

Cytological analysis of complex-heterozygotes in populations of *Oenothera grandiflora* (*Onagraceae*) in Alabama

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Abstract: Genetic analysis of unusual complex-heterozygous genotypes in populations of *O. grandiflora* from Alabama (USA) has shown that these strains are composed of a typical *grandiflora* (B) complex and an altered B complex (designated as B^A) which probably contains genetic elements derived from an A genotype such as the beta complex of *O. biennis* group 1. Analysis of the meiotic configurations of artificial hybrids between the new strains and a series of complexes of known segmental arrangement allowed determination of the arrangements of the unknown complexes. These data are evidence for origin of the altered B complexes.

Until the late 1970's *Oenothera grandiflora* was regarded as a self-compatible, structurally homozygous relic species (CLELAND 1972), the members of which more or less uniformly possessed the ancestral segmental arrangement of chromosomes characteristic of subsect. *Oenothera*, namely 1·2 3·4 5·6 7·10 9·8 11·12 13·14 (STEINER 1952). The discovery of self-incompatible individuals in several populations in Alabama (STUBBE & RAVEN 1979) stimulated interest in a more detailed study of this species which is believed to be one of the progenitors of the complex-heterozygous species, *O. biennis* and *O. parviflora*. *O. grandiflora* is distributed throughout the southeastern United States and is not restricted to the vicinity of Mobile, Alabama, as once thought. Study of earlier, as well as more recent collections from a number of different localities in Alabama (STEINER & STUBBE 1984, 1986) brought new insights into the population structure of *O. grandiflora*; a greater diversity of chromosome arrangements was observed and a number of structurally heterozygous individuals was found, as to be expected for an open-pollinated species, their occurrence apparently related to the presence of numerous Si alleles.

Special attention was directed toward several unusual genotypes within populations of *O. grandiflora* which were complex-heterozygotes with a meiotic config-

Table 1. Representative strains from *Oenothera grandiflora* populations in Alabama analysed in the current study. For geographic origin see STEINER & STUBBE (1986)

| Strain | Chromosome configuration | Original culture number |
|-------------------|--------------------------|-------------------------|
| Bay Minette A-6 | 7 pairs | 84/340-1 |
| Bigbee 2 | 7 pairs | 84/372-1 |
| Bolinger 4 | 7 pairs | 84/363-1 |
| Cantonment 1 | 7 pairs | 84/331-3 |
| Castleberry A-1/1 | ⊙ 10, 2 pairs | 84/301-1 |
| Castleberry A-1/2 | ⊙ 10, 2 pairs | 84/301-2 |
| Castleberry A-4 | ⊙ 12, 1 pair | 84/304-1 |
| Castleberry A-7 | ⊙ 14 | 84/307-1 |
| Castleberry A-9 | ⊙ 10, 2 pairs | 84/309-1 |
| Castleberry B-8 | 7 pairs | 84/318-7 |
| Chastang 1 | ⊙ 12, 1 pair | 84/350-3 |
| Chastang 7 | ⊙ 8, 3 pairs | 84/356-1 |
| County Road 6-1 | ⊙ 4, 5 pairs | 84/368-1 |
| Flomaton 1 | 7 pairs | 84/321-1 |
| Flomaton 6 | ⊙ 4, ⊙ 4, 3 pairs | 84/326-1 |
| Frankville | 7 pairs | 84/370-2 |
| Sims Chapel | 7 pairs | 84/359 b |

uration of either a circle of 10 and 2 pairs, a circle of 12 and 1 pair, or a circle of 14 chromosomes. Genetic analysis of the complex-heterozygotes has shown them to be composed of a typical *grandiflora* complex (B type) and a complex which is distinctly different, tending phenotypically toward the A type characteristic of *O. villosa* and the beta complexes of the *O. biennis* group 1. This latter complex, designated as B^A, generally lacks an Si allele or a lethal; therefore, upon selfing of the complex-heterozygotes viable homozygotes, B^AB^A, may appear among the progeny, although in varying numbers, depending upon the particular strain.

