THE EFFECT OF LIGHT INTENSITY ON SEX EXPRESSION IN SPECIES OF *CYCNOCHES* AND *CATASETUM* (ORCHIDACEAE)[1]

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INTRODUCTION

Charles Darwin (1865) considered the three genera comprising the subtribe Catasetinae Pfitz., *Catasetum* L. C. Rich., *Cycnoches* Lindl., and *Mormodes* Lindl., to be "the most remarkable of all Orchids" because of their unique pollination mechanisms and their extraordinarily different male and female flowers. Of the several hundred genera comprising the orchid family, only members of *Catasetum*, *Cycnoches* and *Mormodes* exhibit male and female flowers. This unusual trait is responsible for a colorful taxonomic history, fraught with misunderstanding and carelessness.

In the first third of the nineteenth century, collectors sent specimens of rare and unusual orchids to John Lindley from Central and South America. Often having only a single plant to study, Lindley described and named the species as they arrived, often giving two specific names to each species of *Cycnoches* sporting unlike male and female flowers. Plants of *Catasetum* rated three different generic names based on their sexual morphologies. Specimens that produced flowers of one species in the field sometimes produced flowers of another species in the greenhouse in England; or a particularly devilish plant might produce flowers of two or three genera at one time. Such occurrences led Lindley to observe that "with such cases as this, . . . all ideas of species and stability of structure in the vegetable kingdom are shaken to their foundation" (Allen, 1952).

Collectors and botanical illustrators compounded the taxonomic problems. Collectors occasionally placed flowers from different plants on the same herbarium sheet and labeled them as coming from the same individual. Preserved specimens of the male flowers of one species of *Cycnoches* were illustrated meticulously as female flowers of another which were too dried to draw (Allen, 1952). Finally, Darwin (1862) recognized the simple explanation of the mystery to be the production of dissimilar male and female flowers, generally on different plants. Darwin, too, made an error, however, and mistakenly called a peculiar male flower an hermaphrodite. Rolfe (1889) resolved Darwin's misunderstanding.

Although Darwin and Rolfe finally cleared up the taxonomic problems plaguing the two genera, an explanation for the sexual dimorphism was not advanced until Dodson (1962) suggested that the control of sex expression in the Catasetinae appeared to be an environmentally controlled phenomenon. His conclusion was based on 14 months of field studies of two species of *Catasetum* and one species each of *Cycnoches* and *Mormodes* in coastal Ecuador. He observed that plants growing in full sunlight with adequate moisture were robust and generally produced female flowers. Less robust plants, often growing in the shade or lacking adequate moisture, produced male flowers.

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Dodson (1962) concluded that sunlight was particularly important in determining sex. When he moved 15 plants of *Catasetum macroglossum* Rchb. f. exhibiting female flowers from natural full sun into dense shade, they then produced all male inflorescences. Of 15 control plants brought in from full sun in the field and kept in full sun, 13 continued producing female flowers and two produced inflorescences with both male and female flowers. Also, several large plants which had produced male flowers under shady conditions produced female inflorescences after being placed in full sun.

Dodson (1962) found few plants with female flowers in wild populations of *C. macroglossum*. In a population growing in a coastal tropical deciduous forest there were 21 male flowers present for every female. Approximately 46 males to one female were counted in a shadier cacao plantation. In plants of *Cycnoches lehmannii* Rchb. f. growing in old cacao plantations near Quevedo, Ecuador, Dodson found 27 male flowers for each female.

Several orchid enthusiasts have also suggested that sex expression in the Catasetinae may be controlled by environmental factors. Vickers (1968) reported that full morning sun was apparently the most important factor in obtaining female flowers in plants of *Cychnoches ventricosum* Batem., and that size and vigor of the plants was not a factor. Brubaker (1969), on the other hand, emphasized that "nature has apparently limited the honor of seed bearing to the strongest plants with the best prospects for active photosynthesis." He advised that female flowers could be obtained from well-established plants of *Catasetum* given high light intensities and manure; however, he was not sure that manure was essential. Teuscher (1965) mentioned that although some growers thought that "very strong plants" flowered female, his own observations on several species of *Catasetum* discounted the theory.

