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Allozyme Genetics in Permanent Translocation Heterozygotes of the *Oenothera biennis* Complex

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Allozyme inheritance and transmission genetics of 11 enzyme systems were determined in the permanent translocation heterozygotes Oenothera biennis, Oe. strigosa, *and* Oe. parviflora. *Electrophoretic variation was examined first among 164 strains of structural heterozygotes. Allelic configurations were then judged from inheritance patterns in reciprocal F_1 hybrids between each of 22 ring-forming strains and tester strains of the related bivalent-formers,* Oe. hookeri *and* Oe. grandiflora. *Allozymes are inherited as codominant markers, and, as dictated by the genetic system, within a strain individual allelic variants are generally transmitted through only one germ line. Of the 20 loci resolved, only eight are polymorphic in any species, and, within species, generally only two alleles are present at each polymorphic locus. Despite the relatively meager allelic array, each of the 22 strains whose chromosome complexes were characterized is genotypically unique. Generally, within taxa, α (egg) and β (sperm) complexes differ in allele frequency at several polymorphic loci. Such variability is correlated with differences in the phylogenetic origins of complexes and not with differences in segmental arrangement within a group of related complexes.*

KEY WORDS: allozyme genetics; *Oenothera*; translocation heterozygosity.

INTRODUCTION

The cytogenetic studies of Cleland and associates (*cf.* Cleland, 1972) in *Oenothera* have provided insight into the phylogeny and the evolution of complete and permanent translocation heterozygosity in certain taxa of the

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genus. However, investigations of population dynamics and ecological genetics have been hampered by the lack of single locus markers which can be readily identified. With the development of gel electrophoresis and substrate-specific straining recipes, allozyme variants may be utilized as such markers, thus permitting rapid analyses of genetic variation and heterozygosity in populations and population systems. The present study focuses on the genetic bases of electrophoretic variation in the permanent translocation heterozygotes of the North American subgenus *Euoenothera*, *Oe. biennis*, *Oe. strigosa*, and *Oe. parviflora*. Companion studies utilizing allozyme variation to investigate geographical variation, phylogenetic affinity, and population structure in these taxa and related bivalent-forming oenotheras appear elsewhere (Levin *et al.*, 1972; Levy and Levin, 1975; Levin, 1975).

The major features of structural hybridity in the *Oenothera biennis* complex are as follows (*cf.* Cleland, 1972). Each structurally heterozygous species contains two seven-chromosome genomes or "Renner" complexes which differ completely in chromosome end (segmental) arrangement. A ring of 14 chromosomes is formed at diakinesis, and, following alternate disjunction, each complex is reconstituted within single gametes. Structural hybridity is maintained by a system of balanced gametophytic and sporophytic lethals; each complex tends to be transmitted exclusively through only one of the germ lines. The genetic system thus insures that strains are true-breeding and that heterozygosity is maintained despite predominant self-fertilization.

Egg (α) and sperm (β) complexes in each ring-forming taxon uniformly manifest distinct morphological syndromes; ostensibly each taxon is a stabilized hybrid derivative. *Oenothera biennis* has diverged into three groups, *Oe. biennis I* and *Oe. biennis II*, which contain a "biennis" and a "strigosa" genome, and *Oe. biennis III*, which contains two "biennis" genomes. Genome transmission in *Oe. biennis I* and *Oe. biennis II* is reversed, the "biennis" genome residing in the α complex of *Oe. biennis I* and in the β complex of *Oe. biennis II*. Ancestral sources of α and β complexes in the other ring-forming taxa are not as well defined. *Oenothera strigosa* contains two very similar "strigosa" genomes. Both groups of *Oe. parviflora* contain highly disparate genomes. Morphological syndromes of the β complexes of both groups resemble the relict *Oe. argillicola*; α-*parviflora I* complexes are "biennis"-like, and α-*parviflora II* complexes manifest "strigosa" morphology.

