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CHIASMA FREQUENCY EVIDENCE ON THE EVOLUTION OF AUTOGAMY IN *LIMNANTHES FLOCCOSA* (LIMNANTHACEAE)¹

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Limnanthes floccosa Howell and *L. alba* Benth. are conspicuous elements of the vernal flora of California and southern Oregon. Evidence suggests that *L. floccosa* is a recent autogamous derivative of *L. alba* (Kalin, 1971) which is adapted for outcrossing. The purpose of this paper is to outline changes in chiasma frequency that have accompanied the evolution of autogamy in *L. floccosa*, and to discuss the significance of these changes in relation to the origin of autogamy in this species.

MATERIALS AND METHODS

The breeding systems of *Limnanthes alba* and *L. floccosa* were determined using plants grown from seed in greenhouses, and from field observations on pollination. Estimates of the number of pollen grains produced per flower were obtained with the use of a haemocytometer. Automatic selfing ability was measured in 15–30 plants per population grown under pollinator-free conditions in greenhouses. Natural pollination was measured by counting the number of seeds produced per flower in a large number of plants following bee pollination in the field.

Chiasma frequencies were determined at diakinesis from flower buds fixed in a 6:3:2 mixture of ethanol:chloroform:propionic acid. Chiasmata were counted for five plants per population from material grown from field-collected seed in growth chambers with similar conditions of light,

humidity and temperature. The chiasmata of 25 pollen mother cells (PMCs) were counted for each plant studied.

THE ECOLOGY AND RELATIONSHIPS OF *Limnanthes floccosa* AND *Limnanthes alba*

Autogamous *Limnanthes floccosa* and its outcrossing relative, *L. alba*, are annuals that occur in California and southern Oregon. Seed germination occurs during the rains of late autumn and winter (November–January) and flowering and seed set correspond with the cessation of the rains and the initiation of drought in the spring (March–May). *Limnanthes alba* is adapted to wet habitats exposed to full sun. It occurs primarily on the eastern margin of the Sacramento Valley of California and in the adjacent foothills of the Sierra Nevada from Merced County, north to Shasta County, along streamsides and pool edges, and in damp meadows. On the valley edge it is restricted almost entirely to the edges of vernal pools and ephemeral streams. In contrast with *L. alba*, *L. floccosa* is adapted to a wide range of ecological conditions. Three of its five subspecies (ssp. *californica*, in Butte County, California, ssp. *grandiflora* on the Medford Plains in Jackson County, Oregon, and ssp. *pumila* on Upper and Lower Table Rock, respectively in Jackson County, Oregon) occur in vernal pools. The most widespread subspecies of *L. floccosa* (ssp. *floccosa*, Shasta County and Siskiyou County, California, and Jackson County, Oregon) is adapted to habitats where the length of the growing season which is limited by moisture in the soil may be very short, e.g., sparsely vegetated flats, road edges, and in

¹ This investigation constitutes part of a dissertation submitted in partial fulfillment of the requirements of the degree of Doctor of Philosophy in Botany at the University of California, Berkeley.

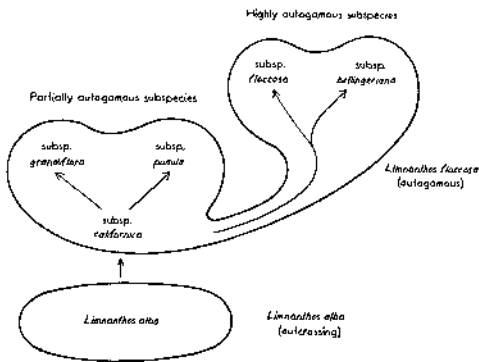


FIG. 1. The relationships of subspecies of *Limnanthes floccosa* and of *L. floccosa* to *L. alba* based on taximetric, electrophoretic and interfertility criteria.

cultivated fields. This subspecies of *L. floccosa* may flower as much as one month earlier than the vernal pool subspecies in the same geographical area. The fifth subspecies of *L. floccosa* (ssp. *bellingermana*) is known only from three populations on the eastern upland margin of the distribution of ssp. *floccosa*. It occurs in damp,

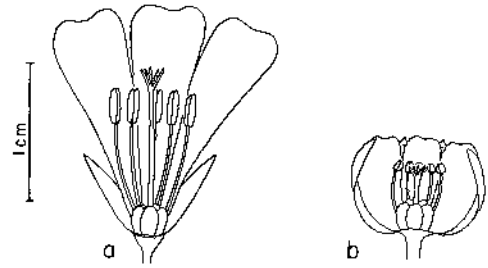


FIG. 2. Floral morphology of outcrossing *Limnanthes alba* (a) and autogamous *L. floccosa* (b).

shaded meadows which may be covered by snow for several months of the winter.