The origin of the B^A genotype is of particular interest. To test the hypothesis that hybridization between *O. grandiflora* and *O. biennis* played a role in the evolution of this new genotype, it is necessary to determine the segmental arrangement of its chromosomes and to compare it with those of the homozygous strains of *O. grandiflora* and of *O. biennis*. This is a report of such cytological analysis.

Material and methods

The strains under investigation were obtained from seeds collected in Alabama as reported in STEINER & STUBBE (1986). They are listed in Table 1 together with their meiotic configurations and initial culture numbers. The complexes of these strains were combined with a series of complexes of known segmental arrangement (Table 2). Analysis of the meiotic

Table 2. Chromosome formulae of complexes used in the present analysis

| Complex | Segmental arrangement | | | | | | |
|----------------------------------|-----------------------|------|------|------|------|-------|-------|
| ^h hookeri deVries | 1·2 | 3·4 | 5·6 | 7·8 | 9·10 | 11·12 | 13·14 |
| ^h hookeri Johansen | 1·2 | 3·4 | 5·6 | 7·10 | 9·8 | 11·12 | 13·14 |
| ^h elata Guatemala | 1·2 | 3·10 | 5·9 | 7·4 | 6·8 | 11·12 | 13·14 |
| ^h elata Cholula | 1·4 | 3·2 | 5·9 | 7·10 | 6·8 | 11·12 | 13·14 |
| ^h grandiflora Brewton | 1·3 | 2·4 | 5·14 | 7·10 | 9·8 | 11·12 | 13·6 |
| ^h grandiflora York | 1·2 | 3·4 | 5·6 | 7·10 | 9·8 | 11·12 | 13·14 |
| excellens chicaginensis | 1·2 | 3·4 | 5·6 | 7·10 | 9·8 | 11·12 | 13·14 |
| punctulans chicaginensis | 1·4 | 3·9 | 5·2 | 7·8 | 6·12 | 11·10 | 13·14 |
| undans hungarica | 1·4 | 3·2 | 5·10 | 7·6 | 9·13 | 11·12 | 8·14 |
| α Forsberg | 1·7 | 3·4 | 5·8 | 2·10 | 9·11 | 6·12 | 13·14 |
| α Fruitland | 1·2 | 3·5 | 6·12 | 7·10 | 9·4 | 11·8 | 13·14 |
| α Iowa II | 1·2 | 3·14 | 5·6 | 7·11 | 9·6 | 10·12 | 13·4 |
| α Littleton | 1·10 | 3·4 | 5·8 | 7·2 | 9·11 | 6·12 | 13·14 |
| α Monett | 1·2 | 3·10 | 5·12 | 7·14 | 9·8 | 11·6 | 13·4 |
| α Yamika | 1·8 | 3·14 | 5·11 | 7·10 | 9·12 | 2·6 | 13·4 |
| gaudens lamarckiana | 1·2 | 3·12 | 5·6 | 7·11 | 9·4 | 8·14 | 13·10 |
| velans lamarckiana | 1·2 | 3·4 | 5·8 | 7·6 | 9·10 | 11·12 | 13·14 |
| ^h blandina | 1·2 | 3·4 | 5·6 | 7·10 | 9·14 | 11·12 | 13·8 |
| α Bestwater | 1·4 | 3·8 | 5·14 | 7·10 | 9·2 | 11·12 | 13·6 |
| β Bestwater | 1·14 | 3·2 | 5·9 | 7·8 | 6·12 | 11·10 | 13·4 |
| α Birch Tree II | 1·2 | 3·4 | 5·14 | 7·10 | 9·8 | 11·12 | 13·6 |
| β Birch Tree II | 1·13 | 3·2 | 5·7 | 4·12 | 9·6 | 11·10 | 8·14 |
