THE INTERACTION OF LIGHT INTENSITY, PLANT SIZE, AND NUTRITION IN SEX EXPRESSION IN *CYCNOCHES* (ORCHIDACEAE)

*Katharine B. Gregg**

Introduction

Exposure to high intensities of sunlight stimulates female flowering in species of *Catasetum* and *Cycnoches*, subtribe Catasetinae, Orchidaceae (Dodson, 1962; Gregg, 1975). The interaction of additional factors, such as nutrition and plant size, in the sex regulatory system of the Catasetinae has also been suggested (Dodson, 1962; Brubaker, 1969; Gregg, 1975).

There is much in the literature relating good nutrition, especially high nitrogen levels, to female flowering in several other species of angiosperms. Nitrogen has been found to be important in sex expression in hemp (Talley, 1934; Schaffner, 1925; Borthwick and Scully, 1954), cucumber (Tiedjens, 1928; Minina, 1938; Hall, 1949; Kooistra, 1967), muskmelon (Brantley & Warren, 1960), tomatoes (Kraus & Kraybill, 1918; Howlett, 1939), spider flower (*Cleome spinosa* L., Murneek, 1927), and spinach (Thompson, 1955).

In addition to promotion of female flowering, increased nitrogen feeding increased the growth of spider flower (Murneek, 1927). Supplemental nitrogen produced taller, healthier cucumber (Tiedjens, 1928) and hemp plants (Borthwick and Scully, 1954). Furthermore, nitrogen was more abundant in female hemp plants. These female hemp plants generally had greater total wet weights than did male plants at flowering time (Talley, 1934).

Maekawa (1926) discovered a progression from non-flowering to male-flowering to female-flowering states in plants of *Arisaema japonica* Bl. Lightweight corms did not flower; heavy corms produced female flowers; and intermediate corms produced male flowers.

Ordinarily, shade-grown plants of *Cycnoches* and *Catasetum* are moderate in size and produce only male flowers (Dodson, 1962). One orchid grower in Miami, however, has grown exceptionally large plants of *Cycnoches* with llama manure from her pet llamas. The large plants produced female as well as male flowers in the shade (B. Wilkins, personal communication). Brubaker (1969) recommended feeding plants of *Catasetum* and *Cycnoches* with sheep manure to obtain female flowers. Twelve percent of the racemes produced by large, healthy plants of *Cycnoches densiflorum* and 7% of the racemes of *C. warscewiczii* were female when sheep manure was applied to shade-grown plants in the University of Miami greenhouse in 1969 (Gregg, 1975).

This paper reports the results of experiments testing the effects of light intensity, plant size, and nutrition on sex expression in two species of *Cycnoches*. Experiments dealing with species of the genus *Catsetum* will be presented in a later paper.

The scope of the present investigation of sex expression in *Cycnoches* can be summarized by the following questions. 1) What is the relationship between plant size and sex? Do larger plants actually produce more female flowers than smaller ones? 2) What is the role of nutrition in plant growth and sex expression? Specifically, what is the effect of enriching the potting medium of *Cycnoches* with manure? Future studies might investigate the role of individual nutrients, such as nitrogen, on sex expression. 3) Is sex expression affected by interaction among the various environmental factors

Department of Biology, Wesleyan College, Buckhannon, West Virginia 26201, U.S.A.

implicated in the control of sex expression? 4) What is the possibility of incorporating the results of these studies into a reasonable physiological explanation of sex control?

Materials and Methods

Plants of *Cycnoches densiflorum* Rolfe and *C. warscewiczii* Rchb. f. were grown under conditions described previously as Greenhouse Experiments, 1970 (Gregg, 1975). At the beginning of the growing season all plants were freshly-potted and consisted of newly-rooted young pseudobulbs which matured and flowered during the experimental period. Except for the manure treatments described below, plants of *C. warscewiczii* were grown without sheep manure. All plants of *C. densiflorum* were manured and grown in medium shade (1/3 full sunlight, under 73% polypropylene mesh screening from the Chicopee Manufacturing Company of Cornelia, Georgia).

