POLLINATION MECHANISMS AS A LIMITING FACTOR
IN THE DEVELOPMENT OF THE ORCHIDACEOUS FLORA OF HAWAI'I

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INTRODUCTION

One of the most intriguing aspects of the endemic Hawaiian flora is the obvious lack of orchids. There are an estimated 2678 endemic taxa of plants which occur throughout the Hawaiian Islands (St. John 1973) and yet the world's largest family of flowering plants, the Orchidaceae, is represented by only three endemic and four naturalized species. The uniqueness of this situation becomes even more apparent when one considers the fact that horticulturally grown orchid plants and cut flowers are major cash crops in Hawai'i. This apparent poverty of orchids in the Hawaiian Islands has not gone unnoticed. MacCaughey (1916), Degener (1930), Ridley (1930), Neal (1938), Fosberg (1948), Degener and Degener (1965), and Carlquist (1966a, 1966b, 1967, 1970) have all commented on Hawai'i's depauperate orchid flora. Many of these authors have even speculated as to the cause of the family's poor showing throughout the Hawaiian Islands. Some felt that a lack of suitable pollinators in Hawai'i may have been the major reason (MacCaughey 1916; Carlquist 1966a, 1967, 1970), while others have suggested that pollination is only part of the problem and that the absence of orchids in Hawai'i is due to high levels of extinction (MacCaughey 1916), lack of suitable mycorrhizae (Degener 1930), or loss of viability in orchid seeds which have been exposed to the rigors of long distance dispersal (Neal 1938; Carlquist 1970). All of these tentative hypotheses could explain the scarcity of orchids throughout the Islands but none has been substantiated by any experimental evidence prior to this study.

It is suggested in this study that the success of orchids in the Hawaiian Islands has been restricted by a shortage of suitable pollinators within the insular biota capable of utilizing the family's complex pollination mechanisms (Carlquist 1966b). The elaborate floral structure of most orchids precludes their pollination by a wide range of insects (Dodson 1962; Dressler 1968; van der Pijl & Dodson 1969). As a result, species dependent upon such reproductive systems would encounter limited success in establishment while successful emigrants would face strong selective pressures toward the development of more generalized pollination mechanisms or asexual means of propagation in their new environment. These could include the development of promiscuous entomophilic pollination systems, anemophily, autogamy, or asexual means of reproduction. All of these mechanisms

tend to reduce the species' dependence upon a particular group of insect pollinators and would enhance the organism's potential for survival in an environment deficient in possible pollinators. Since the floral forms of native entomophilous plants will tend to reflect the nature of the insect faunas (Carlquist 1966b), a high incidence of non-specific pollination mechanisms or asexual reproduction in the endemic and naturalized species of orchids present throughout the Hawaiian Islands would be indicative of a shortage of suitable insect pollinators within the insular biota.

This paper describes the pollination mechanisms utilized by the endemic and naturalized orchids of the Hawaiian Islands, and discusses some of the effects different modes of pollination would have upon the evolutionary potential of the species which adopt them.

MATERIALS AND METHODS

Seven species of orchids found throughout the Hawaiian Islands were examined for adaptations in their floral morphology which would facilitate self-pollination. Individual flowers and buds of different ages were selected from each of the species studied, dissected, and examined for adaptations which would render autogamy feasible. After the initial examination, the seven species were tentatively classified as to their probable mode of pollination and then reexamined in the field utilizing fresh material. As part of this study the mean number of flowers per inflorescence and the number of capsules formed per 100 flowers were determined for each species. Samples used to determine these figures ranged from nine to 42 inflorescences. Specimens of the orchids utilized in this study were collected mainly on the island of O'ahu. Additional material was obtained from the islands of Kaua'i and Hawai'i.

