

## Origin of gynodioecy in *Limnanthes*: evidence from ecogeographic patterns of variation

R. Kesseli and S. Jain

Department of Agronomy and Range Science, University of California, Davis, CA 95616, USA

Received January 2, 1987; Accepted March 20, 1987  
Communicated by P. M. A. Tigerstedt

**Summary.** Evidence for hybrid origin of gene-cytoplasmic gynodioecy in *Limnanthes douglasii* is presented in terms of the parapatric distributions of putative parental taxa and the increased levels of genetic variation in gynodioecious populations. Attempts to produce gynodioecy through artificial hybridization between different accessions apparently failed due to the limited number of parental combinations used in making hybrids. Further studies are proposed on the hybrid origin model and on selective forces determining the fate of gynodioecy with its contributions to higher levels of hybridity and genetic variation.

**Key words:** Gynodioecy – Natural hybridization – Gene-cytoplasmic control – Genetic variation – Anther color polymorphism

### Introduction

Studies in numerous crop species have shown gene-cytoplasmic male-sterility to arise frequently from inter-varietal or inter-specific hybridization (e.g. *Nicotiana*, Chaplin 1964; *Gossypium*, Meyer and Meyer 1961; *Brassica*, Pearson 1972). These hybridizations presumably introduce foreign nuclear alleles into different plasma types. Despite many useful agricultural examples and evidence suggesting that the gene-cytoplasmic mode may be the most common form of male sterility (Edwardson 1970; Ross 1978; Kheyr-Pour 1981; Van Damme and Van Delden 1982; Kesseli and Jain 1984a), most workers have neither discussed the origin of gynodioecy specifically in natural populations nor tested the predicted outcomes from the postulated hybrid mode of origin. Gynodioecy has also been reported in

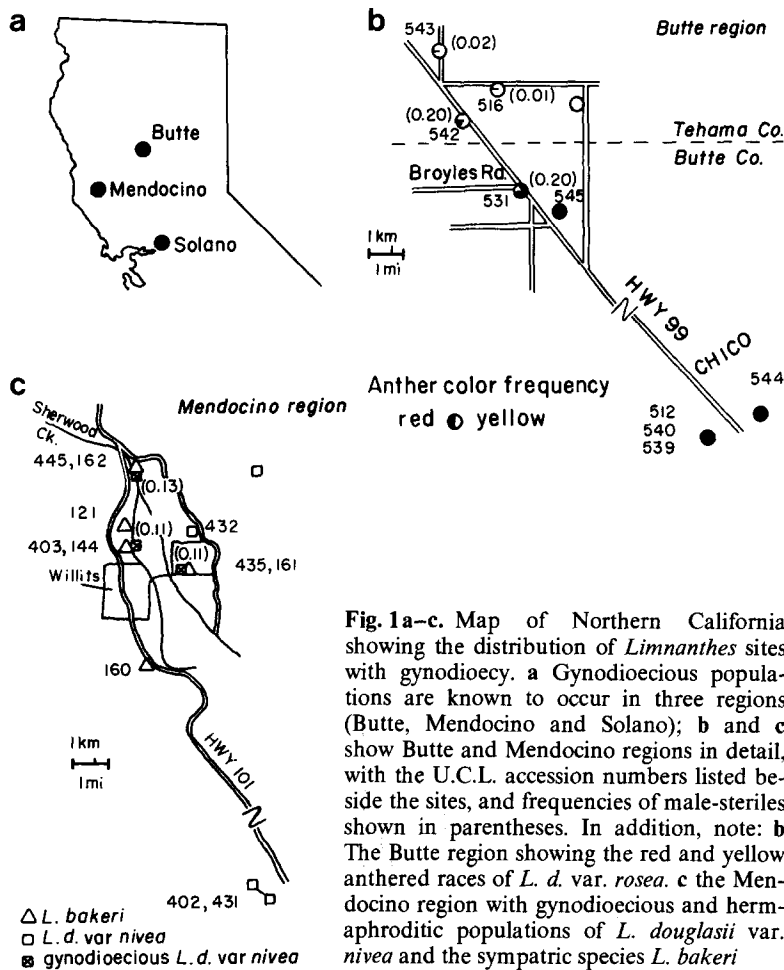
*Limnanthes* (Baker 1966) and investigated for its genetic control and maintenance (Kesseli and Jain 1984a). Several biosystematic studies in this genus have identified nearly 20 operational taxonomic units (Mason 1952; Ornduff and Crovello 1968; McNeill and Jain 1983; Kesseli and Jain 1984b) which commonly occur as partially subdivided and discrete populations in vernal pools or streams; additionally, surveys of genetic variability of all known taxa have shown high levels of intra- and inter-population diversity.

