USE OF INHIBITORS OF ETHYLENE ACTION

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1. Introduction

The final stage in plant development is senescence. Senescence can be defined as an irreversible process of gradual degeneration and disintegration of plant tissue, eventually leading to the death of the organism (Bruinsma, 1983). Detachment of plant organs, like cut-flowers, usually advances the onset of senescence. Flowers wilt sooner, leaves will yellow earlier than when they remain attached to the plant.

Senescence is under hormonal control. This enables the grower to use chemicals to affect (promote or delay) the longevity and shelf life of postharvest commodities, like cut-flowers and fruits. By using promoters or inhibitors of hormone action it is possible to interfere with the hormonal homeostatic system within the plant.

Webster's Dictionary describes homeostasis as "A tendency toward maintenance of a relatively stable internal environment in the bodies of higher animals through a series of interacting physiological processes". A classical example is the maintenance of a fairly constant degree of body heat in the face of widely varying external temperatures. In the present report the concept of homeostasis will be restricted to physiological processes related to senescence and hormones.

Cohen and Bandurski (1982) described hormonal homeostasis as "The maintenance of a steady state concentration of the hormone in the receptive tissue appropriate to any fixed environmental condition". During plant development the information issued by the genome will change under the influence of exogenous and/or endogenous factors, and this will result in a new homeostatic system such that the steady state concentration of the hormone is fixed at a new level.

2. Ethylene homeostasis

Bangerth (1983) pointed out that hormone biosynthesis, transport, metabolism, and action as well as tissue sensitivity to the hormone are contributing factors to the hormonal homeostatic system. In the present report this system will only be illustrated for ethylene. The pathway of ethylene biosynthesis has been elucidated and the possibilities to interfere by means of chemicals have been discussed. Transport of ethylene is - due to its fast diffusibility - not an endogenous regulating mechanism to maintain ethylene concentrations inside the tissue. The role of the ethylene-precursor 1-aminocyclo-propane-1-carboxylic acid (ACC) as a correlation signal is not well understood. It seems likely that ACC plays a role in the root-shoot interaction in waterlogged plants, and as a signal between the gynaecium and other flower parts in pollination phenomena.

In the present report the carnation flower will be used as a model system to demonstrate the possibilities of regulating ethylene homeostasis at its action level. The carnation flower may be considered to be a climacteric flower. Exogenous and endogenous ethylene is effective in shortening post-harvest life by triggering autocatalytic ethylene production. The postulation by McMurchie et al. (1972) that two systems are involved in ethylene production by ripening fruit also holds for carnation flowers. System 1 involves the low preclimacteric ethylene production; this ethylene triggers some process by which the formation of huge amounts of ethylene in System 2 is initiated. This autocatalytically produced ethylene is regulated in carnation flowers by the induction of ACC-synthase and the ethylene-forming enzyme (EFE), (Manning, 1985).

By blocking the binding sites of ethylene with various chemicals, like silver thiosulphate and 2,5-norbornadiene, the production of System 2 ethylene is prevented and flower senescence will continue without entering a postclimacteric phase. Furthermore, chemicals like benzyladenine, are able to lower the responsiveness of the flower tissue to ethylene, and thereby delay the onset of autocatalytic produced ethylene.

Like in climacteric fruits, the sharp increase in ethylene production is associated with a rise in respiration. Romani (1984) suggested that the respiratory climacteric may be regarded as a mitochondrial homeostatic response to compensate for the degradative effects of the incipient programmed cellular senescence. According to Romani, the postclimacteric phase then is a consequence of an unsuccessful attempt. The transient wilting response to short-time exposure to ethylene, observed in carnation flowers (Nichols, 1968) may in this respect be considered to be a successful homeostatic regulation.