The probable evolutionary relationships of *Limnanthes floccosa* and *L. alba* have been discussed elsewhere (Kalin, 1971) but are briefly summarized here (Fig. 1). The most primitive subspecies of *L. floccosa* are the vernal pool subspecies (ssp. *californica*, ssp. *grandiflora* and ssp. *pumila*). Subspecies *floccosa* is a small-flowered lineage that differentiated from ssp. *californica* on the eastern margin of

TABLE 1. Morphological and phenological features of flowers and the breeding systems of *Limnanthes floccosa* and *Limnanthes alba*.

Species and subspecies	Petal length (mm)	Pistil length (mm)	Pollen ¹ production ($\times 1000$)	Anther position relative to receptive stigma	Degree of pro-tandry ²	Greenhouse selfing (% of field seed set)	Actual breeding system
<i>L. floccosa</i>							
subspecies <i>californica</i>	8.00-8.49	3.50-3.81	100-246	above	1-2	100	approx. 50% selfing and 50% outcrossing
subspecies <i>grandiflora</i>	7.75-8.50	3.32-3.87	53-98	above	1-2	93	approx. 50% selfing and 50% outcrossing
subspecies <i>pumila</i>	7.53-8.00	3.12-3.42	57-102	above	1-2	89	approx. 50% selfing and 50% outcrossing
subspecies <i>floccosa</i>	5.50-8.00	2.00-3.32	5-21	above	0-1	95-100	predominant selfing
subspecies <i>bellingermana</i>	6.10-7.55	2.30-2.40	8-27	above	0	69-100	predominant selfing
<i>L. alba</i> ³	11.83-14.70	4.07-8.03	467-933	below	3	3-32	predominant outcrossing

¹ All species of *Limnanthes* have 5 ovules per flower; pollen production measured per flower.

² Number of days separating anther dehiscence and stigma receptivity.

³ Based on 11 populations.

its range. Subspecies *bellingermana*, known only from three widely separated populations, is a recent ecologically marginal derivative of ssp. *floccosa*.

BREEDING SYSTEMS AND POLLINATION

The breeding systems of *Limnanthes alba* and *L. floccosa* are strongly correlated with floral morphology (Fig. 2). *Limnanthes alba* which is outcrossed, has large fragrant flowers with well developed nectaries and nectar guides and copious quantities of pollen ($467-933 \times 10^3$ grains per flower; Table 1). Although self-compatible, very little seed is set by self-pollination in the absence of pollinators (3-32%; Table 1). Self-pollination is largely prevented by protandry in which there is a difference of 2-3 days in the timing of anther dehiscence and stigma receptivity, and by the position of the receptive stigmas above the level of the anthers. In nature, *L. alba* is pollinated by native solitary and semi-social bees mostly of the genera *Panurginus* and *Andrena* (Kalin, 1971). All subspecies of *L. floccosa* are adapted for self-pollination. In contrast with *L. alba*, the stigmas of the flowers of *L. floccosa* mature at the same level as the anthers (Fig. 2). When grown under insect-free conditions 69-100% of the ovules of this species are automatically self-pollinated (Table 1). There is, however, variation in the degree of protandry and general attractiveness of the flowers to bees among the subspecies of *L. floccosa* and actual levels of self-pollination may be significantly lower than those obtained in the greenhouse. In the three vernal pool species, a number of features normally associated with outcrossing (fragrance, nectar guides and protandry) are retained (1-2 days between the time of stigma receptivity and anther dehiscence). When bees are abundant, such subspecies have high levels of self-pollination, but as pollinators may be absent in the habitats of these subspecies in many years, self-pollination must also be important. Levels of self-pollination in the early-flowering