MATERIALS AND METHODS

Samples of geographically widespread strains, cytogenetically characterized by Cleland and others, were obtained from the U.S. National Seed Storage Laboratory, Fort Collins, Colorado. These included representatives of *Oe.*

biennis I (57), *Oe. biennis II* (43), *Oe. biennis III* (6), *Oe. strigosa* (29), *Oe. parviflora I* (19), and *Oe. parviflora II* (10). Individual 2-week-old seedlings of each strain were assayed electrophoretically for acid phosphatase (ACP), alkaline phosphatase (ALP), glucose 6-phosphate dehydrogenase (G6PD), glutamate oxalate transaminase (GOT), leucine aminopeptidase (LAP), leucyl-glycyl-glycine peptidase (LGGP), leucyl-tyrosine peptidase (LTP), malate dehydrogenase (MDH), phosphoglucose isomerase (PGI), phosphoglucose mutase (PGM), and valyl-leucine peptidase (VLP) following procedures detailed elsewhere (Levy and Levin, 1975).

A total of 22 ring-forming strains, collectively representing nearly all electrophoretic variation detected in the survey, were crossed both as male parent and as female parent to three bivalent-forming tester strains, two of *Oe. hookeri* and one of *Oe. grandiflora*. Three tester strains were used to anticipate potential crossing or F_1 germination difficulties and for independent confirmations of allozyme transmission genetics. Twenty-one of the 22 ring-forming strains were polymorphic for one or more enzyme systems, and each of the tester strains had been inbred for many generations and was monomorphic for all systems. Ostensibly, F_1 hybrids would contain only the α or β complex of a structural heterozygote and, consequently, only those allozymes specific to that complex. Allozyme genetics were judged from inheritance patterns of electrophoretic phenotypes in the reciprocal F_1 hybrids. Fourteen seedlings in each hybrid line were analyzed for each enzyme system.

RESULTS AND DISCUSSION

Electrophoretic Variation

Electrophoretic banding patterns manifest in each taxon as characterized by migration distance relative to the anodal electrophoretic front (R_p) are summarized in Table I. All resolved systems migrated anodally. Multiple zones of staining, distinctive in migration distance and between which no segregation was observed, were present for ACP, ALP, GOT, LGGP, LTP, PGI, and PGM in all taxa. For these enzyme systems, each zone was numbered progressively from least to greatest mobility from the origin. Collectively, 20 staining zones were resolved among the 11 enzymes analyzed. In 18 zones, electrophoretic phenotypes consisted of either single bands or complementary doublets [two bands with equal staining intensity accompanied by a faintly staining band(s) of intermediate mobility]. For G6PD a doublet was present in all strains, and in GOT-1 only doublets or complementary quadruplets were observed.

All taxa exhibited a common and invariant phenotype for ACP-1, ACP-2, ALP-1, ALP-3, G6PD, LGGP-1, LGGP-2, LTP-1, and MDH.

Table I. Electrophoretic Variation in Permanent Translocation Heterozygotes and Tester Bivalent-Forming Strains of *Oenothera*

Enzyme-staining zone	Banding phenotypes ($R_p \times 100$)				
	biennis	*strigosa*	*parviflora*	*hookeri*	*grandiflora*
ACP-1	27	27	27	27	27
ACP-2	61	61	61	61	61
ALP-1	30	30	30	30	30
ALP-2	60	60	—	60	60
	—	—	67	—	—
ALP-3	93	93	93	93	93
G6PD	44/49	44/49	44/49	44/49	44/49
GOT-1	40/49	40/49	—	40/49	—
	40/45/49/51	40/45/49/51	—	—	—
	45/51	—	—	—	45/51
	—	—	38/46	—	—
	—	—	38/43/46/48	—	—
	—	—	43/48	—	—
GOT-2	57	57	—	57	57
	—	—	59	—	—
LAP	65	65	—	65	65
	—	—	60/62	—	—
	—	—	62	—	—
	—	—	62/64	—	—
LGGP-1	50	50	50	50	50
LGGP-2	65	65	65	65	65
LTP-1	33	33	33	33	33
LTP-2	55/60	—	—	—	—
	60	60	—	60	60
	—	—	56/61	—	—
	—	—	61	—	—
LTP-3	77	77	—	77	77
	—	—	74/79	—	—
	—	—	79	—	—
MDH	88	88	88	88	88
PGI-1	22/25	22/25	—	—	—
	25	25	—	25	25
	—	—	16	—	—
	—	—	16/26	—	—
	—	—	26	—	—
PGI-2	40	40	40	40	40
	43	—	—	—	—
	40/43	40/43	40/43	—	—
PGM-1	38	—	—	—	—
	38/43	38/43	—	—	—
	43	43	—	43	43
	43/47	—	—	—	—
	47	47	—	—	—
	—	—	35/39	—	—
	—	—	35/47	—	—
	—	—	39	—	—
	—	—	39/47	—	—
PGM-2	57	57	—	57	57
	—	—	55	—	—