3. Effects of chemicals on ethylene homeostasis

3.1. Antagonistic action of carbon dioxide

Thornton (1930) showed that carbon dioxide (5-15%) retarded bud-opening and prolonged post-harvest life of cut-flowers. It has also been known for many years that carbon dioxide delays fruit ripening (Kidd and West, 1934). Burg and Burg (1967) studied the interaction between carbon dioxide and ethylene using the pea straight growth test. With the aid of Lineweaver-Burk plots they showed that carbon dioxide is a competitive inhibitor of ethylene action and suggested that carbon dioxide delays fruit ripening by displacing ethylene from its receptor site. Lineweaver-Burk plots are generally used as a means to analyse enzyme kinetic data. Analysing developmental and growth data with the same procedure may be critized on theoretical grounds; among others, it is tacitly assumed that there is a simple linear coupling between the amount of hormone-receptor complex and the growth response. Nevertheless, the values so obtained may be useful in showing the kind of competition between hormones and their antagonists, as has been indicated in recent work (Sisler et al., 1985; Veen, 1985).

Sisler (1979) exposed tobacco leaves to ^{14}C-labelled ethylene and studied the displacement of the bound ethylene by carbon dioxide. At 2%, carbon dioxide displaced about 35% of the bound ethylene, but increasing the concentration to 10% did not displace the remaining radioactively labelled ethylene. Sisler, therefore, concludes from his experiments that carbon dioxide acts, not by direct competition, but through some indirect manner.

Carbon dioxide also modifies ethylene metabolism. Increasing the ambient carbon dioxide concentration to 7% has been found to inhibit the conversion of ethylene to carbon dioxide (Smith et al., 1985). The meaning of ethylene metabolism for its biological function is still far from clear. The interaction between carbon dioxide and ethylene metabolism requires further study.

Although it is possible to delay senescence of cut flowers during storage by increasing the carbon dioxide level, it is still an uncommon practice. It may be that the different demands of the various crops will make the control of the atmospheric conditions difficult. Long-term storage of carnation buds has been very successful by the use of a pretreatment with silver thiosulphate, which will be discussed later. Also Staby et al. (1984) showed that pretreatment with silver thiosulphate was more effective for long-term storage of carnations than controlling the atmospheric conditions.

3.2. Oxygen-ethylene interaction

Burg and Burg (1967) also examined the interaction of oxygen with ethylene in the inhibition of pea epicotyl elongation. They suggested that oxygen is a "cooperative effector" of ethylene action. It is well known that oxygen is required for the conversion of ACC to ethylene. In a nitrogen atmosphere carnations do not respond to the application of ACC. The oxidation of ethylene at the hormone binding site as a requirement for ethylene action, as has been postulated by Beyer (1984) is a highly speculative idea. Abeles (1984) reported that while the function of ethylene oxidation is not fully understood, evidence from his experiments suggests that it does not play a role in ethylene action.

3.3. Interaction between ethylene oxide and ethylene

Lieberman et al. (1964) observed that ethylene oxide in a concentration between 0.10 and 0.25% increased the longevity of carnations and roses. Also Nichols (1968) showed that this compound antagonized the action of ethylene and prevented the climacteric rise of ethylene in cut carnations. Baker (1983) stated in his review that ethylene oxide may exert some unknown effect in addition to that of ethylene antagonism in roses, since silver thiosulphate, a typical anti-ethylene agent, is ineffective in delaying flower senescence in roses. Beyer (1985) explained Lieberman's observations by suggesting that the inhibiting effect of ethylene oxide on ethylene action was due to a general suppression of metabolism resulting from the high ethylene oxide concentrations employed. Beyer, using low concentrations of ethylene oxide (0.02% in his abscission experiments) showed that ethylene oxide increases tissue sensitivity to ethylene.

Commercial application of ethylene oxide is unlikely. The gas is explosive and very toxic. Moreover, according to Beyer (1985) toxic symptoms on the plant appear at concentrations higher than 0.1%.

3.4. Antagonistic action of 2,5-norbornadiene

2,5-Norbornadiene (2,5-NBD) is a cyclic olefin and is a very powerful anti-ethylene agent. 2,5-NBD competitively blocks the physiological ethylene-binding sites (Sisler and Yang, 1984; Sisler et al., 1985). According to these authors the compound like ethylene, presumably acts through a double binding bond to a metal. Already in the classical paper of Burg and Burg (1967) it was suggested that the ethylene-receptor should contain a heavy metal, like copper.