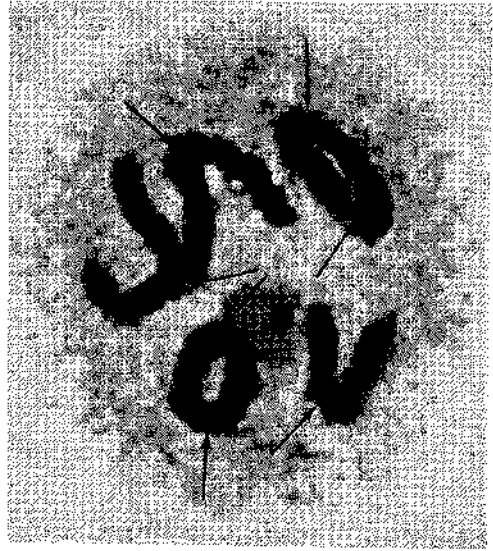


FIG. 3. Diakinesis in *Limnanthes alba* (Lake Co.-2). Arrows indicate location of chiasmata.

subspecies of *L. floccosa* (ssp. *floccosa* and ssp. *bellingermana*), on the other hand, are probably nearly as high as those obtained in greenhouses. The flowers of these subspecies are small and unattractive as food sources to bees (nectar guides are absent and pollen production is reduced; $5-27 \times 10^3$ grains per flower). In most of the populations of these subspecies protandry is almost entirely lacking, such that self-pollination tends to occur before cross-pollination is possible.

CHIASMA FREQUENCIES IN *Limnanthes floccosa* AND *Limnanthes alba*

The genus *Limnanthes* is uniform in chromosome number, size and morphology (Mason, 1952; Ornduff, 1971). All species have five pairs of chromosomes in which chiasmata are easily observed (Fig. 3). Chromosome pairs of *L. alba* and *L. floccosa* may have one, two or three chiasmata which are either terminal or interstitial. The position of chiasmata in each chromosome pair tends to be constant among pollen mother cells of an individual as well as among individuals of the same popula-

