natural senescence. Genetic manipulation, depending on the genes which are targeted, also has this dual potential.

In order to avoid undue exposure to exogenous ethylene, sensitive flowers or pots should not be transported, stored or displayed in close proximity to ethylene-generating commodities such as ripening fruit. Other important management steps for ethylene avoidance include minimizing the use of internal combustion engines during product handling in enclosed spaces, preventing the ingress into stores or handling areas of exhaust fumes from delivery vehicles (or ensure catalytic converters are fitted) and ensuring the efficient functioning of

CO_2 burners if these are located in close proximity to crop handling areas. It is certainly worthwhile for growers and suppliers to monitor ethylene levels in stores, packing areas etc. and useful determinations can be given using low cost gas sampling indicator tubes. Undesirable levels of ethylene in produce storage areas can often be removed by simple ventilation with unpolluted fresh air, and one air exchange per hour has been regarded as generally sufficient. Lowering temperatures during storage, transport and display can also minimize ethylene sensitivity although care must be taken to ensure that low temperature storage will not itself be injurious to the longevity of the product. If sufficient ventilation cannot be provided and low temperatures are not practicable, ethylene removal from the atmosphere by 'scrubbing' is an option. Products incorporating potassium permanganate are in common use, but for efficient performance the air needs to be drawn through the scrubber and the effective life of such products is short. Catalytic reactors offer a potentially much more efficient scrubbing system and are widely used in fruit and vegetable stores to maintain ethylene below critical threshold levels. However these are expensive. Ethylene avoidance strategies will not protect flowers against internally generated ethylene; this requires the use of substances which inhibit ethylene synthesis or prevent ethylene action.

The pathway of ethylene biosynthesis in the plant is shown in Figure 1. The rate limiting step is the conversion of SAM to ACC, catalyzed by the enzyme, ACC synthase. Inhibiting the activity of ACC synthase will, therefore, inhibit ethylene production by the plant and this can be accomplished by the application of chemical substances such as aminooxyacetic acid (AOA) and aminoethoxyvinylglycine (AVG). Commercial preparations of AOA-like and AVG-like compounds are available such as Pokon & Chrysal's EVB, although this is not registered for use in the UK. Such compounds reduce internal ethylene production, and can increase longevity. However, they give no, or little, protection against exogenous ethylene.

For ethylene to elicit its characteristic promotion of senescence it must first bind to a specific receptor. However, other compounds have been found which also bind to this receptor and these, by their competitive action, reduce or prevent ethylene activity and promote longevity. The best known example of such a compound is silver thiosulphate (STS) and more than 400 articles have now been written on the effectiveness of STS in promoting longevity in flower crops.

STS is available commercially as numerous products including Argylene (which is registered for use in the UK) and AVBS (which is not so registered). Such is the benefit that STS confers on post-harvest longevity that it is currently mandatory to use it on 13 species of cut flowers delivered to the Dutch auctions (see Table 4), and is recommended for the treatment of many others. It is recommended for use on numerous pot plant species by Argylene Biochem ApS of Denmark (see Table 5) where the use of STS on pot plants is common.

More recently, the binding competitor, 1-methylcyclopropene (1-MCP) has been extensively tested. It appears to be every bit as effective as STS in promoting longevity and protecting against exogenous ethylene at extremely low concentrations. It is expected that the commercial product will be released in 1997 by Floralife of Chicago, Illinois as a powder which, when mixed with water, releases 1-MCP as a gas.

Considerable progress has been made using genetic engineering techniques to modify plants so that ethylene-mediated senescence is delayed. Key steps in ethylene biosynthesis and

action are regulated by the activity of enzymes (see Figure 1) and these enzymes are the products of specific genes. Preventing these genes functioning efficiently (down-regulation) will restrict enzyme production, and this can be expected to modify the senescence process. Down-regulation can be achieved by introducing laboratory-constructed, reverse copies of the genes (antisense genes) into plants.

It seems clear that the introduction of genetically modified carnation plants with enhanced post-harvest longevity is not far away. However, the scientific effort in achieving this will have been far from trivial and extremely costly. It seems likely that the transgenic approach will only be adapted to other ethylene-sensitive ornamental species if the anticipated financial returns justify the costs involved, and this must be questionable in all but a few cases.

Increasing concern is being expressed over the long-term effects of using STS for the amelioration of ethylene effects because heavy metals (such as silver) remain in the soil and ground water for long periods and may infiltrate drinking water supplies. Once absorbed by the human body, such metals accumulate to toxic levels and cause harm to the nervous system. On the other hand the quantities of silver used are extremely small, and it has been argued that if the film industry can safely dispose of the many thousand times larger quantities of silver that they use, why not the ornamentals industry?

So far as I am aware, there are currently no restrictions anywhere in the world on the use of registered STS preparations for pulse-treating cut flowers. There are, of course, strict regulations in place on the safe disposal of spent solutions. There is, however, a ban on the use of STS on pot plants supplied to the Dutch Auctions, presumably because spraying releases far more silver into the environment than does the pulse-treating of cut stems. There are no such restrictions on the use of STS on pot plants in any country other than Holland so far as I am aware. Certainly, it is allowed in the UK, Denmark, Norway, Belgium, Germany, Japan and the USA. Further, it appears to be generally believed that there are no imminent plans to restrict the use of STS in any of these countries.

STS products require PSD registration in the UK under the Control of Pesticide Regulations 1986 (as amended) and the Plant Protection Products Regulations 1995 (as amended) as they 'aim to regulate the growth of plant products'. Argylene is so registered, but PSD have ruled that Chrysal AVB and Chrysal EVB 'need to be approved for use in the UK' and that 'these products cannot be used legally in the UK'. The situation on registration varies greatly from country to country.

The issue of whether registration is required for an anti-ethylene agent used to promote post-harvest longevity is particularly important since 1-MCP is expected to be released as a commercial product in 1997. This appears to offer an environmentally-friendly, highly effective, non phytotoxic and easy to use alternative to STS. Growers will need to know whether this will be available for use immediately, or whether prior registration will need to be sought by Floralife.

The review cites about 130 references on ethylene action and ethylene avoidance, and an appendix is provided which expands on the responses of particular species to ethylene and on the usefulness of anti-ethylene agents to protect these species against the effects of ethylene.

2. INTRODUCTION

Senescence has been broadly defined as those processes that follow physiological or horticultural maturity (harvest stage) and lead to the death of the whole plant, organ, tissue or cell (Watada *et al.*, 1984). The senescence process is mediated by a series of highly co-ordinated physiological and biochemical changes, such as increased activity of hydrolytic enzymes, degradation of starch and chlorophyll and a climacteric surge in respiration, and is associated with changes in gene expression and protein synthesis (Van Altvorst & Bovy, 1995). In practical terms, post-harvest longevity is determined by the onset and rapidity of senescence and in the case of flowers, can be a matter of hours only as in *Hibiscus trionum* and *Oxalis stricata*, or be a matter of days or even weeks as in most species which are grown commercially (Stead, 1992). The duration of flower longevity is regulated in many species by the plant growth hormone, ethylene.

3. ETHYLENE IN SENESCENCE

3.1. The Role of Ethylene

Ethylene is a hydrocarbon gas which has been shown to be produced in minute quantities from most types of plant tissue during normal metabolism and during senescence, and also as a response to injury or fungal infection. It has, for example, long been known that ethylene is a constituent of the volatile gases given off by many types of ripening fruit, and that ethylene production increases markedly during the fruit ripening process. Similarly, Nichols (1966) working at GCRI, Littlehampton, showed that there was a characteristic sharp rise in the production of ethylene from carnation flowers during senescence and petal wilting, and similar associations between ethylene generation and flower senescence have since been shown in other plant species with ephemeral flowers such as *Hibiscus* (Woodson *et al.*, 1985).

Ethylene production in flowers of species such as carnation typically follows a profile with three distinct stages (Halevy & Mayak, 1981): 1), a low steady rate of production; 2), an accelerated rise to maximum production and 3), a final phase in which production declines. Associated with the second phase is a marked rise in CO_2 evolution (which parallels the climacteric increase in respiration associated with fruit ripening). Usually, clear visual symptoms of flower senescence can be distinguished by the end of the second phase. Thus, the onset of the second phase is important because it signals the terminal stage of senescence and will, for example, occur earlier in short-lived flowers than in longer-lived ones. The onset of the second phase may be induced by various means such as exposure to ethylene as an aerial pollutant or by pollination and these are dealt with in Sections 3.2. and 3.4.

More direct evidence that ethylene plays a regulatory role in flower senescence has come from studies using chemicals which block ethylene production. Thus, for example, when Fujino *et al.* (1980) used aminooxyacetic acid as an additive in the vase solution, the respiration and ethylene climacterics typical of control carnations during senescence were suppressed, and vase-life was extended. The use of anti-ethylene agents to extend post-harvest longevity is extensively covered in Section 5.

Since ethylene is a gas, it can readily escape from the plant. There are no means by which

it can be transported around the plant and, to have a senescence effect, it has to be generated in the tissues in question, such as in the carnation flowers. The quantities of ethylene produced are very low and, where the mass of tissues concerned is small, detection is difficult. It is largely because of this that there is still some controversy over the role of ethylene in the regulation of senescence-induced abscission or 'drop' of flowers and leaves (as opposed to flower wilting). Nevertheless, the demonstration that anti-ethylene agents such as 'silver' can protect against the abscission of flowers of species such as *Schlumbergera (Zygocactus) truncata* (Christmas cactus) (Cameron & Reid, 1981) has led Reid (1985) to argue that ethylene plays a similar role in regulating flower and leaf abscission as it does in regulating flower wilting. Evensen *et al.*, (1993a) have recently reported findings consistent with the hypothesis that ethylene induces petal abscission in geranium by activating the rapid enzymic degradation of cell walls in the abscission layer.

3.2. Exogenous Ethylene

Perhaps the most convincing evidence for a role of ethylene in regulating senescence has come from studies in which plants have been exposed to ethylene in the air (exogenous ethylene). In many species this results in premature senescence with all the symptoms associated with natural senescence: the typical in-rolling and wilting of the petals of carnation (Nichols, 1968) and *Kalanchoe* (Marousky & Harbaugh, 1979a), the induction of anthocyanin pigments in *Cymbidium* orchid flowers (Arditti *et al.*, 1973) and the abscission of flowers or petals in geranium (Armitage *et al.*, 1980). Response is dosage dependent and in carnation, for example, the capacity for exogenous ethylene to induce petal senescence is a function of concentration and duration of exposure (Mayak & Kofranek, 1976).

Exogenous ethylene applied to plant tissue can stimulate the production of ethylene by the plant itself (Nichols, 1968; Woodson & Lawton, 1988), and this phenomenon is known as autocatalysis. Stimulation of ethylene production has also been reported in carnation following exposure to propylene (Nichols, 1977; Mayak *et al.*, 1977). Since the onset of senescence symptoms and autocatalytic production of ethylene appear to occur together in species such as carnation and *Ipomoea* (morning glory), it may be that autocatalysis plays a significant part in giving rise to the frequently dramatic effects associated with exposure of flowers to exogenous ethylene.