Structure-activity relationships have been studied by Sisler and Yang (1984). A number of cyclic olefins were examined for their anti-ethylene activity. 2,5-NBD with two double bonds had the highest activity.

Double reciprocal plots of the data suggest that the antagonism is competitive in nature. However, the same critical comments as made before apply here. It is questionable whether a procedure for analysing enzyme kinetics may be used for interpreting growth data. Yet, 2,5-NBD is a very usefool tool in the study of ethylene action. Sisler proposed that a "trans effect" mechanism is likely to be involved in ethylene action. He suggested that such a "trans effect" would result in a structural modification of a receptor protein which brings about the subsequent biochemical events and physiological response. It is assumed that 2,5-NBD, which structurally resembles ethylene, competes with it for the same binding site and that the resulting 2,5-NBD-receptor complex is biologically inactive.

Hence, 2,5-NBD is a highly interesting compound for fundamental research on the action mechanism of ethylene. Sisler et al. (1983) also showed that 2,5-NBD effectively delays the onset of wilting in carnations. However, horticultural application will be rather limited, as 2,5-NBD is a highly volatile compound with an unpleasant smell. Moreover, Smith and Hall (1985) remarked that the potential usefulness of this compound in reversing or preventing ethylene effects is much limited by its carcinogenic properties. So, there is certainly a need to develop analogues of 2,5-NBD which are non-volatile, harmless, and non-pungent.

3.5. Effects of silver salts

3.5.1. Silver-ethylene interaction

The silver ion (Ag^+) has been shown to be a potent ethylene antagonist (Beyer, 1976). One of the typical anti-ethylene effects of silver is the delay in senescence of ethylene-sensitive flowers. Halevy and Kofranek (1977) showed that the longevity of cut carnations can be increased by pretreatment with silver nitrate. A treatment of the stem base with this silver salt had far less effect on the longevity than a direct spraying or dipping of the flower, the reason being that silver ions are not readily translocated to the carnation flower. This relative immobility can be caused by the participation of the silver ions in the cation-exchange processes at the negatively charged sites of the walls of the xylem vessels. By studying the behaviour of silver chelates, it has been found that the anionic silver thiosulphate complex is transported through the xylem at a speed which is much faster than that of the silver cation (Veen and Van de Geijn, 1978). The anti-ethylene effects of silver are preserved in this complex (Veen and Van de Geijn, 1978; Veen, 1979a; Veen, 1979b). Even a short treatment of 20 min with an STS solution delayed flower senescence (Reid et al., 1980).

Pretreatment of carnation flowers with STS completely blocks the ethylene surge preceding the wilting of the petals. In addition, such a pretreatment causes the flowers to become insensitive to an ethylene treatment (Veen, 1979a). These phenomena can be understood if it is realized that the ethylene surge preceding the wilting of the petals is itself a consequence of system 1 ethylene. By blocking the "receptor site" for ethylene, the climacteric increase of ethylene is prevented. This model fits a positive-feedback mechanism, in which the binding of ethylene to its receptor tends to increase its own biosynthesis.

3.5.2. Localization of silver thiosulphate

It has been shown that there is a distinct accumulation of silver in the receptacle tissue of the flower (Veen and Van de Geijn, 1978). The ultrastructural localization of silver in this flower part was investigated by electron microscopy (Veen et al., 1980). Electron dense deposits were observed at the inner side of the cell wall as well as inside the cell wall region, and much of it accumulated in intercellular spaces. The presence of silver and sulphur atoms in these deposits was verified by X-ray analytical electron microscopy. Similar localization of silver particles has been observed by Hobson et al. (1984) in their investigations on the inhibiting effect of STS on tomato fruit ripening. The presence of silver particles in the intercellular spaces suggests that the movement of silver is largely apoplastic. No evidence of deposits in the cytosol was found. It cannot be excluded, however, that soluble silver salts did pass the plasmalemma but were washed out during the fixation procedures.