Plants of *C. warscewiczii* were divided arbitrarily into two groups, those grown in bright shade (1/2 full sunlight, under 50% polypropylene mesh screening from the above-cited company) and those grown in full sunlight. Twenty-one shade-grown plants of *C. warscewiczii* were given approximately 50 ml Armour-brand sheep manure (1.25-1.00-2.00) in one dose. The potting medium of these plants, watered daily with an overhead misting system, retained the bulk of the manure throughout the experimental period. Fifteen sun plants received approximately 50 ml manure plus two additional 15-ml doses because watering with the hose washed the manure from the pots. Since sun and shade manure treatments were different, they were not compared. Comparisons were made of plant size and sex expression between manured (21) plants and non-manured (113) plants in the shade and between manured (15) and non-manured (37) plants in the sun.

Calculation of a Pseudobulb Index (PI)

The bulk of a cycnoches plant consists of its one or more pseudobulbs which serve as both stems and storage organs. At the end of the flowering season, 25 pseudobulbs of *Cycnoches densiflorum* were weighed after removal of roots, leaves and inflorescences. Length and maximum diameter of the youngest pseudobulb of each plant were measured for all plants of *C. densiflorum* and *C. warscewiczii.* A pseudobulb index, abbreviated PI, was calculated for each plant by multiplying the length times the maximum diameter of the youngest pseudobulb. The PI was designed to facilitate plant size comparisons without severely disturbing the plants.

Statistical Methods

Quantitative data tabulated in r $\times$ 2 tables were tested for interaction using a two-way analysis of variance with unequal subclass numbers, the method of weighted squares of means (Steele & Torrie, 1960). Because there was no interaction in any of the experiments, the remainder of the analyses were carried out by t-tests using the pooled mean square calculated in the analysis of variance in place of s^2, the sample variance. The regression equation and the correlation coefficient were calculated after Goldstein (1964). Enumeration data were analyzed by the chi-square test using the Yates correction.

RESULTS

Effect of Plant Size on Sex Expression

Relationship between pseudobulb weight and pseudobulb index. A high linear correlation exists between the pseudobulb index (PI) and pseudobulb weight of plants of *C. densiflorum* (Figure 1). The correlation coefficient was 0.98 and the equation of the regression line was $y = 1.62x - 12.58$.

A similar high correlation was assumed to exist between PI and weight for *C. warscewiczii* although a regression line was not determined. The high correlation suggests that PI may be substituted for weight in the statistical analysis.

Relationship between PI and sex expression. Because the production of hermaphrodite flowers or racemes was considered an indication of radical developmental change from the male condition, female and hermaphrodite flowers were grouped in the statistical analyses. Female- and hermaphrodite-flowering plants of *C. warscewiczii* had significantly higher PI's than male-flowering plants (Table I). The PI's of female- and hermaphrodite-flowering plants ($\bar{x} = 34.7$ for 33 plants) of *C. densiflorum* were also significantly higher ($P = .001$) than those of male-flowering plants ($\bar{x} = 24.7$ for 32 plants). The mean PI of the female-flowering plants of *C. densiflorum* was 32.2, while that of the hermaphrodite-flowering plants was 45.8.

Table I. Relationship between Pseudobulb Index (PI) and Sex Expression in Plants of *Cycnoches warscewiczii.* PI was calculated by multiplying the length times the maximum diameter of the youngest pseudobulb of each plant.

	PI Mean of Male-Flowering Plants	PI Mean of Female-and Hermaphrodite-Flowering Plants
Sun-grown[1]	27.4 (4 plants)	77.2 (9 plants)
Bright-shade-grown (½ full sunlight)[2]	52.7 (56 plants)	87.2 (9 plants)

[1] Significant, P = .05.
[2] Significant, P = .01.

Effect of Growing Conditions on Pseudobulb Index

Light Intensity. The PI's of sun-grown ($\bar{x} = 44.3$ for 37 plants) and shade-grown ($\bar{x} = 36.8$ for 113 plants) plants of *C. warscewiczii* were not significantly different ($P = .20$), although the mean index of the sun plants was higher than that of the shade plants.