The purpose of this study is to report the distribution of gynodioecy in *Limnanthes* spp. in relation to the evidence for its hybrid origin. Specifically, we test the hybrid origin hypothesis using (a) the patterns of geographic distribution of closely related taxa, (b) data on allozyme and morphological variability between the neighboring hermaphroditic and gynodioecious populations, and (c) certain parental combinations to re-create and transfer male sterility through hybridizations.

### Materials and methods

Variation surveys of 113 populations of *Limnanthes* taxa (McNeill and Jain 1983; Kesseli and Jain 1984b) reported until 1983, showed only two populations (UCL529 from Solano county and UCL435 from Mendocino county) to be gynodioecious. Additional populations in the vicinity of the original gynodioecious populations in these two regions and in a third recently discovered area (Butte region) (Fig. 1) which also has gynodioecy, were surveyed for male-steriles by scoring individuals along several linear transects through each of the populations.

In each of the Solano and Mendocino regions, five populations (one gynodioecious and four neighboring hermaphroditic) were sampled and 10 to 12 plants per population were grown in greenhouses. We scored these plants for 12 morphological characters namely; petal length, petal width,



**Fig. 1 a-c.** Map of Northern California showing the distribution of *Limnanthes* sites with gynodioecy. **a** Gynodioecious populations are known to occur in three regions (Butte, Mendocino and Solano); **b** and **c** show Butte and Mendocino regions in detail, with the U.C.L. accession numbers listed beside the sites, and frequencies of male-steriles shown in parentheses. In addition, note: **b** The Butte region showing the red and yellow anthered races of *L. d. var. rosea*. **c** the Mendocino region with gynodioecious and hermaphroditic populations of *L. douglasii* var. *nivea* and the sympatric species *L. bakeri*

style length at anthesis, stamen length, anther color, sepal pubescence, length of leaf subtending the first flower; and leaf form in terms of the number of leaflets, basal leaflet length, and the number and width of lobes on the leaflets as well as the depth of sinus indentation.

Allozyme variation data from our earlier studies were used in conjunction with data from five populations of the Butte region, including the newly discovered gynodioecious population (UCL531). For all populations, we scored a minimum of 40 plants. Electrophoretic techniques and statistical analyses were identical to those of Kesseli and Jain (1984 b).

Crosses between the postulated progenitor taxa of gynodioecious populations as well as other parental combinations were made in the greenhouse. Transfers of male sterility from the two original gynodioecious populations, *L. douglasii* var. *rosea* (UCL529) and *L. douglasii* var. *nivea* (UCL435) only used male sterile plants as the maternal parent.

## Results

Among the 123 populations which have now been assayed for genetic variation, the hundreds of specimens from herbaria at the Davis and Berkeley campuses of the University of California and the field observations of all taxa in the genus, only eight popula-

tions were gynodioecious. These cluster into three disjunct regions; five populations in two regions (Solano, Butte) are *L. douglasii* var. *rosea* (*L. d. var. rosea*) and three population in the Mendocino region are *L. d. var. nivea* (Fig. 1). There are still areas where the occurrence of male sterility may be likely but so far undetected. Herbert Baker (personal communication) did note male sterility in a fourth Central California region, San Joaquin County, but we have been unable to relocate this site, possibly because of extensive habitat losses due to agricultural development in this region.