Ethylene is a major source of problems during transport and marketing. Background levels of ethylene in the UK range from 0.001 to 0.01 vpm (volumes per million) in rural areas, 0.005 to 0.05 vpm in urban areas, and from 0.05 to 0.5 vpm in industrial areas (Fitter & Hay, 1981), with about 90% of ethylene released into the air being produced by automobiles (Abeles, 1971). Levels as high as 1000 vpm have been quoted for airport terminals by Halevy & Mayak (1981).

Fruit and vegetables constitute a particularly important source of ethylene pollution since these are frequently transported with or displayed alongside ornamental plants. Researchers at Rehovot Hebrew University, Israel, for example, have recorded ethylene production rates ranging from melon (2,400 µl/kg/hour at 25°C), through apple, pear, avocado, banana and tomato (about 1,000 µl/kg/hour), broccoli and celery (750 µl/kg/hour), pepper, aubergine and citrus (about 500 µl/kg/hour) to lettuce and cauliflower (0.05 µl/kg/hour) (Halevy & Mayak,

1981). Carnations were not damaged when associated with cabbage, cucumber, carrot, sweet potato, lettuce, potato, grapes and cauliflower (Wintz, 1954). Ethylene production rates can be expected to be much lower in cool storage areas.

The flowers themselves can contribute to aerial ethylene pollution. Nichols (1979), for example, found that one or two pollinated carnation flowers in the box caused reduced longevity of unpollinated flowers (see Section 2.4.), and Akamine (1976) reported a similar phenomenon in orchid marketing.

With such large differences in the sensitivity to ethylene of ornamental subjects (see Section 4), and an influence not only of ethylene concentration, but also of duration of exposure, it is difficult to set 'danger' levels of aerial contamination. However, Hoer (1989), in studying ethylene exposure during transport, set the critical exposure for sensitive species at 0.05 vpm for 24 hours at a temperature of 15 - 18°C. This was exceeded in the case of one truck studied, transporting pot plants from Denmark (2 - 3 days per trip), on 15 out of 41 journeys, and was put down to a low air exchange rate in the truck, combined with ethylene production by the plants themselves, release of ethylene adsorbed on the walls of the truck, production of ethylene from the materials from which the truck walls were constructed, and release of ethylene previously dissolved in water condensate from preceding journeys when fruit and vegetables had been transported.

3.3. Ethylene and Flower Age

In general, older flowers are more sensitive to the effects of ethylene than younger flowers (Halevy & Mayak 1981; Woodson & Lawton, 1988). Thus, premature petal wilting in carnation is not shown when flowers at the 'tight bud' stage are exposed to ethylene in the air, and there is no induced production of ethylene by the petal tissues (Camprubi & Nichols, 1978). However, this changes rapidly as the flower ages with rapid senescence and ethylene production being shown by 'open' flowers.

A similar flower age effect is shown by the regal pelargonium (*P x domesticum*) in which petal abscission is the typical ethylene response. Florets become increasingly responsive to applied ethylene as they age, with the greatest change in responsiveness occurring in the first two days after anthesis (Evensen, 1991). This is consistent with the finding that ethylene production by the flower itself increases greatly between the first and twelfth day after anthesis (Deneke *et al.,* 1990). *Dendrobium* orchid 'Pompadour' also showed accelerated senescence and abscission of fully mature flowers when ACC, the immediate precursor of ethylene, was applied, but immature flowers were unaffected (Nair & Tung, 1987). It can be generalized that older flowers are more sensitive to ethylene than younger flowers (Woltering, 1987) and, it follows from this that applications of ethylene inhibitors will have less effect in prolonging longevity when applied to older flowers than to younger flowers.

3.4. Ethylene and Pollination

Pollination of flowers results in very rapid and controlled flower senescence in many species such as carnation (Nichols, 1977) and petunia (Whitehead *et al.*, 1984). Thus, pollinated flowers of carnation wilt within 1 - 2 days, whilst unpollinated flowers do not wilt until 5 - 6 days later. Pollination results in up to ten-fold increases in ethylene production within the

carnation flower, initially in the styles (within 1 - 2 hours of pollination) and later in the petals (between 8 and 24 hours after pollination). Pech *et al.* (1987) have shown that ethylene production in petunia flowers occurs within 5 minutes of pollination. The rapidity of this increase in ethylene production after pollination shows that the trigger is pollen tube growth rather than fertilisation. The later increase in other flower parts appears to be due to the production of some transmitted ethylene-promoting factor, the nature of which is still uncertain (Stead, 1992).

Pollination-induced flower senescence, associated with ethylene production and prevented by the use of anti-ethylene agents, can be shown by species which are otherwise little affected by exogenous ethylene, and would not be classified as highly sensitive to ethylene. An example of such a species is cyclamen (Halevy et al., 1984). In unpollinated cyclamen, very low ethylene production rates are shown throughout the whole life span of the flower, and exposure to exogenous ethylene has relatively little effect in hastening senescence. Following pollination, however, there is a dramatic increase in ethylene evolution, culminating in a peak four days after pollination when petal abscission typically occurs. In such cases as cyclamen, it is not so much the effect of pollination in increasing ethylene production which gives rapid senescence, but rather the effect of pollination in conferring increased sensitivity of the flower to ethylene.

Plant breeders have sought to overcome the problem of pollination-induced senescence by developing lines which are pollen sterile or which lack sexual organs. Semi-double or double geraniums, for example, are more resistant to petal shatter than are single flowered forms (Wallner *et al.*, 1979). Similar resistance has been claimed for double flowered forms of *Antirrhinum* (snapdragon) (Kofranek, 1958) and there was a programme of work at the John Innes Institute, Norwich in the late 1960s to introduce pollen sterility into F1 hybrids of *Antirrhinum* (Marks, 1970).

3.5. Ethylene and Flowering

Although, perhaps, a side issue in a consideration of post-harvest longevity, it is worth noting that ethylene can have striking effects on flowering itself, both positive and negative. Ethylene promotes the flowering of bromeliads, and ethephon (see Section 4.1.) is used commercially in the production of pineapples and the various ornamental bromeliads grown as pot plants (De Proft *et al.*, 1986). Ethylene also regulates the natural opening of flowers of citrus species (Zacarias et al., 1991). Reid et al. (1989) have shown that ethylene can accelerate, inhibit or have no effect on the opening of rose flowers, depending on cultivar but, in this case, ethylene is probably not the natural regulator of flower opening. Ethylene inhibits flowering in chrysanthemums when present as a pollutant in the glasshouse growing environment (Tjia *et al.*, 1969), or when plants are sprayed with ethephon (Cockshull *et al.*, 1979). It also has deleterious effects on the flowering of other species, particularly bulbous species, and exposure to ethylene of tulip bulbs during storage or of tulip plants during growth, for example, causes 'blasting', the inhibition of normal floral development (De Munk, 1973).

3.6. Ethylene and Stress

Ethylene production is induced in plants by many forms of environmental stress. These

include mechanical wounding, physical load or pressure, water deficit, flooding and low temperature (Hyodo, 1991). In addition, ethylene can be produced as a response to chemical stimuli such as herbicides, SO_2 and ozone, and to infection by pests, fungi, bacteria and viruses. It is not unusual, for example, for cut flowers such as carnation which are exposed to drought, even for short periods, to show increased ethylene production and earlier appearance of senescence symptoms (Borochov et al., 1982). Similarly, water stress has been reported to increase petal and flower abscission in pot plants such as calceolaria and bougainvillaea (Cameron & Reid, 1983), and effects can, in part, be reduced by prior treatment with anti-ethylene agents (see Section 5 and under the species in Appendix). Ethylene also appears to be implicated in the low-light inhibition of flowering shown by 'Enchantment' lilies, since sprays of anti-ethylene agents prevent this (Van Meeteren & de Proft, 1982).

4. SENSITIVITY TO ETHYLENE

Kader (1985) lists the main effects of ethylene in accelerating the senescence of ornamental plants as: the acceleration of chlorophyll break-down leading to leaf yellowing, leaf abscission (leaf 'drop'), flower fading and wilting, the abscission of flowers or flower parts (such as petals) and the stimulation of fungal infections and rots. However, some species are far more sensitive to ethylene than others, and strategies to combat ethylene and to promote increased longevity need to take this into account. Indeed, some of the major commercial ornamental species are insensitive to ethylene and these will neither show premature senescence when exposed to ethylene as a contaminant, nor prolonged longevity following treatment with anti-ethylene agents.

4.1. Test Procedures

In practice, the sensitivity of a species to ethylene has generally been judged by the effects of exposing plants to controlled levels of ethylene gas for defined periods, or to sprays of the ethylene-releasing compound, 2-chloroethylphosphonic acid (ethephon) at appropriate concentrations. However, because methodologies differ in the many research reports concerning single species, relative sensitivities are hard to judge. However, Woltering (1987), working at the Sprenger Institute, Wageningen (Holland), tested the sensitivity of 52 foliage and flowering pot plant species under standardized conditions, and this comparative data is summarized in Tables 1 and 2. Subsequently, the comparative responses of cut-flower species were tested (Woltering & van Doorne, 1988) and summarized data are presented in Table 3.

4.2. Pot Plants

Plants used in Woltering's (1987) study were obtained form commercial growers and were exposed to ethylene gas under standardized conditions when at the 'normal' harvest stage. Thus, flowering pot plants typically had both open (mature) flowers and developing flower buds. Plants were exposed to three concentrations of ethylene (3, 9 and 15 vpm) in fumigation chambers at 20°C in darkness, for either 24 or 72 hours, with CO_2 controlled at a steady 0.25%. Control plants were held under identical conditions except that ethylene was removed from the recirculating air stream by the use of 'Ethysorb' (potassium permanganate adsorbed on aluminium oxide). All plants were then removed to a controlled environment

shelf-life room and observed over a three-week period. Species were categorized into nine sensitivity classes which, for simplicity, have been amalgamated into five classes (insensitive to very highly sensitive) in Table 1 (flowering pot plants) and four classes (insensitive to highly sensitive) in Table 2 (foliage pot plants).

Leaf abscission was shown in about 30% of the flowering pot plants and about 50% of the foliage plants and generally required 72 hours of treatment to elicit effects. However, *Beloperone, Clerodendron and Solanum pseudocapsicum* exhibited leaf abscission after only 24 hours. Older leaves generally abscised first but, in the case of *Capsicum annuum*, the younger leaves were first affected. Of the foliage plants, *Schefflera* was particularly badly affected by ethylene in terms of percentage leaves abscised (100% abscission caused by 9 vpm ethylene exposure for 72 hours), with *Dizygotheca* close behind. An additional experiment showed that the minimum ethylene exposure time to induce leaf abscission in this latter species was about 30 hours, with maximum response (100% abscission) resulting from exposure for about 90 hours.