After examining all seven species for morphological adaptations which would facilitate self-pollination, detailed field studies were initiated for Anoectochilus sandvicensis Lindl., the only endemic species of orchid which appeared to be normally allogamic. Field work was carried out in an area of cloud forest located on the summit of Ka'ala, O'ahu (alt. 4025 ft). The orchid studied occurred terrestrially in low density throughout the area surveyed. Flowering specimens of A. sandvicensis within the study site were utilized in a number of experiments in an attempt to determine the species' natural pollinator. These experiments included bagging trials, insect trapping in the vicinity of blooming orchids, and artificial cross- and self-pollination. A detailed description of the techniques utilized in this study appears in Kores (1979).

RESULTS

A summary of the reproductive methods utilized by the seven species of orchids, based upon studies of their floral morphology, appears in Table 1. Based on floral morphology Anoectochilus sandvicensis, Arundina graminifolia (D. Don) Hochr., Epidendrum X Obrienianum Rolfe, and Phaius tankarvilleae (Banks ex L'Her) Bl. have normally developed flowers, are functionally allogamic throughout the Hawaiian Islands, and apparently require some external agent to bring about pollination. This conclusion is supported by the low number of capsules formed by the four supposedly allogamic species. Field surveys of wild populations of the four species throughout Hawai'i indicate that only 1.6% to 7.7% of the flowers produce capsules (Table 2). Similar studies of allegedly autogamic orchids in Hawai'i indicate that they produce over 10 times as many capsules as the allogamic species.

In addition to sexual means of reproduction three of the four allogamic orchids in Hawai'i are capable of asexual propagation. Arundina graminifolia and E. X Obrienianum develop new plantlets along the lower nodes of the old inflorescences. The third species, A. sandvicensis, develops new axes along the older portions of the fleshy, decumbent rhizomes; the new shoots ultimately become established and the connection between the new and old growing points break down, leaving two plants. Phaius tankarvilleae, the fourth allogamic species, does not appear to reproduce actively by asexual means of propagation though the species is capable of doing so if plants are forcibly divided.

The remaining three species of orchids studied are all listed in Table 1 as autogamic. All three species appear to have some structural adaptations in their floral morphology which facilitate self pollination. In the case of Liparis hawaiensis Mann, autogamy occurs as the result of a sequence of movements by the pollinium which ultimately bring the organ in contact with the stigma. These movements are the result of a differential drying out of the plant tissues and are a common phenomenon within the Orchidaceae (Darwin 1862; Knuth 1909). Spathoglottis plicata Bl., the second of the autogamic species listed in Table 1, effects self-pollination by producing an excess of stigmatic fluid which floods the anther causing the pollen to germinate in situ. This process is aided by movements of the column and labellum during anthesis. The entire sequence of events leading to pollination requires approximately 72 hours to complete and agrees with the findings of Ridley (1888), who first described S. plicata as being autogamic.

Platanthera holochila (Hbd.) Krzl. also appears to have specially modified flowers which facilitate self-pollination but the actual sequence of events which leads to pollination is still somewhat questionable. The species has small, green, fairly inconspicuous flowers which develop capsules 86% of the time. Platanthera holochila has been collected only once during the past 39 years and the observations presented in this paper are based on an analysis of spirit material from that collection.

Flowers of P. holochila have specially modified lateral petals which assist in self-pollination. These petals have a relatively narrow, club-like apex which is incurved against the column while the flowers are in bud. The pollen is granular and the elastic connective tissue which usually holds the grains together in other species of Platanthera appears to be absent from the Hawaiian species. Self-pollination in the species probably occurs when loose, granular pollen is compressed in the anther cells and eventually forced out over the lower edge of the anther. This extruded pollen is trapped between the incurved, fleshy tips of the lateral petals and the nonreceptive stigma. The pollen is held in this position and the stigma eventually becomes receptive, effecting pollination.

