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POSTPOLLINATION PHENOMENA IN ORCHID FLOWERS. VIII. WATER AND DRY WEIGHT RELATIONS[1]

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Pollination causes increases in FW and DW of *Cymbidium* ovaries and gynostemia. It also initiates FW losses in perianth segments. Auxin (NAA) applications to the stigma have the same effects except that FW of ovaries decreases. All segments of unpollinated flowers increased in DW, whereas FW variations were minimal. These weight changes reflect the aging and subsequent death and/or redifferentiation and further development of pollinated and/or unpollinated orchid flowers.

Introduction

Wilting of sepals, petals, and labella (lips); swelling of gynostemia (columns) which subsequently become green; and increases in the diameter of ovaries are among the most easily observable postpollination phenomena in orchid flowers. One intuitive explanation (HUBERT and MATON 1939; HSIANG 1951*a*) for these phenomena is water gains in organs which swell and water losses in those that wilt. Increases and decreases in dry-matter content of floral segments may also occur, thereby affecting FW and DW. The available evidence indicates that, after pollination, substances are mobilized from the perianth into gynostemia and ovaries (FITTING 1909*a*, 1909*b*, 1910; SCHUMACHER 1931; SESHAGIRIAH 1941; OERTLI and KOHL 1960; HARRISON and ARDITTI 1976).

Should the movement of water and dry matter be simultaneous, FW changes would reflect both, whereas DW variations can indicate only the latter. The relationship between water and dry matter determines the hydration of tissues and is expressed as HV (BALDOVINOS 1953; HINNAWI 1973), which is a parameter that can provide information on whether the gains or losses of dry matter and water differ in magnitude.

Material and methods

FLOWERS.—Racemes of *Cymbidium* 'Jungfrau' (lathhouse-grown plants, U.C.I. orchid collection), harvested after all but the two or three apical buds had opened, were placed in water for 12–16 h. Flowers were cut at the pedicel base just before the start of the experiments. Ovaries and pedicels were decontaminated by a 5-min immersion in saturated calcium hypochlorite (ARDITTI and KNAUFT 1969).

CULTURE MEDIUM AND CONDITIONS.—Modified Knudson C medium (ITO 1961) was dispensed into rubber-capped tubes of the kind used to ship orchid flowers (Acme Glass and Vial Co., Los Angeles), sterilized by autoclaving, and allowed to stand on a bench top for 48 h to allow for dispersion of any ethylene which might be produced by the caps as a result of the sterilization. Pedicels were inserted through holes in the rubber caps (ARDITTI, JEFFREY, and FLICK 1971*b*), and the tubes were placed in small cans. All flowers were maintained at room temperature under continuous light and a light intensity of 0.85 mW/cm² provided by two 40-W Gro-Lux lamps.

TREATMENTS.—One-third of the flowers were self-pollinated. Auxin (25 g NAA per flower) was applied in 5 μl drops of warm liquefied lanolin to the stigmas of flowers of a second group. Untreated flowers served as controls, since lanolin had no significant effects in previous studies (ARDITTI and KNAUFT 1969; ARDITTI, FLICK, and JEFFREY 1971*a*; ARDITTI et al. 1971*b*).

SAMPLING.—Flowers were harvested 0, 3, 8, 24, 48, 96, and 168 h after the treatments (HARRISON and ARDITTI 1976) and divided into gynostemia (columns, one per flower), ovaries (one per flower), dorsal (median) sepals (one per flower), lateral sepals (two per flower), petals (two per flower), and labella (lips, median sepals; one per flower). The segments were weighed while fresh, dried at 80 C for 24 h, and reweighed. In preliminary experiments, longer drying periods did not result in additional weight losses. Initial weights were obtained from 10 freshly cut untreated flowers. Results were uniform and are presented as FW, DW, and HV (figs. 1–4) and percentage of gain (+) or loss (−) at the end of the experiment (table 1). All treatments were replicated nine times.

Results

UNTREATED FLOWERS.—The DW of all segments increased (figs. 1*a*, 2*a*, 3*a*, 4*a*; table 1). Gains in the perianth were smaller than in the gynostemia and ovaries (table 1). After 24 h, the DW of all segments

[1] Abbreviations used: DW = dry weight; FW = fresh weight; HV = hydration value (FW-DW)/DW; NAA = naphthaleneacetic acid.