Table I. Continued

Enzyme-staining zone	Banding phenotypes ($R_p \times 100$)				
	biennis	*strigosa*	*parviflora*	*hookeri*	*grandiflora*
VLP	*48*	—	—	—	—
	48/51	*48/51*	—	—	—
	48/55	*48/55*	—	—	—
	51	*51*	—	—	*51*
	55	*55*	—	*55*	—
	—	—	*50*	—	—
	—	—	*50/51*	—	—
	—	—	*51/53*	—	—
	—	—	*53*	—	—

Each taxon also exhibited only one phenotype for ALP-2, GOT-2, and PGM-2, with *Oe. parviflora* bands being distinctive from those shared by *Oe. biennis* and *Oe. strigosa*. Variation within a taxon was detected in only eight of the 20 staining zones. Each taxon was polymorphic for GOT-1, PGI-1, PGI-2, PGM-1, and VLP. Polymorphism for LTP-2 was detected only in *Oe. biennis* and *Oe. parviflora* and for LTP-3 and LAP only in *Oe. parviflora*. In polymorphic systems, *Oe. biennis* and *Oe. strigosa* exhibited common variants while those of *Oe. parviflora* were distinctive except for PGI-2. Each tester strain was monomorphic for 18 zones, expressed the usual doublet at G6PD and GOT-1, and exhibited a composite phenotype common only to *Oe. biennis* and *Oe. strigosa*. The *Oe. hookeri* and *Oe. grandiflora* testers were distinctive *inter se* for GOT-1 and VLP (see Table II).

Inheritance Patterns and Allozyme Genotypes

Eighty-seven hybrid lines, established from 110 attempted crosses, yielded electrophoretic phenotype data. Crossing and germination difficulties were greatest among the tester × *Oe. parviflora* crosses. Six of these failed to produce germinable seed and two produced partially or wholly chlorotic seedlings. Such results are consistent with those obtained in other interspecific crosses with *β-parviflora* complexes (Cleland, 1972).

A sample of the F_1 electrophoretic phenotype data, illustrating the spectrum of inheritance patterns observed, is presented in Table II. With certain exceptions, the salient features of the synthetic stocks are that (1) each hybrid line is phenotypically uniform, (2) reciprocal crosses yield different phenotypes for each parental polymorphism, and (3) the phenotype of F_1 lines is dependent on the direction of the cross. Consider F_1 phenotype patterns for GOT-1 in crosses involving the *Oe. biennis I* strain *Bloomington II*, which exhibits the polymorphic quadruplet *40/45/49/51* (Table II).

Table II. Electrophoretic Phenotypes for Polymorphic Systems in Selected *Oenothera* Strains and F_1 Hybrids