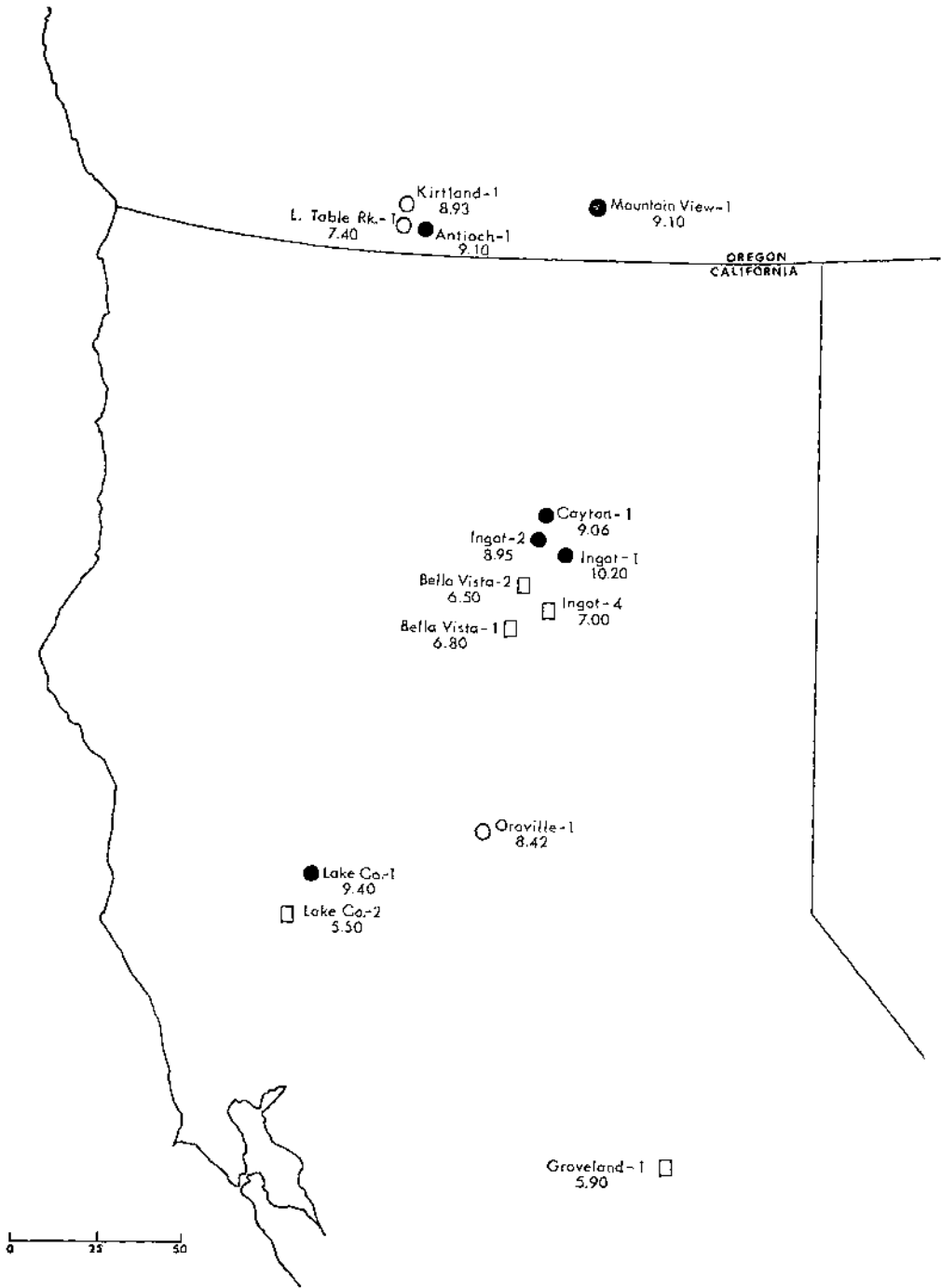


FIG. 4. Chiasma frequencies and locations of populations of *Limnanthes floccosa* and *L. alba*. Open circles, partially autogamous population of *L. floccosa*; closed circles, highly autogamous populations of *L. floccosa*; open squares, *L. alba*.

TABLE 2. *Chiasma frequencies in Limnanthes floccosa and Limnanthes alba.*

Species and subspecies	Population	Average chiasma frequency (average no. of chiasma per PMC per plant ¹)	Inter-plant chiasma frequency variance	Average no. of chiasmata per bivalent
<i>L. floccosa</i>				
subspecies <i>californica</i>	Oroville—1	8.42	0.05	1.68
subspecies <i>grandiflora</i>	Kirtland—1	8.93	0.49	1.78
subspecies <i>pumila</i>	Lower Table	7.40	0.02	1.48
	Rock—1			
subspecies <i>floccosa</i>	Ingot—1	10.20	0.01	2.04
	Antioch—1	9.10	0.27	1.82
	Lake Co.—1	9.40	0.00	1.90
	Cayton—1	9.06	0.06	1.81
subspecies <i>bellingneriana</i>	Ingot—2	8.95	0.00	1.80
	Mountain View—1	9.10	0.08	1.82
<i>L. alba</i>				
	Lake Co.—2	5.50	0.50	1.10
	Groveland—1	5.90	0.02	1.18
	Bella Vista—1	6.80	0.13	1.36
	Bella Vista—2	6.50	0.00	1.32
	Ingot—4	7.00	0.02	1.40

¹The data are based on 25 PMC per each of 5 plants.

tion. In both species, intra-population variation in the number of chiasmata per pollen mother cell is low ($\sigma = 0.00-0.50$). There is a slight tendency for individuals within populations of *L. floccosa* to show greater variation in chiasma frequency than those of *L. alba* but there are populations of *L. alba* which nevertheless show greater variation than some of those of *L. floccosa* (Table 2). The low level of variation in the chiasma frequency at the population level in *L. floccosa* and *L. alba* is surprising, especially in view of the fact that the plants used in the analysis were chosen from populations of plants established from field-collected seed. The low level of variation is probably due in part to the use of standardized growing conditions which would be expected to minimize the amount of environmental variation in chiasma frequency both within and between populations. The data suggest that each population of both species has a characteristic chiasma frequency which is, at least in large measure, genetically determined.

The chiasma frequencies of all popula-

tions of *Limnanthes floccosa* (7.40-10.20; Table 2) exceed those of all populations of *L. alba* (5.50-7.00), although this difference is not statistically significant ($t_{14} = 2.1$). Within *L. floccosa*, all populations of the partially autogamous subspecies or vernal pool subspecies (7.40-8.93) have lower chiasma frequencies than those of the two highly autogamous subspecies (8.95-10.20; $t_7 = 0.5$; not significant). The highest chiasma frequencies obtained in *L. floccosa* are from populations on the eastern margin of its range, where the level of autogamy is greatest for the species as a whole (Fig. 4; e.g. Ingot-1, 10.20).