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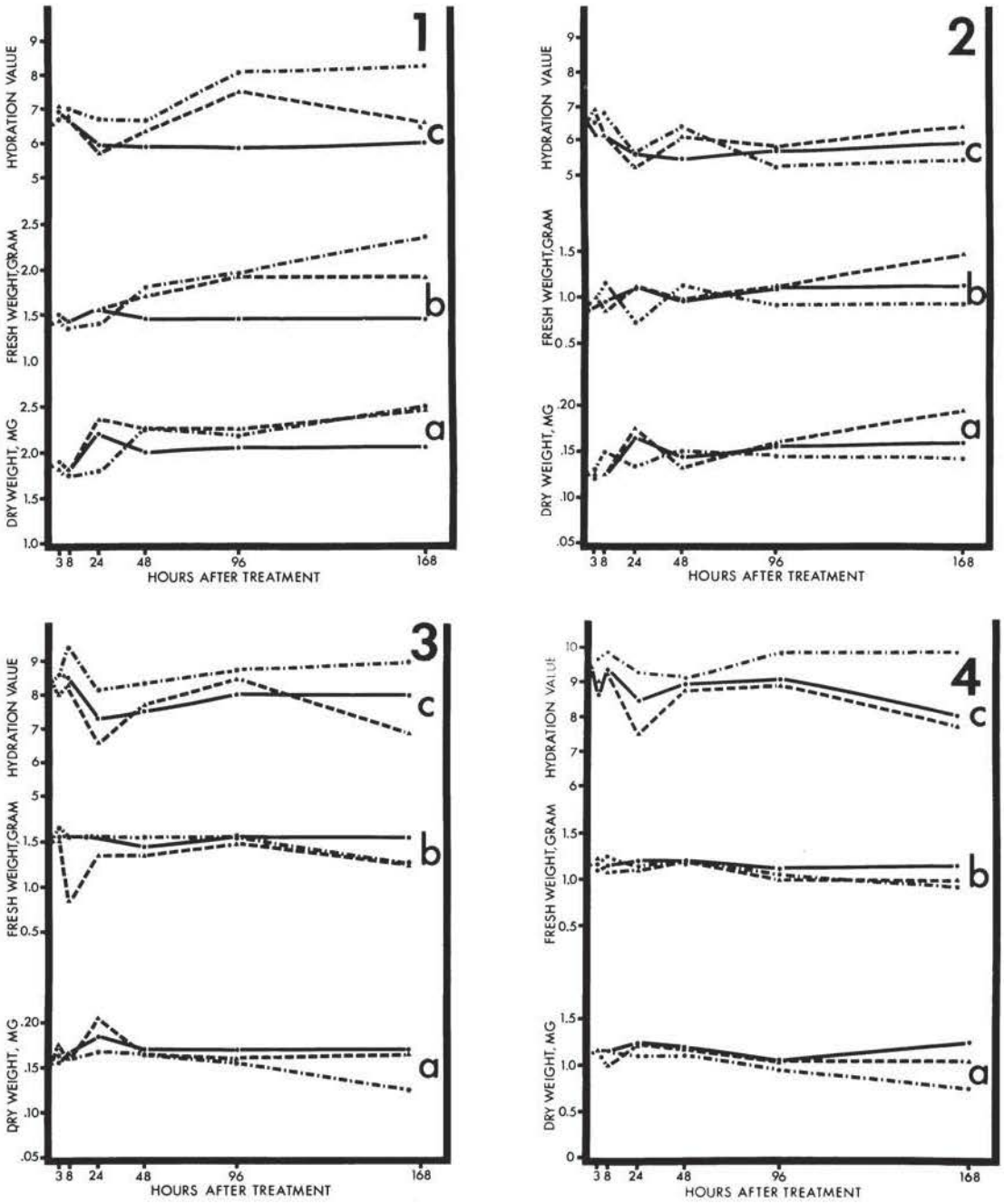
had increased; it dropped at 48 h and did not change very much thereafter (figs. 1*a*, 2*a*, 3*a*, 4*a*).

Labella (fig. 3*b*) and sepals (fig. 4*b*) showed no FW changes, but petals (table 1) and ovaries (fig. 2*b*) gained. Gynostemia (fig. 1*b*) lost FW slightly. Gains in FW by the gynostemia and ovaries were 5 times higher than those of the perianth (table 1).

Except labella, all floral segments decreased in HV (table 1). Following a drop at 24 h, HV of ovaries (fig. 2*c*) and labella (fig. 3*c*) increased, but by the end of 168 h still showed a loss. Petals, which behaved like the other perianth segments, as exemplified by dorsal sepals (fig. 4*c*), decreased in HV at 24 h, increased during the next 72 h, and then dropped again. The HV of columns (fig. 1*c*) decreased during the first 24 h and did not change thereafter.