Taxon: strain or cross	Banding patterns ($R_p \times 100$)						
	GOT-1	PGI-1	PGI-2	PGM-1	LTP-3	LTP-3	VLP
Oe. hookeri:							
hookeri (H)	*40/49*	*25*	*40*	*43*	*60*	*77*	*55*
Johansen (H-12)	*40/49*	*25*	*40*	*43*	*60*	*77*	*55*
Oe. grandiflora:							
Biebel (Gr)	*45/51*	*25*	*40*	*43*	*60*	*77*	*51*
Oe. biennis I:							
Bloomington II (B-9)	*40/45/49/51*	*22/25*	*40/43*	*38/43*	*60*	*77*	*51*
B-9 × H	*40/45/49/51*	*22/25*	*40/43*	*38/43*	*60*	*77*	*51/55*
B-9 × H-12	*40/45/49/51*	*22/25;25*[a]	*40/43;40*[a]	*38/43*	*60*	*77*	*51/55*
B-9 × Gr	*45/51*	*22/25*	*40/43*	*38/43*	*60*	*77*	*51*
H-12 × B-9	*40/49*	*25*	*40*	*43*	*60*	*77*	*51/55*
Gr × B-9	*40/45/49/51*	*25*	*40*	*43*	*60*	*77*	*51*
Lake (B-14a)	*40/45/49/51*	*25*	*40*	*38/43*	*55/60*	*77*	*48/55*
B-14a × H	*40/45/49/51*	*25*	*40*	*38/43*	*55/60*	*77*	*48/55*
B-14a × H-12	*40/45/49/51*	*25*	*40*	*38/43*	*55/60*	*77*	*48/55*
B-14a × Gr	*45/51*	*25*	*40*	*38/43*	*55/60*	*77*	*48/51*
H-12 × B-14a	*40/49*	*25*	*40*	*43*	*60*	*77*	*55*

Oe. biennis II:							
Elma V (B-65)	*40/45/49/51*	*22/25*	*40/43*	*43*	*55/60*	*77*	*51*
B-65 × H	*40/49*	*25*[b]	*40*	*43*	*60*	*77*	*51/55*
B-65 × Gr	*40/45/49/51*	*22/25*	*40*	*43*	*60*	*77*	*51*
H-12 × B-65	*40/45/49/51*	*25*	*40/43*	*43*	*55/60*	*77*	*51/55*
Gr × B-65	*45/51*	*25*	*40/43*	*43*	*55/60*	*77*	*51*
Oe. strigosa:							
Forsberg (S-29)	*40/49*	*25*	*40/43*	*43*	*60*	*77*	*48/51*
S-29 × H	*40/49*	*25*	*40/43*	*43*	*60*	*77*	*48/55*
S-29 × H-12	*40/49*	*25*	*40/43*	*43*	*60*	*77*	*48/55*
S-29 × Gr	*40/45/49/51*	*25*	*40/43*	*43*	*60*	*77*	*48/51*
H-12 × S-29	*40/49*	*25*	*40*	*43*	*60*	*77*	*51/55*
Gr × S-29	*40/45/49/51*	*25*	*40*	*43*	*60*	*77*	*51*
Oe. parviflora II:							
Nobska (P-25)	*38/43/46/48*	*16/26*	*40/43*	*35/39*	*56/61*	*74/79*	*53*
P-25 × Gr	*38/45/46/51*	*16/25*	*40/43*	*39/43*	*56/60*	*74/77*	*51/53*
Gr × P-25	*43/45/48/51*	*25/26*	*40*	*35/43*	*60/61*	*77/79*	*51/53*

[a] Respective phenotype ratio of 12:2.
[b] Does not conform to phenotypic transmission patterns indicated in other F_1 hybrid lines.

Bloomington II × *Oe. hookeri* (*40/45/49/51* × *40/49*) produces only *40/45/49/51* progeny. The reciprocal cross produces only *40/49* progeny. *Bloomington II* × *Oe. grandiflora* (*40/45/49/51* × *45/51*) produces only *45/51* progeny. The reciprocal cross produces only *40/45/49/51* progeny. The preceding segregation patterns are consistent solely with exclusive transmission of the *45/51* doublet via *Bloomington II* ovules and the *40/49* doublet via *Bloomington II* pollen. The uniformity within hybrid lines and the segregation of polymorphic systems solely among reciprocal crosses are consistent with the general absence of independent assortment among α and β chromosome complexes and the predominant, exclusive transmission of complexes via opposite germ lines that characterizes permanent structural hybridity in *Oenothera*.