The data on chiasma frequency strongly suggest that the evolution of autogamy in *Limnanthes floccosa* has been accompanied by an increase in chiasma frequency. Chiasma frequency and selfing potential as measured under greenhouse conditions are significantly correlated ($r = 0.72$; $P = 0.001$; Fig. 5). In itself, however, selfing potential is not a good index of the amount of self-pollination that occurs under natural

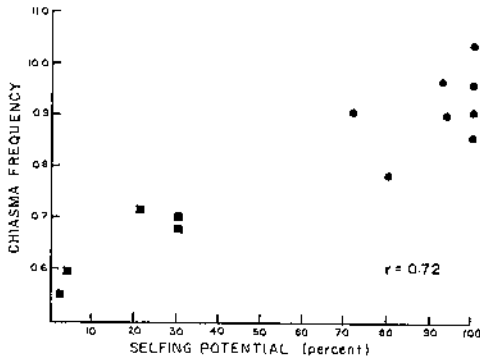


FIG. 5. The relationship between chiasma frequency and selfing potential in populations of autogamous *Limnanthes floccosa* and outcrossing *L. alba*. *Limnanthes floccosa*, circles; *L. alba*, squares.

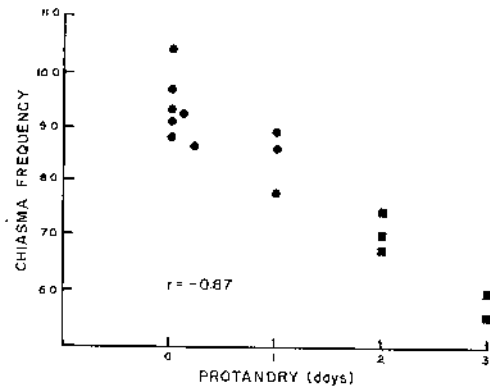


FIG. 6. The relationship between chiasma frequency and degree of protandry (number of days between stigma receptivity and anther dehiscence) in populations of autogamous *Limnanthes floccosa* and outcrossing *L. alba*. *Limnanthes floccosa*, circles; *L. alba*, squares.

circumstances because as noted earlier the actual amount of self-pollination occurring in the field will also depend upon the probability that self-pollination is not precluded by cross-pollination, or in other words, the degree of protandry. But chiasma frequency is also significantly correlated ($r = -0.87$; $P = 0.001$; Fig. 6) when the chiasma frequency is compared with the degree of protandry as a comparative measure of the level of self-pollination. Such correlations indicate that the trend for increase in chiasma frequency not only accompanied the original change from outcrossing to autogamy in *L. floccosa*, but that it also persisted with the differentiation of subspecies with higher levels of self-pollination.

DISCUSSION

The effect of chiasma frequency changes in Limnanthes floccosa.—Chiasma frequency has been shown to reflect the amount of genetic recombination in chromosomes at meiosis in a wide range of organisms (Lewis and John, 1963; Bodmer and Parsons, 1962). Like other components of the genetic system affecting levels of variability in populations, chiasma frequency is also known to be subject to selection which may decrease or increase the amount of genetic variability

in populations due to recombination alone (Lewis and John, 1963). The increase in chiasma frequency accompanying the evolution of autogamy in *Limnanthes floccosa* more than likely has led to an increase in the level of variability due to recombination. In the partially autogamous subspecies of *L. floccosa*, where the increase in chiasma frequency over that in *L. alba* has been due to an increase in the number of ring type bivalents with two localized terminal or subterminal chiasma over the number of rod type bivalents with a single chiasma, the increase in recombination potential in fact must be very small, as substantial lengths of the chromosomes of these subspecies still remain unrecombinable. In the highly autogamous subspecies, however, where interstitial, as well as terminal and subterminal chiasmata are present in one or more of the five chromosomes, the increase in chiasma frequency has probably led to a substantial increase in the level of recombination.

Hypotheses concerning the evolution of autogamy.—The presence in *Limnanthes floccosa* of subspecies showing increasing levels of self-pollination along with the

trend toward increasing chiasma frequency provides a favorable situation for testing hypotheses concerning the selective origin of autogamy. Hypotheses concerning the evolution of autogamy essentially fall into two categories. Early naturalists (e.g., Darwin, 1876; Müller, 1883; Henslow, 1888) and some recent workers (Lloyd, 1965; Moore and Lewis, 1965; Hagerup, 1950, 1951; in part Stebbins, 1957; Stebbins, 1970) consider autogamy as a *fertility insurance* which arises under ecological situations unfavorable for insect mediated cross-pollination. Autogamy is also considered advantageous for establishment following long-distance dispersal, in that only a single propagule would be required for successful colonization (Baker, 1955). Neither of these prefertilization hypotheses for the evolution of autogamy assume that any reduction in genetic variability following establishment of autogamy is selectively advantageous. Rather, it is regarded as the effect of an adaptation necessary for evolutionary survival.