Abscission of flowers, flower buds or whole inflorescences occurred in about 65% of the flowering plants tested. Exposure for just 24 hours was generally sufficient to induce this symptom in sensitive species, and mature flowers abscised at lower concentrations than did flower buds. However, in *Fuchsia*, flower buds appeared most sensitive. In terms of percentage flowers abscised, the most sensitive species were *Rechsteineria, Hibiscus and Fuchsia*, with *Browallia, Streptocarpus* and *Vinca* close behind. Species that exhibited abscission of leaves as well as flowers (eg *Hibiscus* and *Clerodendron*), showed the latter at lower ethylene concentrations or after shorter exposure times. However, species exhibiting abscission of leaves and whole inflorescences (eg *Beloperone* and *Pachystachus*) showed similar sensitivities to both.

All fruit-bearing plants exhibited fruit drop; in *Capsicum annuum* and *Solanum pseudocapsicum*, leaf abscission was more pronounced than fruit drop, but in *Ficus deltoidea*, the situation was reversed. Fruit of *Solanum pseudocapsicum* and *Ficus deltoidea* rapidly ripened, turning to yellow and red respectively.

Severe yellowing of leaves due to ethylene was observed only in *Rhaphidophora aurea* and geranium, although some other species showed slight yellowing of older leaves. With the exception of *Hibiscus, Euphorbia keysii* and *Euphorbia pseudocactus*, leaf yellowing was not accompanied by abscission.

Some plants showed premature wilting of the flowers and this was sometimes accompanied by buds failing to open (bud blasting) (*Campanula, Kalanchoe* and geranium). Only in the case of *Cyclamen* was flower wilting accompanied by flower abscission. Premature leaf wilting was never observed.

Some species were totally unaffected by ethylene exposure and these included *Primula acaulis, Senecio cruentus*, and the foliage species *Anthurium, Asplenium, Chaemaedorea, Codiaeum, Cordyline, Nephrolepis and Scindapsus*. Chrysanthemum was also physiologically unaffected although the incidence of fungal infections was increased, possibly due to the effects of ethylene stimulating fungal spore germination. It is also well known that, whilst

Table 1. Ethylene sensitivity - flowering pot plants (based on Woltering, 1987)

Species	Flower wilt	Petal / flower drop	Leaf yellowing Leaf drop	Leaf wilt
INSENSITIVE				
Dendranthema grandiflora (chrysanthemum)				
Primula acaulis hybrids				
Senecio cruentus (cineraria)				
SLIGHTLY SENSITIVE				
Euphorbia pulcherrima (poinsettia)		✓	✓	✓
Exacum affine	✓			
Sinningia hybrids (gloxinia)		✓		
MODERATELY SENSITIVE				
Azalea indica			✓	
Calceolaria x herbeohybrida		✓		
Cyclamen persicum	✓	✓		
Pelargonium zonale (geranium)**	✓		✓	
Saintpaulia ionantha (African violet)	✓			
HIGHLY SENSITIVE				
Achimenes		✓		
Begonia (Rieger)		✓		
Begonia semperflorens		✓		
Campanula isophylla		✓		✓
Kalenchoe blossfeldiana	✓			
Kohleria		✓		
Pachystachus lutea		✓	✓	
Rechsteineria cardinalis		✓		
Streptocarpus (Cape primrose)		✓		
Vinca minor		✓		
VERY HIGHLY SENSITIVE				
Beloperone guttata (shrimp plant)		✓	✓	
Browallia speciosa		✓	✓	
Clerodendron thomsoniae		✓	✓	
Fuchsia x hybrida		✓	✓	✓
Hibiscus rosa-sinensis		✓	✓	

** Petal abscission is the usual symptom for geranium- e.g. Armitage *et al.*, 1980.

Table 2. Ethylene sensitivity - foliage pot plants (based on Woltering, 1987)

Species	Leaf yellowing	Leaf drop	Fruit drop	Fruit ripening	Leaf wilt
INSENSITIVE					
Anthurium scherzerianum					
Asplenium nidus					
Chamaedorea elegans					
Codiaeum variegatum					
Cordyline fruticosa					
Nephrolepis exaltata					
Scindapsus pictus					
SLIGHTLY SENSITIVE					
Asparagus densiflorus		✓			
Capsicum annuum		✓	✓		
Dieffenbachia	✓				
Dracaena marginata	✓				
Dracaena sanderiana		✓			
Eucharis grandiflora	✓				
Fatsia japonica		✓			✓
Ficus benjamina		✓			
Ficus pumila		✓			
Hedera canariensis		✓			
Yucca elephantipis	✓				
MODERATELY SENSITIVE					
Dizygotheca elegantissima		✓			
Euphorbia keysii	✓	✓			
Ficus deltoidea		✓	✓	✓	
Philodendron scandens		✓			
Rhaphidophora aurea	✓				
Schefflera compacta		✓			✓
HIGHLY SENSITIVE					
Euphorbia pseudocactus	✓	✓			
Solanum pseudocapsicum		✓	✓	✓	

ethylene does not impair post-harvest longevity of chrysanthemum, it can seriously delay flowering when present as a pollutant in the glasshouse (Tjia *et al.*, 1969).

Greater detail is given of the effects of ethylene on individual species in the Appendix. This includes several commercially important pot plant species which have been shown to be sensitive to ethylene, but which were not included in the comparative tests of Woltering (1987): *Bougainvillaea, Impatiens* (New Guinea impatiens), *Pelargonium x domesticum* (regal pelargonium), *Rosa* (pot rose) and *Schlumbergera (Zygocactus) truncata* (Christmas cactus).

4.3. Cut Flowers

Woltering & van Darkness (1988) comparative cut-flower study used commercial species obtained from growers or from the Dutch auctions, and wild species obtained from botanical gardens (results for these not shown). Stems were stood in water overnight in the dark at 6 - 10°C, and were then taken out of water and exposed 'dry' to ethylene (about 0.3 Pa) in chambers for 22 - 24 hours. Stems were then re-cut, and plants were placed in vases of water in a shelf-life room (12 hours light per day from fluorescent lamps at about 3 Wm^{-2}, 60% RH and 20°C) and scored for senescence symptoms daily against control plants which had not been exposed to ethylene. Effects of ethylene were expressed as percentage reduction in vase life or percentage stimulation of abscission. The percentage responses were then grouped to give five classes: no response (insensitive); up to 33% reduction / stimulation (slightly sensitive); 33 - 66% reduction / stimulation (moderately sensitive); 66 - 99% reduction / stimulation (highly sensitive); immediate dramatic response (very highly sensitive). These groupings for the commercial species are shown in Table 3.

In general, the commonest symptom of senescence was wilting of the flowers followed, at some later stage, by abscission (denoted as 'flower wilt' in Table 3). More rarely, flowers abscised without prior wilting (denoted as 'abscission' in Table 3); this response was not shown by any of the monocot species tested, but was shown in about half of the dicot families represented. In alstroemeria and some other species, the interval between wilting and abscission was very short (denoted by 'flower wilt and abscission' in Table 3). In *Cymbidium*, the initial symptom of senescence was a colour change to the petals.

High sensitivity to ethylene was found in many botanical families, but occurred in all *Campanulaceae, Caryophyllaceae, Geraniaceae, Labiatae, Malvaceae, Orchidaceae, Primulaceae, Ranunculaceae* and *Rosaceae* species investigated. Low sensitivity or insensitivity was shown by all the *Compositeae* and *Iridaceae* species investigated, and also by most of the *Amaryllidaceae* and *Liliaceae* species. In general, sensitivity was similar for species within a genus and for cultivars within a species. Species showing flower or petal abscission without prior wilting were generally sensitive to ethylene: *Geraniaceae, Labiatae, Primulaceae, Ranunculaceae, Rosaceae and Scrophulariaceae.* Wilting flowers with high sensitivity to ethylene were found only in: *Campanulaceae, Caryophyllaceae, Dipsacaceae, Malvaceae and Orchidaceae.* These family relationships ought to be useful pointers to the likely performance of other, untested species.

Table 3. Ethylene sensitivity - cut flowers (based on Woltering & van Doorn, 1988)

Species	Senescence symptoms
INSENSITIVE	
Achillea filipendulina (yarrow)	flower wilt
Allium sphaerocephalon (drumstick chives)	flower wilt
Anethum graveolens (flowering dill)	flower wilt
Aster novi-belgii (Michaelmas daisy)	flower wilt
Chrysanthemum maximum	flower wilt
Chrysanthemum parthenium (feverfew)	flower wilt
Chrysanthemum segatum (corn marigold)	flower wilt
Dendranthema grandiflora (chrysanthemum)	flower wilt
Eremurus (foxtail lily)	flower wilt
Erigeron (fleabane)	flower wilt
Helianthus annuus (sunflower)	flower wilt
Helipterum roseum (sunray everlasting)	flower wilt
Kniphofia (red hot poker)	flower wilt
Liatris spicata (button snakeroot)	flower wilt
Nerine sarniensis (Guernsey lily)	flower wilt
Rudbeckia (cone flower)	flower wilt
Solidago (golden rod)	flower wilt
Zinnia elegans	flower wilt
SLIGHTLY SENSITIVE	
Allium caeruleum (blue globe onion)	flower wilt
Centaurea cyanus (knapweed)	flower wilt
Crocosmia x crocosmiiflora (montbretia)	flower wilt and abscission
Dahlia	flower wilt
Euphorbia fulgens (spurge)	flower wilt
Freesia x hybrida	flower wilt
Gerbera jamesonii (Transvaal daisy)	flower wilt
Gladiolus	flower wilt
Gloriosa superba	flower wilt
Iris	flower wilt
Lilium (lily)	flower wilt
Narcissus pseudonarcissus (daffodil)	flower wilt
Nerine bowdenii	flower wilt
Ornithogalum thyrsoides (star of Bethlehem)	flower wilt
Triteleia laxa (Brodiaea)	flower wilt

Continued over page

Table 3. Continued

Species	Senescence symptoms
MODERATELY SENSITIVE	
Alstroemeria spp.	flower wilt and abscission
Asclepias tuberosa (Madagascar jasmine)	flower wilt
Chelone obliqua (turtle head)	abscission
Matthiola incana (stock)	flower wilt
Tulipa (tulip)	flower wilt and abscission
HIGHLY SENSITIVE	
Aconitum napellus (monkshood)	abscission
Antirrhinum majus (snapdragon)	abscission
Cattleya orchid	flower wilt
Dendrobium phalaenopsis orchid	flower wilt
Paphiopedilum orchid	flower wilt
Phalaenopsis orchid	flower wilt
Physostegia virginiana (obedient plant)	flower wilt and abscission
Scabiosa caucasica (scabious)	flower wilt
Trachelium caeruleum (throatwort)	flower wilt
VERY HIGHLY SENSITIVE	
Campanula pyramidalis (bellflower)	flower wilt
Cymbidium orchid	coloration and wilting
Delphinium ajacis (larkspur)	abscission
Dianthus barbatus (sweet William)	flower wilt
Dianthus caryophyllus (carnation)	flower wilt
Gypsophila paniculata (baby's breath)	flower wilt
Lychnis chalcedonica (Maltese cross)	flower wilt
Lysimachia clethroides (loosestrife)	abscision
Nigella damascena (love-in-a-mist)	abscission
Phlox paniculata	flower wilt and abscission
Rosa (rose)	abscission
Saponaria	flower wilt

5. AMELIORATION OF ETHYLENE EFFECTS

There are four levels of manipulation which can be used to regulate or suppress ethylene-mediated senescence responses (Yang, 1985): removal of ethylene as an aerial pollutant, inhibition of ethylene biosynthesis, inhibition of ethylene binding and genetic manipulation. Ethylene removal removes the threat posed by exogenous ethylene but does not delay natural senescence. Ethylene inhibitors can delay natural senescence in ethylene-free air, but cannot protect against exogenous ethylene. However, binding inhibitors have the potential both to protect against exogenous ethylene and delay natural senescence. Genetic manipulation, depending on the genes which are targetted, also has this dual potential.