| α Camp Peary | 1·2 | 3·4 | 5·14 | 7·10 | 9·8 | 11·12 | 13·6 |
| α Delaware | 1·2 | 3·4 | 5·14 | 7·10 | 9·8 | 11·12 | 13·6 |
| β Delaware | 1·4 | 3·8 | 5·7 | 2·14 | 9·6 | 11·10 | 13·12 |
| α Lanoraie | 1·4 | 3·12 | 5·2 | 7·11 | 9·8 | 6·10 | 13·14 |
| β Lanoraie | 1·2 | 3·12 | 5·6 | 7·4 | 9·11 | 10·14 | 13·8 |
| α Richmond | 1·9 | 3·10 | 5·14 | 7·4 | 2·8 | 11·12 | 13·6 |
| albicans suaveolens Grado | 1·12 | 3·6 | 5·7 | 2·14 | 9·4 | 11·10 | 13·8 |
| flavens suaveolens Grado | 1·4 | 3·2 | 5·6 | 7·10 | 9·8 | 11·12 | 13·14 |
| albicans biennis deVries | 1·4 | 3·6 | 5·7 | 2·14 | 9·8 | 11·10 | 13·12 |
| α Buck Creek | 1·4 | 3·10 | 5·7 | 2·6 | 9·8 | 11·12 | 13·14 |
| β Buck Creek | 1·2 | 3·5 | 6·8 | 7·12 | 9·13 | 11·4 | 10·14 |
| β Elma II | 1·2 | 3·12 | 5·6 | 7·10 | 9·4 | 11·13 | 8·14 |
| α Indian River | 1·4 | 3·2 | 5·7 | 6·10 | 9·8 | 11·12 | 13·14 |
| α Micaville | 1·5 | 3·9 | 2·6 | 7·10 | 4·8 | 11·12 | 13·14 |
| α Wakefield | 1·7 | 3·10 | 5·4 | 2·6 | 9·8 | 11·12 | 13·14 |
| β Wakefield | 1·2 | 3·5 | 6·8 | 7·12 | 9·13 | 11·4 | 10·14 |
| α Williamsville | 1·4 | 3·2 | 5·6 | 7·10 | 9·8 | 11·12 | 13·14 |
| rigens ammophila | 1·2 | 3·4 | 5·6 | 7·11 | 9·10 | 8·14 | 13·12 |
| percurvans ammophila | 1·14 | 3·5 | 6·8 | 7·10 | 9·2 | 11·4 | 13·12 |
| α angustissima | 1·13 | 3·4 | 5·8 | 7·14 | 9·2 | 11·12 | 6·10 |
| α Camas | 1·9 | 3·5 | 4·6 | 7·10 | 2·8 | 11·14 | 13·12 |
| α biennis 1 | 1·2 | 3·4 | 5·14 | 7·10 | 9·8 | 11·12 | 13·6 |
| rubens biennis deVries | 1·2 | 3·12 | 5·6 | 7·11 | 9·4 | 8·14 | 13·10 |
| B type Brewton | 1·2 | 3·4 | 5·6 | 7·10 | 9·8 | 11·12 | 13·14 |
| B ^A type Brewton | 1·6 | 3·2 | 5·11 | 7·10 | 9·4 | 8·12 | 13·14 |

Table 3. Chromosome configurations of hybrids between various homozygous strains of *Oenothera grandiflora*

| Cross | Chromosome configuration |
|------------------------------|--------------------------|
| Bay Minette A-6 × York | 7 pairs |
| Flomaton 6 × York | 7 pairs |
| York × Bigbee 2 | ⊙ 4, 5 pairs |
| York × Frankville | ⊙ 4, ⊙ 4, 3 pairs |
| Bigbee 2 × Bolinger 4 | ⊙ 4, 5 pairs |
| Castleberry B-8 × Bolinger 4 | 7 pairs |
| Castleberry B-8 × Frankville | ⊙ 4, 5 pairs |
| Flomaton 1 × Bigbee 2 | 7 pairs |
| Flomaton 1 × Bolinger 4 | ⊙ 4, 5 pairs |
| Flomaton 1 × Frankville | 7 pairs |
| County Road 6-1 × Brewton | 7 pairs |
| Flomaton 1 × County Road 6-1 | ⊙ 4, 5 pairs |
| Castleberry B-8 × Brewton | ⊙ 4, ⊙ 4, 3 pairs |
| Bigbee 2 × Brewton | ⊙ 4, 5 pairs |
| Flomaton 1 × Brewton | ⊙ 4, 5 pairs |
| Bolinger 4 × York | 7 pairs |