Deviations from the predominant transmission patterns occur in some hybrids of ten of the 22 ring-forming strains (noted in Table IV). However, such deviations are manifest only in a few individuals of one or two F_1 lines involving each strain, and are concentrated in PGI systems. For example, the cross between a *Bloomington II* ovule parent and the *Johansen* strain of *Oe. hookeri* (B-9 × H-12, Table II) produces a 12:2 ratio of phenotypes *22/25* and *25* for PGI-1, and *40/43* and *40* for PGI-2. The minority phenotypes are otherwise restricted to hybrid lines derived from a *Bloomington II* pollen parent. No segregants for either PGI system were observed in any other *Bloomington II* hybrids. Rare segregants of polymorphic PGI systems also occur in hybrids of four other ring-forming strains and of polymorphic VLP systems in hybrids of two additional ring-formers. Completely anomalous PGI transmission sequences are manifest in one cross of each of three ring-formers. For example, the reciprocal crosses between the *Oe. biennis II* strain *Elma V* (B-65, Table II) and *Oe. grandiflora* testers and the *Elma V* × *Johansen* cross indicate that the *22* singlet of PGI-1 resides in *Elma V* ovules. However, the *Elma V* × *hookeri* progeny exhibit only the *25* singlet and not the expected *22/25* doublet. Other polymorphic systems segregate as expected in the last cross.

The frequency of segregants within hybrid lines derived from polymorphic ring-forming parents is within the normally observed range of recombination, 0.1–10.0% in hybrids of ring-forming oenotheras. Such rates tend to be higher in hybrid progeny than in the ring-forming strains themselves and restricted to genes positioned at the ends of chromosomes (for discussion, see Cleland, 1972, Chapter 10). However, in three instances of segregation within an F_1 line, we cannot distinguish between recombinational segregation and leakage in the gametophytic lethal or incompatibility systems. The frequency of such leakage, as judged from morphological segregation, is also enhanced in hybrid crosses (Cleland, 1972) and may be greater in the hybrid lines of the present study than indicated by electro-

phoretic phenotypes (E. Steiner, unpublished). Nevertheless, the precise nature of both segregants within lines and anomalous transmission patterns remains to be resolved.

The F_1 phenotype data also demonstrate that for each staining zone (1) all crosses between parents with the same phenotype produce progeny with only that phenotype and (2) all crosses between parents with different singlet phenotypes (or different doublets at GOT-1) produce progeny with only complementary phenotypes. In combination with the inheritance patterns in polymorphic systems, these results indicate that electrophoretic variation within each polymorphic staining zone is encoded by codominant alleles at one locus. The absence of phenotypic segregation between multiple staining zones of GOT, PGI, PGM, and LTP also indicates that variation between zones is determined by separate loci. The encoding of enzyme morphs in each of the staining zones of the invariant systems ACP, ALP, and LGGP by separate loci may be inferred on bases of large mobility differences and differential rates of staining between morphs. This inference is further supported by the observation (Levin *et al.*, 1972) of a rare doublet in ACP-1 which includes band *27* and exhibits no change in phenotype in ACP-2. The long-term selfing of the bivalent-forming tester strain reasonably insures that the nonsegregating doublets observed at G6PD and GOT-1 are encoded by homozygous genotypes. However, the present data do not resolve how many loci are responsible for such phenotypes. Preliminary results obtained from reelectrophoresis of some individual bands at GOT-1 suggest that the doublets may be mixtures of configurational isomers generated during electrophoretic procedures (M. Levy, unpublished). Tentatively, we will assume the most parsimonious explanation, single-locus determination.

Summarizing, we judge that, collectively, the electrophoretic variation resolved in the 11 enzyme systems assayed is under the genetic control of 20 loci. Allozymes encoded by *Acp-1*, *Acp-2*, *Alp-1*, *Alp-2*, *Alp-3*, *Got-2*, *Lap*, *Lggp-1*, *Lggp-2*, *Ltp-1*, *Ltp-2*, *Ltp-3*, *Mdh*, *Pgi-1*, *Pgi-2*, *Pgm-1*, *Pgm-2*, and *Vlp* occur as single bands and those at *G6pd* and *Got-1*, ostensibly, are manifest as nonsegregating doublets. All allozymes resolved are expressed codominantly, and heterozygotes (when present) exhibit additive phenotypes. Allelic designations which encode each of the allozymes observed in the study are summarized in Table III.