Attempts at determining how A. sandvicensis is pollinated were not as successful as the studies carried out on L. hawaiensis and P. holochila. The species is apparently allogamic but extensive field studies failed to identify its natural pollinator. During the species' eight-week flowering season no natural pollination occurred in any of the samples under observation at the Ka'ala site. Inflorescences of A. sandvicensis left exposed as controls, those partially surrounded by insect traps, and bagged flowers all failed to set seed. However, artificially selfed or crossed flowers did show signs that pollination had taken place by the following week and ovaries collected from these flowers at the end of the study did contain seed.

The fact that artificially pollinated flowers of A. sandvicensis set seed, while the remainder of the flowers from the Ka'ala sample did not, strongly suggests that the species is allogamic. These findings confirm those presented earlier in this paper based on the species' floral morphology. The absence of natural pollination within the Ka'ala sample of A. sandvicensis, during the species' 1973 flowering season, is probably best explained in terms of the small number of suitable pollinators and the limited quantity of flowers present at the site.

Insect traps surrounding inflorescences of A. sandvicensis yielded very few insects, predominantly Diptera (Drosophilidae), Hymenoptera (Ichneumonidae), Lepidoptera (Phycitidae), and Heteroptera (Reduviidae). None of these families listed above offer many promising potential pollinators for orchids (Faegri & van der Pijl 1966; van der Pijl & Dodson 1969) and it is suggested that the actual pollinator of A. sandvicensis may not be present in the sample of insects collected from Ka'ala.

DISCUSSION

The most prominent feature which emerged from the study of the seven endemic and naturalized orchids in Hawai'i was the non-specific nature of their pollination mechanisms. Orchids are usually dependent upon very specific pollinators to ensure adequate seed set, and yet in Hawai'i 42.8% of the species examined appear to be autogamic. If one considers just the endemic

species this figure jumps to 66%. The estimated rate of autogamy suggested by van der Pijl & Dodson (1969) for the rest of the family is only about 3%, approximately one-twentieth of the level found among the endemic Hawaiian orchids. This high incidence of autogamy prevalent in the Hawaiian orchids becomes even more significant when one examines the allogamic species included in this study. Although the majority of orchids studied proved to be allogamic, three of the four allogamic species appear to reproduce primarily by some form of vegetative propagation. Anoectochilus sandvicensis, Arundina graminifolia, and Epidendrum X Obrienianum are all capable of asexual reproduction. As a result six out of seven species, or 85.7% of the orchids studied, have alternative means of reproduction.

The apparent absence of specific entomophilic pollination mechanisms within the seven species of orchids examined, the high incidence of autogamy, and the prevalence of asexual reproduction are not typical of the Orchidaceae in general. The fact that so many orchids which have become successfully established in Hawai'i share these traits suggests that their presence has been favored by selective pressures within the insular environment. The most obvious environmental condition which would favor tran- sitions toward autogamy or asexual reproduction within the endemic and naturalized orchids present in the Hawaiian Islands would be lack of suitable insect pollinators. It is well known that islands generally have very depauperate insect faunas (Wal- lace 1891) and the Hawaiian Islands are certainly no exception (Zimmerman 1948). The generalized, non-specific reproductive mechanisms found in many orchids present in Hawai'i certainly suggest a lack of suitable insect pollinators and this lack of pollinators has probably been a major factor in restricting the development of an orchidaceous flora in the area.

A shortage of suitable pollinators would restrict the devel- opment of orchids within the region for a variety of reasons, the most obvious of these being the influence a lack of potential pollinators would have upon the reproductive success of the group. Long distance dispersal of orchids to the Hawaiian Islands would almost certainly exclude the emigrant species' natural pollinator, imposing a further restriction upon estab- lishment and success. Emigrant species would be faced with the task of finding a suitable substitute pollinator within their new environment or developing non-entomophilic pollination mech- anisms. The greater the specificity of the emigrant species' pollination mechanism the more difficult the problem of adap- tation becomes. This point is illustrated by the absence of certain orchids in the Caribbean Islands, although the distances between land masses are relatively small. Janzen (1974) has sug- gested that this absence of certain orchids from these insular floras may be due solely to the lack of Euglossine bees which serve as their natural pollinators. This situation is by no means unique to just the Orchidaceae. Ramirez (1970) has made similar suggestions concerning the influence the distribution of fig wasps (Agaonidae) has had upon the dispersal of Ficus throughout the world. In the case of the Hawaiian Islands, the depauperate insect fauna would tend to exlude emigrant species