Distribution patterns of several *Limnanthes* spp. showed a close association between gynodioecy and sympatry of different taxa or evidence of introgression. In all three gynodioecious *L. d. var. nivea* populations in the Mendocino region, a second species, the narrowly distributed *L. bakeri*, was also found. Pure stands of *L. d. var. nivea* or *L. bakeri* had no male sterile individuals (Fig. 1c). In Butte region, a mapping of morphological variants at a locus controlling anther color showed that male sterility occurred at the interface

Table 1. A comparison of morphological variation in hermaphroditic and gynodioecious populations

	Petal length (mm)	Petal width (mm)	Style length at anthesis (mm)	Style length at maturity (mm)	Stamen length (mm)	Leaflet number	Leaflet length (mm)	Leaflet width (mm)	Lobe indentation (mm)	Lobe number	Sepal <sup>a</sup> pubescence	Anther <sup>b</sup> color
Solano Co., <i>L. d. rosea</i>												
Gynodioecious (UCL529)												
Mean	11.8	6.2	5.5	7.9	5.5	7.4	8.5	0.96	2.2	4.5	0-2	R, Y
SE	0.58	0.25	0.22	0.31	0.48	0.40	0.58	0.14	0.28	0.46		
C.V. <sup>c</sup>	17.7	14.6	14.2	13.7	31.4	19.6	24.9	54.0	45.4	36.7		
Hermaphroditic												
Mean ± SE of 4 populations	14.7	8.3	5.4	9.0	6.4	7.5	7.6	1.1	2.1	4.1	0-1	R
Mean C.V.	6.7	10.7	11.3	11.3	12.4	17.2	23.8	29.5	40.7	44.7		
Mendocino Co., <i>L. d. nivea</i>												
Gynodioecious (UCL435)												
Mean	12.6	5.3	5.1	8.6	5.9	9.4	6.1	1.1	1.9	3.8	1-2	Y
SE	0.70	0.28	0.26	0.30	0.48	1.17	0.33	0.10	0.33	0.86		
C.V. <sup>c</sup>	19.3	16.8	15.3	9.2	27.6	27.7	12.2	20.3	39.0	50.6		
Hermaphroditic												
Mean ± SE of 4 populations	13.8	6.2	4.9	7.9	6.5	9.2	8.8	3.0	2.5	5.4	1	Y
Mean C.V.	8.0	18.9	11.4	6.9	7.4	10.9	22.1	29.7	39.1	35.5		

<sup>a</sup> Sepal pubescence: 0 = absence, 1 = moderate, and 2 = highly dense pubescence

<sup>b</sup> Anther color: R = red, Y = yellow

<sup>c</sup> A sign test comparing the C.V.s for all characters of the gynodioecious with those of each hermaphroditic population showed the gynodioecious to be higher in 32 of 40 comparisons in *L. d. var. rosea* ( $P < 0.01$ ) and 28 of 40 comparisons in *L. d. var. nivea* ( $P < 0.05$ )

**Table 2.** A comparison of allozyme variation in hermaphroditic and gynodioecious populations. G, gynodioecy present

Population (UC accession no. in parentheses)	Loci and alleles												
	Adh-1			Pgm-1			Pgm-2				Pgi-1		
	100	98		100	102	99	100	96	94	102	100	102	98
Lenninger (543)	0.93	0.07		0.82	0.07	0.11	0.53	0.45	0.02		1.0		
Vina (516)	1.0			1.0			0.88	0.08		0.04	0.95		0.05
Broyles (531) G	0.86	0.14		0.78	0.17	0.05	0.63	0.37			0.99	0.01	
Shippee (512)	1.0			1.0			0.71	0.29			0.90	0.05	0.05
Skillen (540)	1.0			0.88	0.12		0.56	0.44			0.96		0.04
<i>L. d. rosea</i> (13 popn.)	0.99	0.01		0.82	0.16	0.01	0.78	0.21		0.01	0.80	0.15	0.05
Jepson (529) G	1.0			0.80	0.20		0.81	0.19		0.01	0.77	0.18	0.04
<i>L. d. nivea</i> (14 popn.)	0.99	0.01		0.77	0.11	0.09	0.18	0.79	0.01	0.02	0.93	0.02	0.04
Adams (435) G	0.99	0.01		0.63	0.33	0.04	0.19	0.81			0.87	0.12	0.01
<i>L. bakeri</i> (3 popn.)	1.0			1.0			1.0				0.81	0.19	