configurations of these hybrids allowed determination of the arrangements of the unknown complexes.

The large-circled complex-heterozygous strains were first crossed as pollen parents with the artificial heterogamous hybrids *albicans-percurvans* and *albicans-undans* as seed parents.

The offspring consisted of twin hybrids in which the egg complex, *albicans*, was combined with either the typical B complex or with the B^A complex. These two types were then combined with a series of complexes of known segmental arrangement. By determining the configuration at meiosis of each of these complex combinations data were obtained that allowed determination of the segmental arrangements of the B and B^A complexes of the various collections.

The meiotic chromosome configurations of the hybrids were determined using the acetocarmine method for anther squashes as described by STEINER & STUBBE (1984). The method of analysis for determining the segmental arrangement of a complex is described by CLELAND (1972: 61, 65). Such analysis is now facilitated by a computer program devised by WASMUND (1980).

In addition, appropriate complex combinations permitted recognition of the presence of a self-incompatibility allele in the complexes under investigation.

Results

Tables 3, 4, 6, and 7 list the chromosome configurations of the new races in combination with those of known segmental arrangements.

Table 4. Chromosome configurations of hybrids between the type B *grandiflora* complex of the complex-heterozygous strains and complexes with known segmental arrangements

| Complex combination | Chromosome configuration |
|---|--------------------------|
| albicans Grado · B Castleberry A-1/1 | ⊙ 14 |
| β Bestwater · B Castleberry A-1/1 | ⊙ 8, ⊙ 6 |
| α biennis 1 · B Castleberry A-1/1 | ⊙ 6, ⊙ 4, 2 pairs |
| ^h blandina · B Castleberry A-1/1 | ⊙ 6, ⊙ 4, 2 pairs |
| β Buck Creek · B Castleberry A-1/1 | ⊙ 10, ⊙ 4 |
| ^h hookeri deVries · B Castleberry A-1/1 | ⊙ 4, ⊙ 4, ⊙ 4, 1 pair |
| α Indian River · B Castleberry A-1/1 | ⊙ 4, ⊙ 4, 3 pairs |
| ^h hookeri Johansen · B Castleberry A-1/1 | ⊙ 4, ⊙ 4, 3 pairs |
| α Micaville · B Castleberry A-1/1 | ⊙ 8, ⊙ 4, 1 pair |
| α Williamsville · B Castleberry A-1/1 | ⊙ 4, 5 pairs |
| α Delaware · B Castleberry A-1/2 | ⊙ 6, ⊙ 4, 2 pairs |
| ^h blandina · B Castleberry A-1/2 | ⊙ 6, ⊙ 4, 2 pairs |
| excellens chicag. · B Castleberry A-1/2 | ⊙ 4, ⊙ 4, 3 pairs |
| ^h hookeri Johansen · Castleberry A-1/2 | ⊙ 4, ⊙ 4, 3 pairs |
| albicans Grado · B Castleberry A-4 | ⊙ 10, ⊙ 4 |
| ^h hookeri deVries · B Castleberry A-4 | ⊙ 4, ⊙ 4, 3 pairs |
| ^h hookeri Johansen · Castleberry A-4 | ⊙ 4, 5 pairs |
| α Richmond · B Castleberry A-4 | ⊙ 6, ⊙ 4, ⊙ 4 |
| albicans Grado · B Castleberry A-7 | ⊙ 14 |