POLLINATED FLOWERS.—Small DW gains were



FIGS. 1–4.—FW, DW, and HV in floral segments of *Cymbidium*. Fig. 1, Gynostemium (column). Fig. 2, Ovary. Fig. 3, Labellum (lip). Fig. 4, Dorsal sepal. Explanation of symbols: *a*, DW; *b*, FW; *c*, HV. Solid line and solid circles, control; single (equal length) dashes with triangles, pollinated flowers; double (unequal length) dashes and asterisks, NAA-treated blossoms. DW ranges from 10.0 to 2.5 mg; FW from 0.5 to 2.5 g, and HV from 5 to 10.

TABLE 1

FW AND DW CHANGES IN UNDISTURBED, POLLINATED, AND NAA-TREATED CYMBIDIUM FLOWERS AND THEIR SEGMENTS

	Initial weight, g			Gain or loss after 168 h, % of initial weight								
				Control			Pollinated			NAA		
Floral segments	FW	DW	HV	FW	DW	HV	FW	DW	HV	FW	DW	HV
Labellum (lip)[a]	1.5	.16	8.4	0	+6.3	+17.9	−14.5	+1.9	−18.2	−15.7	−21.9	+7.1
Ovary[a]	.95	.125	6.6	+17.9	+30.4	−9.0	+43.8	+55.2	−4.0	− 2.9	+12.0	−15.5
Gynostemium (column)[a]	1.4	.185	6.57	−.6	+5.4	−6.5	+37.0	+34.0	−.1	+65.4	+35.1	+25.7
Lateral petals[b]	1.4	.14	9.0	+6.0	+4.7	−4.7	−18.0	+3.5	−23.2	+23.8	−28.5	+7.3
Dorsal sepals[a]	1.15	.11	9.45	0	+37.9	−13.2	−20.9	−5.5	−23.28	−26.7	−25.0	+5.0
Lateral sepals[a]	1.85	.195	8.48	0	+12.8	−9.8	−17.2	0	−18.1	−23.0	−24.1	+3.6
Lateral petals and labellum[c]	2.9	.3	8.67	+2.9	+8.3	−9.1	−16.1	+2.7	−20.5	−20.1	−25.0	+7.15
All sepals[c]	3.0	.305	8.83	0	+13.1	−12.9	−18.7	−1.9	−18.9	−24.5	−26.2	+2.7
Entire perianth	5.9	.605	8.75	+1.4	+10.7	−9.3	−17.4	+.3	−19.7	−22.3	+24.0	+2.4
Gynostemium and ovary	2.35	.31	6.58	+6.9	+14.5	−7.7	+40.4	+42.5	−1.8	+37.7	+25.8	+10.9
Whole flower	8.25	.915	8.91	+9.1	+12.2	−12.6	−1.0	+14.7	−22.4	−5.2	−8.1	−6.8

[a] One per flower. [b] Two per flower. [c] A total of three.

evident in labella (fig. 3*a*) and petals, whereas ovaries (fig. 2*a*) and gynostemia (fig. 1*a*) showed much larger increases (table 1). The perianth remained unchanged, and the DW of whole flowers increased (table 1).

Ovaries (fig. 2*b*) and gynostemia (fig. 1*b*) increased in FW. All perianth segments (figs. 3*b*, 4*b*) lost FW, and the net change for the entire flower was also negative (table 1).

Gynostemia (fig. 1*c*) decreased in HV during the first 24 h. Their HV increased for the next 72 h and then decreased again. The HV of ovaries (fig. 2*c*) also decreased during the first 24 h but increased by 48 h, dropped at 96 h, and showed a second increase. Labella (fig. 3*c*) and other perianth segments (fig. 4*c*) decreased in HV at 24 h, showed increases at 96 h, and registered losses thereafter.

NAA-TREATED FLOWERS.—Ovaries (fig. 2*a*) gained in DW as did gynostemia (fig. 1*a*). All other segments (figs. 3*a*, 4*a*) lost in DW. A net loss in DW was recorded for whole flowers (table 1).

All segments (figs. 2*b*, 3*b*, 4*b*) except the gynostemia (fig. 1*b*) lost in FW (table 1). Gains in FW by gynostemia were consistent from the start. The HV increases were registered by all segments (figs. 1*c*, 3*c*, 4*c*) except ovaries (fig. 2*c*), but the entire flower lost (table 1).