Population (UC accession no. in parentheses)	Loci and alleles															
	Lap-1			Lap-2		Skd-1				Prx-1			Prx-2			
	100	98	102	100	102	100	102	104	98	100	96	94	100	96	104	92
Lenninger (543)	0.69	0.31		0.57	0.43	0.80	0.19	0.01			1.0		0.70	0.30		
Vina (516)						0.89	0.13	0.02	0.07	0.05	0.95		0.91	0.09		
Broyles (531) G	0.87	0.11	0.02	0.51	0.49	0.67	0.18	0.11	0.05		1.0		0.67	0.33		
Shippee (512)						0.62	0.36	0.02			1.0		0.99	0.01		
Skillen (540)	0.96	0.04		0.71	0.29	0.71	0.08	0.21			1.0		0.96	0.04		
<i>L. d. rosea</i> (13 popn.)						0.74	0.22	0.03	0.01	0.40	0.60		0.97	0.02		0.01
Jepson (529) G						0.84	0.08		0.08	0.22	0.77	0.01	0.96	0.03	0.01	0.01
<i>L. d. nivea</i> (14 popn.)						0.60	0.35	0.05		0.37	0.46	0.17	0.75	0.25	0.01	
Adams (435) G						0.55	0.45			0.05	0.66	0.29	0.64	0.32	0.04	
<i>L. bakeri</i> (3 popn.)						1.0				0.30	0.70		0.28	0.04	0.40	0.29

of a northwestern yellow anther race and a southeastern red anther race of *L. d. var. rosea* (Fig. 1 b). Pure stands of red or yellow anther forms of *L. d. var. rosea* had no male sterility while polymorphic stands have male sterility. The most polymorphic stands (e.g. UCL531, 542) had the highest frequency of male-steriles. We have not thoroughly explored the regions north of this interface, but to the south all populations in the northern Central Valley are generally monomorphic for the red anther allele.

In the Solano region we found no geographical evidence for the extant sympatry of species or races. All hermaphroditic populations are nearly monomorphic for red anthers. However, as in the case of Butte region, all gynodioecious populations are highly polymorphic for anther color. The yellow anther taxon, *L. d. var. nivea*, does inhabit the same drainage systems but at higher elevations of the coastal range.

Levels of variation were higher in the gynodioecious populations than the average population of the taxa. In addition to anther color, the gynodioecious *L. d. var. rosea* and *L. d. var. nivea* populations showed greater amounts of variation for other floral and vegetative morphological characters as well (Table 1). The coefficients of variation (C.V.) in a pairwise comparison of gynodioecious with each of four hermaphroditic populations for 10 characters showed that populations UCL 529 and UCL 435 were significantly more variable than the hermaphroditic populations of their respective taxa (sign test,  $P < 0.01$  and  $P < 0.05$ , respectively).

The allozyme data also showed greater levels of variability in gynodioecious populations than the mean of other populations within each respective taxon (Table 2). For all three regions, the average number of alleles per locus was consistently higher in the gynodioecious populations. Also, estimates of intra-popula-

Table 2 (continued)