Other authors consider the change from outcrossing to autogamy to be positively related to supposed effects autogamy has on the genetic structure of populations. In assuming that autogamy will lead to *actual* reduction in genetic variability they argue that this breeding system will arise in situations in which a genetic system favoring close adaptation (fitness) is favored over one emphasizing evolutionary longevity or flexibility (Mather, 1943, 1953), or in ecologically marginal and temporary habitats where there might be a high premium on rapid population build-up and the maintenance of individuals with a particular adaptive gene combination (Stebbins, 1950, 1957, although this view appears to be no longer held in Stebbins, 1970).

One important step in determining whether autogamy has arisen in relation to a prefertilization effect or in relation to certain of its genetic effects will be the determination of whether the reduction in genetic variability that results from self-

pollination in the autogamous derivative is selectively advantageous. In *Limnanthes floccosa*, increase in the level of autogamy is positively correlated with increase in the chiasma frequency. Because none of the populations of *L. floccosa* are obligately self-pollinated, all populations of this species can be expected to have considerable levels of heterozygosity. The increase in chiasma frequency in *L. floccosa*, therefore, must lead to an increase in genetic variability in its populations over that which would be due to outcrossing alone. That selection has favored a trend for increasing the level of variability in autogamous *L. floccosa* strongly suggests that levels of variability resulting from self-pollination in this species are lower than that which would be required to maintain a viable balance between short-term adaptability and long-term evolutionary survival. It is unlikely therefore, that autogamy in *L. floccosa* has arisen in relation to its direct effect of reducing genetic variability in populations. The trend for increase in chiasma frequency with increase in the level of autogamy can, however, be interpreted otherwise. Stebbins (1950), who regards autogamy as a means for the production and maintenance of a large number of well-adapted, genetically similar individuals in marginal and temporary habitats, views increase in chiasma frequency associated with autogamy as a means for populations to adapt during their colonizing phases, without destroying adaptedness to their existing conditions. Such an argument, however, has several short comings. That an increase in the recombination potential will afford self-pollinating populations flexibility without a loss of uniformity will only be valid when the level of self-pollination is very high, or when recombination tends to be ineffective in producing genetic variability. When the level of autogamy is not high, however, increase in chiasma frequency must always lead to an increase in genetic variability. Under these

circumstances, a high recombination potential must influence short-term as well as long-term evolution. In *L. floccosa*, the level of autogamy in the partially autogamous subspecies is probably no higher than 50% on the average (Kalin, 1971). The chiasma frequencies of these subspecies, nevertheless, are higher than those of populations of the outcrossing *L. alba*. It must be concluded therefore, that if autogamy arose in *L. floccosa* in conjunction with the need for closer adaptation purchased through population uniformity, the simultaneous establishment of a trend that opposes this effect would hardly be likely. Increase in chiasma frequency in *L. floccosa* over that in *L. alba*, seems to indicate that reduction in genetic variability resulting from the change from outcrossing to autogamy is an effect of the evolutionary change rather than its cause.

Ecological factors affecting the evolution of autogamy in Limnanthes floccosa.—In *Limnanthes floccosa* autogamy almost certainly evolved in relation to certain of its prefertilization effects. *Limnanthes floccosa* evolved on the dry northwestern margin of the range of *L. alba* in the Sacramento Valley of California. The extent to which *L. alba* penetrates into the relatively dry Sacramento Valley from the Sierra Nevada in any year depends upon fluctuations in seed output and seed germination due to yearly differences in winter rainfall. Dry years result in reduced germination, stunted plant growth, and, probably because of larval death due to drought, early bee emergence and shorter flight periods, the absence of bees at the time of flowering. Even if cross-pollination is mediated in such years, inadequate soil moisture may entirely prevent ovules from maturing to seed. In the relatively dry spring of 1970, when the only pollinator visiting ecologically marginal populations of *L. alba* in the Sacramento Valley was the introduced honeybee, seed output was reduced to an average of 9.3 seeds per plant, or approximately $\frac{1}{4}$ the number of seeds produced in

