

## Effects of floral display and plant abundance on fruit production of *Ryncholaelia glauca* (Orchidaceae)

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**Abstract:** Flowering plant density can increase number of visits and fruit set in multi-flowering plants, however this aspect has not been studied on few flower species. We studied the effects of individual floral display and plant density on the fruit production of the epiphytic, moth-pollinated orchid, *Ryncholaelia glauca*, in an oak forest of Chavarrillo, Veracruz, Mexico. Species is non-autogamous, and produced one flower per flowering shoot each flowering season. We hypothesized that orchids with more flowering shoots and those on trees with clumps of conspecific should develop more fruits than isolated ones. *R. glauca* population flowers synchronously, and individual flowers last up to 18 days, with flowers closing rapidly after pollination. Individuals produced few flowers per year, although some plants developed flowers in both seasons and fewer of them developed fruits both years. There was no relationship between flower number per orchid, or per host tree, with the number of fruits developed per plant. Host trees with flowering and fruiting orchids were randomly dispersed and the pattern of distribution of flowering and fruiting plants was not related. Apparently, pollinators visit the flowers randomly, with no evidence of density dependence. The fruit set of *R. glauca* was as low as fruit set of multi-flowered orchids moth pollinated, suggesting that fruit set on moth pollinated orchids could be independent of the number of flowers displayed.

**Key words:** Floral display, abundance, reproduction, *Ryncholaelia glauca*, orchid, fruit set, spatial distribution.

Inflorescence size and population density are important features influencing the reproductive success of animal-pollinated plants (Schmitt *et al.* 1987, House 1992, Kearns and Inouye 1993, Widén 1993, Kunin 1997, Groom 1998). Both, large inflorescence size and density of reproductive individuals, increase flower display, visitor frequency, and fruit set on multi-flowered non-orchid species (Pleasants and Zimmerman 1990, Kilnkhamer and de Jong 1993, Ågren 1996, Kunin 1993, 1997), and multi-flowered orchid species (Montalvo and Ackerman 1987, Rico-Gray and Thien 1987, Wolfe 1987, Firmage and Cole 1988, Calvo 1990b, Robertson and Wyatt 1990, Rodríguez-Robles *et al.* 1992, Sabat and Ackerman 1996). Despite their importance, the

effects of these factors have not been studied on few-flowered species. Fruit production in plants with many flowers may depend on several reproductive characteristics as flower size, shape, color, rewards, breeding systems, and resources (Zimmerman and Pyke 1988), these characteristics could be even more critical in plants with few flowers. Fruit set should be higher on clumped of few flowering plants than on isolated ones, because pollinators may be more likely to visit high density of flowers (enlarging the overall floral display, as many flowers they have together). We studied the effects of floral display and plant abundance on fruit set of the non-autogamous orchid *Ryncholaelia glauca* (Lindl.) Schltr. (Orchidaceae). We hypothesized that: 1) clumped plants should produce relatively more

fruits than isolated plants, and 2) plants with several flowering shoots should develop more fruits than plants with one flowering shoot.

## MATERIALS AND METHODS

**Study area:** Fieldwork was done in an oak-forested hill near Chavarrillo, Coatepec, Veracruz, Mexico (19°24'24" N, 96°48'19" W; altitude 900 - 1000 m). The climate is warm subhumid with a mean temperature of 24.5 °C. Total annual precipitation is 1 106.4 mm, mostly falling between June and September (García 1981). The forest grows on limestone soils with many superficial rocks. Tree height ranged between 6 to 20 m. The most common species in this area include *Quercus oleoides* Schlecht. and Cham., *Quercus laurina* Humb. and Bonpl., and *Quercus peduncularis* Nee (Fagaceae). Epiphytes are abundant, especially *Cattleya aurantiaca* (Batem. ex Lindl.) P.N. Don., *Encyclia cochleata* (L.) Lemee, *Laelia anceps* Lindl., *Nageliella purpurea* (Lindl.) L.O. Wms., *Notylia barkeri* Lindl., *Oncidium maculatum* Lindl., *Oncidium stramineum* Batem. ex Lindl., *Ryncholaelia glauca* (Lindl.) Schltr. (Orchidaceae), *Tillandsia ionantha* Planchon, *Tillandsia schiedeana* Steudel, *Catopsis* spp. (Bromeliaceae), and *Pepperomia* spp. (Piperaceae) (Castillo 1985, Flores-Palacios 1995).