The particular association of silver deposits with the middle lamella leads Hobson and co-workers to suggest that the silver may be involved in inhibiting the polygalacturonase activity, by binding to sites concerned with increasing sensitivity to ethylene, or to specific sites for ethylene action. According to these authors, a direct effect of silver on the mechanism of protein synthesis is not thought likely. For example, Hobson and co-workers showed that the synthesis of nitrate reductase was not affected by the presence of silver within the tomato tissue. In carnations, the physiological importance of the particles observed in the receptacle tissue is still unclear.

3.5.3. The site of action of silver thiosulphate

Ethylene is thought to bind to a receptor molecule that as a result is activated. The activated receptor molecule triggers the primary response, which then initiates the chain of reactions leading to the physiological effect. One of these effects in carnation is the autocatalytic production of ethylene, as a consequence of the development of the activities of ACC synthase and ethylene-forming enzyme (EFE). Moreover, the outburst of this System 2 ethylene is accompanied by a climacteric increase in respiration. As the respective K_m-values (ethylene concentrations which gives half-maximal stimulation) are similar in apple tissue for increased respiration (1.0 µl l^{-1}), development of ACC synthase activity (0.8 µl l^{-1}), and EFE activity (0.9 µl l^{-1}), a common binding site for ethylene in autocatalytic ethylene production and climacteric increase in respiration has been suggested (Bufler, 1986). This implies one initial event of ethylene action. The inhibiting action of STS on all three phenomena supports this view. The silver ion may prevent the primary receptor-ethylene binding by modifying the receptor molecule, as has been suggested by Yang (1985).

Does the silver ion compete with the ethylene molecule for the same binding site (like 2,5-NBD) or does it act at a different place within the receptor-system? Yang (1985) published a model in which a ligand in the receptor site facilitating the binding of ethylene, interacts with the silver ion. The result will be that the receptor has little capability to bind ethylene, or that the ethylene-receptor complex becomes biologically inactive.

In a recent paper it has been shown that the growth promotion of pistils in carnation buds by ethylene can be reversed by administering STS via the stem or 2,5-NBD in the ambient atmosphere (Veen, 1985). In both cases, the inhibition has been suggested to be competitive. However, it is not likely that ethylene and silver ions compete for the same site. Beyer (1976) suggested that the silver ion could replace the copper ion within the receptor unit. To explain the competition between ethylene and 2,5-NBD and between ethylene and silver ions, a model which shows some resemblance to the calcium-calmodulin scheme has been proposed (Veen, 1986).

It is hypothesized that the ethylene receptor is composed of a sub-unit A of proteinaceous nature and one or more enzymic sub-units (sub-unit B). Binding of ethylene to sub-unit A will cause an activating allosteric change in that protein. The activated sub-unit A will act as a regulatory system for the sub-unit B. The activation of sub-unit A is thought to be analogous to the allosteric activation of calmodulin by calcium. The binding of calcium to calmodulin allows this complex to become bound to various target proteins. By analogy, the type of response caused by ethylene may depend on which enzymic sub-units B are present.

The similarity in chemical structure between ethylene and 2,5-NBD makes it likely that both compounds compete for the same site in sub-unit A. However, binding of 2,5-NBD does not lead to activation of sub-unit A, while that of ethylene does. In the model it is suggested that activation of sub-unit A involves exposure of copper atoms, before encapsulated within sub-unit A. This exposed copper may activate the enzymic sub-unit(s) B. The similarity in atomic structure between copper and silver makes it likely that the latter displaces the copper in the receptor sub-unit B. Binding of activated sub-unit A (with copper as a coupling factor) leads to activation of sub-unit B and finally to a growth response. Binding of silver to sub-unit B prevents this compling, and blocks the action of ethylene.

3.5.4. Use of silver thiosulphate in commercial horticulture

A review on horticultural applications of STS has been published (Veen, 1983). Moreover, in two recent ISHS symposia (Skierniewice, 1984 and Noordwijkerhout, 1985) several reports have been presented on the use of STS in ornamentals (Acta Horticulturae vol. 167 (1985) and 181 (1986)).