These earlier observations, made on small numbers of plants, have shown that ecological factors such as light intensity, nutrition and plant size may be important in the regulation of sex in members of the Catasetinae. To learn the relative importance of these factors in sex regulation, a series of studies using relatively large numbers of plants was planned to make quantitative measurements, both in the field and in the greenhouse, of the effects of light intensity, nutrition and plant size on sex expression in some species of *Catasetum* and *Cycnoches*. This paper reports the results of experiments testing the effect of light intensity on sex expression; another paper in preparation will describe relations among sunlight, plant size, nutrition and sex expression in these two genera.

Materials And Methods

Importation and Culture of Plants

Approximately 300 plants of *Cycnoches spp.* were imported from Panama from December, 1968, through early spring, 1969. Upon flowering, 115 of the plants proved to be *C. densiflorum* Rolfe, *C. stenodactylon* Schltr., *C. dianae* Rchb. f. and *C. aureum* Lindl. The remainder were *C. warscewiczii* Rchb.f. Approximately 100 plants of *Catasetum expansum* Rchb. f. were imported from Ecuador in the early spring of 1969 to supplement those on hand in the University of Miami greenhouse. Plants of *C. tabulare* Lindl., originally from Colombia, were present in the University of Miami collection. Voucher specimens of the species of *Cycnoches* and

Catasetum studied are on file at the herbarium of the University of Miami, Coral Gables, Florida.

Imported plants arrived in a dormant state and were fumigated with methyl bromide at the Plant Inspection Station of the United States Department of Agriculture in Miami. Plants were stored dry until new growths appeared. When the new growths produced roots, plants were potted in chopped treefern fiber and watered liberally with mist early each morning. When leaves first opened and the root systems were fairly well-established, plants were usually given from 50 to 100 ml of Armour sheep manure (1.25-1.00-2.00), which was replenished as needed. When plants were two months old, they were fertilized once a week with an aqueous spray (diluted 1/1357 by volume) of Peters 18-18-18. Plants were sprayed with a 0.4% solution of Ortho Malathion as needed.

Plants were grown out of doors either in full sunlight or under polypropylene screening, wooden slats, or a combination of both. At the end of the flowering season when plants had lost all their leaves, the fat storage stems, called pseudobulbs, were unpotted, trimmed of roots and kept in a dry shed. The pseudobulbs were watered about once a week. Plants were repotted when roots appeared on the new growths.

Greenhouse Experiments, 1969

In 1969, recently imported plants of *Catasetum* were divided into plants with three pseudobulbs each. Plants of *Cycnoches* were divided into plants with only one pseudobulb each because the pseudobulbs of these species from previous seasons usually died during the growing season. At the beginning of the season there were 171 plants of *Catasetum expansum*, 21 of *C. tabulare*, 260 of *Cycnoches warscewiczii*, 25 of *C. dianae*, 18 of *C. aureum* and 52 of *C. densiflorum*.

At the start of the experiments all plants were grown under 73% polypropylene mesh screening (Chickapee-Lumite Co.). Light intensities were measured with a Weston Illumination Meter, Model 756 and were approximately ⅓ that of full sunlight (about 35,000 Lux). (Daubenmire stated in 1959 that plants are exposed to 107,000 Lux at sea level). This treatment was designated medium shade.

Plants were graded subjectively according to size and approximately 1/3 of the plants in each size category were chosen to be grown in full sunlight, and the remainder were grown in medium shade.

In order to make a gradual transition from the medium shade to the full sun treatment, plants to be grown in full sun were placed on benches under wooden slats for two or three days before being moved into full-sun benches. The slatted roof was constructed with boards 2.5 cm wide by 2.5 cm thick spaced so that plants received light intensities approximately ½ that of full sunlight. The move to full sun was made during the first week in June. Plants on the sun benches badly sunburned as the summer progressed. To prevent further damage, one layer of cheesecloth was spread above the sun benches in early August, reducing the light intensity to approximately ¾ that of full sunlight. Sun plants were also given an additional early afternoon watering to cool the leaves. Sex of the inflorescences produced by each plant was recorded.