Sheep Manure. The PI was significantly higher with sheep manuring in sun-grown plants of *C. warscewiczii* (Table II). The PI's of manured shade-grown plants also tended to be higher ($P = .10$) than those of non-manured plants.

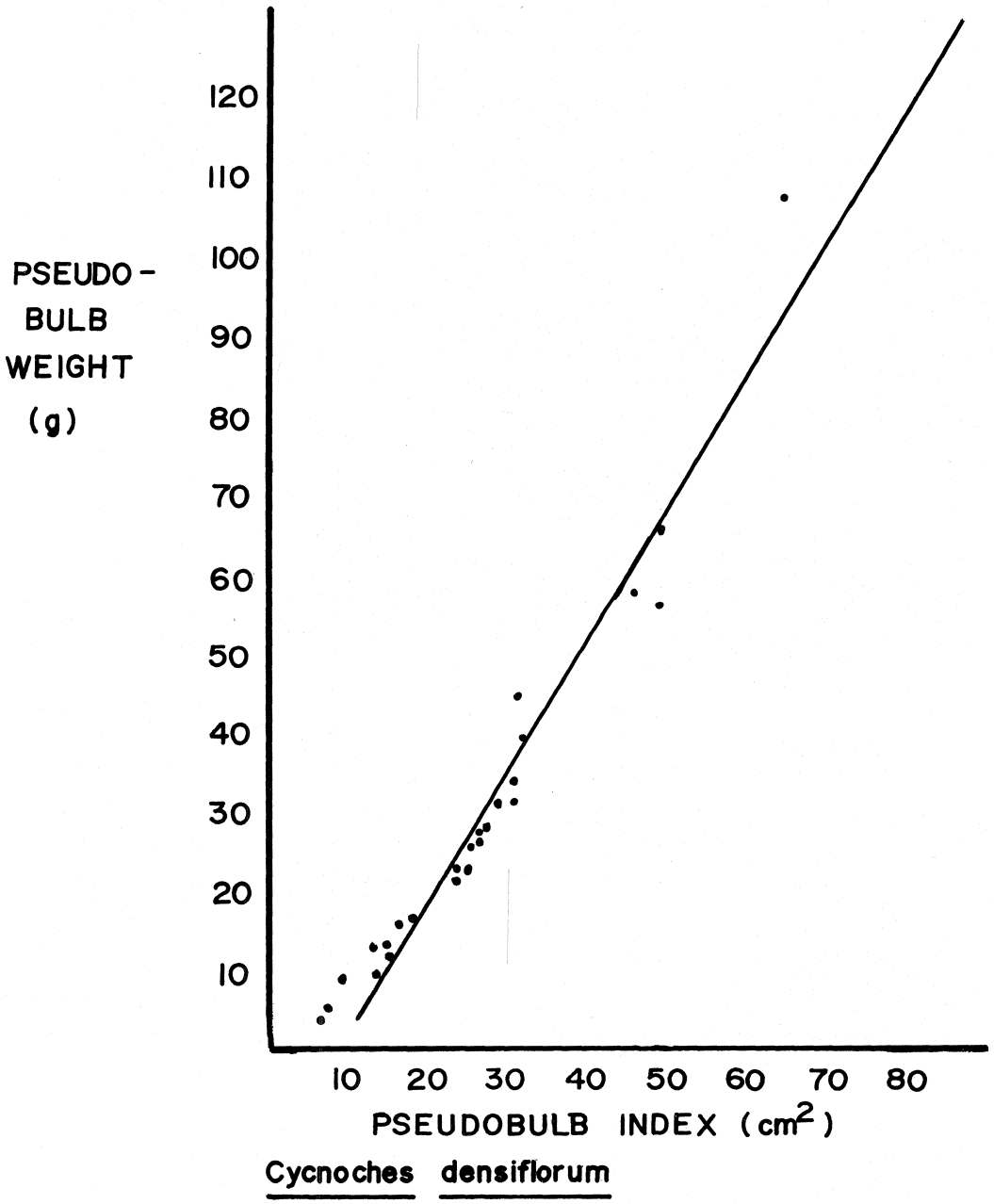

Figure 1. Relationship between pseudobulb index (PI) and pseudobulb weight in 25 plants of *Cycnoches densiflorum*. The PI was calculated by multiplying the length times the maximum diameter of the youngest pseudobulb per plant. The correlation coefficient was 0.98 and the equation of the regression line, y = 1.62x - 12.58.