| α Birch Tree II · B Castleberry A-7 | ⊙ 4, 5 pairs |
| β Birch Tree II · B Castleberry A-7 | ⊙ 14 |
| β Buck Creek · B Castleberry A-7 | ⊙ 6, ⊙ 4, 2 pairs |
| elata Cholula · B Castleberry A-7 | ⊙ 10, 2 pairs |
| ^h hookeri deVries · B Castleberry A-7 | ⊙ 6, ⊙ 4, 2 pairs |
| α Indian River · B Castleberry A-7 | ⊙ 10, 2 pairs |
| ^h hookeri Johansen · B Castleberry A-7 | ⊙ 6, 4 pairs |
| α Lanoraie · B Castleberry A-7 | ⊙ 12, 1 pair |
| α Littleton · B Castleberry A-7 | ⊙ 10, ⊙ 4 |
| α Micaville · B Castleberry A-7 | ⊙ 10, 2 pairs |
| α Wakefield · B Castleberry A-7 | ⊙ 10, 2 pairs |
| α Williamsville · B Castleberry A-7 | ⊙ 8, 3 pairs |
| ^h hookeri Johansen · B Castleberry A-9 | 7 pairs |
| albicans Grado · B Chastang 1 | ⊙ 14 |
| α Delaware · B Chastang 1 | ⊙ 4, 5 pairs |
| ^h blandina · B Chastang 1 | ⊙ 8, 3 pairs |
| elata Guatemala · B Chastang 1 | ⊙ 10, 2 pairs |
| ^h hookeri deVries · B Chastang 1 | ⊙ 6, ⊙ 4, 2 pairs |
| ^h hookeri Johansen · B Chastang 1 | ⊙ 6, 4 pairs |
| punctulans chicag. · B Chastang 1 | ⊙ 14 |
| albicans Grado · B Chastang 7 | ⊙ 14 |
| α biennis 1 · B Chastang 7 | ⊙ 4, ⊙ 4, 3 pairs |
| ^h blandina · B Chastang 7 | ⊙ 4, ⊙ 4, 3 pairs |
| ^h hookeri Johansen · B Chastang 7 | ⊙ 4, 5 pairs |
| punctulans chicag. · B Chastang 7 | ⊙ 10, 2 pairs |

Table 5. Chromosome formulae of the B complexes of the complex-heterozygous strains newly found in populations of *Oenothera grandiflora*

| | | | | | | | |
|-------------------|-----|-----|------|------|-----|-------|-------|
| Castleberry A-1/1 | 1·4 | 3·2 | 5·6 | 7·10 | 9·8 | 11·13 | 12·14 |
| Castleberry A-4 | 1·2 | 3·4 | 5·6 | 7·10 | 9·8 | 11·13 | 12·14 |
| Castleberry A-7 | 1·2 | 3·5 | 4·14 | 7·10 | 9·8 | 11·12 | 13·6 |
| Castleberry A-9 | 1·2 | 3·4 | 5·6 | 7·10 | 9·8 | 11·12 | 13·14 |
| Chastang 1 | 1·2 | 3·5 | 4·14 | 7·10 | 9·8 | 11·12 | 13·6 |
| Chastang 7 | 1·4 | 3·2 | 5·6 | 7·10 | 9·8 | 11·12 | 13·14 |

The chromosome formulae of the homozygous strains of *O. grandiflora* determined from these data can be summarized as follows: The strains Bay Minette A-6, Bolinger 4, Castleberry B-8 and one of the complexes of Flomaton 6 exhibit the segmental arrangement believed to be ancestral for subsect. *Oenothera*, namely 1·2 3·4 5·6 7·10 9·8 11·12 13·14. The formulae of the strains Bigbee 2, Flomaton 1, and Frankville are one translocation removed from the foregoing, i.e., 1·3 2·4 5·6 7·10 9·8 11·12 13·14. One complex of the strain County Road IV-1 has the same formula as one of the homozygous Brewton races, namely 1·3 2·4 5·14 7·10 9·8 11·12 13·6. Cytological data were insufficient to fully establish the segmental arrangements of Cantonment and Sims Chapel, but they appear to be close to the former.