dependent upon specialized pollination mechanisms. This would effectively reduce the number of prospective emigrants within the Orchidaceae to a small portion of the family adapted to less specialized pollinators.

A second point to consider is the influence a shortage of suitable pollinators has had upon the evolutionary potential of the endemic Hawaiian orchids. In the case of the Hawaiian Islands, experimental evidence suggests that the orchids examined depend upon relatively non-specific entomophilic pollination systems, autogamy, or asexual reproduction to maintain populations of the species. From an evolutionary standpoint none of these mechanisms offers the individual as much opportunity for speciation as the specific entomophilic pollination systems which typify the family. This point is relatively clear cut when considering the autogamic or asexually reproducing individuals present within Hawai'i's established orchids. Self-fertilization limits the size of the gene pool accessible to a population for the formation of new combinations to fit changing environmental conditions and this reduces the evolutionary potential of those lines which adopt it (Stebbins 1957). As a result, obligatory self-fertilizing species, while not necessarily on the road to extinction, do represent an evolutionary "blind alley." Asexual reproduction, from an evolutionary standpoint, is often even more deleterious to the future of the species. It almost entirely eliminates recombination and the species frequently becomes evolutionarily moribund.

In the case of species dependent upon non-specific entomophilic pollination mechanisms, the evolutionary potential of the individual is also reduced, but for precisely the opposite reason. Grant (1949) has pointed out that non-promiscuous pollination mechanisms utilizing insects capable of developing flower consistency (the situation for most orchids) can create a system of non-random mating within a population. In this case ethological isolation may prevent or reduce interbreeding between sympatric populations which have acquired different floral characters during a previous period of geographic separation. This condition would augment the efficiency of allopatric speciation within non-promiscuously pollinated groups of flowering plants but would be inoperative in promiscuously pollinated populations because the alleles would be uniformly distributed throughout the entire population of the species. As a result, the Hawaiian representatives of the Orchidaceae with their relatively generalized pollination mechanisms may have had less of an opportunity to undergo speciation than more specialized members of the family present elsewhere. This certainly seems to be the case for the endemic Hawaiian orchids where three original introductions appear to have given rise to only three endemic species. The lack of speciation within the endemic Hawaiian orchids and the restrictions that a shortage of suitable pollinators has imposed upon long distance colonization within the family are probably the major factors which have resulted in the notable scarcity of orchids in the endemic Hawaiian flora.

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TABLE 1. Mode of pollination based on floral morphology.

Species	Allogamic	Autogamic	Asexual
Platanthera holochila	–	+(?)	–
Liparis hawaiensis	–	+	–
Spathoglottis plicata	–	+	–
Arundina graminifolia	+	–	+
Phaius tankarvilleae	+	–	–
Epidendrum X Obrienianum	+	–	+
Anoectochilus sandvicensis	+	–	+

TABLE 2. Percentage of capsules formed in wild populations.

Species	Sample Size	$\overline{X}$ Fls./Infl.	% Fls. Forming Capsules
Platanthera holochila	25*	30.24	86.12
Liparis hawaiensis	42	5.23	66.36
Spathoglottis plicata	35	22.54	66.13
Arundina graminifolia	35	10.42	7.67
Phaius tankarvilleae	35	14.71	4.70
Epidendrum X Obrienianum	32	24.40	3.97
Anoectochilus sandvicensis	9	6.77	1.63

* Based on herbarium specimens at BISH.