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POST-POLLINATION PHENOMENA IN ORCHID FLOWERS. IV. EFFECTS OF ETHYLENE[1, 2]

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ABSTRACT

Treatment of *Cymbidium* (Orchidaceae) flowers with 10 μl/liter ethylene for up to 78 hr induces anthocyanin formation in both gynostemia (columns) and labella (lips). After that, pigment levels decrease. During 24-hr exposures, ethylene concentrations of 0.1, 1, and 10 μl/liter cause increased anthocyanin levels in both lips and columns. Ethylene also brings about color changes in the calli and wilting of the perianth, but it does not cause straightening of gynostemia and stigmatic closure. Emasculation effects are similar to those of ethylene, whereas pollination and NAA induce anthocyanin formation and closing of stigmas, as well as swelling and loss of curvature in gynostemia. The effects of ethylene are correlated with its action in other systems.

ETHYLENE CAUSES certain post-pollination phenomena in orchid blossoms including anthocyanin formation, fading, shortened flower life, and wilting of sepal tips known as "dry-sepal" injury (Crocker, Zimmerman, and Hitchcock, 1932; Lindner, 1946; Davidson, 1949; Fischer, 1950; Akamine and Sakamoto, 1951; Jester, 1952; Saylor, 1954; Kendrick et al., 1956; Middleton et al., 1956; Anonymous, 1960; Akamine, 1963; Burg and Dijkman, 1967; Clayton and Platt, 1967; Dijkman and Burg, 1970; Hindawi, 1970). Pollination, emasculation, and auxin treatments can all cause ethylene evolution which, at least in *Vanda*, is autocatalytic (Akamine, 1963; Burg and Dijkman, 1967; Dijkman and Burg, 1970). This is particularly noticeable during shipment of flowers in closed containers, where damage such as simple dislodgement of pollinia, can induce ethylene evolution from a single flower (Akamine and Sakamoto, 1951). When this happens, a blossom may evolve enough ethylene to cause either direct damage or bring about production by other flowers. Eventually enough ethylene may accumulate in a box to damage all blossoms.

Since auxins induce ethylene formation in a number of systems, including orchids (Burg and Dijkman, 1967), some of their effects have been attributed to the gas. The same is true regarding several post-pollination phenomena in orchid flowers (Burg and Dijkman, 1967; Arditti, 1969, 1971a, b; Arditti and Knauft, 1969; Dijkman and Burg, 1970; Knauft, Arditti, and Flick, 1970; Arditti, Flick, and Jeffrey, 1971; Arditti, Jeffrey, and Flick, 1971). In addition, both abscisic acid (ABA) and gibberellin (GA) have been suggested to initiate ethylene evolution (Addicott and Lyon, 1969; Pratt and Goeschl, 1969). Therefore, their effects on orchid flowers could be due, at least in part, to ethylene evolution they may induce. Thus, to understand the causes of post-pollination phenomena in *Cymbidium* flowers better, it was necessary to determine the exact effects of ethylene itself.

MATERIALS AND METHODS—Flowers of *Cymbidium* 'Samarkand' (Dos Pueblos Orchid Co., Goleta, California) were selected for uniformity and freshness. Ovaries and pedicels were surface sterilized by a 5-minute immersion in saturated calcium hypochlorite (Wilson, 1915)—a treatment previously shown to have no deleterious effects. The flowers were then inserted into rubber-capped tubes (Acme Glass and Vial Co., Los Angeles, CA.) containing a modified Knudson C medium (Knudson, 1946; Ito, 1961; Arditti and Knauft, 1969). Culture vessels and media were sterilized by autoclaving several days before they were used to allow for dissipation of any ethylene

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[2] See Arditti and Knauft, 1969, for part I; Arditti, Flick, and Jeffrey, 1971, for part II; and Arditti, Jeffrey, and Flick, 1971, for part III.