Table II. Effect of Sheep Manure on Pseudobulb Index (PI) in Plants of *Cycnoches warscewiczii.*

	PI Mean of Manured Plants	PI Mean of Non-Manured Plants
Sun-grown[1]	66.8 (15 plants)	44.3 (37 plants)
Bright-shade-grown (½ full sunlight)[2]	50.7 (21 plants)	36.8 (113 plants)

[1] Significant, P = .05. Plants received approximately 80 ml Armour sheep manure.

[2] Not significant, P = .10. Plants received approximately 50 ml Armour sheep manure.

Effect of Manure Treatments on Sex Expression and Flowering

Treatment with sheep manure did not promote female sex expression in either shade- or sun-grown plants of *C. warscewiczii* (Table III). The data in Table IV show that sheep manure treatments also did not affect flowering percentages of plants, whether grown in sun or shade.

Table III. Effect of Sheep Manure Treatment on Sex Expression in Plants of *Cycnoches warscewiczii.*

Growing Conditions	Number of Plants Producing Male Racemes	Hermaphrodite & Female Racemes
Bright-shade-grown[1] (½ full sunlight)		
With approx. 50 ml Armour sheep manure	11	2
Without manure	56	8
Full sun-grown[2]		
With approx. 80 ml Armour sheep manure	6	3
Without manure	4	9

[1] Chi-square test (X^2 = .029): not significant.

[2] Chi-square test (X^2 = 1.51) and Fisher Exact test (P = .11): not significant.

Table IV. Effect of Sheep Manure Treatment on Flowering in Plants of *Cycnoches warscewiczii.*

Growing Conditions	Plants Flowering	Plants Not Flowering	Per Cent Plants Flowering
Bright shade[1] (½ full sun)			
Manured[3]	13	10	56.5
Not manured	64	57	53.0
Full sunlight[2]			
Manured[3]	9	8	53.0
Not manured	13	24	35.0

[1] Chi-square test (X^2 = .008): not significant.
[2] Chi-square test (X^2 = .881): not significant.
[3] See Table II for manure treatments.

Effect of the Interaction Between Plant Size and Light Intensity on Sex Expression

To discover whether the effects of large plant size and high light intensities were additive in promoting female sex expression, all plants of *C. warscewiczii*, whether manured or non-manured, were divided into three groups according to their PI's. The largest PI recorded was 183. Arbitrary groupings were small (PI's of 0-50), medium (PI's of 51-100), and large (PI's of 101 and larger). The percentages of female- and hermaphrodite- flowering of the small, medium, and large plants were compared for sun- and shade-grown plants.

The resulting graph (Figure 2) indicates that exposure of large plants to full sunlight resulted in the highest percentage of female and hermaphrodite flowering. That is, the combination of exposure to high light intensity and large plant size promoted higher percentages of female and hermaphrodite flowering than did either factor alone.

Discussion and Conclusions

Data presented in this paper demonstrate that a number of factors are involved in the control of sex expression in members of the genus *Cycnoches*. Essentially, Dodson's assessment (1962) of the situation seems correct: plants growing in full sunlight, with adequate moisture and embedded in a suitable substrate, are robust and generally produce female flowers. Less robust plants, often growing in the shade or lacking adequate nutrition, tend to produce male flowers.

In an earlier paper it was shown that exposure to high intensities of sunlight stimulates female flowering in *Cycnoches* (Gregg, 1975). Plant size has been shown here to be another important factor in sex expression in the genus. The PI's of female- and hermaphrodite-flowering plants of *C. densiflorum* and *C. warscewiczii* were significantly higher than those which produced male flowers. That is, large plants of the two species produced significantly more female and hermaphrodite flowers than did small plants.