5.1. Ethylene Removal

It is certainly worthwhile for growers and suppliers to monitor ethylene levels in stores, packing areas and during transportation if ethylene-sensitive products are involved. For accurate quantitative determinations, particularly when levels are low, the gas chromatograph is required. However, useful determinations can be given using low cost gas sampling indicator tubes. B.R.M. Agencies (Cheshire House, 164 Main Street, Goostrey, Cheshire), for example, supply 'Gastec' gas sampling pumps (about £200 each) which can be used in conjunction with direct reading, ethylene detector tubes which show a colour change from pale yellow to blue (about £21 for 10 tubes). Tubes are available to monitor concentrations between 0.2 and 50 vpm or between 25 and 800 vpm.

In order to avoid exposure to exogenous ethylene, sensitive flowers or pots should not be transported, stored or displayed in close proximity to ethylene-generating commodities such as ripening fruit (see Section 2.2.). Other important management steps for ethylene avoidance include minimizing the use of internal combustion engines during product handling in enclosed spaces (use electric fork-lifts for example), preventing the ingress into stores or handling areas of exhaust fumes from delivery vehicles (or ensure catalytic converters are fitted) and ensuring the efficient functioning of CO_2 burners if these are located in close proximity to crop handling areas. Studies by Hand (1986) at GCRI Littlehampton, for example, have shown that atmospheric concentrations of ethylene from inefficient combustion in a moderately well-sealed glasshouse can fall within the range 0.02 - 1.0 vpm, sufficient to cause premature senescence of sensitive ornamental crops.

Undesirable levels of ethylene in produce storage areas and during transportation can often be removed by simple ventilation with unpolluted fresh air, and one air exchange per hour has been regarded as generally sufficient (Sherman, 1985). Lowering temperatures during storage, transport and display can also minimize ethylene sensitivity, and it is claimed, for example, that a carnation flower is 1,000x more sensitive to ethylene at 18°C than at 1.5°C (Nell, 1992). However, care must be taken to ensure that low temperature storage will not itself be injurious to the longevity of the product. This is particularly important in the case of foliage pot plants (Poole & Conover, 1983). Retail areas have the potential to be particularly damaging to ethylene-sensitive species since relatively high temperatures are maintained for the comfort of shoppers, and because ornamental plants are frequently located near to fruit and vegetable displays.

If sufficient ventilation cannot be provided, ethylene removal from the atmosphere by

'scrubbing' is an option. Products commonly in use, particularly in the USA, incorporate potassium permanganate, adsorbed on a suitable carrier with a large surface area (Sherman, 1985). Such a product is 'Ethysorb' which is marketed in the UK in sachets, blankets and tubes by Molecular Products Ltd., Stayfresh Division, Mill End, Thaxted, Essex CM6 2LT. In this case, potassium permanganate is adsorbed on pellets of aluminium oxide. The potassium permanganate oxidizes ethylene to CO_2 and water, and shows a colour change from purple to brown. Replacement is needed when the colour change is complete, which can be after a relatively short period if ethylene levels in the air are high. For efficient performance, the air needs to be drawn through the scrubber and an Ethysorb forced air filter unit is available with a capacity to scrub 125 m^3 of air per hour. Ethysorb was used by Woltering (1987) in his pot plant sensitivity study to ensure his control plants received no exposure to ethylene.

Catalytic reactors also provide an efficient scrubbing system and are widely used in fruit and vegetable stores to maintain ethylene below critical threshold levels. These are units which employ platinum-coated ceramic beads, heated to 250°C, over which air from the store is re-circulated to catalyze the breakdown of ethylene to CO_2 and water. Their claimed efficiency is 80 - 97% removal of ethylene, and the catalyst can be expected to have a long, useful life (4 - 5 years) before replacement is needed. B.R.M. Agencies (Cheshire House, 164 Main Street, Goostrey, Cheshire) supply 'Swingcat' reactors which are manufactured by 'Turbamet AG' in Switzerland in a range of sizes to process between 50 and 400 m^3 of air per hour (about £7 - 11k per unit). Units suitable for use during transit are not yet available, and a recently introduced cool reactor model (to reduce heat inputs into stores) has not performed as well as the heated catalyst models.

Both Molecular Products Ltd and B.R.M. Agencies have expressed interest in assisting with trials to demonstrate the potential usefulness of their products for the ornamentals supply industry. It has to be stressed, however, that ethylene avoidance strategies will not prolong natural senescence. This requires the use of substances which inhibit ethylene synthesis or prevent ethylene binding.

5.2. Ethylene Biosynthetic Pathway

To understand how inhibitors of ethylene biosynthesis and ethylene binding work, it is necessary to know something of the pathway of ethylene biosynthesis in the plant. This is shown in simplified form in Figure 1 (based on Van Altvorst & Bovy, 1995). The pathway was first elucidated by Adams & Yang (1979) in ripening apples, but has since been shown to be operative in all other tested plant tissues, including flowers.

Methionine is the starting point. This is converted to S-adenosyl methionine (SAM) by the catalytic activity of the enzyme, SAM synthase, in a process involving the energy-rich, adenosine triphosphate. SAM is then converted by the enzyme ACC synthase to 1-amino cyclopropane-1-carboxylic acid (ACC) and 5-methylthioadenosine (MTA). MTA can be recycled back to methionine, thus allowing high rates of ethylene production even if methionine concentrations are low. ACC is the immediate precursor of ethylene and is oxidized to ethylene by ACC oxidase (also known as ethylene-forming enzyme, EFE).

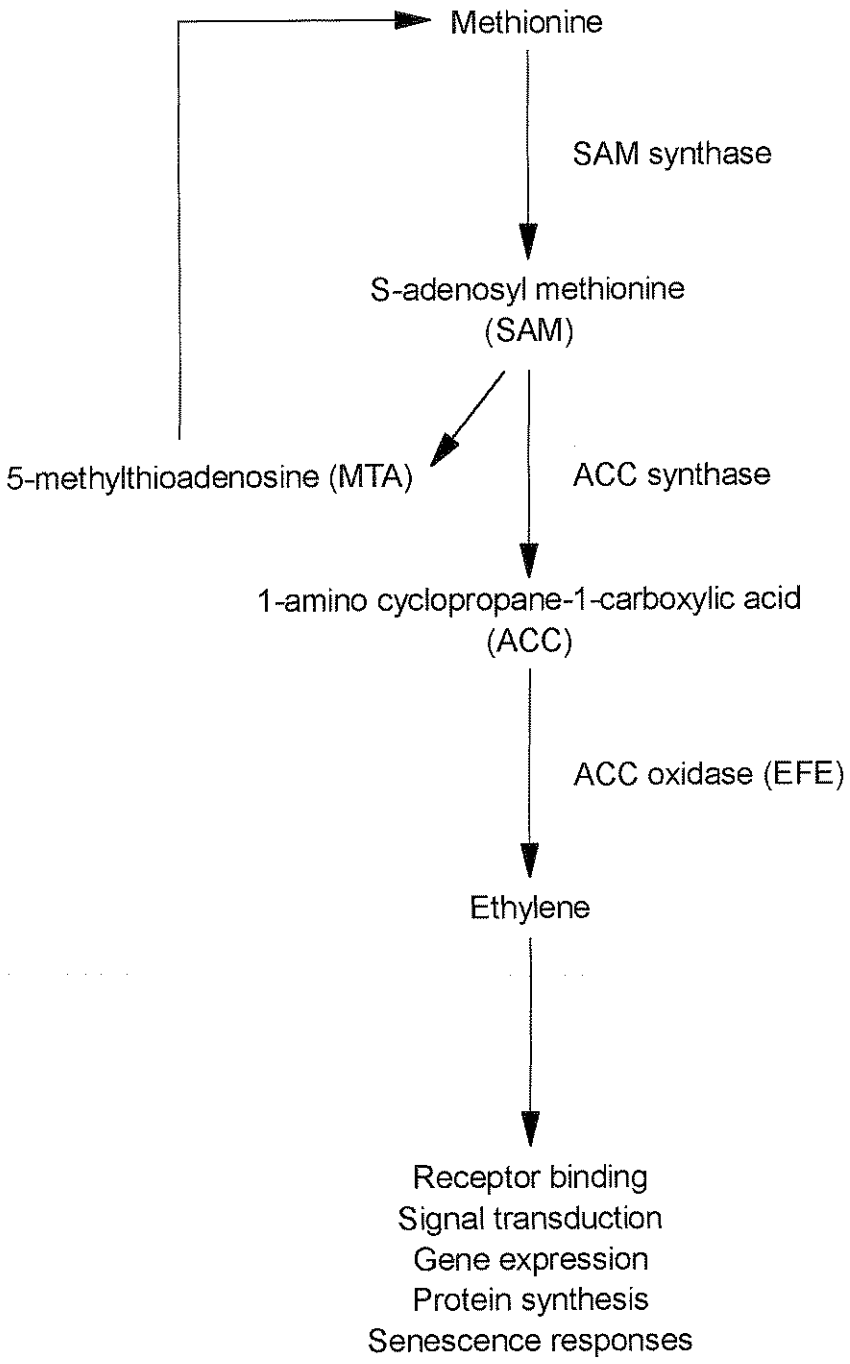

Figure 1. Pathway of ethylene biosynthesis (after Van Altvorst & Bovy, 1995).

For ethylene to have a biological effect it has to bind to a specific (but, as yet, uncharacterized) membrane-based, binding site. Binding of ethylene to form an activated complex triggers a signal which causes senescence genes to be expressed, producing proteins which give rise to the characteristic expression of senescence.

5.3. Inhibitors of Ethylene Synthesis

The rate limiting step in ethylene biosynthesis is the conversion of SAM to ACC, catalyzed by the enzyme, ACC synthase (see Figure 1). This is supported by the observation that application of ACC generally results in a marked increase in ethylene biosynthesis (Cameron *et al.*, 1979). Inhibiting the activity of ACC synthase will, therefore, inhibit ethylene production by the plant and this can be accomplished by the application of chemical substances such as aminooxyacetic acid (AOA) and aminoethoxyvinylglycine (AVG). However, since inhibitors of ACC synthase only prevent ethylene synthesis, they can be expected to offer little protection in ethylene polluted atmospheres (Van Altvorst & Bovy, 1995).