Greenhouse Experiments 1970

During repotting for the 1970 flowering season, plants of *Cycnoches* were again divided into one pseudobulb each but those of *Catasetum* were not redivided. Plants were again arranged in groups according to size and approximately ⅓ of the plants in each category were chosen to be grown in full sunlight. Plants were chosen with no regard for whether they had been grown in the sun or shade in 1969.

Shade plants were grown under mesh screening known as 50% polypropylene mesh screening (Chickapee-Lumite Co.); they were exposed to light intensities approximately ½ that of full sunlight. This treatment was designated bright shade. Shade plants received a daily misting from an automatic watering system.

Sun plants were grown on benches in the greenhouse compound where they were exposed to full sunlight. In 1969 the sun benches had been surrounded on all sides by buildings and tall shrubs; ventilation was poor and plants became badly sunburned. In 1970 the sun benches were moved away from the buildings for better ventilation and no sunburning occurred. Sun plants were watered once a day.

Plants of *Cycnoches warscewiczii*, *Catasetum tabulare* and *C. expansum* were grown either in full sunlight or in bright shade. Plants of *Cycnoches densiflorum* were grown in either medium or bright shade. With the exception of plants of *C. warscewiczii*, plants were given sheep manure as in 1969. Sex of the inflorescences for each plant was recorded when the flowers opened.

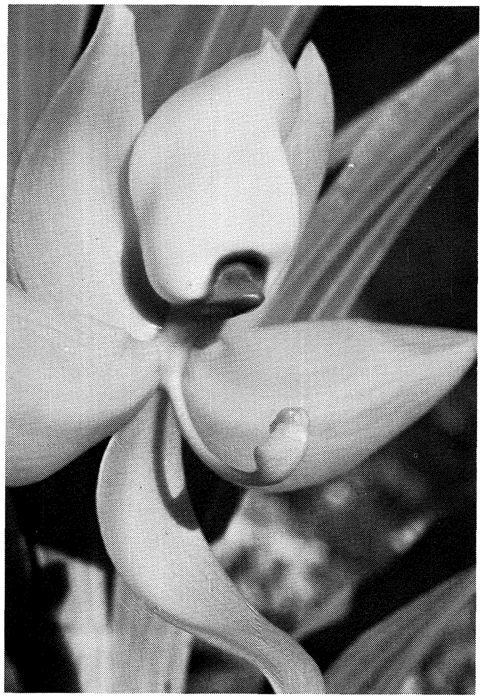
Field Study, Guyana, 1970

In late March and early April, 1970, sex expression was studied in a large population of *Catasetum macrocarpum* L. C. Rich. ex Kunth growing on dead trees in the lake of the Dawa Water Conservancy Area on the Tapakuma River, Essequibo District, Guyana. The lake was created in 1963 when part of the forest was inundated to form a reservoir. The population of *Catasetum* was flourishing in full sunlight. Sex expression was recorded for 151 plants.

Raceme Capping Experiments

Catasetum expansum. The racemes of twelve sun-grown plants, nine of which had flowered female earlier in the flowering season and three of which had not flowered, were covered with loosely-fitting aluminum foil caps when they were from 1.7 to 5.6 cm long. The caps were left on the racemes from five to 22 days. In order to bias the experiment toward female flower production, the plants with racemes to be capped were chosen for their large sizes because large plant size has been shown to favor female flowering (Gregg, 1973). The pseudobulb index, calculated by multiplying the length times the maximum diameter of the youngest pseudobulb, was used as an estimate of plant size. The pseudobulb index average for the plants with capped racemes was 32.0 while that of the sun-grown female-flowering uncapped controls was 30.3.