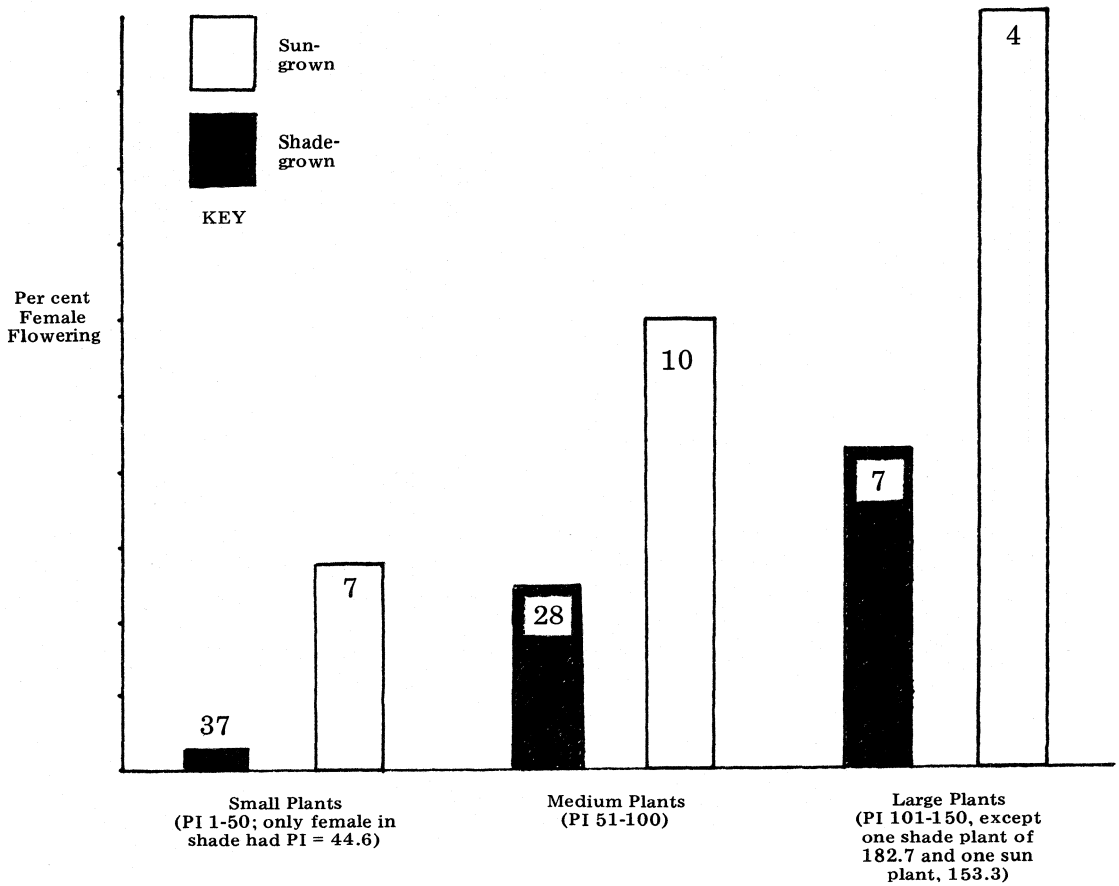

Figure 2. The effect of the interaction between plant size and light intensity on sex expression in *Cycnoches warscewiczii*. PI is assumed to be directly proportional to pseudobulb weight. Shaded bars represent shade-grown plants and non-shaded bars, sun-grown plants. The numbers within each bar indicate the number of plants in each group.

Effect of Nutrition on Plant Size and Sex

These data indicate that sheep manure contributed significantly to the development of greater plant size in sun-grown plants of *C. warscewiczii*. A significant increase in growth of manured shade-grown plants did not occur; however, there was a tendency toward larger plant size in the manured plants. Plants growing under high intensities of full sunlight probably use nutrients at a fairly rapid rate due to their high rate of photosynthesis. Added nutrients, in the form of sheep manure (PKN = 1.25-1.00-2.00), could thus result in higher than normal rates of growth in sun-grown plants. On the other hand, shade-grown plants, photosynthesizing at slower rates and using fewer nutrients, might not benefit as much from added nutrients. It is possible that high light intensity and rich nutrition act synergistically in this manner to promote growth of large, robust plants. It is not possible to document that conclusion, however, because sun and shade manure treatments were different. These experiments will be repeated with identical sun and shade treatments.