5.3.1. AOA and AVG

Commercial preparations of AOA-like and AVG-like compounds are available, although not registered for use in the UK, (eg 'EVB' from Pokon & Chrysal, 'Diaflor' from Brinkman, 'Florissant 150' from Van de Sprong and 'Prima Fleur Carnation' from Benfried, 'Florish' from Abbott Laboratories) and it is clearly of interest to know how these are likely to perform. Using AOA for example, Fujino *et al.* (1980) demonstrated that the respiration and ethylene production climacterics typical of control carnations during senescence were suppressed and that when used as a vase solution at 2mM concentration increased longevity of cut carnations from 8 to 15 days. AOA also gave as good an increase in longevity when used as a single 10 minute 100nM pulse. However, AOA gave no protection when cut carnation flowers were exposed to 10 µl/l of ethylene in air.

Similar increases in longevity due to the use of AOA in cut carnations in the absence of applied ethylene have been reported by Wang & Baker (1980), Broun & Mayak (1981) and Harkema *et al.* (1987). However, Broun & Mayak (1981) and Harkema *et al.* (1987) did find AOA to give some protection against ethylene as an aerial contaminant (claimed also in the literature for Pokon and Chrysal 'EVB'), and similar findings have been reported for geranium (*Pelargonium x hortorum*) where AOA gave some protection against petal drop following the application of ethylene (as ethephon) (Anderson *et al.*, 1993). The human toxicity of AOA was found by Woltering *et al* (1987) to be very low and, following unpublished testing, the Westland and Aalsmeer Auctions in Holland decided to permit spray carnations (and standard carnations at Westland) to be pre-treated with the chemical (van Doorn & Woltering, 1991). More recently, Staby *et al.* (1993) in the USA have reported the results of their own tests of Chrysal EVB on cut carnations exposed at various times to several concentrations of applied ethylene. They conclude that the commercial AOA analog, Chrysal EVB, offers no improved vase life over the control, even at low ethylene concentrations (they did not test the product in air free of ethylene) (See also Section 5 for the current status of this compound in Holland).

Experiments using AVG and AVG analogs have given comparable results to those with AOA. Ethylene synthesis is prevented or reduced, but little or no protection is offered against the effects of applied ethylene on flower wilting in carnation (Wang & Baker, 1980; Staby *et al.*, 1993) or flower bud abscission in Christmas cactus, *Schlumbergera (Zygocactus) truncata* (Serek & Reid, 1993). Conflicting results have been found for geranium; Miranda & Carlson (1991) found that AVG gave little or no protection against petal abscission, whilst Anderson et al. (1993) found flower drop to be reduced. van Doorn & Woltering (1991) have pointed out that AVG is less useful than AOA as a potential commercial product because it is very much more expensive.

5.3.2. Other Inhibitors

Just as the activity of ACC synthase can be blocked, so can the activity of ACC oxidase which catalyses the conversion of ACC to ethylene (see Figure. 1). Effective substances include Triton X-100 and aminoisobutyric acid (AIB).

Harkema *et al.* (1987) showed that Triton X-100, which modifies membrane structure, extended the longevity of carnations, when used alone or in combination with AOA. However, Triton X-100 contains an aromatic residue which has ruled it unacceptable for commercial use (van Doorn & Woltering, 1991). AIB has also been shown to delay petal wilting in carnation when included in the vase solution (Serrano *et al.*, 1990). It has also been shown to be effective when given as a pulse but, at high concentration, gives white leaf spotting on some cultivars (van Doorn & Woltering, 1991). These latter workers have suggested the evaluation of AIB in combination with AOA as a commercial post-harvest treatment, enabling AIB to be used at low concentration but providing an additional additive effect to that of AOA. It needs to be remembered, however, that like the inhibitors of ACC Synthase, Triton X-100 and AIB can be expected to give little or no protection against ethylene as an aerial pollutant.

5.4. Inhibitors of Ethylene Binding

For ethylene to elicit its characteristic promotion of senescence it must first bind to specific receptors which are produced as flowers age or are activated by a 'sensitivity factor' when flowers age (Reid & Wu, 1992). However, other compounds have been found which also bind to this receptor and these, by their competitive action, reduce or prevent ethylene activity and promote longevity. Because exogenous ethylene has the same requirement to bind to the receptor as internally produced ethylene in order to have a physiological effect, such compounds have the potential to delay senescence in plants exposed to ethylene as an aerial pollutant, a characteristic not shared by inhibitors of ethylene synthesis such as AOA and AVG (Section 5.3.1.). Beyer (1976) showed that silver (Ag^{+}) applied as silver nitrate was a potent binding competitor, blocking the ability of exogenous ethylene to, amongst other things, induce senescence in *Cattleya* orchids. However, silver nitrate has not been useful in commercial horticulture since it is relatively immobile in plant tissues and is phytotoxic at effective concentrations (Cameron & Reid, 1883). It is not, for example, transported in measurable amounts to the flowers when supplied to cut carnations in the vase solution and, because of this, does not protect against exogenous ethylene (Kofranek & Paul, 1972), although it does act as an effective bactericide. Far more useful, has been silver thiosulphate (STS).

5.4.1. Silver Thiosulphate (STS)

Veen & Van de Geijn (1978) showed that whilst silver nitrate moved upwards in the carnation stem at only about 3 cm / day, the STS anionic complex produced by combining silver nitrate and silver thiosulphate, was transported in the transpiration stream at about 2 m / hour. Furthermore, STS preserved its anti-ethylene binding activity after transport to the flower, so prolonging flower longevity, and was much less phytotoxic than silver nitrate. In a later publication, Veen (1983) summarized the benefits of STS pre-treatment of: *Antirrhinum* (to prevent floret abscission), *Bougainvillea* (to reduce bracteole drop due to drought), *Calceolaria* (to reduce dark-induced flower abscission), *Delphinium* (to prevent flower drop), *Dendrobium* orchids (to extend vase life), carnation (to extend vase life), poinsettia (to eliminate leaf epinasty), *Lathyrus* (to prevent flower drop and extend vase life), lily (to extend vase life), *Matthiola* (stock) (to improve flower quality and to double vase life), geranium (to inhibit petal shatter), rose (to protect against exogenous ethylene-induced petal shatter and leaf abscission), *Schlumbergera* (to prevent flower drop) and tulip (to overcome ethylene-induced inhibition of stem elongation). On the negative side, STS had little or no effect on *Gladiolus* and tended to be phytotoxic to *Gerbera*. Staby *et al.*, (1993) claim that more than 400 articles have now been written on the effectiveness of STS in promoting longevity in flower crops.

STS is available commercially as Argylene which is registered for use in the UK (Argylene Biochem ApS, Denmark, supplied by Applied Horticulture (Fargro), Littlehampton), and products such as AVBS (Pokon & Chrysal, Holland), Florever (Brinkman, Holland) and Florissant 100 (V. de Sprong, Holland) which are not registered in the UK. Such is the benefit that STS confers on post-harvest longevity that it is currently mandatory to use it on 13 species of cut flowers delivered to the Dutch auctions (see Table 4), and is recommended for the treatment of many others. However, environmental concerns (see Section 6) cast some doubt on its continued availability and it cannot, for example, be used for the treatment of pot plants in the Netherlands. It is recommended for use on numerous pot plant species by Argylene Biochem ApS of Denmark (see Table 5) where the use of STS on pot plants is allowed. Commercial recommendations are to use a 0.1% solution of Argylene in tap water (equivalent to a 0.2 mM solution) between 8 - 14 days before marketing (see recommendations on timing for geranium in Appendix). For particularly sensitive pot plant species such as geranium and Zygocactus, higher rates are suggested.

5.4.2. 1-MCP

Compounds other than STS have also been shown to be potent ethylene-binding competitors, and one such is the ethylene analogue, 2,5-norbornadiene (NBD) (Sisler *et al.*, 1986). However binding by NBD is reversible, and its anti-ethylene effects are not permanent. It also has a foul odour and is reputed to be carcinogenic.

Another binding competitor is diazocyclopentadiene (DACP) and this has advantages over NBD in that it binds irreversibly (Sisler & Blankenship, 1993). Serek et al., (1994) tested it on pot roses and found it effective in inhibiting leaf and bud drop caused by exogenous ethylene. However, DACP is unstable and potentially explosive!

Table 4. Cut-flower species requiring STS treatment by the Dutch VBN Auctions (1 May 1996) (information supplied by Pokon & Chrysal, Naarden, Holland.

Treatment Compulsory	Treatment Recommended[1]
Aconitum napellus	*Alstroemeria*
Aquilegia	*Antirrhinum majus*
Asclepias tuberosa[2]	*Bouvardia*
Delphinium	*Campanula glomerata*
Dianthus (carnation)[3]	*Cymbidium*
Dicentra	*Dianthus barbatus*
Euphorbia fulgans	*Freesia*
Gypsophila[4]	*Lisianthus (Eustoma)*
Lathyrus oderatus	*Scabiosa*
Lavatera	
Lilium	
Physostegia	
Veronica	

1 Many other species of lesser commercial importance are included by Pokon & Chrysal in this 'recommended' category.
2 AOA is compulsory for *Asclepias* 'Serenade'.
3 AOA can be used instead of STS.
4 STS is compulsory for *Gypsophila* in boxes, but only recommended for *Gypsophila* in containers.

Table 5. Pot plant species benefitting from treatment with STS (information supplied by Argylene Biochem ApS, Denmark)[1]

Abutilon	*Catharanthus*	*Fuchsia*	*Primula malacoides*
Acalypha	*Cestrum*	*Gardenia*	*Primula obconica*
Achimenes	*Cineraria*	*Hibiscus*	*Rhipsalidopsis*
Aeschynanthus	*Clerodendrum*	*Hoya carnosa*	*Saintpaulia*
Aphelandra	*Columnea*	*Impatiens*	*Schizanthus*
Azalea	*Crossandra*	*Ixora*	*Schlumbergera*
Begonia	*Cyclamen*	*Jacobinia*	*Solanum*
Bougainvillea	*Cytisus*	*Jasminum*	*Stephanotis*
Browallia	*Dianthus*	*Mimulus*	*Streptocarpus*
Brunfelsia	*Diplodenia*	*Pachystachys*	*Verbena*
Calceolaria	*Epiphyllum*	*Pelargonium*	*Zygocactus*
Camellia	*Euphorbia pulcherrima*	*Petunia*	
Campanula	*Eustoma*	*Plumbago*	
Capsicum	*Exacum*	*Primula acaulis*	

1 Suggested rates of use of 'Argylene' are available from the suppliers, Applied Horticulture, Fargro Ltd., Toddington Lane, Littlehampton, W. Sussex.