Cycnoches warscewiczii. Six racemes of five large sun-grown plants were covered with aluminum foil caps when they were from 2.1 to 3.7 cm long. This experiment was also purposely biased toward large plants. The pseudobulb index average was 67.1 for the experimental plants with capped



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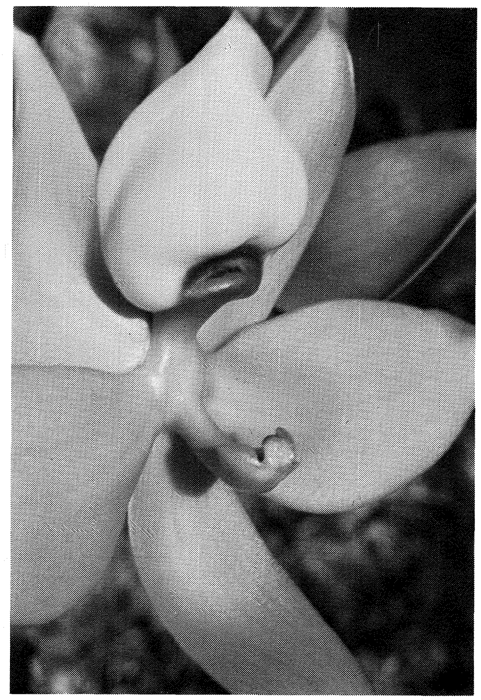

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1. Male flower of *Cycnoches warscewiczii.* × 1

2. Female flower of *Cycnoches warscewiczii.* × 1

3. Mixed raceme of *Cycnoches dianae.* Two male flowers (right) and a hermaphrodite flower are contained in this raceme. The hermaphrodite flower (left) has knobby projections (K) on the lip, vestiges of the fingers exhibited by the normal male flowers on the right. The column of the hermaphrodite flower is intermediate in size between that of normal female and male flowers. × 1.5

racemes and 44.3 for the uncapped controls of both sexes. Indices of uncapped female-flowering plants averaged 77.2 while the indices of uncapped male-flowering plants averaged only 27.4.

Statistical Analyses

Data were analysed by the chi-square test using the Yates correction. For expected values less than five, the Fisher exact test was used. Because the production of hermaphrodite flowers or mixed (hermaphrodite) racemes was considered an indication of radical developmental change from the male condition, female and hermaphrodite flowers were grouped in the statistical analyses whenever they occurred.

Results

Comparison between the Effects of Full Sunlight and Medium Shade on Sex Expression

Sun-grown plants of *Cycnoches warscewiczii* and *Catasetum tabulare* produced significantly more female racemes (Table 1) than did plants grown in medium shade (light intensity approximately ⅓ that of full sunlight). Figures 1 and 2 illustrate male and female flower morphology of *Cycnoches warscewiczii.* Sun-grown plants of *Cycnoches dianae, C. densiflorum* and *Catasetum expansum* produced higher percentages of female and hermaphrodites racemes than did plants grown in medium shade, although the differences were not significant. An hermaphrodite raceme of *Cycnoches dianae* containing two male and one hermaphrodite flower is pictured in Figure 3. A male raceme is shown in Figure 4. Plants of *Cycnoches aureum* produced no female racemes in 1969.

Comparison between the Effects of Full Sunlight and Bright Shade on Sex Expression

Cycnoches warscewiczii. Sex expression in the sun was significantly different from that in bright shade where plants received approximately ½ the light intensity of full sunlight (Table 2). Flowering was 55% female in the sun and only 12% female and hermaphrodite in the shade.

Catesetum expansum. Sex expression in the sun was significantly different from that in bright shade (Table 2). Sex expression was 63% female in the sun and only 3% female in the shade. Male sex expression was 93% in the shade and 37% in the sun. A small percentage of hermaphrodite racemes was produced by shade-grown plants. Male, female and hermaphrodite expression are shown in Figures 5, 6, and 7.