The use of STS can be very profitable for the grower. In principle, all processes in which ethylene plays a decisive role (e.g. wilting, abscission) can be delayed or even prevented by a pretreatment with STS. The key to its succesful use is to choose a suitable combination of pretreatment time, STS concentration and pretreatment conditions such as relative humidity and temperature. STS pretreatment will extend vase life of many flowers. It will also be beneficial in preventing shedding of leaves in potplants when these plants are subjected to stress conditions during transport and storage.

STS is used to prevent abscission in cut flowers, such as snapdragons, sweet peas, and lily of the Nile (Farnham et al., 1980; Mor et al., 1984a, 1984b). Abscission in potted flowering plants is inhibited, e.g. Christmas Cactus, Impatiens, Pelargonium, Calceolaria, Bougainvillea. Leaf abscission in Schefflera is also inhibited (Cameron and Reid, 1983). In potted flowering plants STS can be applied before the flower buds show colour, thus avoiding any possible phytotoxicity to the petals (Reid and Goszczynska, 1985).

Losses during winter production of 'Enchantment' lilies is a common situation in The Netherlands due to the low light conditions (Van Meeteren and Slootweg, 1986). Supplemental illumination is necessary to prevent the abscission of the developing flower buds. This abscission is mediated by elevated ethylene production from the developing anthers caused by low-light stress. Treatment with STS overcomes this problem and makes supplemental illumination needless. However, silver pretreatment of flowers, especially as a spray to e.g. potted plants, might lead to objections for environmental reasons, which could force authorities to issue restrictions. In The Netherlands, for example, spray applications of STS are not presently permitted. One argument is that the silver ion is a potent biocide, although in its formulation as silver thiosulphate it seems not to have any bactericidal action. It is important that research will go on to study ethylene action in flower senescence in the hope of finding other chemicals that can be used. In this respect, the late Staden from the Sprenger Institute in The Netherlands (Staden and Beekhuizen, 1986) showed that a combination of aminooxy acetic acid, gibberellic acid, kinetin, daminozide and a detergent like Triton X-100, extended the longevity of cut carnations as much as did STS.

The contamination of the environment by silver applications in horticulture is of minor importance compared to the production of silver by other human activities. Anthropogenic emission amounts to $50 \cdot 10^5$ kg/yr in the atmosphere (In: Salomons and Förstner, 1984). Also volcanic dust contaminates the atmosphere with silver, $0.6 \cdot 10^5$ kg/yr. Cut carnations are completely protected against ethylene if they have taken up 20-30 μg of silver. Hence, a total number of 10^9 carnations pretreated with STS will contaminate the environment with 20-30 kg of silver. Moreover, in The Netherlands the spent STS solutions are delivered by the growers to the auctions, which take care of recycling the remaining silver by means of a specially developed installation.

Cameron et al. (1985) showed that a number of recommended formulation procedures are unnecessarily stringent and that long-term cold storage of STS solutions (3 months in glass) is feasible.

Nowadays, in The Netherlands pretreatment of carnations, Aconitum, Delphinium, Euphorbia, Lathyrus and lilies with STS has been made compulsory by the auctions. The growers must pretreat the flowers directly after harvesting. Auctions test whether growers have pretreated their flowers in a correct way. Presently, pretreatment of Alstroemeria, Antirrhinum, Campanula, Freesia, Phlox and Physostegia is recommended, but not yet compulsory.

Three different pretreatment solutions containing STS are now commercially available. The first is a concentrate which must be diluted by the grower, the second is a powder to be dissolved in water (1 gr in 1 liter gives 0.2 mM) and the third consists of two concentrates to be mixed together and diluted.

4. Conclusion

By the use of chemicals or physical methods it is now possible to control the production of ethylene (e.g. AOA) the accumulation of ethylene (e.g. ventilation) or its action (e.g. STS). Thereby, the homeostatic equilibrium inside the plant parts is extended and therefore post-harvest life of the flower is prolonged. Hence, STS is not only an experimental tool in the hands of plant physiologists studying the action of ethylene, it is also a powerful instrument in the hands of the grower to improve the quality of his product.

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