More recently, 1-methylcyclopropene (1-MCP) has been extensively tested (Serek *et al.*, 1994, 1995). This gaseous compound is chemically related to DACP and also shows irreversible binding. However, It is non-toxic and is effective in inhibiting ethylene responses at extremely low concentrations. Serek *et al.*, (1994) showed that, at a concentration of only 20 v.p.b. (billion), it was as effective as STS in protecting the pot plant species, elatior Begonia, *Begonia x tuberhybrida*, *Kalenchoe* and rose against the effects of exogenous ethylene. Similarly, Serek *et al.*, (1995) showed that it was as effective as STS in protecting the cut flower species, carnation, *Mattthiola, Consolida, Penstamon* and *Antirrhinum.* Given environmental concerns over the use of STS (Section 6), great hopes are pinned on 1-MCP as providing an effective substitute. It is expected that the commercial product will be released in 1997 by Floralife of Chicago, Illinois (Staby, Serek, personal communication). The product will be sold as a powder which, when mixed with water, releases 1-MCP as a gas.

5.5. Genetic Manipulation

Considerable progress has been made using genetic engineering techniques to modify plants so that ethylene-mediated senescence is delayed (Van Altvorst & Bovy, 1995). Key steps in ethylene biosynthesis and action are regulated by the activity of enzymes (Figure 1) which are the products of specific genes. Preventing these genes functioning efficiently (down-regulation) will restrict enzyme production, and can be expected to modify the senesence process. Down-regulation can be achieved by introducing laboratory-constructed, reverse copies of the genes (antisense genes) into plants.

Recently, the expression of the carnation ACC oxidase gene has been suppressed by the antisense approach (Michael et al., 1993). Ethylene production was reduced by 90%, petal inrolling was inhibited and post-harvest life was increased. However, the flowers had fewer petals and these showed decreased pigmentation. Similarly, antisense ACC synthase has been introduced into carnation (Savin et al., 1995). Transformed plants also exhibited low climacteric ethylene production and enhanced longevity but, as would be expected, the transformants were not protected from the effects of exogenous ethylene.

Inhibition of ethylene binding by genetic modification is now also a real possibility. Recent advances in molecular genetics have resulted in the isolation of several genes which are likely to encode and so be responsible for the production of the ethylene receptors in plants (Bleeker & Schaller, 1996). So, although many issues remain to be resolved concerning the mode of action of ethylene, modulation of ethylene sensitivity in flowers should now be technically possible.

It seems clear that the introduction of genetically modified carnation plants with enhanced post-harvest longevity is not far away. However, the scientific effort in achieving this will have been far from trivial and extremely costly. It seems likely that the transgenic approach will only be adapted to other ethylene-sensitive ornamental species if the anticipated financial returns justify the costs involved, and this must be questionable in all but a few cases.

6. ENVIRONMENTAL CONCERNS AND CHEMICAL REGISTRATION

Increasing concern is being expressed over the long-term effects of using heavy metals, such as silver, for the amelioration of ethylene effects (Nell, 1992). This is because heavy metals remain in the soil and ground water for long periods and may infiltrate drinking water supplies. Once absorbed by the human body, such metals accumulate to toxic levels and cause harm to the nervous system.

In response to Nell's article, Staby *et al.*, (1993) have compared the use of STS in commercial growing to that of the use of the essentially identical product by the film-processing industry. They point out that there is sufficient recoverable silver from processing one roll of most films to treat thousands of flowers and that there is enough recoverable silver in one year in North America associated with domestic film processing, to treat more than 4 trillion carnations! If the film industry can safely dispose of the many thousand times larger quantities of silver that they use, why not the ornamentals industry?

So far as I am aware, there are no restrictions anywhere in the world on the use of registered STS products for pulse-treating cut flowers. Indeed, it is mandatory to prior-treat 13 species of cut flowers with STS before these are delivered to the Dutch Auctions (see Table 4). There are, of course, strict regulations in place on the safe disposal of spent solutions. Residual silver has to be recovered by precipitation from spent solutions and information supplied in the UK with Argylene (Fargro Ltd) suggest that this is done using potassium iodide from local chemists. In Holland it is recommended that sodium sulphide is used to precipitate silver sulphide and that this is then taken to the Auctions where systems exist for its collection (van Doorn & Woltering, 1991). Pokon & Chrysal supply a 'neutralization powder' to be used on the residual solution before this is discharged into the sewers.

There is, however, a ban on the use of STS on pot plants supplied to the Dutch Auctions, presumably because spraying releases far more silver into the environment than does the pulse-treating of cut stems. There are no such restrictions on the use of STS on pot plants in any country other than Holland so far as I am aware. Certainly, it is allowed in the UK, Denmark, Norway, Belgium, Germany, Japan and the USA. Further, it appears to be generally believed that there are no imminent plans to restrict the use of STS in any of these countries. A private view expressed by one research worker in Denmark is that a ban on the use of STS in Denmark would be unworkable since the chemicals to make STS are readily available and there is no easy way of detecting whether STS has been used on pot plants.

STS products require PSD registration in the UK under the Control of Pesticide Regulations 1986 (as amended) and the Plant Protection Products Regulations 1995 (as amended) as they 'aim to regulate the growth of plant products'. Argylene is so registered, but PSD have ruled that Chrysal AVB and Chrysal EVB 'need to be approved for use in the UK' and that 'these products cannot be used legally in the UK'. The situation on registration varies greatly from country to country. In the USA, STS is legally used without registration although the US Environmental Protection Agency is currently claiming that STS is a growth regulator and ought to be classed as a chemical requiring registration (Staby, personal communication). A similar situation pertains in Holland and, currently, official registration (for use with cut flowers) is being sought (Vonk Noordegraaf, personal communication). There appears to be no requirement for registration of STS products in Germany (Ludolph, personal

communication). In Belgium, STS is classed as a 'pesticide' and the only product registered is that from Pokon & Chrysal (Bodson, personal communication). Registration is also required in Norway (Fjeld, personal communication).

The issue of whether registration is required for an anti-ethylene agent used to promote post-harvest longevity is particularly important since 1-MCP is expected to be released as a commercial product in 1997 (see Section 5.4.). This appears to offer an environmentally-friendly, highly effective, non phytotoxic and easy to use alternative to STS. Growers will need to know whether this will be available for use immediately, or whether prior registration will need to be sought by Floralife.

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APPENDIX - responses of individual species to ethylene and to anti-ethylene agents

Alstroemeria

Alstroemeria is not greatly affected by ethylene, responding with only a minor increase in flower wilting and abscission. Prolongation of vase life is not assured by the application of STS, and this practice is recommended (rather than compulsory) for stems supplied to the Dutch Auctions. A much greater post-harvest problem is leaf yellowing due to breakdown of chlorophyll, which can be shown only a few days after cutting, even on stems kept in the light. However, this can be largely prevented by the application of gibberellins (Van Doorn *et al.*, 1992) and treatment with gibberellin-based preparations such as SVB (Pokon and Chrysal) is compulsory for stems of alstroemeria supplied to the Dutch Auctions.

Antirrhinum

Floret drop is a particular problem of cut antirrhinums exposed to exogenous ethylene and the species is classified by Woltering & van Doorn (1988) as highly ethylene sensitive. STS can protect against this damage, and Anderson *et al.* (1993) demonstrated the efficacy of standing antirrhinums for 12 hours in a holding solution containing STS prior to ethephon application. Veen (1983) has also shown the value of pre-treatment with STS, and STS pulsing is currently recommended for cut antirrhinums by the Dutch Auctions (but is not mandatory).

Begonia

All begonia species appear to be highly sensitive to exogenous ethylene. Moe & Smith-Eriksen (1986) found that applications of ethephon to *B x cheimantha* (Lorraine begonia) increased the incidence of bud malformation and prevented flowers opening when applied to plants at the tight bud stage, and promoted flower abscision when applied to plants at the open flower stage. Similar results were obtained by Fjeld (1989) when ethylene gas was used. STS largely suppressed flower abscission when applied as a 1.05mM solution immediately before ethephon treatment (Moe & Smith-Eriksen, 1986), but the protection was relatively short-lived since ethephon treatment given 8 days after STS application again caused rapid flower abscission. The highest concentration of STS used (6.25mM) gave some petal necrosis, and Moe & Smith-Eriksen recommended frequent applications of STS at low concentration before flowers opened rather than a single spray at high concentration (although this was not tested experimentally).

Serek *et al.* (1994b) showed that exogenous ethylene applied continuously at 1.0 vpm caused about 70% of flowers of *B x hiemalis* (elatior begonia) to abscise within 1 day. In contrast, plants treated with STS (0.5mM) or 1-MCP (5.0 vpb) did not show this level of abscision until after 5 days. There was, however, no obvious benefit gained from the application of either STS or 1-MCP to plants maintained in an ethylene-free environment; regardless of treatment, 'display life' in ethylene-free air was judged to have been between 26 and 28.5 days. Hoyer (1985) also observed rapid flower drop following exposure to ethylene. Symptoms showed up after exposure for 24 hours at just 0.1 vpm, and market value was significantly reduced following exposure for 24 hours at 1.0 and 5.0 vpm. Ethylene did not cause damage to leaves.

B x tuberhybrida 'Non Stop' plants have also been shown to exhibit premature senescence following exposure to ethylene (Serek et al., 1994b), with a concentration of 1.4 vpm for 6 days giving 100% flower and bud abscision, even after pre-treatment with 5.0 vpb 1-MCP.

Bougainvillea

Cameron & Reid (1983) found that bracteole drop in Bougainvillea was extremely sensitive to drought conditions, and that drop continued even after watering was resumed. However, foliar sprays of STS offered good protection, reducing abscission under drought conditions by about two thirds.

Calceolaria

Cameron & Reid (1983) found that a 0.5mM STS spray (to run-off) reduced flower abscission when, one week later, plants were either stressed by being placed in drought conditions for 4 days in the dark (83% flower drop down to 22% drop) or exposed to 1 vpm. ethylene for 2 days (91% flower drop down to 36%). However, mature, open flowers were removed prior to STS application and the protection would not have appeared so good had this not been done!

Camellia

Flower bud abscission has been claimed to be promoted by ethylene produced by the leaves under confined conditions (Song & Lee, 1994), and could be significantly reduced by application of STS 10 days before plants were moved indoors. By reducing abscission, treatment increased the cumulative number of unopened flowers on a plant and extended the duration of flowering.

Carnation

Carnation is in the category of very highly ethylene-sensitive species, and typical ethylene symptoms are an in-rolling and wilting of the petals. It has been the model species for a majority of the studies on ethylene and flower senescence. Pulses of STS for as short a period as 10 minutes are sufficient to double cut-flower longevity (Reid *et al.*, 1980a), but effectiveness can decline considerably if treatment is not given on the day of harvest (Nichols *et al.*, 1982). Effectiveness is frequently greater on standard carnations than on miniature carnations (Sytsema, 1981). Longevity can be increased up to fourfold by combining STS with commercial vase preservatives (Reid *et al.*, 1980b). It is compulsory for growers to apply either STS or AOA to cut carnations other than 'Pink Roland', 'Roland' and 'Taiga' for supply to the Dutch VBN Auctions. It is recommended (rather than mandatory) that STS is used on cut flowers of *Dianthus barbatus* (Sweet William).