Even though manuring sun-grown plants significantly enhanced the development of large pseudobulbs, the corollary that manuring also in-

creased female sex expression in these sun-grown plants was not supported. The obvious correlation between manure treatment and increased female flowering was attempted but statistical analysis showed none occurred. A trend opposite to that expected was noted: fewer female and hermaphrodite flowers were produced by manured plants rather than more. No attempt was made here to account for the discrepancy because the experimental group contained a relatively small number of plants. The small numbers were due to small sample size and not to any effect on flowering by the sheep manure treatments.

Manuring clearly had no effect on sex expression in the shade-grown plants. Exposure to high intensities of light apparently played a far more important role in promoting female sex expression than did the nutrients contained in sheep manure.

Effect of the Interaction Between Light Intensity and Plant Size on Sex

Both exposure to high light intensities and largeness of plant size have been shown independently to promote female flowering in *C. warscewiczii* and *C. densiflorum*. Further, the effects of these two factors were shown here to be synergistic in promoting female sex expression in *C. warscewiczii:* exposure of large plants to high intensities of full sunlight produced the highest percentage of female flowering.

An attempt was made to discover whether high light intensity and rich nutrition in the form of sheep manure contributed to the development of large plants. Because the pseudobulb indices of shade- and sun-grown plants were not significantly different, it was not possible to conclude that exposure to full sunlight produced larger plants. Addition of sheep manure increased plant size only when plants were also exposed to the high intensities of full sunlight. Further, although high intensity sunlight promotes female sex expression, sunlight is not itself an absolute requirement for female flowering in *C. warscewiczii* because developing racemes deprived of sunlight by foil caps were capable of becoming female (Gregg, 1975). Obviously, there are complex interactions among light intensity, photosynthetic rate, and nutrition involved in the female flowering process. At present it seems fair to conclude merely that large plant size appears at least equally important as high light intensity in promoting female sex expression in plants of *Cycnoches.*

A Possible Physiological Explanation of the Roles of Nutrition, Plant Size, and Light Intensity in the Control of Sex Expression in Cycnoches

Indications that sex expression in other species is related to the presence of large quantities of metabolites. A number of workers have related female sex expression in several non-orchidaceous species to the large quantities of metabolites believed to be present within female flowering plants. Maekawa (1926) concluded that the primary factor in female flowering by large corms of *Arisaema japonica* was the presence of larger quantities of stored food than was present in the smaller, male-flowering corms.

Defoliation, defloration, and mutilation experiments have indicated that female flowering is associated with large quantities of metabolites. Atkinson (1898), Schaffner (1922), and Maekawa (1926) discovered that wounding or removing portions of the leaves or corms of *Arisaema* caused

sex reversion from female to male and from male to non-flowering states. Upon recovery, plants returned to their former flowering conditions (Maekawa, 1926). In hermaphrodite papaya trees (*Carica papaya* L.), Lange (1961) and Awada (1967) observed that defoliation increased the production of staminate flowers (those with ten stamens and a non-functional pistil). Awada hypothesized that the decreased level of metabolites following removal of photosynthetic tissue caused male flowering. Male flowering was also associated with low leaf weight and low rates of trunk growth.