**Study species:** *Ryncholaelia glauca* is a sympodial epiphytic herb with compressed oblong-fusiform pseudobulbs (Ames and Correll 1954). As other orchids (Zotz 1995), each terminal shoot develops one pseudobulb yearly. The new pseudobulb produces a single, large creamy-white flower 10-12 cm in diameter (A. Palacios-Rios and J.G. García-Franco pers. obs.). As a consequence, the number of flowers depends on the number of new shoots developed by the plant. Each flower produces 1.0 to 10.5 µl of nectar with  $10.25 \pm 3.02\%$  total sugars on wt/wt basis (mean  $\pm$  S.D., n = 5), individual flowers last from 15 to 18 days, and fruit development starts immediately after

pollination (Flores-Palacios 1995). Plants bloom synchronously between January and February, and fruits take one year to develop. Flowers are non-autogamous but they are self-compatible (100%), and geitonogamy and xenogamy could exist (100% each) (Flores-Palacios 1995). The large white flowers are pollinated by hawkmoths (Sphingidae) (Dressler 1990) (phalaenophily syndrome *sensu* Pjil and Dodson 1966).

**Data collection:** We mapped all trees in two study plots (each 0.15 ha). On each tree we counted and recorded the spatial location of all individual orchids (using x, y, z coordinates). Plants of *R. glauca* were usually found isolated with one rhizome line and few pseudobulbs; each of them was considered an individual. We also recorded plants with mixed rhizomes (clump) as a single individual. Throughout two reproductive seasons (1993 and 1994), we surveyed each individual every 2-3 days to record the number of flowers and fruits.

**Data analysis:** The effects of abundance and floral display on fruit production were analyzed at three levels: a) individual plant, b) clumped individuals on host trees (each tree supporting different orchid numbers), and c) spatial distribution (two and three dimensions) of the reproductive orchids.

a) Effect of individual floral display on the fruit production. We compared flower and fruit numbers developed per individual plant of *R. glauca*. We expected to find a positive relationship between the number of flowers and fruits. We used a non-parametric correlation procedure to test this hypothesis (Spearman rank correlation test, StatView 1996).

b) Effect of the total flower number of *R. glauca* per host tree on the fruit production. We related the number of reproductive orchids and the total number of flowers produced per tree, with the pooled fruit set recorded for each tree. Each tree was considered a unit. We expected to find a positive relationship between number of flowering plants and number of fruits on the host trees. Once again, we

used a non-parametric correlation procedures to test our hypothesis (Spearman rank correlation test, StatView 1996).

c) Spatial distribution of reproductive orchids. The spatial pattern of host trees supporting reproductive orchids was obtained for each plot and season using the nearest-neighbor method (Clark and Evans 1954). If clumping in reproductive plants is an important factor determining fruit production, we would expect to record more orchid fruits on clumped host trees. The spatial pattern of flowering and fruiting individuals of *R. glauca* was tested using the Zorro Program (Romesburg 1989). This program, based on the nearest-neighbor distance, can test for three-dimensional spatial patterns. The program performs a conditional randomization test based on three hypotheses:  $H_0$ , the spatial distribution of two or more types of individuals is random;  $H_1$ , individuals of the same type are attracted to each other, and  $H_2$ , individuals of the same type repel each other. The program estimates p-values using Monte Carlo sample iterations. We used 10 000 iterations to estimate the p value. When  $p < 0.025$ ,  $H_0$  is rejected in favor of  $H_1$ ; if  $p > 0.975$ ,  $H_0$  is rejected in favor of  $H_2$ , and when

$0.025 \leq p \leq 0.975$ ,  $H_0$  is accepted (Romesburg 1989). We expected an attraction relationship between the spatial pattern of flowering and fruiting plants of *R. glauca* ( $H_1$ ).

## RESULTS

### General reproductive characteristics:

We recorded a total of 115 *Q. peduncularis* trees in our study plots, but only 56 of them (48.7%) supported plants of *R. glauca*. A total of 223 individuals of *R. glauca* were recorded. The number of flowering plants and number of flowers increased rapidly during the first twelve days since the start of the bloom season (Fig. 1). Seventy five plants flowered during the first study year (1993) producing 132 flowers, this was 33.63% of the total orchids considered. During the second year (1994) 123 individuals flowered (55.16% of the total) producing 238 flowers (Table 1). The number of flowering orchids and the total number of flowers produced were different between years ( $\chi^2_c = 9.91$ ;  $p < 0.005$ ; and  $\chi^2_c = 28.35$ ;  $p < 0.001$ , respectively). Twenty four plants (11.21%) failed to develop flowers in either season.