TABLE 1. *Effects of 10 μl/liter ethylene on* Cymbidium *cv Samarkand flowers one week after treatment with ethylene and/or auxin*

Treatment	Duration, hours	Column width, mm[a]	Condition of			
			Stigma	Column	Calli[b]	Sepals & Petals[c]
Untreated	0	10.3	open	curved	Y	NW
Untreated	164	10.6	open	curved	O	NW
Pollinated	164	14.3	closed	straight	R	SW
Emasculated	164	11.0	open	curved	R	SW
Lanolin	164	11.0	open	curved	YO	NW
NAA (25 μg/flower)	164	16.3	closed	straight	OR	SW
Ethylene (10 μl/liter)	½	10.8	open	curved	OR	VSW
Ethylene (10 μl/liter)	1	10.5	open	curved	OR	VSW
Ethylene (10 μl/liter)	2½	10.5	open	curved	OR	VSW
Ethylene (10 μl/liter)	5½	10.0	open	curved	OR	VSW
Ethylene (10 μl/liter)	7	11.5	open	curved	OR	VSW
Ethylene (10 μl/liter)	16	11.0	open	curved	OR	VSW
Ethylene (10 μl/liter)	21½	10.5	open	curved	OR	SW
Ethylene (10 μl/liter)	64	10.8	open	curved	OR	SW
Ethylene (10 μl/liter)	78	10.5	open	curved	OR	SW
Ethylene (10 μl/liter)	111	11.0	open	curved	OR	SW
Ethylene (10 μl/liter) plus NAA (25 μg/flower)	164	15.0	closed	straight	OR	SW

[a] Indicative of swelling, measured along the lower edge of the stigma.
[b] *O*, orange; *R*, red; *Y*, yellow.
[c] *NW*, not wilted; *SW*, slightly wilted; *VSW*, very slightly wilted.

that might be produced by the autoclaved rubber caps.

Treatments were carried out in 1-liter jars whose lids were fitted with ampule caps. One flower was placed in each jar. Ethylene was introduced with disposable plastic syringes. The jars were placed on a laboratory bench at room temperature under fluorescent lights and 16-hr photoperiods. In experiments designed to determine the effects of different ethylene concentrations (0.1, 1, and 10 μl /liter) exposure lasted 24 hr (Fig. 2). In order to determine the effects of prolonged exposure, flowers were subjected to 10 μl/liter ethylene for periods ranging from ½ to 164 hr (Table 1; Fig. 1). NAA was applied at 25 μg/flower (Arditti and Knauft, 1969).

Anthocyanins were extracted by steeping and maceration in 1 % methanolic HCl (Arditti, Flick, and Jeffrey, 1971) one week after the experiments were started. The homogenates were centrifuged to remove debris and adjusted to a constant volume (25 ml). Optical density at 525 nm (OD_{525}) was determined in a Beckman DBG spectrophotometer. Concentration of anthocyanins is expressed as OD_{525}/g tissue (Arditti and Knauft, 1969). Since pollinated or NAA-treated columns swell and increase in fresh weight, values for these treatments were corrected by calculating OD_{525}/g tissue on the basis of unswollen columns whose average weight was 1.5 g (Fig. 3).

Wilting, color of calli, straightening of the column, and condition of the stigmas are described in subjective terms. Swelling of the columns was measured as width at the lower edge of the stigma (Arditti, Flick, and Jeffrey, 1971; Arditti, Jeffrey, and Flick, 1971).

All experiments were replicated three times. The values presented are averages of all replications, except in a few cases where individual flowers were damaged.

RESULTS—Ethylene (10 μl/liter) did not cause stigmatic closure or swelling of columns, but it did bring about color changes in the calli and slow, yet perceptible, wilting (Table 1).

Anthocyanin content at the end of one week varied in flowers exposed to 10 μl/liter ethylene for less than an hour. Following longer exposures, anthocyanin content after 7 days increased and remained high (Fig. 1). Gynostemia (also known as columns—a fusion of stamens, styles, and stigmas) and labella (or lips—a modified petal) followed parallel courses, but the latter contained more anthocyanins (Fig. 1).

