BULB-TYPE FLOWER SENESCENCE

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Abstract

In order to study the senescence of flowers of geophytes, many of which are important commercial cut flowers but last poorly in the vase, we chose day lilies as a model system. the flowers of daylilies (*Hemerocallis* species). The rapid senescence of these flowers was accompanied by a transient respiratory climacteric but not by any appreciable evolution of ethylene. Since the application of silver thiosulfate (STS), an inhibitor of ethylene action, or of aminooxyacetic acid (AOA), an inhibitor of ethylene biosynthesis, did not delay senescence of daylilies, we conclude that ethylene is not involved in this process. Daylilies treated with cycloheximide, an inhibitor of protein synthesis on 60-S ribosomes, lasted as long as six days in the vase. The implications of these findings to our understanding of bulb-type senescence are discussed.

1. Introduction

The senescence of cut flowers involves a coordinated series of complex physiological and biochemical events leading to eventual collapse and death of the petals. The physiology of these processes has been studied almost entirely using, as models, carnation, morning glory, and tradescantia flowers (Halevy and Mayak, 1979). In these flowers senescence is accompanied by increased respiration and ethylene production, induction of catabolic enzymes and a resulting decrease in protein, complex carbohydrate and nucleic acid content, and loss of membrane function (Halevy and Mayak 1979, 1981).

Some important commercial monocotyledonous flowers such as iris, tulip, and narcissus have relatively short vase life. The vase life of others, such as daylilies, Mexican shellflowers, and bearded iris is so short that they are normally not used commercially as cut flowers. Until now, because of the model systems normally used to study it, rapid petal senescence has been considered to be to be ethylene-dependent, but there has been no evidence for this in any of the bulb-type flowers. We report here preliminary studies of the physiology of senescence in such flowers, using, as a model system, flowers of the daylily (*Hemerocallis* spp.).

Daylilies are herbaceous garden perennials commonly grown for their showy display of lily-like flowers. Much hybridized since their original discovery in Asia, these plants are now widespread throughout temperate climate zones and have been selected for variable blooming seasons, a broad spectrum of overall plant size, and flower colors ranging from typical yellow through red, pink, and purple. Members of the plant family Liliaceae, daylilies have three sepals and three petals, as do lilies. Unlike true lilies, however, daylily flowers last only one day - hence their name. The inflorescence (a branched scape with several flowers at different stages of development) may last up to six weeks, but each individual bloom lasts for only one day. Preliminary findings (Lukaszewski and Reid, unpublished 1987) indicate that the senescence of daylilies, like the relatively rapid senescence of a number of commercially-important geophytes, is ethylene-independent. If a directed sequence of gene derepression is responsible for senescence in bulb-type flowers and this process can be understood, it might then be possible to interrupt the natural course of senescence and improve the vase life of these flowers.

2. Materials and methods

Flowers of the yellow 'Cradle Song' cultivar were produced in the greenhouse under normal production conditions (day/night temperatures of 24/18°C, natural photoperiods). Individual flowers or inflorescences were harvested as needed for experiments. Individual flowers were cut with 0.5 cm of pedicel attached, and placed in small vials containing DI water or, where desired, test solutions.

2.1. *Observation of morphological changes during opening and senescence.* The changes occurring in harvested daylily buds were recorded using time-lapse photography.

2.2. *Measurement of water uptake during opening and senescence.* Buds were suspended with the pedicel immersed in water in a vial on the pan of a balance with digital output. The output was connected to a computer, and the weight of the vial was recorded at 10 min intervals.

2.3. *Measurement of respiration and ethylene production.* Harvested flowers were placed in 1.0 l glass jars ventilated with a stream of humidified ethylene-free air (1 l/hr). The concentrations of ethylene and CO_2 in the effluent air stream were determined at intervals using a gas chromatograph (equipped with a photoionization detector) and an infrared gas analyzer, respectively.