Allelic Characterization of Chromosome Complexes

The genotypes and the distribution of allozyme alleles at polymorphic loci among the chromosome complexes of the 22 ring-forming strains are presented in Table IV. Generally, within each species there are only two alleles per

Table III. Allozyme Genotypes in *Oenothera*

Locus	Allele	Phenotype ($R_p \times 100$)
Acp-1	*b*	*27*
Acp-2	*b*	*61*
Alp-1	*b*	*30*
Alp-2	*a*	*60*
	b	*67*
Alp-3	*b*	*93*
G6pd	*b*	*44/49*
Got-1	*a*	*40/49*
	b	*45/51*
	c	*38/46*
	d	*43/48*
Got-2	*a*	*57*
	b	*59*
Lap	*a*	*65*
	b	*60*
	c	*62*
	d	*64*
Lggp-1	*b*	*50*
Lggp-2	*b*	*65*
Ltp-1	*b*	*33*
Ltp-2	*a*	*55*
	b	*60*
	c	*56*
	d	*61*
Ltp-3	*a*	*77*
	b	*74*
	c	*79*
Mdh	*b*	*88*
Pgi-1	*a*	*22*
	b	*25*
	d	*16*
	e	*26*
Pgi-2	*a*	*40*
	b	*43*
Pgm-1	*a*	*38*
	b	*43*
	c	*47*
	d	*35*
	e	*39*
Pgm-2	*a*	*57*
	b	*55*
Vlp	*a*	*48*
	b	*51*
	c	*55*
	d	*50*
	e	*53*

Table IV. Distribution of Alleles at Polymorphic Loci[a] Among Chromosome Complexes in *Oenothera*

Taxon:	*Got-1*		*Pgi-1*		*Pgi-2*		*Pgm-1*		*Ltp-2*		*Ltp-3*		*Vlp*	
strain	α	β	α	β	α	β	α	β	α	β	α	β	α	β
Oe. biennis I:														
Baltimore	*b*	*a*	*b*	*b*	*b*	*a*	*b*	*b*	*b*	*b*	*a*	*a*	*a*	*b*
Bestwater I	*a*	*a*	*b*	*b*	*a***	*b*	*b*	*b*	*a*	*b*	*a*	*a*	*a*	*b*
Bestwater II	*a*	*a*	*b*	*b*	*a*	*a*	*b*	*b*	*b*	*b*	*a*	*a*	*a*	*b*
Birch Tree I	*b*	*a*	*b*	*b*	*b**	*a**	*a*	*a*	*b*	*b*	*a*	*a*	*a*	*b*
Bloomington II	*b*	*a*	*a*	*b*	*b**	*a**	*a*	*b*	*b*	*b*	*a*	*a*	*b*	*b*
Chicaginensis	*a*	*a*	*b*	*b*	*a*	*a*	*b*	*b*	*b*	*b*	*a*	*a*	*a**	*c*
Coshocton I	*b*	*b*	*b*	*b*	*a*	*b*	*b*	*b*	*b*	*b*	*a*	*a*	*b*	*b*
Hot Springs	*b*	*b*	*b*	*b*	*a*	*a*	*b*	*b*	*b*	*b*	*a*	*a*	*a*	*b*
Lake	*b*	*a*	*b*	*b*	*a*	*a*	*a*	*b*	*a*	*b*	*a*	*a*	*a*	*c*
Oe. biennis II:														
Buck Creek	*a*	*b*	*b*	*a*	*a***	*b*	*b*	*b*	*b*	*b*	*a*	*a*	*b*	*a*
Corning II	*a*	*a*	*b**	*a*	*b**	*a**	*b*	*b*	*b*	*b*	*a*	*a*	*b*	*b*
Elma II	*a*	*b*	*b*	*b*	*a*	*a*	*b*	*b*	*b*	*a*	*a*	*a*	*b*	*b*
Elma V	*a*	*b*	*a***	*b*	*a*	*b*	*b*	*b*	*b*	*a*	*a*	*a*	*b*	*b*
Tonawanda I	*a*	*b*	*b*	*b*	*a*	*a*	*b*	*b*	*b*	*b*	*a*	*a*	*c*	*c*
Oe. strigosa:														
Fargo	*a*	*a*	*b*	*b*	*a*	*a*	*b*	*b*	*b*	*b*	*a*	*a*	*b*	*b*
Forsberg	*a*	*a*	*b*	*b*	*b**	*a*	*b*	*b*	*b*	*b*	*a*	*a*	*a*	*b*
Heber	*a*	*a*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*b*	*a*	*a*	*c**	*a*
N. Colorado Springs	*a*	*a*	*b*	*b*	*b*	*a*	*b*	*b*	*b*	*b*	*a*	*a*	*b*	*b*
Oe. parviflora:														
Angustissima	*d*	*d*	*e*	*e*	*a*	*b*	*e*	*e*	*c*	*d*	*b*	*c*	*d*	*b*
Eriensis	*d*	*c*	*e**	*d**	*a*	*a*	*e*	*e*	*c*	*d*	*c*	*c*	*b*	*b*
Iron Mountain	*d*	*c*	*e*	*e*	*a*	*a*	*d*	*e*	*d*	*d*	*c*	*c*	*e*	*e*
Nobska	*c*	*d*	*d*	*e*	*b*	*a*	*d*	*e*	*c*	*d*	*b*	*c*	*e*	*e*