Christmas cactus (*Schlumbergera (Zygocactus) truncata*)

Flower aging is characterised by a gradual loss of turgor and colour fading, leading to flower desiccation and abscission of the entire flower from the phylloclade (Scott *et al.*, 1994). Flower longevity depends on cultivar but is typically about 4 - 6 days (for an individual flower). Up to 30% of flowers can be lost during long distance transit and this abscission

is promoted by high temperatures and darkness (Cameron & Reid, 1981). Ethylene is implicated in natural flower senescence and Serek & Reid (1993) have shown that STS applied at a 0.2mM concentration increased display life in a simulated interior environment by about 20% (by about 4 - 5 days). The species is extremely sensitive to exogenous ethylene (Cameron & Reid, 1981); following exposure, plants typically dropped all their flowers and buds within 24 hours when the concentration was 50 vpm, within 48 hours when the concentration was 5 vpm and within 5 days when the concentration was 0.5 vpm. Control plants held in clean air still retained most of their buds and flowers after 7 days. STS has been shown to offer significant protection against the effects of exogenous ethylene (Cameron & Reid, 1981; Serek & Reid, 1993) and protection is retained for at least 4 weeks. After 7 days exposure to 0.5 vpm ethylene, for example, untreated plants had dropped over 90% of their flowers and buds, while plants treated with 2 or 4 mM STS had dropped none of their flowers or buds (Cameron & Reid, 1981). However, some phytotoxicity was shown when a 4mM concentration was used, but STS damage was minimal when the concentration was 2mM or less. These researchers found that the degree of protection conferred declined when lower concentrations of STS were used, but Serek & Reid (1993) still found that treatment with 0.2mM STS reduced flower drop from 50% to 20% following 7 days of exposure to 1 vpm ethylene. In addition to giving protection against exogenous ethylene, STS has also been shown to protect plants against premature senescence caused by the stress effects of high temperature and darkness during marketing (Cameron & Reid, 1981).

No research reports have been found for Easter cactus (*Rhipsalidopsis*), but the close genetic relationship between this and Christmas cactus, and the similarities in symptoms of post-harvest senescence suggest that responses to ethylene and STS may also be similar. It should be noted that Argylene is recommended for use with Easter cactus in Table 5.

Chrysanthemum

As with other members of the *Compositeae* which have been tested, post-harvest longevity in chrysanthemum is not noticeably affected by exogenous ethylene (Woltering, 1987), and anti-ethylene agents confer no clear benefits in either clean air or ethylene-contaminated air.

***Citrus* spp**

Cunningham & Staby (1975) have reported that ethylene concentrations greater than 1 vpm introduced to ornamental lime plants (*C. latifolia*) in air-tight containers caused serious defoliation. However, there appear to be no published reports on the effectiveness of anti-ethylene treatments to prevent such shipping damage. Defoliation of foliage species is a common problem during prolonged transit and ethylene is not necessarily associated with this; inappropriate temperatures can also have severe adverse effects (Poole & Conover, 1983: Buck & Blessington, 1982).

Coleus

Baird *et al.*, (1984) have reported that petioles of *C. blumei* exposed to 20 vpm ethylene abscissed within 36 hours, but that this could be prevented by prior treatment with 4mM STS.

Freesia

Longevity of cut freesia is often unsatisfactory as a result of rapid wilting, malformation of buds and florets and dying of small buds at the apex of the inflorescence (Spikman, 1989). It has been shown that whilst ethylene production of mature florets is low, sharp increases in ethylene production are characteristic of small green buds, 2 - 3 days after harvest and just prior to the first symptoms of dying (white margins on the flower tepals) (Spikman, 1987). The implication is that ethylene is generated in the young buds as a consequence of harvesting stress, and that this results in premature senescence of these buds. Furthemore, exogenous ethylene is particularly harmful to the young flower buds (Spikman, 1986), and STS (4 hour pulse treatment at a 0.4mM concentration) significantly aids young bud development and opening (Spikman, 1989). On the other hand, AVG (which inhibits ethylene production after harvesting) does not fully prevent bud death (Spikman, 1989) and it may be that the primary cause of death is carbohydrate deficiency, with ethylene playing only a secondary role. In support of this view, sucrose treatments have also been shown to promote the development of young buds (Spikman, 1989). Relative to some other species, freesia is only slightly sensitive to ethylene (Woltering & Van Doorn, 1988), but the use of STS and/or sucrose can be expected to have some beneficial effect on the opening of young flower buds.

Fuchsia

Although fuchsia has been rated by Woltering (1987) as among the most ethylene-sensitive of ornamental pot plants, amelioration of flower and bud drop appears to have been little researched. However, the effectiveness of STS was investigated on photoperiod-lit, early fuchsia crops at the Lee Valley EHS in the early 1980s (Anon., 1984a). STS (as a mixture of 35 ppm silver nitrate and 350 ppm sodium thiosulphate) was applied either at the 'green bud' stage or immediately prior to simulated marketing and supermarket display lasting 11 days in total. Both treatments reduced bud drop to a limited extent, with application immediately prior to marketing being the more successful of the two; this reduced bud drop from 64.2% to 42.6% in cultivar 'Display' and from 36.5% to 26.8% in 'Heidi Ann'. Some petal spotting was observed on treated plants. Doubtless, bud drop would have been much more serious had the plants been exposed to exogenous ethylene, and STS may well have provided greater relative protection under such conditions.

Geranium

As with the regal pelargonium, the major post-harvest problem associated with geraniums is severe petal abscission or 'shattering' during transit and marketing. This occurs in ethylene-free air, but is greatly increased by exogenous ethylene (Armitage *et al.*, 1980). Recent research has shown that petal abscission begins about 60 minutes after flowers are exposed to 1 vpm ethylene, and is complete after 90 minutes (Evensen et al., 1993b). Less severe or less rapid damage can, of course, be expected at lower ethylene concentrations. Some amelioration is given by transporting plants cool (2 - 5°C) (Armitage *et al.*, 1980), but greater control has been reported by spraying entire plants or developing inflorescences with STS (Cameron & Reid, 1983). These workers found that 0.5mM foliar sprays applied 2 - 3 weeks before marketing, protected the plants during simulated packing, transit and retail display (but in their experimental protocol, mature flowers were removed before STS

application). A 48% reduction in petals dropped was given by a 0.1mM spray, but a 98% reduction was given by a 0.5mM spray. Protection was even afforded to inflorescences which were not yet visible at the time of treatment. Phytotoxicity (necrotic patches near the margins of leaves) was sometimes shown when 2mM sprays were used, but never when 0.5 mM sprays were used.

Farthing and Chappell (1982) developed this approach at the Lee Valley EHS and showed that best results were given by application of sprays of STS (they used a home-made mixture of 35 ppm silver nitrate and 350 ppm sodium thiosulphate) 7 - 10 days before marketing. Spraying much before this time had reduced efficacy. As well as significantly reducing petal drop, treatment with STS enhanced flower and foliage colour, and reduced the incidence of *Botrytis*. Spraying just the foliage gave best results, and avoided the slight petal spotting which sometimes occurred. However, it is difficult to see how this could be implemented in practice! A note of caution also needs to be sounded concerning the use of STS on geraniums following the observation that treatment with STS can markedly increase premature plant death due to infection by *Pythium ultimum* (Hausbeck *et al.*, 1989).

Gerbera

Although slightly sensitive to ethylene (Woltering & van Doorn, 1988), STS cannot be used to prevent flower wilting in gerbera since it has been shown to be phytotoxic (Nowak, 1979).

Hibiscus

Hibiscus is among the most sensitive of pot plants to ethylene (Woltering, 1987), and flower bud abscission can be a major problem during marketing (Thaxton et al., 1988). Senescence is associated with increased ethylene production (Woodson *et al.* 1985) and severe abscission can be shown even in the absence of exogenous ethylene. Factors exaccerbating this include darkness (Hoyer, 1984) and high temperature (Thaxton et al., 1988). STS can partially protect against marketing-induced abscission, and Thaxton et al. (1988) showed that a 4mM spray with STS, 7 days prior to dark storage (4 days) and simulated 'office environment' (16 days) reduced bud abscission from 97.1% to 5.3% at 30°C, from 45.2% to 0.0% at 20°C and from 66.7% to 7.1% at 10°C. The effects of exogenous ethylene are dependant on both concentration and duration of exposure, and extensive bud abscission can be expected after exposure to ethylene at just 0.05 vpm for 24 hours (Hoyer, 1996). Buds showing colour are particularly sensitive, followed by green buds and, finally, leaves (which can also absciss if ethylene levels are high enough). Bud drop caused by exogenous ethylene can be largely prevented by the application of STS at 4mM concentration, 11 or 7 days before exposure (Hoyer, 1986; Thaxton et al., 1988). However, whilst these latter workers found no phytotoxicity at this concentration, Hoyer found flower damage when buds opened. Application of STS at a 0.45mM concentration had little protective effect (Hoyer, 1986). The timing of STS treatment in relation to flower opening seems critical, since Woodson *et al.* (1985) reported that application of STS the day before a flower opened prevented petal senescence, but that application on the morning of flower opening was ineffective.

Kalanchoe

Although flowers of kalanchoe have the potential to last for many weeks, the species is highly sensitive to exogenous ethylene. Symptoms are an in-rolling of the petals and irreversible closure of the flowers, petal fading followed by desiccation, leaf yellowing and abscission (Marousky & Harbaugh, 1979a). These workers showed that severe damage occurs when open flowers are exposed to concentrations of ethylene greater than 0.5 vpm for two or more days at 23.5°C. Flowers still in the bud stage are less affected and open when plants are removed from ethylene contamination. However, opening is delayed. Lower holding temperatures reduce the severity of symptoms. Protection from exogenous ethylene is given by sprays of STS and by treatment with 1-MCP (Serek *et al.*, 1994b).

Lily

Low light-mediated flower bud abscission in 'Enchantment' lilies is mediated via ethylene and can be prevented by the use of STS applied either as a bulb treatment (Van Meeteren & de Proft, 1982) or as a spray applied to the growing plants (Malorgio *et al.*, 1990). Potted Easter lilies (*L. longiflorum*) also benefit from STS treatment (0.5 - 2.0mM) prior to harvest to reduce storage-induced bud abortion, to increase flower longevity and to protect against the effects of exogenous ethylene (Prince *et al.*, 1987). These latter researchers have shown that a peak of ethylene production is shown during the senescence of lily flowers and that STS reduces the magnitude of this, but does not delay its onset.