2.4. *Treatment with ACC or ethylene.* To determine the effects of 1-aminocyclopropane-1-carboxylic acid (ACC), the immediate precursor of ethylene in plants, buds were placed in vials containing 1 mM ACC. To test the effects of exogenous ethylene, harvested flowers were placed in 40 l chambers ventilated with a flowing stream of air (ca. 30 l/hr) containing different concentrations of C_2H_4.

2.5. *Determination of the effects of inhibitors.* Buds or opening flowers were placed either continuously or for short periods (pulsing) in solutions containing inhibitors of ethylene synthesis (1 mM aminooxyacetic acid {AOA}), ethylene action (1 mM silver thiosulfate {STS} prepared as described by Reid *et al.* {1980}), or 6-benzylaminopurine (BA, 1 mM), or protein synthesis (1 μM - 1 mM cycloheximide). Vase life of the flowers was measured as time to the start of wilting of the perianth.

3. Results

3.1. *Changes during development and senescence of daylily flowers.* An individual daylily flower bud enlarges steadily until, the evening before opening, it reaches nearly full size. By this time the bud also achieves a significant degree of coloration, and the sepals begin to separate at the tip of the bud. The next morning, the daylily petals and sepals separate fully, unfold, and expand rapidly. By midday the petals and sepals open fully and recurve to form the typical lily flower. Within six to twelve hours, the blossom wilts. Translucent areas develop in the anthers and along the margins of the petals and sepals; these areas enlarge and coalesce, and the flower finally collapses. In some cases (especially in red and purple cultivars) pigmented liquid exudes from the petals and sepals as they collapse. The total elapsed time from bud opening to collapse is typically 12 to 18 hours. During this time an abscission zone also develops directly beneath the point of attachment of the petals and sepals to the pedicel, and by the end of the following day the entire corolla and the anthers abscise from the scape. If unpollinated, the pistil also abscises at that time.

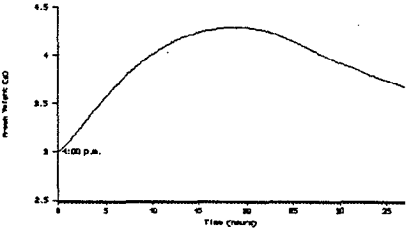

Fig. 1 Fresh weight of a daylily flower during opening and senescence

3.2. *Changes in fresh weight during opening and senescence.* As their buds opened, the fresh weight of daylily flowers (mean bud fresh weight was ca. 3 g) increased markedly to a broad plateau, then fell again as the flower senesced (Fig. 1).

3.3. *Respiration and ethylene production during senescence.* Production of ethylene by daylily flowers was below the limits of detection (5 nl/flower/hr) of our experimental system. The respiration of the flowers was high, and fairly constant during opening, rose somewhat as the flowers started to senesce, and then fell when the perianth had collapsed completely (Fig. 2). Often the respiration subsequently increased again, probably reflecting microbial contamination of the dead petals.

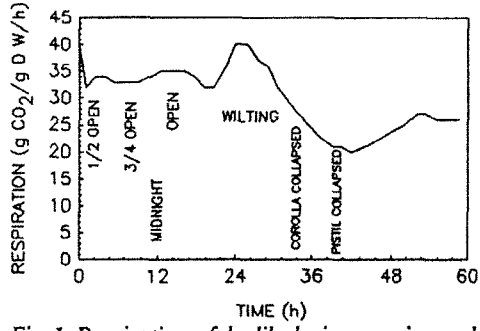

Fig. 1 Respiration of daylily during opening and senescence

3.4. *Response to applied ACC and ethylene.* The timing of senescence of daylily flowers was not appreciably affected by application of ACC, or of exogenous ethylene (data not shown).

3.5. *Effect of inhibitors.* Pretreatment of buds with AOA (to inhibit ACC synthase) or silver thiosulfate (to block the action of ethylene) had no effect on the longevity of daylily flowers. Treatment with the BA was also without visible effect. When treated with cycloheximide, daylily buds did not open (data not shown). When flowers were treated with this inhibitor during the rapid opening period (midnight), opening was unaffected, but flower longevity was greatly prolonged (Fig 3). The flowers lasted several days in the vase and wilted gradually without the normal rapid collapse and leakage of cell contents.