Pgi-2			Got-1				Got-2			Got-3			Est-1		Est-2				
100	104	96	100	98	102	88	100	95	105	100	93	107	100	96	100	96	103		
0.97	0.03		1.0				0.94	0.06		0.94	0.06		1.0			0.67	0.33		
0.97		0.03	0.97	0.03	0.01		0.99	0.01		0.99	0.01		1.0				0.98	0.02	
0.95	0.01	0.04	0.88	0.12			0.79	0.15	0.06	0.98	0.02		0.94	0.05	0.01	0.66	0.29	0.05	
0.98		0.02	0.98		0.02		0.99	0.01		0.97	0.03		0.98	0.02		0.60	0.40		
1.0			0.96	0.04			0.92	0.08		1.0			0.92	0.04	0.04	0.46	0.54		
0.96	0.02	0.01	0.97	0.02	0.01		0.98	0.02		0.90	0.04	0.06	0.98	0.02		0.58	0.35	0.02	0.06
0.97	0.01	0.02	0.97		0.03		0.89	0.11		0.97	0.01	0.02	1.0			0.75	0.25		
0.94	0.05	0.01	0.93	0.04	0.02		0.99	0.01	0.01	0.83	0.11	0.05	0.97	0.03		0.74	0.23	0.02	
1.0			0.87	0.10	0.02		1.0			0.93	0.01	0.06	0.98	0.02		0.70	0.30		
1.0						1.0	0.93		0.07	1.0			1.0			0.49	0.51		

Mdh-1		Mdh-2				Acp-2				No. of plants	Frequency of ms in population	H <sub>s</sub>	No. of alleles/ locus/ population
100	103	100	85	95	97	100	95	90	104				
0.97	0.03	0.06	0.94			0.91	0.09			31	0	0.20	1.9
1.0		0.23	0.74		0.03	0.97	0.02	0.01		38	0	0.11	2.1
0.95	0.05	0.10	0.89	0.01		0.86	0.12	0.02		40	0.20	0.25	2.5
1.0		0.19	0.81			0.89	0.11			38	0	0.12	1.9
1.0		0.14	0.86			0.96		0.04		39	0	0.16	1.8
		0.15	0.80	0.05		0.92	0.06	0.01		455	0	0.14±0.02	1.9
		0.17	0.74	0.06	0.04	0.90	0.08	0.01		111	0.15	0.020	2.5
		0.85		0.13	0.02	0.86	0.06			490	0	0.17±0.01	2.2
		0.99		0.01		0.94	0.06			67	0.12	0.23	2.3
		1.0				1.0				44	0	0.07±0.02	1.2

tion diversity ( $H_s$ ) of the gynodioecious populations were significantly higher than the respective taxon means ( $P < 0.05$ ,  $t$ -test). In the Butte region, allozyme markers did not provide diagnostic identification of the potential ancestral races, so the verification of introgression is not yet possible. In the Mendocino region, several loci showed allelic differences between the sympatric species *L. d. var. nivea* and *L. bakeri*. At three of these loci (Pgi-1, Got-3, and Acp-2), the allelic frequencies of the gynodioecious *L. d. var. nivea* populations were intermediate or more similar to those of *L. bakeri*. One locus, Got-1, has alternate alleles present in the sympatric species but the *L. bakeri* allele Got-1<sup>88</sup> was not detected in the gynodioecious populations. These allozyme data did not provide a rigorous test but appeared consistent with the hybrid origin hypothesis.

Male sterility has been successfully transferred to *L. striata* and all the *L. douglasii* varieties including *L. d.*

*var. sulphurea* and *L. d. var. douglasii* in which no gynodioecious populations are known (Table 3). Backcrosses have been attempted to stabilize the gynodioecy trait in some other varietal backgrounds. The de novo derivation of male sterility through artificial hybridization has not yet been successful as preliminary attempts to hybridize the sympatric species *L. d. var. nivea* and *L. bakeri* did not yield viable progeny, and crosses between different *L. douglasii* varieties produced only hermaphroditic progeny.