After 24-hr exposure to 0.1 μl/liter ethylene, anthocyanin content in columns of treated flowers was higher at the end of one week than that in columns of fresh flowers but about equal to that in columns of blossoms kept in 1-liter jars for 164 hr (Fig. 2, 3). The effects of 1.0 μl/liter ethylene were less pronounced following 7 days, whereas 10 μl/liter caused a marked increase. After the same period of time, 0.1 and 1.0 μl/liter ethylene had no appreciable effect on anthocyanin content

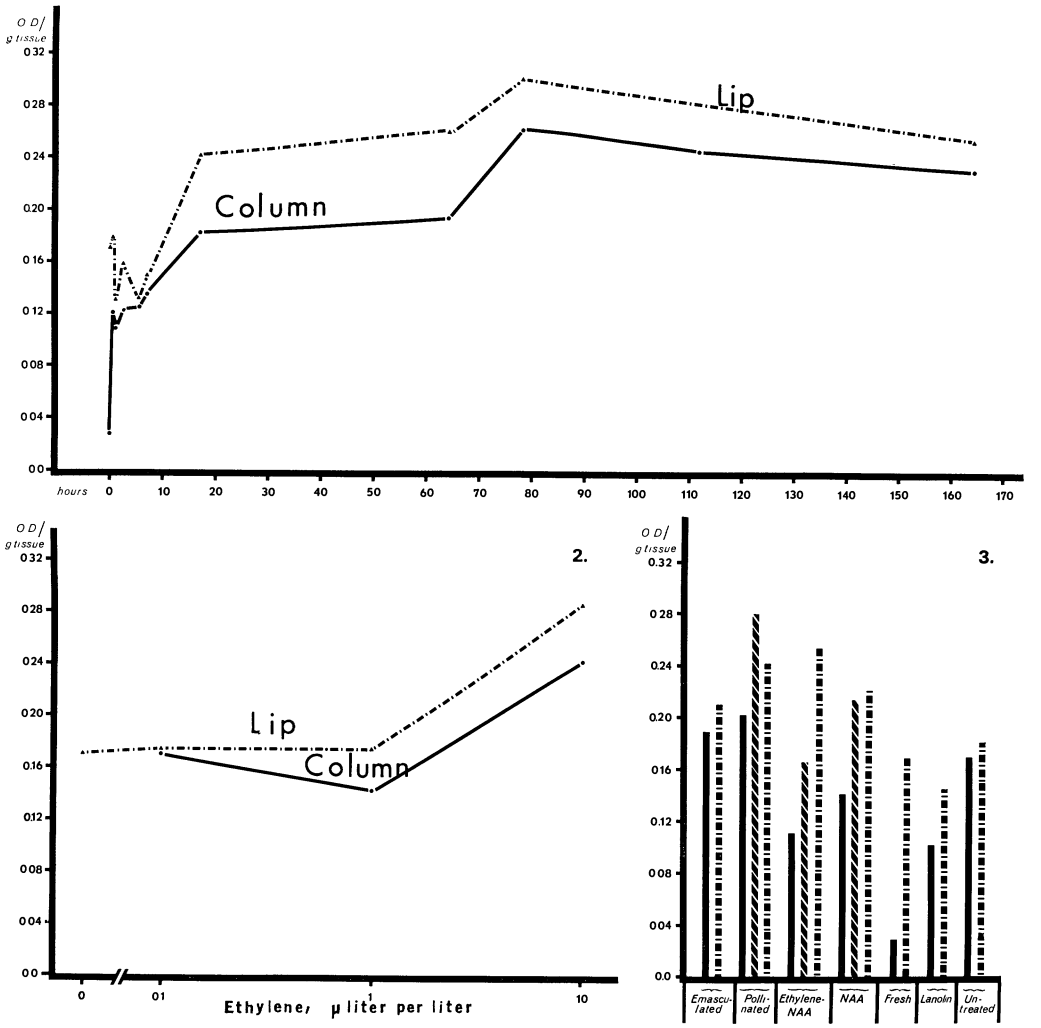

Fig. 1–3. **1.** Anthocyanin levels in *Cymbidium* 'Samarkand' columns (gynostemia) and lips (labella) following exposure to 10 µl/liter ethylene over extended periods of time. Inasmuch as there were no marked visual changes in flowers not subjected to ethylene, none were extracted until the end of the experiment. **2.** Anthocyanin content in *Cymbidium* 'Samarkand' columns (gynostemia) and lips (labella) one week after a 24-hr exposure to 0.1, 1.0, and 10 µl/liter ethylene. **3.** Anthocyanin concentration in *Cymbidium* 'Samarkand' flowers: Fresh, untreated, emasculated, pollinated, and following applications of NAA (25 µg/flower) plus ethylene (10 µl/liter) or lanolin. Bars, gynostemia (columns); dashed lines, labella (lips); slashed line, gynostemia corrected for swelling. In all cases, anthocyanins were extracted and measured one week after the start of the experiments.