Discussion

UNTREATED FLOWERS (CONTROL).—The DW increases in all segments and the entire flower indicate dry matter (sugar, minerals) uptake from the culture medium. Photosynthesis may occur in green *Cymbidium* flowers (DUEKER and ARDITTI 1968), but in this flower the perianth was white. Ovaries (the only green segments) were essentially in the dark because of the position of the tubes inside the small cans. The increases in DW and losses in HV during the first 24 h also indicate dry-matter uptake regardless of water movement. Similar uptake of sucrose, fluoride (as Na^+), and red dye has been reported for *Gladiolus*, *Gerbera*, *Chrysanthemum*, and snapdragons (MAROUSKY 1971, 1972; MAROUSKY and WOLTZ 1975).

The DW losses by all segments between 24 and 48 or 96 h may be the result of reduced uptake and increased utilization, or a combination of the two. Although firm evidence is not available, it appears reasonable to assume that the increased utilization is through respiration. Reports regarding respiration in orchid flowers support this assumption despite lower rates in older blossoms (HSIANG 1951*b*; SHEEHAN 1954; ROSENSTOCK 1956). Our findings (HARRISON and ARDITTI 1976) showed that leakage (at least of ^{32}P) into the medium does not occur.

Life of *Cymbidium* flowers exceeds 1 wk. Therefore, it is not surprising that at the end of 7 days the flowers gained in DW (figs. 1*a*, 2*a*, 3*a*, 4*a*; table 1). The transpiration stream (GOLDSCHMIDT and HUBERMAN 1974) results in the uptake and accumulation of minerals and sugars from the medium. We have no evidence for active uptake.

Increases in FW (except in the labellum) after 24 h are the result of higher water uptake brought about by elevated osmotic concentrations which have been reported in orchid flowers (HSIANG 1951*a*). Reduced subsequent water uptake, increased transpiration losses, or a combination of the two can account for the low final FW (table 1). The sizable FW gains by ovaries (fig. 2*b*; table 1) are due both to water uptake and the fact that they were either submerged in medium or inside the tubes where transpiration is reduced.

Water losses occur through cuticular transpiration

in the absence of stomata on the perianth of *Cymbidium* flowers (HSIANG 1951*a*).

POLLINATED FLOWERS.—As in control flowers, gains in DW during the first 24 h are due to uptake of solutes from the medium. Uptake is also a contributing factor to the subsequent DW increases in gynostemia (fig. 1*a*) and ovaries (fig. 2*a*). One suggestion (FITTING 1909*a*, 1909*b*, 1910; SCHUMACHER 1931; SESHAGIRIAH 1941; GESSNER 1948; HARRISON and ARDITTI 1976) is that at least part of the increase is due to transport of substances from the perianth. Our data support this view with respect to the sepals (table 1).

The DW gains by the entire flower (14.7%) and petals (2.7%) were much lower than those by the ovaries and gynostemia (42.5%). Losses in DW by all sepals (1.9%) were minimal (table 1). These figures indicate that (1) uptake from the medium does take place, and (2) substances are transported preferentially into gynostemia and ovaries which act as sinks because of newly initiated developmental processes and increased metabolic activity. Selective transport has been reported for ^{32}P in *Cymbidium* (OERTLI and KOHL 1960; HARRISON and ARDITTI 1976) and tomato (ARNON, STOUT, and SIPOS 1940) flowers as well as for ^{14}C sucrose, ^{14}C-acetate, and ^{3}H-acetate in *Citrus sinensis* 'Shamouti' blossoms (GOLDSCHMIDT and HUBERMAN 1974). Creation of sinks in pollinated orchid flowers is evident (FITTING 1909*a*, 1909*b*, 1910; SCHUMACHER 1931; HUBERT and MATON 1939; SESHAGIRIAH 1941; DUNCAN and CURTIS 1942*a*, 1942*b*, 1943; GESSNER 1948; HSIANG 1951*a*, 1951*b*; ROSENSTOCK 1956; HESLOP-HARRISON 1957; OERTLI and KOHL 1960; HARRISON and ARDITTI 1976).

All perianth segments should lose DW if there is transport of dry matter from them into columns and ovaries. However, this is not the case. Labella (fig. 3*a*) and petals gained very slightly (table 1). Uptake from the medium, translocation patterns, and physiological differences between perianth segments can account for this apparent anomaly. *In situ* translocation of sugars into flowers is in the phloem, but distribution of substances taken up through cut peduncles or pedicels may be via the xylem (GOLDSCHMIDT and HUBERMAN 1974). Should this be true for *Cymbidium* flowers, the increased transpiration stream into perianth segments will bring in a higher amount of solutes. This would lead to dry-matter accumulation and gains in DW.