TABLE 1  
Reproductive data of *R. glauca* (Rg) per host tree (a) and per individual orchid (b) for the 1993 and 1994 reproductive seasons. (values are means  $\pm$  S.D, in parenthesis the range or percentage)

Reproductive Characteristics	Season 1993	Season 1994
a)		
Rg No./tree (range)	5.03 $\pm$ 5.58 (1-21)	2.68 $\pm$ 2.43 (1-11)
Trees with flowering Rg (% of total)	33 (31.58)	47 (43.86)
Flowering Rg/tree (range)	2.27 $\pm$ 1.96 (1-9)	2.64 $\pm$ 2.42 (1-10)
Total flower No./tree (range)	4 $\pm$ 3.66 (1-17)	5.06 $\pm$ 5.16 (1-20)
Trees with fruiting Rg	16	12
Total fruit No./tree (range)	1.13 $\pm$ 0.34 (1-2)	1.33 $\pm$ 0.65 (1-3)
b)		
Flowering Rg No. (% of total)	75 (33.33)	124 (51.92)
Total flower No.	132	238
Flower No./Rg (range)	1.7 $\pm$ 1.16 (1-13)	1.8 $\pm$ 1.44 (1-17)
Fruiting Rg No.	18	14
Total fruit No.	18	16
Fruit No./Rg (range)	1.0 (1)	1.14 (1-2)
Fruit set (Total No. Fruit/Total No. Fl)	0.136	0.067

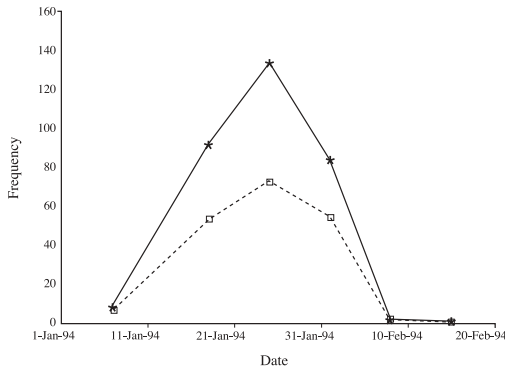


Fig. 1. Frequency of flowering individuals of *R. glauca* (broken line) and total number of flowers (solid line) recorded during the reproductive season 1994 in hill Chavarrillo, Coatepec, Veracruz, Mexico.

Reproductive plants did not develop the same flower and fruit number in both years. Eighty orchid plants flowered in only one year (16 in 1993, and 64 in 1994), and 59 individual plants flowered in both years (26.46% of the total orchids). In plants that flowered both years, 28 individuals (47.46%) produced the same number of flower both seasons, 24 plants (40.68%) increased their flower display and 7 orchids (11.86%) decreased their flower number in 1994.

Few plants developed fruits (Table 1). Most fruiting *R. glauca* produced one fruit per plant in 1993, but in 1994 we recorded two individuals with two fruits each (Table 1). Mean fruit number per plant was low ( $1.21 \pm 0.5$ ) and also the fruit set (0.136 and 0.672, respectively for each study season). Twelve individuals (66.67%) from those fruiting in 1993 flowered again in 1994, but only four of them developed fruits again in the second season (22.22%).

**Effect of the total flower number of *R. glauca* per host tree on the fruit production:** Individuals of *R. glauca* produced few flowers during both seasons. In 1993, 49 flowering individuals (65.33%) developed only one flower, whereas the remaining plants (26) produced 2 to 13 flowers. In 1994, 58.54% of the total flowering individuals (72 plants) developed one flower, and the remaining plants (52)

produced 2 to 17 flowers. Individuals with more than two flowers were probably mixed clumps of multiple individuals. Mean flower number per *R. glauca* individual was not different between years (Mann-Whitney  $U = 4261$ ,  $p = 0.369$ , Table 1).

Plants developed few fruits during both seasons (Table 1). Individual fruit production was not related to flower number per individual plant ( $r_{s\ 1993} = 0.120$  and  $r_{s\ 1994} = 0.158$ ,  $p > 0.05$ ). There was no difference between fruit set of plants with one flower and fruit set of individuals with more than one flower ( $\chi^2_c = 0.18$  in 1993 and  $\chi^2_c = 0.45$  in 1994,  $p > 0.05$ ).