In the inflorescence of the plantain (*Musa paradisiaca* L.), a series of female flowers is normally followed by a terminal series of male flowers. Joshi (1939) produced a new zone of female flowers at the growing apex by removing the older female flowers at the base of the inflorescence. The normal inflorescence of *Cleome spinosa* is indeterminate, with alternating male- and female-flowering zones. Removal of flowers or fruits from lower zones promoted production of female instead of male flowers in apices entering a male phase (Murneek, 1927). Tiedjens (1928) discovered that removal of female flowers at anthesis increased further female flower production in cucumber. Awada (1967) observed that removal of both flowers and developing fruits increased female flower production in hermaphrodite papaya trees. He hypothesized that removal of the flowers prevented development of fruits (i.e., metabolic sinks), thereby increasing the level of available metabolites and promoting the production of additional carpellodic flowers (those with a functional pistil and fewer than ten stamens — compare these to the staminate papaya flowers described above). Consistent with this hypothesis was his observation that female flowering was associated with high leaf weight.

Indications that female sex expression in Cycnoches *is related to the presence of large quantities of metabolites.* Most members of the deciduous Catasetinae lose their leaves just prior to or shortly after flowering. Therefore, adequate food reserves must be stored in the pseudobulbs to sustain development of the large seed capsules, which require several months to mature. Data in this paper have shown that female flowering in *Cycnoches* is usually restricted to plants with large pseudobulbs. Thus, there appears to be a causal relationship between large plant size and female flowering in the genus. It could be hypothesized that the mechanism of induction of female flowering involves high quantities of metabolites found in large plants or in plants growing under high light intensities and consequently photosynthesizing at relatively high rates.

Any proposed explanation of the mechanism of sex control in *Cycnoches* must account for the significant promotion of female flowering by these two separate factors, large plant size and exposure to high intensities of sunlight. A photo-chemical induction, probably involving photosynthesis, has been suggested for sun-stimulated female flowering (Gregg, 1973). Large quantities of photosynthates might be expected in sun-grown plants since higher light intensities generally promote higher rate of photosynthesis than lower light intensities (Gaffron, 1960; Rabinowitch & Govindjee, 1969). Female flowering in the shade is generally restricted to large, robust plants within which large quantities of photosynthates might also be expected. If the presence of large quantities of photosynthates within a plant initiates female flowering in shade-grown plants, then it is possible that photosynthesis might be involved in female flowering in the shade as well as in the sun.

The occurrence of high levels of metabolites, or photosynthates, may coincide with high hormone levels. Atsmon & Galun (1962) concluded that there was a close association between hormone concentration and sex expression in cucumber. They found that female flowers tended to develop next to younger leaves which are sites of relatively high auxin concentration. Male flowers commonly developed next to older leaves where auxin concentrations are lower. Galun, Izhar, & Atsmon (1965) reported that the auxin content of hermaphrodite cucumber plants was higher than that of male plants. Byers, Baker, Sell, Herner, & Dilley (1972) proposed ethylene gas to be an endogenous regulator of sex expression in cucumber and muskmelon. They suggested that high endogenous levels of auxin within plants producing female flowers may determine the high levels of ethylene gas associated with female flowering; i. e., ethylene may be an intermediate effector molecule which promotes femaleness. Another paper in preparation will show that within developing racemes of *Cycnoches*, endogenous production of high levels of ethylene gas is consistently associated with both exposure to high light intensity and female sex expression. Lower levels of ethylene gas production by the developing buds are consistently associated with exposure of the plants to low light intensity and male flowering.

Summary

1. Large plants of *Cycnoches warscewiczii* and *C. densiflorum* produced significantly more female and hermaphrodite racemes than did smaller plants.

2. Treating sun-grown plants of *C. warscewiczii* with approximately 80 ml Armour sheep manure significantly increased plant size; however, treatment of shade-grown plants with approximately 50 ml sheep manure did not affect plant size.

3. The effects of large plant size and exposure to high intensities of sunlight were synergistic in promoting female sex expression in plants of *C. warscewiczii.* Exposure of large plants to full sunlight resulted in the highest percentage of female and hermaphrodite flowering.

4. A pseudobulb index (PI) was calculated for each plant by multiplying the length times the maximum diameter of the youngest pseudobulb. The index was used to correlate plant size with other factors involved in sex expression within a give species. PI was substituted for pseudobulb weight in the statistical analysis.

5. The hypothesis that female flowering in *Cycnoches* is promoted by high levels of metabolites, including hormones, was discussed.

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