in labella, but 10 µl/liter increased pigment levels considerably (Fig. 2).

Within a week after emasculation, anthocyanin formation in columns roughly equaled that brought about by 16-hr exposure to 10 µl/liter ethylene (Fig. 1, 3). During the same period, pollination induced anthocyanin levels (uncorrected) in gynostemia close to those obtained following 64-hr exposures to ethylene (Fig. 1, 3). In labella, concentrations 7 days after pollination were also equal to those resulting from 64-hr exposures to 10 µl/liter ethylene and somewhat higher than in emasculated flowers (Fig. 1, 3).

Ethylene (10 µl/liter) plus NAA (25 µg/flower) brought about anthocyanin levels (uncorrected) for columns equaling those obtained following 1-hr exposures. When these values are corrected for swelling, they rise to just below those following a 16-hr treatment with ethylene only (Fig. 1, 3). Levels in the labella are also very similar to flowers exposed for 16 hr to 10 µl/liter ethylene (Fig. 1, 3).

One week after the application of only NAA, anthocyanin content in labella increased to levels equaling those obtained following 4-hr exposure to 10 µl/liter ethylene. In columns (uncorrected)

the level equaled a 65-hr exposure, but correction brought the concentration up to that of a 70-hr treatment.

DISCUSSION—In *Cymbidium*, column swelling seems to be the result of radial enlargement rather than proliferation of cells (Hubert and Maton, 1939). This response is typical of that mediated by ethylene (Burg and Burg, 1966; Chadwick and Burg, 1967). For this reason the swelling of orchid columns following pollination or auxin treatment can be interpreted as being a typical ethylene effect. The swelling could also be due to a combination of effects resulting either from pollination (i.e., pollen-borne growth factors) or experimental application of ethylene and/or auxins. Pollination or auxin cause swelling and straightening of the column as well as stigmatic closure in *Cymbidium* flowers. Ethylene does not, indicating that these aspects of post-pollination are not mediated by the gas. It is possible, of course, that the response to ethylene by other orchid species may not be like that of *Cymbidium*.

An influx of water into the column is brought about by pollination or auxin treatments (Hubert and Maton, 1939; Oertli and Kohl, 1960; Harrison and Arditti, unpublished). It would seem, therefore, that auxins cause swelling of the columns simply by increasing the plasticity of the cell walls. This, in turn, would bring about cell expansion due to increased water uptake. Presence of ethylene may stimulate radial enlargement to a larger degree, but the gas alone has no effect on swelling and straightening of *Cymbidium* columns.

Stigmatic closure and straightening of the columns are also initiated by auxin and pollination (Arditti and Knauft, 1969). Other plant hormones we have used cannot induce them, although combinations of 10 μg/flower kinetin with 0.01 μg/flower, 0.05 μg/flower, or 0.1 μg/flower ABA cause stigmatic closure, but not column straightening. Histological evidence suggests that, like stigmatic closure, swelling may be due to an increase in cell size (Hubert and Maton, 1939). As with swelling of the column, these phenomena cannot be induced by treatment with ethylene only. Auxin (NAA) and pollination cause ethylene formation in *Cymbidium* (Chadwick, Hogan, and Arditti, unpublished) as they do in *Vanda* (Burg and Dijkman, 1967; Dijkman and Burg, 1970). There are also good reasons to believe that dislodgement of *Phalaenopsis* (Orchidaceae) pollinia may have the same effect (Curtis, 1943). No information is available at present regarding the sites(s) of ethylene evolution in either *Phalaenopsis* or *Cymbidium* flowers. In *Vanda* 'Petamboeran', ethylene production following auxin treatment is centered in the column for up to 10 hr. After 10 hr, production by the lip exceeds that of the column (Dijkman and Burg, 1970). Following treatments with 10 μl/liter ethylene, production is lower and initiated later; and even after 24 hr, the column produces more than the lip.