Catasetum tabulare. Plants of *C. tabulare* grown in bright shade produced six male and one female raceme. Only one plant flowered in the sun and it produced one female raceme. (Table 2)

Comparison between the Effects of Bright Shade and Medium Shade on Sex Expression

Plants of *Cycnoches densiflorum* appeared to produce more ($P<0.10$) female and hermaphrodite inflorescences in bright shade (light intensity approximately ½ that of full sunlight) than in medium shade (light intensity approximately ⅓ that of full sunlight, Table 2). Male and hermaphrodite racemes are illustrated in Figures 8 and 9; female flowers are pictured in Figure 10.

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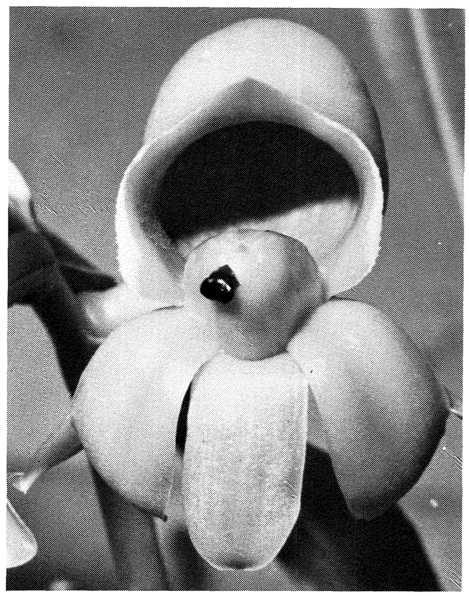

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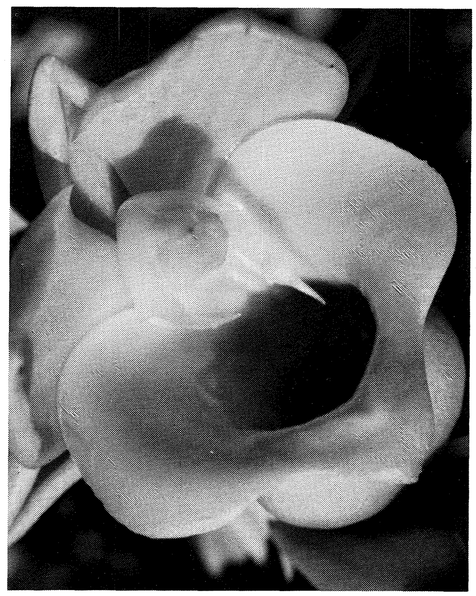

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4. Male flowers of *Cycnoches dianae*. X 1.2

5. Male flower of *Catasetum expansum*. X 1

6. Female flower of *Catasetum expansum*. X 1.2

7. Hermaphrodite flower of *Catasetum expansum*. The hermaphrodite flower has a lip intermediate in appearance between a normal male and female flower and exhibits antennae about half the size of those of normal male flowers. X 1.8

A slight increase in female sex expression was observed in plants of both *Catasetum expansum* and *Cycnoches warscewiczii* when plants were grown in bright rather than medium shade. Seven per cent of the plants of *Cycnoches warscewiczii* produced female inflorescences in medium shade in 1969 while 12% produced female inflorescences in bright shade in 1970. No female racemes were produced by plants of *Catasetum expansum* grown in medium shade in 1969 while 3% of the plants grown in bright shade in 1970 produced female racemes. No mixed racemes were produced by plants of either species grown in medium shade but mixed racemes appeared in plants of both species when grown in bright shade.

Sex Expression in a Wild Population Growing in Full Sunlight

In a count of 151 inflorescences of plants of *Catasetum macrocarpum* growing in full sun on dead trees in Lake Tapakuma in Dawa, Guyana, there were 125 female, 25 male and one hermaphrodite.