**Reproductive success of the *R. glauca* individuals per host tree:** Host trees support  $3.98 (\pm 4.5)$ , range 1-21) orchids (reproductive and non-reproductive individuals). Almost half of the trees supported one flowering *R. glauca* in both seasons (48.5% in 1993 and 47% in 1994), while the remaining trees supported two or more flowering orchids (21-27.3% two plants, and 24.2-32% more than two orchids, respectively). The mean number of flowering *R. glauca* per tree and the total number of flowers per tree (Table 1) were not different between seasons ( $U = 728$ ,  $p = 0.64$ ; and  $U = 732.5$ ,  $p = 0.67$ ).

We recorded only 16 host trees in 1993 and 12 in 1994 with *R. glauca* fruiting plants. Fruit number per tree (Table 1) was not different between seasons ( $U = 83$ ,  $p = 0.546$ ). We found a weak positive correlation between the number of flowering individuals and the number of fruiting *R. glauca* per host tree in the first reproductive season ( $r_{s\ 1993} = 0.37$ ,  $p = 0.036$  and  $r_{s\ 1994} = 0.231$ ,  $p = 0.117$ ).

**Spatial distribution of reproductive orchid plants:** We found a random pattern of distribution for the host trees of *R. glauca* (plot A:  $R = 1.14$ , and plot B:  $R = 1.09$ ,  $p < 0.05$ ). Host trees with flowering orchids were randomly distributed in both seasons (plot A:  $R_{1993} = 1.35$  and  $R_{1994} = 1.02$ ; plot B:  $R_{1993} = 0.95$  and  $R_{1994} = 1.01$ ;  $p < 0.05$ ). Also, host trees with fruiting plants of *R. glauca* showed a random spatial pattern (plot A:  $R_{1993} = 1.01$  and  $R_{1994} = 0.46$ ; plot B:  $R_{1993} = 1.49$  and  $R_{1994}$

= 0.76;  $p < 0.05$ ). Flowering and fruiting *R. glauca* plants were randomly distributed in both plots and seasons, as suggested by the randomization test (plot A:  $R_{1993} = 154.14$ ,  $p = 0.12$  and  $R_{1994} = 694.39$ ,  $p = 0.59$ ; plot B:  $R_{1993} = 287.47$ ,  $p = 0.483$  and  $R_{1994} = 150.95$ ,  $p = 0.26$ ).

## DISCUSSION

*Ryncholaelia glauca* is abundant at the studied forest; however only half or less of the studied population reproduces each year. Resources and previous reproductive efforts could influence new reproductive events in some orchid species (Montalvo and Ackerman 1987, Ackerman 1989, Ackerman and Montalvo 1990, Murren and Ellison 1996). Plant size (v.gr., total shoots and leaf number) should be a good indicator of potential reproductive capacity (v.gr., total flower number) (Murren and Ellison 1996), particularly in *R. glauca* where the number of inflorescences and flowers developed is constrained by the number of shoots and new pseudobulbs produced. We observed some large plants (clumps with many growing shoots and leaves) developing only one flower, and nearby small ones (with few growing shoots and leaves) developing two flowers. Large *R. glauca* plants with few flowers could be old ones. Also, we recorded some *R. glauca* individuals flowering and fruiting both study years. Apparently, in this species, previous reproductive effort does not limit the next one reproductive expression.

Individual floral display of *R. glauca* was low (1.8 flowers/plant). However flower lifetime (15-18 days, from one quarter to half of the flowering season) increases each individual floral display and the flower population density. Flower display and density have been associated with female and male function (Kunin 1993, 1997, Murren and Ellison 1996). Therefore longer flower life span could increase pollen export and pollination possibilities. On multi-flowered plants, large inflorescence size could result in increasing pollinia

removal (Sutherland 1986, Rodríguez-Robles *et al.* 1992) and high fruit set (Murren and Ellison 1996); though it is not a general pattern in orchids (Calvo 1990a). On the other hand, floral display and flower lifetime should influence pollinator behavior (Sih and Baltus 1987, Strauss and Conner 1996). Longer display period might be a result of scarcity of pollinators (Firmage and Cole 1988). Flower characteristics of *R. glauca* suggest a specialist pollinator (hawkmoth syndrome). Apparently, this type of relationship could be constant despite the number of flowers present, because specialists are efficient pollen vectors (Nilsson *et al.* 1987, Kunin 1993). Though we did not record pollinium removal, as on many orchid species, flowers of *R. glauca* close immediately after pollination even without pollinium removal (Flores-Palacios 1995). Infrequency of pollinators and low fruit set are common conditions for most orchid species (Ackerman and Montalvo 1990, Calvo 1990a, 1993, Dressler 1990, Sabat and Ackerman 1996). As other outbreeders species (Primack 1985), the extended flower life span in *R. glauca*, could increase individual pollination probabilities.