Increased ethylene production following pollination has been reported in flowers of *Vaccinium angustifolium* Ait (lowbush blueberry) and strawberry, *Fragaria ananasa* Duch 'Cavalier' (Hall and Forsyth, 1967). IAA also caused increased ethylene production in *Vaccinium angustifolium* flowers. Stigmas and styles of unpollinated blueberry flowers produce the greatest amounts of ethylene (136.58 μg/100 g fresh weight vs. 1.58 μg /100 g fresh weight for corolla and stamens). The same organs may also produce ethylene in orchids since dislodgement of pollinia involves the interface between viscidium and rostellum (a nonfunctional stigma). It would, therefore, be interesting to determine exactly which part of an orchid flower is most intimately connected with ethylene evolution and its control. The reports for *Vaccinium angustifolium* and surgical experiments with *Cymbidium* (Arditti, unpublished) point to interesting physiological roles for the rostellum.

ABA enhances ethylene producton in bean explants and citrus fruits (Addicott and Lyon, 1969) and GA may have similar effects in some systems (Pratt and Goeschl, 1969). In rose petals, ethylene induces "an increase in abscisic acid activity which in turn may control ethylene evolution via a feedback mechanism" (Mayak and Halevy, 1972). It is not inconceivable that similar mechanisms may exist in *Cymbidium* flowers and could be used to explain the effects of GA and ABA on their post-pollination phenomena.

Ethylene has been implicated in the induction of anthocyanin production by ripening fruits (Biale, 1950; Craker, 1971) and certain vegetative tissues (Craker, Standley, and Starbuck, 1971). In the latter, ethylene may stimulate or retard anthocyanin formation, depending on experimental conditions. The same is true in orchids. Ethylene may enhance anthocyanin formation or loss (the former in *Cymbidium* and the latter in *Vanda*) depending on species or duration of treatment (as in *Cymbidium*).

Exposures to ethylene of up to 78 hr increased anthocyanin content in both columns and labella after a week. With larger exposures, pigment levels dropped slightly (Fig. 1), suggesting that both processes may be occurring sequentially. Thus, it appears that ethylene may play two roles in connection with anthocyanins. It can raise their levels, probably by enhancing synthesis, and also stimulate their destruction. In *Cymbidium* flowers, degradation, if it occurs, seems to be preceded by synthesis. Not so in fading *Vanda* flowers where destruction seems to be the only process. A situation similar to that in *Cymbidium* occurs in sorghum seedlings where initial treatment with ethylene induces anthocyanin produc-

tion, whereas continuous presence of the gas inhibits its formation (Craker, et al., 1971). It is unclear what determines the sequence of events. Possibly, ethylene initiates destruction of anthocyanin only when pigment content is relatively high, or exceeds threshold levels.

Depending on the species and plant or tissue age, auxin, gibberellins, kinetin, and abscisic acid have all been shown to enhance or depress anthocyanin content. Therefore, it is not surprising that ethylene behaves in a similar fashion, but, as with the other hormones, presently available information is insufficient for definitive conclusions regarding its mode of action.

Emasculation-induced post-pollination phenomena are of the type caused by ethylene (Table 1, Fig. 3). Anthocyanin production in gynostemia roughly equals that of a 64-hr exposure to 10 μl/liter ethylene or, by interpolation, 5 μl/liter for 24 hr. Indeed, removal of pollinia initiates ethylene evolution in *Cymbidium* flowers as it does in *Vanda* blossoms (Burg and Dijkman, 1967; Dijkman and Burg, 1970; Chadwick, Hogan, and Arditti, unpublished).