Sex Expressed by Sun-grown Racemes Capped with Aluminum Foil Caps

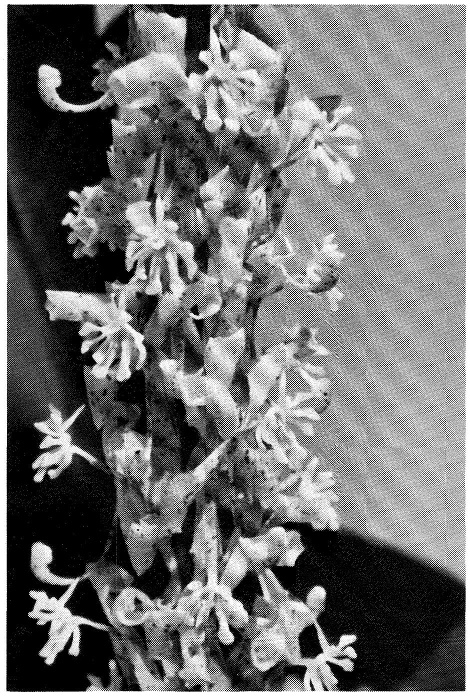
Catasetum expansum. All twelve capped racemes produced male flowers while uncapped controls produced 52% female, 41% male and 7% hermaphrodite inflorescences (Table 3). Nine of the plants with capped racemes had already produced female flowers earlier in the season; thus the results were considered significant because previous observations (Gregg, 1973) established that sun-grown plants continued producing inflorescences of the same sex 90% of the time in the same flowering season.

Cycnoches warscewiczii. Ten of 14 uncapped control racemes flowered female and three of six capped racemes produced female flowers. (Table 3) Although capping reduced female sex expression by 21%, the difference was not significant. No hermaphrodite inflorescences were produced by the control or experimental plants.

Discussion And Conclusions

Results indicate that exposure to high intensities of sunlight is an important factor in stimulating female flowering in members of the Catasetinae. Plants of *Cycnoches* and *Catasetum* produced more female inflorescences when grown under high light intensities of full sunlight than when grown under light intensities from ⅓ to ½ that of full sunlight. The promotion of female flowering by high light intensities is not unique to the Catasetinae. It has been reported in cucumbers (Kooistra, 1967) and in the oil palm (Broekmans, 1957; Williams and Thomas, 1970).

Species differences in light intensity required for female flowering were observed. While plants of *Catasetum expansum*, *C. tabulare* and *Cycnoches warscewiczii* required full sunlight to produce substantial percentages of female inflorescences, plants of *Cycnoches densiflorum* produced large numbers of female flowers in bright shade (½ full sunlight). A slight increase in female flowering was observed in plants of *Catasetum expansum* and *Cycnoches warsewiczii* when they were grown in bright shade rather than in medium shade. The sex regulatory system of some species thus appears able to discern smaller differences in light intensity than can that of other species.



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8. Male flowers of *Cycnoches densiflorum*. × 1

9. Mixed raceme of *Cycnoches densiflorum*. The apical hermaphrodite flowers have knobby projections (K) on the lips which are remnants of the fingers exhibited by the lips of the normal male flowers seen at the basal end of the inflorescence. The columns of the hermaphrodite flowers are intermediate in size between normal male and female flowers. × .5

10. Female flowers of *Cycnoches densiflorum*. × 1.1

Dodson (1962) showed that sex expression of plants of *Catasetum macroglossum* could be changed from female to male by moving plants from full sunlight into dense shade. Raceme capping experiments reported here show that sex expression can be changed from female to male by placing aluminum foil caps over developing racemes of sun-grown plants of *Catasetum expansum.* Capping developing racemes of sun-grown plants of *Cycnoches warscewiczii* did not affect sex expression. These results indicate that the sex regulatory system appears to be located within the raceme apex of plants of *Catasetum expansum* but may be located elsewhere in plants of *Cycnoches warscewiczii.*