As can be expected in a wilting tissue, all perianth segments lose FW (figs. 3, 4; table 1). A similar decrease in the weight of cut rose flowers occurs when transpiration is greater than water uptake (MAYAK et al. 1974). Water balance is considered to be an important factor in the determination of cut-flower longevity (MAYAK et al. 1974). Our results confirm this by demonstrating that pollinated or auxin-treated flowers (which senesce and die quickly) show higher FW losses than unpollinated ones (which age and die at a slower rate). The FW gains by gynostemia (fig. 1*b*) and ovaries (fig. 2*b*) result from the increased water content which is also the reason for their swelling (HUBERT and MATON 1939).

Perianth segments (figs. 3*c*, 4*c*; table 1) become drier and have a lower HV because water losses are proportionally higher than those of dry matter. The reduced HV of gynostemia (fig. 1*c*) and ovaries (fig. 2*c*) is due to a disproportionately higher influx of water than that of dry matter.

NAA-TREATED FLOWERS.—Auxins, including NAA, can mimic pollination or emasculation in orchid flowers. The overall effect is accelerated aging, sometimes, as observed here, even more than after pollination (FITTING 1909*a*, 1909*b*, 1910; HUBERT and MATON 1939; GESSNER 1948; HSIANG 1951*a*, 1951*b*; BURG and DIJKMAN 1967; DOLCHER 1967; ARDITTI and KNAUFT 1969; ARDITTI et al. 1971*a*, 1971*b*). Hence FW and DW losses in perianth segments of NAA-treated flowers may be higher than those of pollinated blossoms. The NAA application mimics pollination in respect to DW of gynostemia (fig. 1*a*) and FW of perianth segments (fig. 3*b*, 4*b*; table 1), but not in ovaries.

Pollination initiates ovule formation in orchid ovaries, but auxin applications do not always have the same effect. Thus, NAA-treated ovaries may be senescing, and this is reflected in their FW, DW, and HV (fig. 2; table 1). In gynostemia these differences between pollination and NAA treatment may be due to (1) faster destruction of IAA (the auxin found in pollen), (2) the presence of other hormones in pollinia (R. MA, unpublished results), and/or (3) auxin-induced synthesis of other substances such as ethylene (ARDITTI, HOGAN, and CHADWICK 1973).

The observed FW, DW, and HV changes in *Cymbidium* 'Jungfrau' are fully in line with our previous observations and suggestions regarding pre- and postpollination phenomena and aging in orchid flowers. These observations also indicate that the labellum is physiologically similar to perianth segments, thereby supporting the view that it has originated from a petal (VERMEULEN 1959; NELSON 1965, 1967).

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LITERATURE CITED

ARDITTI, J., B. H. FLICK, and D. C. JEFFREY. 1971*a*. 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.

ARDITTI, J., N. M. HOGAN, and A. V. CHADWICK. 1973. Post-pollination phenomena in orchid flowers. IV. Effects of ethylene. Amer. J. Bot. **60**:833–888.

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

ARDITTI, J., and R. L. KNAUFT. 1969. The effects of auxin, actinomycin D, ethionine and puromycin on post-pollination behavior in orchid flowers. Amer. J. Bot. **56**:620–628.

ARNON, D. I., P. STOUT, and F. SIPOS. 1940. Radioactive phosphorus as an indicator of phosphorus absorption of tomato fruits at various stages of development. Amer. J. Bot. **27**:791–792.

BALDOVINOS, G. 1953. Growth of the root tip. Pages 27–54 *in* W. E. LOOMIS, ed. Growth and differentiation in plants. Iowa State College Press, Ames.

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

DOLCHER, T. 1967. Relazioni ormonali nella fruttificazione delle orchidee. III. Induzione della fruttificazione mediante trattementi auxinice. G. Bot. Ital. **101**:41–57.

DUEKER, J., and J. ARDITTI. 1968. Photosynthetic $^{14}CO_2$ fixation by green *Cymbidium* (Orchidaceae) flowers. Plant Physiol. **43**:130–132.

DUNCAN, R. E., and J. T. CURTIS. 1942*a*. Intermittent growth of fruits of *Phalaenopsis*. A correlation of the growth phases of an orchid fruit with internal development. Bull. Torrey Bot. Club **69**:167–183.