Raised anthocyanin levels are just one post-pollination phenomenon in *Cymbidium* flowers. In unpollinated, hormone-treated flowers they are merely a prelude to death for both columns and labella. Pollination does not change this for the labellum, but in the columns, the appearance of anthocyanins precedes development of chlorophyll and a modification in function. Anthocyanin production cannot, therefore, be considered to be a mere aspect of aging. Initially, anthocyanins may render a pollinated flower unattractive to pollinators (Arditti, Jeffrey, and Flick, 1971). With wilting (Table 1), anthocyanin levels in labella and columns drop (Fig. 1, 2, 3), due to destruction. This may allow for the transport and recycling of some of their components from the lips and columns as well as unmask the newly synthesized chlorophyll in gynostemia.

A combination of 10 μl/liter ethylene and 25 μg NAA/flower decreased anthocyanin content relative to treatments with the gas only (Table 1; Fig. 2, 3). Levels in the labellum increased relative to applications of only NAA but were reduced in the columns. The combination does not prevent swelling or stigmatic closure. All this is not fully in line with previous suggestions that ethylene and IAA from pollinia act synergistically as in the case of dry sepal (Saylor, 1954); but here, the effects may be due to supraoptimal auxin concentrations (25 μg NAA/flower). In any case, the effects of ethylene-NAA combinations resemble those of other hormone pairs (Arditti, Flick, and Jeffrey, 1971; Arditti, Jeffrey, and Flick, 1971). This tends to substantiate our previous suggestions that post-pollination phenomena, although all initiated by pollination, are each controlled in different ways. Clearly, a pollinated *Cymbidium* flower is not just wilting. On the contrary, it is a highly complex developmental system, only one aspect of which is senescence of the perianth. Other aspects include redifferentiation of gynostemia, development of ovules, recycling of substances, anthocyanin synthesis or destruction, and chlorophyll production.

LITERATURE CITED

ADDICOTT, F. T., AND J. L. LYON. 1969. Physiology of abscisic acid and related substances. Annu. Rev. Plant Physiol. 20: 139–164.

AKAMINE, E. A. 1963. Ethylene production by fading *Vanda* orchid blossoms. Science 140: 1217–1218.

———, AND H. I. SAKAMOTO. 1951. Brominated charcoal to prevent fading of Vanda orchid flowers. Amer. Orchid Soc. Bull. 20: 149–152.

ANONYMOUS. 1960. Ethylene, p. 85. *In* Technical report of California standards for ambient air quality and motor vehicle exhaust. State of California, Dept. of Public Health, Berkeley.

ARDITTI, J. 1969. Post-pollination phenomena in orchid flowers. Aust. Orchid Rev. 34: 155–158.

———. 1971a. The place of the orchid pollen "poison" and Pollenhormon in the history of plant hormones. Amer. J. Bot. 58: 480–481. (Abstr.)

———. 1971b. Orchids and the discovery of auxin. Amer. Orchid Soc. Bull. 40: 211–214.

———, B. FLICK, AND D. C. JEFFREY. 1971. Post-pollination phenomena in orchid flowers. II. Induction of symptoms by abscisic acid and its interactions with auxin, gibberellic acid and kinetin. New Phytol. 70: 333–341.

———, D. C. JEFFREY, AND B. FLICK. 1971. Post-pollination phenomena in orchid flowers. III. Effects and interactions of auxin, kinetin, or gibberellin. New Phytol. 70: 1125–1141.

———, AND R. L. KNAUFT. 1969. The effects of auxin, actinomycin D, ethionine and puromycin on post-pollination behavior in *Cymbidium* (Orchidaceae) flowers. Amer. J. Bot. 56: 620–628.

BIALE, J. B. 1950. Postharvest physiology and biochemistry of fruits. Annu. Rev. Plant Physiol. 1: 183–206.

BURG, S. P., AND E. A. BURG. 1966. The interaction between auxin and ethylene and its role in plant growth. Proc. Nat. Acad. Sci. (USA) 55: 262–269.

———, AND M. J. DIJKMAN. 1967. Ethylene and auxin participation in pollen-induced fading of Vanda orchid blossoms. Plant Physiol. 42: 1648–1650.

CHADWICK, A. V., AND S. P. BURG. 1967. An explanation of the inhibition of root growth caused by indole-3-acetic acid. Plant Physiol. 42: 415–420.