## Discussion

We have suggested that gynodioecy in *Limnanthes douglasii* has arisen via hybridization events involving different progenitor taxa. Clearly, all hybridization events do not necessarily result in the production of

**Table 3.** Hybridization attempts for (a) the transfer of male-sterility trait among taxa and (b) the production of male-sterility de novo in crosses with hermaphrodites as female parent

Female parent	No. of plants used as female parent <sup>a</sup>	Male parent	No. of viable plants phenotype <sup>b</sup>
<b>Male sterile</b>			
rosea (529)	5	sulphurea, nivea, douglasii (400, 406, 441)	35 ms
nivea (435)	3	sulphurea, nivea douglasii striata (400, 406, 404, 441, 117)	57 ms 1H
F <sub>1</sub> (435 ms × 400)	12	sulphurea, nivea, rosea (440, 406, 405, 435, 516, 512, 511)	56 ms 1H <sup>c</sup>
nivea (435)	2	alba, grandiflora (312, 224)	0
<b>Hermaphrodite<sup>a</sup></b>			
nivea (435)	4	bakeri (144)	0
bakeri (144)	4	nivea (435)	0
nivea (416, 431, 435)	10	nivea, rosea, sulphurea douglasii (406, 435, 529, 441)	52 H
rosea (529, 511)	24	rosea, nivea, sulphurea douglasii (511, 512, 516, 406, 431, 400, 441)	84 H

<sup>a</sup> Between five and ten flowers per plant were emasculated and used for each cross

<sup>b</sup> Phenotype: ms indicates male sterile plant; H indicates hermaphroditic plant

<sup>c</sup> Morphological characters indicate that this hermaphroditic individual may be a contaminant

male sterility. There are a minimum of 16 areas where species or varieties have overlapping distribution patterns and congeners lie within a few kilometers of each other. Field observations show that sympatry occurs for five pairs of diagnostically distinct taxa. *Limnanthes d.* var. *nivea* is sympatric with *L. d.* var. *douglasii*, *L. bakeri* and *L. vinculans* in three separate areas and *L. alba* is sympatric with *L. striata* and *L. floccosa*, ssp. *floccosa* in two separate areas. Thus, even with the possible discovery of additional zones of hybridization, only rarely would this yield gynodioecy. Many workers have reported in situ hybridizations, the outcomes of which can be loosely grouped into five categories (some of which may be transitory stages of others). These are: (1) a "swamping out" or loss of immigrant variation via genetic drift or selection causing no long-term evolutionary change in the native population or species (Lewis 1961; Levin 1983); (2) the production of a narrow hybrid zone presumably maintained by continuous hybridization with no introgression (Antonovics et al. 1971; Leslie and Dingle 1983; Millar 1983); (3) maintenance of increased and novel genetic variation (Stebbins and Daly 1961; Baetcke and Alston 1968; Anderson and Gage 1952; Grant 1971); (4) introgression and the development of clines (Mason 1949; Heiser 1949; Endler 1977); and (5) one of several routes toward speciation (Grant 1971; Lewis and Epling 1959; Turner et al. 1980; Goldman et al. 1983). We

have shown evidence in *Limnanthes* for outcome (3) in this paper. Other outcomes have also been noted in this genus (Kesseli 1984).

We also postulate that gynodioecy has arisen at least 3 times (a polyphyletic origin) in *L. douglasii*. A single origin is unlikely since cytoplasmic male sterility would not generally be carried along in long distance dispersal events. The rationale somewhat follows Baker's (1967) rule explaining the disadvantage of self-incompatible species in colonizing events. Gynodioecy could not establish from a single seed or even many seeds from a single mother, since only a single plasma type would be transmitted in these situations. Nuclear male sterility could establish but the fitness requirements for this mode of male sterility are much more stringent (Charlesworth and Ganders 1979; Kesseli and Jain 1984a). Gynodioecy is not common on islands (Carlquist 1966; Godley 1979; McComb 1966) while dioecy (nuclear inheritance), which is common, presumably represents a reversion to an outcrossing system from the self-compatible colonizer. Cytoplasmic male sterility may evolve if there are multiple colonization events and hybridizations of closely related taxa leading to a de novo origin.