We found a weak relationship between individual floral display (flower number) and fruit set. Almost all flowering individuals of *R. glauca* developed one fruit over the two study years; only two plants developed two fruits each. Presence of conspecifics increased flower visitation rate on *Nepeta cataria*, but not all pollinator showed significant relationship (Sih and Baltus 1987). In nontropical areas hawkmoths show constancy when large patches of food plants are available, but inconstancy when resources are scarce (Nilsson *et al.* 1987). On the other hand, despite difference in total flowers of *R. glauca* produced each season, the mean number of flowering plants, orchid flower number, and fruits present per host tree were not different. These trees had a random spatial pattern, and the spatial pattern of flowering and fruiting orchid plants were not related. This suggests there is no density dependence effect on the flower visitors. Pollinators do visit the flowering plants of *R.*



*glauca* and host trees randomly, independently of flower number.

In general, the fruit set recorded for the few-flowered *R. glauca* was similar to multi-flowered orchid species that have the same breeding system (Flores-Palacios 1995). It is particularly interesting the similarity of the fruit set of *R. glauca* with that of *B. nodosa* and *E. ciliare*, species with the same pollination syndrome (Shemske 1980, Ackerman and Montalvo 1990). Apparently, single and multi-flowering, hawkmoth pollinated species could have similar fruit set. However, plants with one or few flowers per year should have a critical reproductive reduction. A possible benefit of flower display reduction is achieved by a larger fruit size and seed number. *Rhyncholaelia glauca* produces large fruits (10-15 cm long). Moreover, reduction in flower display in not self-pollinated orchids could decrease geitonogamy and increase xenogamy. It has been noted that orchids offering rewards to pollinators have relatively higher fruit set (14.2-26.6%), while deceptive species lower fruit set (9%) (Rodríguez-Robles *et al.* 1992). Fruit set of *R. glauca* occurs between the range of both types of orchids mentioned. However, as in all plant species, flower number in *R. glauca* changes among years and sites (see Table 1), producing differences in reproductive success.

In summary, fruit production of *R. glauca* was not related to individual floral display. Host trees with reproductive orchids were randomly distributed, and the spatial patterns of distribution of flowering and fruiting orchids were not associated. Finally, the fruit set of *R. glauca* is similar to that of multi-flowered orchid species, suggesting that the fitness of few flowered orchids with hawkmoth pollinated flowers could be equal to that of the former species.

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#### RESUMEN

La densidad de plantas floreciendo puede incrementar la tasa de visitas de polinizadores y la producción de frutos en plantas con inflorescencias multiflorales; sin embargo, este aspecto no ha sido estudiado en plantas con inflorescencias de una sola flor. En un encinar tropical de Chavarrillo, Veracruz, México, estudiamos el efecto de la densidad de plantas con flores y del despliegue floral en la producción de frutos de la orquídea epífita, polinizada por polillas, *Rhyncholaelia glauca*. La especie no es autógama y produce sólo una flor por eje de crecimiento, por año. La población de *R. glauca* florece sincronizadamente, las flores individuales duran más de 18 días y aquellas polinizadas se cierran rápidamente. Hipotetizamos que orquídeas con más ejes de crecimiento y aquellas en árboles con grupos de plantas floreciendo deben desarrollar más frutos que aquellas aisladas. Las plantas produjeron pocas flores por año, algunas plantas desarrollaron flores en ambos años y muy pocas desarrollaron frutos en ambos años. El número de frutos producidos por planta no estuvo relacionado con el número de flores por planta ni con el número de flores por árbol hospedero. Tanto los árboles con plantas con flores, como aquellos con plantas con frutos están distribuidos al azar y el patrón de distribución de plantas con flores y frutos no se relacionó. Aparentemente, los polinizadores visitan las flores al azar y no de forma denso-dependiente. La producción de frutos de *R. glauca* fue tan baja como la reportada para orquídeas multiflorales, polinizadas por polillas, lo que sugiere que la producción de frutos producidos en orquídeas polinizadas por polillas podría ser independiente del despliegue floral.

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