The large percentage of female racemes encountered in the population of *Catasetum macrocarpum* growing in full sunlight in Lake Tapekuma in Guyana is quite different from sex ratios observed in populations of *Cycnoches* and *Catasetum* near Quevedo, Ecuador (Dodson, 1962). The habitats of the Ecuadorian populations were considerably shadier and much higher percentages of male flowers than female flowers occurred. Dodson (1962) suggested that these large numbers of male flowers were advantageous to population survival since male flowers of these species are short-lived, lasting from four to five days, while female flowers may persist up to six weeks. That is, large numbers of pollen packets, or pollinaria, would ensure the pollination of the few female flowers occurring. Dodson concluded that pollination of a few female flowers would maintain the population because the seed capsules contain very large numbers of seeds. Numbers as high as two million seeds per capsule have been estimated (Dodson and Gillespie, 1967). However, in December 1974, when I revisited the old cacao plantations near Quevedo, Ecuador, plants of *Cycnoches* and *Catasetum* were scarce. Those present in the dense shade were small and none had capsules.

On the other hand, in Guyana, where catasetums were flourishing in abundance upon the fully exposed dead trees and stumps, large numbers of seed pods were present. In this case probably a very high percentage of the limited pollinaria produced reached female flowers. In a few years the dead trees which serve as perches for the catasetums will be gone; unless enough seeds have reached the surrounding forest, the lake population will perish. Obviously, here, a system of sex regulation based on light intensity appears potentially successful in ensuring population survival.

Although this paper demonstrates that high light intensities stimulate female flowering in members of the Catasetinae, other factors have been found to interact with light intensity in regulating sex (Gregg, 1973). Another paper in preparation will show that large plant size and good nutrition also play important roles in the female flowering process in these plants. The data will further substantiate a difference in the sex regulatory systems of *Catasetum* and *Cycnoches* which is only indicated here.

TABLE I

Sex expression of sun- and shade-grown plants during the 1969 flowering season.

Species and Growing Conditions	Number of plants producing		
	Male racemes	Hermaphrodite racemes[3]	Female racemes
Cycnoches warscewiczii[2]			
Sun	24	0	16
Medium shade (approx. ⅓ full sunlight)	87	0	7
Cycnoches dianae[4]			
Sun	5	1	1
Medium Shade	15	1	0
Cycnoches aureum[4]			
Sun	6	0	0
Medium shade	14	0	0
Cycnoches densiflorum[4]			
Sun	10	1	4
Medium shade	26	3	4
Catasetum expansum[1]			
Sun	12	1	1
Medium Shade	27	0	0
Catasetum tabulare[4]			
Sun	2	0	3
Medium Shade	7	0	0

[1]Significant, $P = .04545$.
[2]Significant, $P < .005$.
[3]Female and hermaphrodite racemes added in statistical analysis.
[4]P = ns.

TABLE II

Sex expression of sun- and shade-grown plants during the 1970 flowering season.

Species and Growing Conditions	Number of plants producing Male racemes	Hermaphrodite racemes[2]	Female racemes
Cycnoches warscewiczii[1]			
Sun	10	0	12
Bright shade (approx. 1/2 full sunlight)	62	2	9
Cycnoches densiflorum[4]			
Bright shade	29	4	27
Medium shade (approx. ⅓ full sunlight)	14	1	4
Catasetum expansum[1]			
Sun	12	0	20
Bright shade	66	3	2
Catasetum tabulare[3]			
Sun	0	0	1
Bright shade	6	0	1

[1]Significant, $P < .005$.
[2]Female and hermaphrodite racemes added in statistical analysis.
[3]$P = ns$.
[4]$P < .10$.

TABLE III

Sex expression in sun-grown racemes capped with aluminum foil caps.

Species and Growing Conditions	Number of plants producing Male racemes	Hermaphrodite racemes[1]	Female racemes
Catasetum expansum[2]			
Control racemes	18	3	23
Capped racemes	12	0	0
Cynoches warscewiczii[3]			
Control racemes	4	0	10
Capped racemes	3	0	3

[1]Female and hermaphrodite racemes added in statistical analysis.
[2]Significant, $P = .00015$.
[3]$P = ns$.

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