The geographic distributions and genetic data also show that gynodioecy may be at different stages of evolution in these populations, possibly having existed for the longest time period in the Mendocino area and

the shortest in Butte area. The recent origin in Butte area is suggested by the extant presence of potential progenitors, the very high levels of male sterility (possibly indicating continued hybridization and a non-equilibrium frequency stage) and high average numbers of alleles per locus. The relative antiquity of gynodioecy in Mendocino is primarily suggested by the absence of certain alleles representing a putative progenitor, namely *L. bakeri* (probably indicating many generations of backcrossing and drift) and low average number of alleles per locus. While high heterozygosity levels are difficult to associate with recent hybridizations since male sterility itself enhances heterozygosity levels, the average number of alleles per locus may be a good index of recency since it is less severely affected by the evolutionary changes in mating systems.

Stronger evidence for the hybrid origin of male sterility would require two additional data sets. First, the experimental re-creation of male sterility should be broadly pursued despite the probability of a low success rate. In a study of gynogenesis in hybrid derived fish *Poecilia formosa*, Turner et al. (1980) failed to reproduce gynogenesis in artificial hybrids of the well known ancestral species. They argued that in populations with large intra-population variation the choice of parents could be critical. In addition to our hybridization efforts, Mason (1952) and Ornduff (1971) both attempted with limited success to cross *L. bakeri* with other species. Mason produced no hybrids in crosses with *L. d.* var. *douglasii* or *L. striata* while Ornduff managed two with *L. striata*. These F<sub>1</sub>'s had low pollen fertility (4% and 16%), indicating some male sterility but no further information was provided.

The second line of evidence requires the discovery of genetic markers which specifically distinguish progenitor populations and demonstrate polymorphism in gynodioecious populations. As yet no enzyme markers surveyed have shown this; however, techniques revealing organelle genome variation might be a more appropriate probe. To have cytoplasmic male sterility, gynodioecious populations must have at least two plasma types. Hermaphroditic populations should generally have one unless the plasma types are not incompatible or they have a nuclear fertility restorer in high frequency. This latter situation may indicate the acquisition followed by the loss of male sterility in a population. Since mitochondria are involved in cytoplasmic male sterility in maize (Levings 1983), this would be the logical choice of organelles.

This report has outlined the breadth of this very interesting evolutionary genetic problem dealing with the origin of a novel trait, a recombination product, and an experimental approach to altering breeding systems. Hybridization events in nature provide opportunities for ecological studies of genetics, recombina-

tion, and evolution of novel traits (Gottlieb 1972). The origin of novel sex forms and breeding system variants such as male sterility, autogamy, apomixis, etc. (Levin 1978, for a review) needs greater emphasis in the population dynamic context.