[a] Not determined for *Lap* in *Oe. parviflora*.
* Minor ($\leq 10\%$) variation in transmission.
** Anomalous transmission in some crosses with *Oe. hookeri*.

polymorphic locus. Despite this meager allelic array, each of the strains is genotypically unique, and a total of 28 different genotypes are manifest among the 44 chromosome complexes characterized.

Most of the genotypic heterogeneity is concentrated among the "biennis" genomes of *Oe. biennis* (*α-biennis I* and *β-biennis II*) and in *Oe. parviflora* complexes. Among the nine *α-biennis I* complexes, only two bear common allelic constitutions. Differences between the complexes range from zero to six alleles, with a majority of comparisons within the group differing by two or three alleles. The genotypes of the five *β-biennis II* complexes are distinctive both *inter se* and in comparison with the *α-biennis I* complexes. Within the *β-biennis II* complexes, allelic differences range from one to four alleles,

with a majority of comparisons differing by three or four alleles. Each of the *Oe. parviflora* complexes exhibits a different genotype, and, by virtue of unique alleles at most loci, all are distinct from genotypes in the other ring-forming taxa. The least genotypic heterogeneity is found among "strigosa" genomes. At polymorphic loci, a genotype containing *Got-1*^{a}, *Pgi-1*^{b}, *Pgi-2*^{a}, *Pgm-1*^{b}, *Ltp-2*^{b}, and *Vlp*^{b} is present in nine of the 22 (41%) *β-biennis I*, *α-biennis II*, and α- and *β-strigosa* complexes. All but two of the remaining *strigosa* complexes differ by only one or two alleles.

As a corollary to the differential heterogeneity among various genomes, striking differences in allele frequency are suggested between α and β complexes of each group of *Oe. biennis* and between those of *Oe. parviflora* (Table V). Differences are most dramatic at *Got-1*, *Ltp-2*, and *Vlp* in *Oe. biennis* and at *Ltp-2* and *Pgm-1* in *Oe. parviflora.* Moreover, such "linkage disequilibria" in *Oe. biennis* include all polymorphic loci and are correlated

Table V. Allele Frequencies (%) at Major Polymorphic Loci in Complexes of Analyzed Ring-Forming Strains of *Oenothera*