———. 1942*b*. Intermittent growth of fruits of *Cypripedium* and *Phaphiopedilum*. A correlation of the growth of orchid fruits with their internal development. Bull. Torrey Bot. Club **69**:353–359.

———. 1943. Growth of fruits in Cattleya and allied genera in the *Orchidaceae*. Bull. Torrey Bot. Club **70**:104–119.

FITTING, H. 1909*a*. Die Beeinflussung der Orchideenblüten durch die Bestäubung und durch andere Umstände. Z. Bot. **1**:1–86.

———. 1909*b*. Entwicklungsphysiologische Probleme der Fruchtbildung. Biol. Zentralbl. **29**:193–206.

———. 1910. Weitere entwicklungsphysiologische Untersuchungen an Orchideenblüten. Z. Bot. **1**:225–267.

GESSNER, F. 1948. Stoffwanderungen in bestäubten Orchideenblüten. Biol. Zentralbl. **67**:457–479.

GOLDSCHMIDT, E. E., and M. HUBERMAN. 1974. The coordination of organ growth in developing citrus flowers: a possibility for sink type regulation. J. Exp. Bot. **25**:534–541.

HARRISON, C. R., and J. ARDITTI. 1976. Post-pollination phenomena in orchid flowers. VII. Phosphate movement among floral segments. Amer. J. Bot. **63**:911–918.

HESLOP-HARRISON, J. 1957. The physiology of reproduction in *Dactylorchis*. I. Auxin and the control of meiosis, ovule formation and ovary growth. Bot. Notis. **110**:28–48.

HINNAWI, E. E. 1973. The growth responses of excised tomato roots to applied gibberellins. Z. Pflanzenphysiol. **69**:1–12.

HSIANG, T.-H. T. 1951*a*. Physiological and biochemical changes accompanying pollination in orchid flowers. I. General observations and water relations. Plant Physiol. **26**:441–455.

———. 1951*b*. Physiological and biochemical changes accompanying pollination in orchid flowers. II. Respiration, catalase activity, and chemical constituents. Plant Physiol. **26**:708–721.

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

ITO, J. 1961. In vitro culture of ovary and seed in orchids. Olericulture Lab., Fac. Agric. Kyoto Prefectual Univ. Kyoto.

MAROUSKY, F. J. 1971. Influence of 8-hydroxyquinoline citrate and sucrose on carbohydrate content of leaves and florets of cut gladiolus spikes. Acta Hort. **23**:127–131.

———. 1972. Water relations, effects of floral preservatives on bud opening, and keeping quality of cut flowers. HortScience **7**:114–116.

MAROUSKY, F. J., and S. S. WOLTZ. 1975. Relationship of floral preservatives to water movement, fluoride distribution and injury in gladiolus and other cut flowers. Acta Hort. **4**:171–182.

MAYAK, S., A. H. HALEVY, S. SAGIE, A. BAR-YOSEPH, and B. BRAVDO. 1974. Water balance of cut rose flowers. Physiol. Plantarum **31**:15–22.

NELSON, E. 1965. Zur organophyletischen Natur des Orchideenlabellums. Bot. Jahrb. Syst. Pflanzengeschichte Pflanzengeogr. **84**:174–214.

———. 1967. Das Orchideenlabellum, ein Homolog des einfachen medianen Petalums der Apostasiaceen oder ein zusammengesetztes Organ? Bot. Jahrb. Syst. Pflanzengesch. Pflanzengeogr. **87**:22–35.

OERTLI, J. J., and H. C. KOHL, JR. 1960. Der Einfluss der Bestäubung und die Stoffbewegung in Cymbidiumblüten. Gartenbauwissenschaft **25**:107–114.

ROSENSTOCK, G. 1956. Die Atmung von Orchideeninfloreszenzen im Verlaufe ihrer Vegetationsperiode. Z. Bot. **44**:77–87.

SCHUMACHER, W. 1931. Über Eiweissumsetzungen in Blütenblättern. Jahrb. Wiss. Bot. **75**:581–608.

SESHAGIRIAH, K. N. 1941. Physiology of pollination in Orchidaceae. Current Sci. **10**:30–32.

SHEEHAN, T. J. 1954. Respiration of cut flowers of *Cattleya mossiae*. Bull. Amer. Orchid Soc. **23**:241–246.

VERMEULEN, P. 1959. The different structure of the rostellum in Ophrydeae and Neottieae. Acta Bot. Neerlandica **8**: 338–355.