4. Discussion

The daylily proved to be a useful and readily manipulable system for studying rapid (bulb-type) flower senescence. The respiratory climacteric accompanying rapid petal collapse was not associated with the ethylene climacteric observed in flowers like carnations and petunias. In recent studies maximizing sensitivity (Stead *et al.*, unpublished), we have found that the senescing petals do produce a small amount of ethylene (1 nl/g F W/hr). The fact that application of ethylene, application of ACC, and treatment with inhibitors of ethylene biosynthesis or ethylene action have no perceptible effect on senescence of these flowers suggests that the process is not controlled by ethylene.

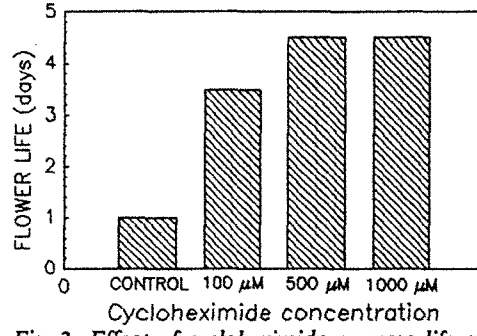

Fig. 3 Effect of cycloheximide on vase life of daylily flowers

Daylily flowers continue to respire throughout senescence, with a peak of activity during the time of most rapid wilting. This respiratory increase is from the corolla, since the respiration of the non-senescing portions of the flower (gynoecium and pedicel) changes little during senescence. As in other climacteric tissues, therefore, the wilting of senescing daylily corollas is not an uncontrolled destruction of tissue, therefore, but a coordinated series of events requiring continued metabolism.

Since daylily petal senescence is an active metabolic process, it is probable that gene derepression, mRNA and protein synthesis are involved. This hypothesis is supported by the dramatic effects on their senescence of cycloheximide, a nonspecific protein synthesis inhibitor that acts by blocking the peptidyl transferase activity of the 60S ribosomal subunit in eukaryotes. Apparently, then, daylily senescence involves the production of a protein or proteins that direct or are responsible for rapid wilting. Isolation and characterization of these proteins and their associated nucleotides would provide tools for studying bulb-type senescence, and, in the future, means of manipulating it.

References

Cameron, A.C. and Reid, M.S., 1983. Use of silver thiosulfate to prevent flower abscission from potted plants. Scientia Hortic. 19:373-378.

Davis, B.A., 1954. Daylilies and how to grow them.

Farnham, D.S., Reid, M.S. and Fujino, D.W., 1981. Shattering of snapdragons - effects of silver thiosulfate and ethephon. Acta Hortic. 113:39-43.

Halevy, A.H. and Mayak, S., 1979. Senescence and postharvest physiology of cut flowers. Part I. Horticultural Review 1:204-236.

Halevy, A.H. and Mayak, S., 1981. Senescence and postharvest physiology of cut flowers. Part II. Horticultural Review 3:59-143.

Hemerocallis Journal (1963-1985).

Reid, M.S., Paul, J.L., Farhoomand, M.B., Kofranek, A.M. and Staby, G.L. 1980. Pulse treatments with the silver thiosulfate complex extend the vase life of cut carnations. Journal of the American Society of Horticultural Science 105:25-27.

Stout, A.B., 1986. *Daylilies*. Sagapress, Inc. New York.

Whitehead, C.S., Halevy, A.H. and Reid, M.S., 1978. Control of ethylene synthesis during development and senescence of carnation petals. Journal of the American Society of Horticultural Science 109:473-475.

Yang, S.F. and Pratt, H.K., 1978. The physiology of ethylene in wounded plant tissues. In: Biochemistry of Wounded Plant Tissues. Kahl, G., editor. Berlin.