		biennis I		*biennis II*		*strigosa*		*parviflora*	
Locus	Allele	α	β	α	β	α	β	α	β
Got-1	*a*	33	78	100	20	100	100	0	0
	b	66	22	0	80	0	0	0	0
	c	0	0	0	0	0	0	25	50
	d	0	0	0	0	0	0	75	50
Lpt-2	*a*	22	0	0	40	0	0	0	0
	b	78	100	100	60	100	100	0	0
	c	0	0	0	0	0	0	75	0
	d	0	0	0	0	0	0	25	100
Pgi-1	*a*	11	0	20	40	0	0	0	0
	b	88	100	80	60	100	100	0	0
	d	0	0	0	0	0	0	25	25
	e	0	0	0	0	0	0	75	75
Pgi-2	*a*	66	78	80	60	25	75	75	75
	b	33	22	20	40	75	25	25	25
Pgm-1	*a*	33	11	0	0	0	0	0	0
	b	66	88	100	100	100	100	0	0
	d	0	0	0	0	0	0	50	0
	e	0	0	0	0	0	0	50	100
Vlp	*a*	78	0	0	20	25	25	0	0
	b	22	78	100	60	50	75	25	50
	c	0	22	0	20	25	0	0	0
	d	0	0	0	0	0	0	25	0
	e	0	0	0	0	0	0	50	50

with the genomic origin of complexes. Among the 14 *Oe. biennis* strains characterized, there are 34 heterozygous loci (Table IV). At 30 of these loci, the minority allele at each locus (Table V) is specific to the "biennis" genome; i.e., *Got-1*^{b}, *Pgi-1*^{a}, *Pgi-2*^{b}, *Pgm-1*^{a}, *Ltp-2*^{a}, and *Vlp*^{a} reside primarily in *α-biennis I* and *β-biennis II* complexes. The opposite situation occurs at *Pgi-2* in *Coshocton I* and *Bestwater I* and at *Pgi-1* in *Buck Creek* and *Elma V*. Curiously, the latter three strains are those in which anomalous PGI transmission was detected. Intergenomic allele frequency differences also are present in *Oe. parviflora*, where the minority alleles *Pgm-1*^{d}, *Ltp-2*^{c}, and *Ltp-3*^{b} are confined to α complexes (non-"parviflora" genomes). However, none of these alleles is present in other "biennis" or "strigosa" genomes.

Correlations between allozymic variation and the genomic origin of complexes do not extend to segmental arrangements within a group of complexes. For example, the segmental arrangement 1·2, 3·4, 5·14, 7·10, 9·8, 11·12, 13·6 is manifest in 56 of the 78 *α-biennis I* complexes fully analyzed by Cleland and associates and is judged to be the original α arrangement in the taxon (Cleland, 1972). Allozyme genotypes in this arrangement have been determined in five polymorphic strains, *Baltimore*, Md., *Birch Tree I*, Mo., *Bloomington II*, Ind., *Hot Springs*, Ark., and *Lake*, Va. (Table IV) and in seven uniformly homozygous strains, *Hilltop*, Ind., *Walkerton*, Ind., *Cardiff Delta*, Md., *Cambridge I*, Ohio, *Lemoyne*, Pa., *Camp Perry*, Va., and *Petersburg*, Va. (Levy and Levin, 1975, their Table 7). Ten genotypes are present in these 12 strains, with most differing by two or three alleles and *Bestwater I* and *Bloomington II* distinct *inter se* at all six polymorphic loci. Conversely, the greatest cytological diversity is found among complexes which are least variable genically, *β-biennis I*, *α-biennis II*, and both complexes of *Oe. strigosa*. Further, it also is apparent from the above homozygous strains that complexes of different origins and completely different segmental arrangements may share the same allozyme genotypes. This phenomenon is also manifest in polymorphic strains, as evidenced by the common genotypes of *α-Elma V* and *β-Corning II* (Table IV).

CONCLUSIONS

Allozymes in the structural heterozygotes of *Oenothera* are inherited as single-locus, codominant markers. However, permanent translocation heterozygosity virtually eliminates the usual independent assortment or recombination of allozyme variants. Within a polymorphic ring-forming strain, an allozyme variant is specific to only one of the seven-chromosome linkage groups, transmitted nearly exclusively through only one germ line, and destined generally for permanent residence in the parental genotype. New allozyme genotypes may arise solely via the infrequent processes of

recombination, hybridization, or mutation. Within taxa, the distribution of allozyme variants among α and β chromosome complexes is nonrandom, and apparent linkage disequilibria for allozyme alleles are correlated with differences in the genomic origin of complexes. However, there is no obvious relationship between allozyme genotype and chromosome segmental arrangement.

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