nearby populations of the same species in the adjacent wetter foothills. The advantages of autogamy under such circumstances are clear. First, there is no dependence upon pollinators for pollen transfer, and secondly, because of their tendency to bloom earlier than their outcrossing relatives (e.g. Lloyd, 1965; Kalin, 1971) self-pollinating genotypes may escape the harmful effects that early soil drying has on ovule maturation. In 1970, when *L. alba* experienced a sharp reduction in seed output, the earlier flowering populations of *L. floccosa* ssp. *californica* in the same area of the Sacramento Valley were virtually unaffected. Self-pollinating genotypes arising in marginal populations of *L. alba* in years of early drought would thus be at a strong selective advantage. If drought were so severe as to prevent the production of outcrossed seed, the success of such variants would be assured. This sequence of events almost certainly accounts for the change from outcrossing to autogamy in *L. floccosa*.

General implications for the evolution of autogamy.—Some of the conclusions presented here are at variance with several ideas on the evolution of autogamy, but nevertheless may have a broader application outside the generic limits of *Limnanthes*. Genetic theories for autogamy revolve around the supposition that self-pollination, through its effect of reducing population variability, can lead to an increase in adaptedness to the immediate environment. The level of self-pollination attained with the evolution of specific morphological and physiological features adapting a species to autogamy, however, is rarely high (Lloyd, 1965; Kalin, 1971). The increase in adaptedness achieved with the initial evolution of self-pollinating mechanisms, therefore, in the majority of species must be very small. A second factor opposing the likelihood that autogamy will arise in relation to "Matherian fitness" concerns the effect of inbreeding in a highly heterozygous outcrossing population.

Among the several effects of inbreeding known in plants are a decrease in vigor and competitive ability (Antonovics, 1968), and a reduction in seed set per fruit following self-pollination (Lloyd, 1965). Unless some means for conserving heterozygosity is available with self-pollination, self-pollinating variants that arise in outcrossing populations will usually be lost. The probability that autogamy will be associated with a *net increase* in fitness therefore must be very low.

It is emphasized here that autogamy must rarely arise in relation to a positive selection pressure for decreasing the level of variability in populations because of the effect of inbreeding. The evolution of autogamy in *Limnanthes floccosa* has been described in relation to certain prefertilization effects of self-pollination. In *Clarkia xantiana* autogamy has arisen through catastrophic selection for early-maturing genotypes (Moore and Lewis, 1965, 1966). Lloyd (1965) describes the evolution of self-compatibility in self-incompatible species of *Leavenworthia* in relation to a paucity of bees in early-flowering dry glade populations. The high frequency of autogamy in the insect impoverished Galápagos Island (Rick, 1966) and Faroes Islands (Hagerup, 1950, 1951) likewise suggests the evolution of autogamy in relation to a fertility insurance. Autogamy could also arise if a particular self-pollinating variant should by chance (e.g., by long-distance dispersal) be separated from its ancestral outcrossing population. All these modes for the evolution of autogamy, including the origin of autogamy through catastrophic selection have one feature in common, namely, at the time of establishment, autogamous genotypes are either spatially separated from competition with outcrossing genotypes or outcrossing genotypes have been removed from the presence of self-pollinating genotypes. Under such arrangements, any bottleneck due to inbreeding depression is easily surmounted, as the survival of the population is dependent upon autogamy alone.

SUMMARY

1) *Limnanthes floccosa* is an autogamous derivative of the outcrosser, *L. alba*. *Limnanthes floccosa* comprises five subspecies of which three are facultatively autogamous, and two are predominantly autogamous.

2) In *Limnanthes floccosa* the increases in chiasma frequency that have paralleled the evolution of autogamy indicate that autogamy has arisen not because of the effects self-pollination has on population structure, but because it serves as an adaptation to secure survival.

3) Hypotheses bearing on the evolution of autogamy are discussed and categorized according to whether the change from outcrossing to autogamy has occurred in relation to the prefertilization or the genetic effects of self-pollination.

4) Fluctuations in pollinator availability and seasonal variations in soil drying in marginal populations of *Limnanthes alba* indicate that autogamy in *L. floccosa* has arisen in relation to its prefertilization effect of securing seed set under circumstances in which insect-mediated cross pollination is unreliable.

5) Several arguments against the likelihood that autogamy arises in relation to the genetic effects of self-pollination are given.

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