Impatiens

Flower abscision is a major factor limiting the successful marketing of New Guinea Impatiens (NGI) plants, and 65% corolla abscision during simulated marketing was reported by Dostal *et al.* (1991). Petals typically abscised whilst still turgid and without showing prior signs of discolouration, damage or wilting. STS and AOA had similar beneficial effects in reducing abscission due to simulated shipping (when stresses other than those relating to ethylene are imposed) from 65% to about 20% when applied 7 - 10 days before harvest at 1.0 mM concentration. These same workers tested the sensitivity of NGI to exogenous ethylene and concluded that the species should be placed in Woltering's (1987) most-sensitive category. As with other species, response was determined by the concentration of exogenous ethylene and by the duration of exposure, but even 1 vpm ethylene for 4 hours caused 80% or more of flowers to drop. STS sprays gave full protection against the effects of exogenous ethylene but, as would be expected, AOA did not.

Recent MAFF-funded trials at the University of Reading and HRI, Efford have also shown that STS can have a beneficial effect on the post-harvest longevity of NGI plants. Not only did STS reduce premature abscission of young flower buds at the colour stage or younger, it also enhanced plant shelf-life greatly since retained buds continued development to the open flower stage.

STS (0.001mM) applied at harvest has also been reported to be effective in preventing or reducing low light induced flower drop in seed-raised impatiens (*Impatiens walleriana*) 'Super Elfin Scarlet' (Doi *et al.*, 1992). However, it did not prevent weak shoot growth.

Petunia

Petunia, like carnation has frequently been used in studies of ethylene-induced flower senescence because it shows high sensitivity, exhibiting rapid petal wilting and abscission. Natural senescence is associated with a climacteric increase in ethylene production within the flower, and the onset of this can be delayed by the use of STS (Whitehead *et al.*, 1984). Pollination significantly advances flower senescence (Gilissen, 1977), but this can also be retarded by the use of STS (Lovell *et al.*, 1987; Whitehead *et al.*, 1984). To my knowledge, STS has not been used to prolong the floral life of bedding petunias during marketing, but the potential for this certainly exists.

Philodendron

Exogenous ethylene is damaging to plants of *Philodendron scandens* with typical symptoms being leaf and stipule abscission and leaf chlorosis (Marousky & Harbaugh, 1979b; Woltering, 1987). Abscission increases as the concentration and/or duration of exposure increases. Thus, plants exposed to 1 vpm ethylene at 23.5°C for 2 - 3 days did not abscise any leaves, while plants exposed to this concentration for 4 days abscised 4% of leaves; plants exposed to 5 vpm ethylene for 3 - 4 days, or to 10 vpm ethylene for 2 days, abscised 50% or more of their leaves (Marousky & Harbaugh, 1979b). Holding plants at 16°C greatly reduced symptom severity and, since this is above the chilling-injury threshold temperature for the species, is recommended during marketing. Although trials of anti-ethylene agents have not been reported, these should reduce senescence-related damage during marketing.

Poinsettia

Poinsettia is very little affected by exogenous ethylene (Woltering, 1987) and can be generally regarded as ethylene insensitive. Nevertheless, the sleeving of poinsettia cultivars such as 'Annette Hegg Diva' has often been reported as resulting in epinasty (drooping of leaves and bracts), usually lasting several days, when the sleeves are removed (Sacalis, 1978; Staby *et al.*, 1978), and ethylene has been implicated in this response. Epinasty is due to the asymmetric distribution of auxin to the upper side of the petiole (in this case as a result of the vertical reorientation of the typically horizontal petioles), giving the upper side a higher growth rate than the lower side (Lyon, 1963). The cause of this redistribution has been ascribed to ethylene generated within the plant as a result of bending stress (Saltveit *et al.*, 1983), and trials have shown an increase in epinasty as a result of applying exogenous ethylene, and a reduction in epinasty following prior treatment with AVG or STS (Saltveit *et al.*, 1979; Saltveit & Larson, 1981). In contrast, other researchers suggest that the observed increase in ethylene production is only a secondary response, and report that AOA and STS do not reduce epinasty (Reid *et al.*, 1981). Scott *et al.*, (1983) showed that the cultivar 'Gutbier V-14 Glory' was epinasty-resistant, and it is probable that newer cultivars are also resistant since the disorder appears not to be troublesome to UK poinsettia growers. There is no evidence to suggest that ethylene is implicated in premature cyathia drop since this is not promoted by exogenous ethylene and is not prevented by the use of STS (Miller & Heins, 1986).

Radermachera sinica

Wang & Dunlap (1990) found that exposure of *Radermachera* plants to 2,000 vpm ethylene for 24 hours caused abscission of all leaflets and most petioles and rachises within 22 hours (i.e. whilst treatment was still proceeding). Exposure to 500 vpm ethylene caused abscission of the leaflets within 30 hours, but there was no petiole or rhachis abscission. These are undoubtedly extreme responses, but it is difficult to judge the relative sensitivity of the species since ethylene concentrations used by Wang & Dunlap were so much higher than those used by Woltering (1987), who did not include this species in his comparative tests. Plants treated by Wang & Dunlap with STS and then exposed to ethylene showed no abscission during the following 30 days. Application of STS at 0.125 mM concentration was effective and no plant damage was observed. However, at higher concentrations, STS proved phytotoxic, inducing necrotic lesions on the leaves.

Regal pelargonium

The regal pelargonium (*Pelargonium x domesticum*) has great potential as a flowering pot plant because of its large showy flowers, but it is very susceptible to petal abscission, 'shattering' (Deneke *et al.*, 1990). Indeed, in an evaluation in a simulated consumer environment (home-life room), petal abscission was the primary factor reducing post-production ratings of advanced breeding lines (Deneke *et al.*, 1992). A climacteric rise in endogenous ethylene precedes abscission, as in carnation and, as might be expected, plants show extreme sensitivity to treatment with exogenous ethylene (Deneke *et al.*, 1990; Evensen, 1991). Exposure to 0.5 vpm ethylene for 1 hour induced abscission, with sensitivity varying between cultivars and increasing with floret age. The greatest change in sensitivity occurred between the day of anthesis and 2 days later, and younger florets required a higher concentration of ethylene and a longer duration of exposure to induce the abscission response. Florets aged 2 - 3 days after anthesis still required exposure to ethylene for at least 40 minutes, regardless of ethylene concentration for rapid abscission to occur. Plants raised at cooler temperatures (18°C Day / 13°C Night as opposed to 21°C Day / 16°C Night) had better post-harvest longevity due to the continued development of flower buds after harvest, and showed less petal abscission when plants were exposed to exogenous ethylene (Evensen & Olson, 1992). STS applied as the first flowers on a plant reached anthesis reduced sensitivity greatly, and often extended longevity to beyond that of the controls (Deneke *et al.*, 1990).

Practical trials of the effectiveness of STS in protecting against petal shatter (without the imposition of exogenous ethylene) were carried out at the Lee Valley EHS in the early 1980s (Anon., 1984b). The effects were not as dramatic as those reported for geranium (Chappell & Farthing, 1982), but petal shatter, averaged over five cultivars, was reduced by 30%. There was an indication that the earliest flowering cultivars which were carrying the most advanced flowers at the time of treatment, benefitted least, and this probably indicates that only the youngest flowers received protection. Petal spotting proved a problem, but this could probably have been avoided by earlier treatment when the first flowers were starting to open (timing of application in relation to harvest not reported).

Rose

Although ethylene has been claimed to be of only minor importance in the natural senescence of cut-flower roses (Reid *et al.* 1989), exogenous ethylene can have very marked deleterious effects (Woltering, 1987; Reid *et al.* 1989). Prediction of likely effects is difficult, however, since these latter researchers found that low concentrations of exogenous ethylene could accelerate flower opening, inhibit flower opening or have no effect, depending on cultivar. Pre-treatment with 0.5mM solutions of STS overcame any effects of exogenous ethylene with no phytotoxicity shown. Cold-stored cut-flower roses tend to have a reduced longevity but STS, applied as a half-hour pulse treatment at 0.5mM concentration, extended this by several days (Mor *et al.*, 1989). It can be concluded that a benefit from the use of STS is far from certain, and STS is not a pre-treatment requirement for cut roses on the Dutch Auctions (but aluminium sulphate pre-treatments to reduce vascular plugging are mandatory).

Typical post-harvest senescence symptoms shown by pot roses are leaf yellowing, flower bud and leaf abscission, and a failure of flower buds to open, and exogenous ethylene exacerbates these symptoms (Serek, 1993; Tjosvold *et al.*, 1994). Serek (1993) found that, in the absence of exogenous ethylene, STS increased pot-rose longevity of cultivar 'Victory Parade' by 66 - 70%, increased flower life by 13 - 37% and promoted flower opening. The optimum STS concentration was considered to be below 0.4mM (largely determined on the basis of environmental protection and cost) and spray application was made 3 days before shipping when plants had 4 - 8 open flowers. However, other cultivars were said to have shown no obvious benefits. Tjosvold *et al.*, (1994) also found that STS (1mM applied the day before harvest) promoted flowering in the pot rose 'Belle Sunblaze' but that it did not reduce leaf yellowing. On the other hand, synthetic cytokinins (a type of plant growth regulator) have been shown to reduce leaf yellowing in rose but to have no effect of flower opening (Halevy & Kofranek, 1976; Clark *et al.*, 1991), and Tjosvold *et al.* (1994) found the best treatment for pot roses to be a combination of the cytokinin, benzyladenine (BA) (100 ppm) and STS (1mM). Serek & Andersen (1993) have reported that AOA is not as satisfactory in extending longevity as either BA or STS (even in the absence of exogenous ethylene), but 1-MCP has been reported to be equally effective as STS (Serek *et al.*, 1994a). These latter researchers showed that STS (0.5mM) or 1-MCP (5 vpb) increased the 'display life' of 'Victory Parade' pot roses from about 3 days to about 9 days in the continuous presence of exogenous ethylene at a concentration of 1 vpm, and from about 21 days to about 30 days in the absence of exogenous ethylene.

Streptocarpus

Streptocarpus responded as highly sensitive to ethylene in Woltering's 1987 comparative tests (Table 1), confirming earlier studies by Agnew et al. (1985) and by Rewinkel-Jansen (1986). Abscission of mature petals during marketing is a particular problem, and growers have resorted to removing open flowers at harvest (Agnew et al., 1985). This strategy of marketing plants in tight bud is successful in eliminating the abscission problem but it is expensive and time-consuming, and resulting plants lack visual impact, so depressing sales. Agnew et al., (1985) showed that the use of STS could effectively eliminate the need for flower removal; the 'best' treatment was to spray plants to run-off with STS at 0.5mM concentration, 1 week before marketing. This completely suppressed abscission following simulated shipping (2 days sleeved in a box in the dark at 25°C) and caused no phytotoxicity

symptoms, even though the plants were heavily budded at the time of treatment. Plants sprayed just 24 hours before 'shipping' showed even more abscission than the unsprayed controls and necrotic lesions appeared on the flowers and leaves. Similar necrotic lesions were observed by Rewinkel-Jansen (1986) after spraying plants with 0.6 mM solutions (and sometimes 0.3mM solutions) 3 days before exposure to exogenous ethylene and/or dark treatment (simulated shipping).