CLAYTON, G. D., AND T. S. PLATT. 1967. Evaluation of ethylene as an air pollutant affecting plant life. J. Amer. Hyg. Assoc. 28: 151–160.

CRAKER, L. E. 1971. Postharvest color promotion in cranberry with ethylene. Hort. Sci. 6: 137–139.

———, L. A. STANDLEY, AND M. J. STARBUCK. 1971. Ethylene control of anthocyanin synthesis in sorghum. Plant Physiol. 48: 349–352.

CROCKER, W., P. W. ZIMMERMAN, AND A. E. HITCHCOCK. 1932. Ethylene-induced epinasty of leaves and the relation of gravity to it. Contrib. Boyce Thompson Inst. 4: 177–218.

CURTIS, J. T. 1943. An unusual pollen reaction in Phalaenopsis. Amer. Orchid Soc. Bull. 11: 258–260.

DAVIDSON, O. W. 1949. Effects of ethylene on orchid flowers. Proc. Amer. Soc. Hort. Sci. 53: 440–446.

DIJKMAN, M. J. AND S. P. BURG. 1970. Auxin-induced spoiling of *Vanda* blossoms. Amer. Orchid Soc. Bull. 39: 799–804.

FISCHER, C. W. 1950. Ethylene gas—A problem in cut-flower storage. Bull. N. Y. State Flower Growers 61: 1–4.

HALL, I. V., AND F. R. FORSYTH. 1967. Production of ethylene by flowers following pollination and treatment with water and auxin. Can. J. Bot. 45: 1163–1166.

HINDAWI, I. J. 1970. Ethylene injures vegetation in urban areas, p. 32. *In* Air pollution injury to vegetation. National Air Pollution Control Administration Publication No. AP-71. U.S. Dept. of Health, Education and Welfare, Public Health Service, Environmental Health Service, Raleigh, N.C.

HUBERT, B., AND T. MATON. 1939. The influence of synthetic growth-controlling substances and other chemicals on post-floral phenomena in tropical orchids. Biol. Jaarboek 6: 244–285.

ITO, I. 1961. In vitro culture of ovary and seed in orchids. Olericulture Lab. Fac. Agr. Kyoto Prefect. Univ., Kyoto.

JESTER, R. A. 1952. A study of dried sepal injury to orchid flowers. M.S. Thesis. Rutgers University, New Brunswick, N. J.

KENDRICK, J. B., JR., E. F. DARLEY, J. T. MIDDLETON, AND A. O. PAULUS. 1956. Plant response to polluted air. Calif. Agric. 10: 9–15.

KNAUFT, R. L., J. ARDITTI, AND B. FLICK. 1970. Postpollinationphänomene an Orchideenblüten. Die Orchidee 22: 132–135.

KNUDSON, L. 1946. A new nutrient solution for germination of orchid seed. Amer. Orchid Soc. Bull. 15: 214–217.

LINDNER, R. C. 1946. Studies on packaging and storage of *Vanda* (Joaquim) flowers. Hawaii Agr. Exp. Sta. Progress Notes, Univ. of Hawaii 49: 1–5.

MAYAK, S., AND A. H. HALEVY. 1972. Interrelationship of ethylene and abscisic acid in the control of rose petal senescence. Plant Physiol. 50: 341–346.

MIDDLETON, J. T., A. S. CRAFTS, R. F. BREWER, AND O. C. TAYLOR. 1956. Plant damage by air pollution. Calif. Agric. 10: 9–10.

OERTLI, J. D., AND H. C. KOHL. 1960. Der Einfluss der Bestäubung auf die Stoffbewegungen in Cymbidiumblüten. Gartenbauwissenschaft 25: 107–114.

PRATT, H. K., AND J. D. GOESCHL. 1969. Physiological roles of ethylene in plants. Annu. Rev. Plant Physiol. 20: 541–584.

SAYLOR, J. C., JR. 1954. A study of ethylene-induced injury to orchid flowers. M.S. Thesis. Rutgers University, New Brunswick, N.J.

WILSON, J. K. 1915. Calcium hypochlorite as a seed sterilizer. Amer. J. Bot. 2: 420–427.