## References

- Anderson E, Gage A (1952) Introgressive hybridization in *Phlox bifida*. *Am J Bot* 39:399-404
- Antonovics J, Bradshaw AD, Turner RG (1971) Heavy metal tolerance in plants. *Adv Ecol Res* 7:1-85
- Baetcke KP, Alston RE (1968) The composition of a hybridizing population of *Baptisia sphaerocarpa* and *Baptisia leucophaea*. *Evolution* 22:157-165
- Baker HG (1966) The evolution of floral heteromorphism and gynodioecism in *Silene maritima*. *Heredity* 21:689-692
- Baker HG (1967) Support for Baker's law as a rule. *Evolution* 21:853-856
- Carlquist S (1966) The biota of long distance dispersal. IV. Genetic systems in the floras of oceanic islands. *Evolution* 20:433-455
- Chaplin JF (1964) Use of male sterile tobacco in the production of hybrid seed. *Tob Sci* 8:105-109
- Charlesworth D, Ganders FR (1979) The population genetics of gynodioecy with cytoplasmic-genic male sterility. *Heredity* 43:213-218
- Edwardson JR (1970) Cytoplasmic male sterility. *Bot Rev* 36:341-420
- Ender JA (1977) Geographic variation, speciation and clines. Princeton University Press, Princeton
- Godley EJ (1979) Flower biology in New Zealand. *NZ J Bot* 17:441-466
- Goldman M, LoVerde P, Chrisman C (1983) Hybrid origin of polyploidy in fresh water snails of the genus *Bulinus* (Mollusca: Planorbidae). *Evolution* 37:592-600
- Gottlieb LD (1972) Levels of confidence in the analysis of hybridization in plants. *Ann Mo Bot Gard* 59:435-446
- Grant V (1971) Plant speciation. Columbia University Press, New York
- Heiser CB (1949) Naturalization with particular reference to introgression. *Bot Rev* 15:645-687
- Kesseli RV (1984) Biosystematics, evolution and breeding system analyses in *Limnanthes*. PhD Dissertation, University of California, Davis
- Kesseli RV, Jain SK (1984a) An ecological study of gynodioecy in *Limnanthes douglasii* (Limnanthaceae). *Am J Bot* 71:775-786
- Kesseli RV, Jain SK (1984b) New variation and biosystematic patterns detected by allozyme and morphological comparisons in *Limnanthes* section *Reflexae* (Limnanthaceae). *Plant Syst Evol* 147:133-165
- Kheyr-Pour A (1981) Wide nucleus-cytoplasmic polymorphism for male sterility in *Origanum vulgare* L. *J Hered* 71:253-260
- Leslie J, Dingle H (1983) Interspecific hybridization and genetic divergence in milkweed bugs (*Oncopeltus*: Hemiptera). *Evolution* 37:583-591
- Levin DA (1978) The origin of isolating mechanisms in flowering plants. *Evol Biol* 11:185-317
- Levin DA (1983) An immigration-hybridization episode in *Phlox*. *Evolution* 37:575-582
- Levings CS III (1983) Cytoplasmic male sterility. In: Kosuge T, Meredith CP, Hollaender A (eds) Genetic engineering of plants. Plenum Press, New York, pp 81-92

- Lewis H (1961) Experimental sympatric populations of *Clarkia*. *Am Nat* 95:155–168
- Lewis H, Epling C (1959) *Delphinium gypsophilum*, a diploid species of hybrid origin. *Evolution* 13:511–525
- Mason CT (1952) A systematic study of the genus *Limnanthes*. *R. Br. Univ Calif Publ Bot* 25:455–512
- Mason HL (1949) Evidence for the genetic submergence of *Pinus remorata*. In: Jepsen GL (ed) *Genetics, paleontology and evolution*. Princeton University Press, Princeton
- McNeill CI, Jain SK (1983) Genetic differentiation studies and phylogenetic inference in the plant genus *Limnanthes* (Section *Inflexae*). *Theor Appl Genet* 66:257–269
- McComb JA (1966) The sex forms of species in the flora of the south west of Western Australia. *Aust J Bot* 14:303–316
- Meyer JR, Meyer NG (1961) Cytoplasmic male sterility in cotton. *Genetics* 46:883–890
- Millar C (1983) A steep cline in *Pinus muricata*. *Evolution* 37:311–319
- Ornduff R (1971) Systematic studies of Limnanthaceae. *Madrono* 21:103–111
- Ornduff R, Crovello TJ (1968) Numerical taxonomy of Limnanthaceae. *Am J Bot* 55:173–182
- Pearson OH (1972) Cytoplasmically inherited male sterility characters and flavor components from the species cross *Brassica nigra* (L.) Koch X *B. oleracea* L. *J Am Soc Hortic Sci* 97:397–402
- Ross MD (1978) The evolution of gynodioecy and subdioecy. *Evolution* 32:174–188
- Stebbins GL, Daly K (1961) Changes in the pattern of a hybrid population of *Helianthus* over an eight-year period. *Evolution* 15:60–71
- Turner BJ, Brett BH, Miller RR (1980) Interspecific hybridization and the evolutionary origin of a gynogenetic fish, *Poecilia formosa*. *Evolution* 34:917–922
- Van Damme JMM, Van Delden W (1982) Gynodioecy in *Plantago lanceolata* L. I. Polymorphism for plasmon type. *Heredity* 49:303–318