Table 4 presents the meiotic configurations of the hybrids with the B type *grandiflora* complex found in the complex-heterozygotes of *O. grandiflora* populations. The formulae obtained from the analysis of these data are found in Table 5. Castleberry A-9 carries the ancestral arrangement. Chastang 7 is one interchange removed from the latter, having the 1·4 and 3·2. Castleberry A-4 is also one interchange removed from the ancestral arrangement, but differs in having the 11·13 and 12·14. Castleberry A-1/1 has a B complex with both interchanges. The translocation 11·13 and 12·14 appears to be rare; it has not previously been found in *O. grandiflora* and has only been reported in certain beta *villosa* complexes. Castleberry A-7 and Chastang 1, which are identical in segmental arrangement, are two interchanges removed from the ancestral arrangement, but differ by only one interchange from the arrangement most common among the alpha *biennis* group 1 complexes (designated as arrangement C by STEINER & STUBBE 1984).

Table 6 lists the meiotic configurations of a series of hybrids combining complexes of known arrangements with the B^A type complexes found in the complex-heterozygotes of the *O. grandiflora* populations. From these data the segmental arrangements of the B^A complexes were determined. The B^A complexes of Castleberry A-1/1 and Chastang 7 proved to be identical with each other as well as with the B^A complex found in the Brewton population, namely 1·6 3·2 5·11 7·10 9·4 8·12 13·14 (STEINER & STUBBE 1986). The formula of the B^A complex of Castleberry A-7 differs from the foregoing by one interchange involving the most conserved chromosomes 7·10 and 13·14; it is 1·6 3·2 5·11 7·14 9·4 8·12 13·10.

Table 6. Chromosome configurations of hybrids between the B^A complexes of the complex-heterozygous strains and complexes with known segmental arrangements

| Complex combination | Chromosome configuration |
|--|--------------------------|
| albicans Grado · B ^A Castleberry A-1/1 | ⊙ 8, ⊙ 4, 1 pair |
| α Bestwater · B ^A Castleberry A-1/1 | ⊙ 12, 1 pair |
| α biennis 1 · B ^A Castleberry A-1/1 | ⊙ 12, 1 pair |
| rubens · B ^A Castleberry A-1/1 | ⊙ 12, 1 pair |
| ^h blandina · B ^A Castleberry A-1/1 | ⊙ 12, 1 pair |
| α Buck Creek · B ^A Castleberry A-1/1 | ⊙ 12, 1 pair |
| α Delaware · B ^A Castleberry A-1/1 | ⊙ 12, 1 pair |
| β Delaware · B ^A Castleberry A-1/1 | ⊙ 6, ⊙ 4, ⊙ 4 |
| α Fruitland · B ^A Castleberry A-1/1 | ⊙ 8, 3 pairs |
| ^h hookeri deVries · B ^A Castleberry A-1/1 | ⊙ 12, 1 pair |
| ^h hookeri Johansen · B ^A Castleberry A-1/1 | ⊙ 10, 2 pairs |
| α Indian River · B ^A Castleberry A-1/1 | ⊙ 10, 2 pairs |
| α Lanoraie · B ^A Castleberry A-1/1 | ⊙ 12, 1 pair |
| β Lanoraie · B ^A Castleberry A-1/1 | ⊙ 14 |
| α Littleton · B ^A Castleberry A-1/1 | ⊙ 12, 1 pair |
| α Monett · B ^A Castleberry A-1/1 | ⊙ 14 |
| α Richmond · B ^A Castleberry A-1/1 | ⊙ 14 |
| velans lamarckiana · B ^A Castleberry A-1/1 | ⊙ 8, ⊙ 4, 1 pair |
| β Wakefield · B ^A Castleberry A-1/1 | ⊙ 14 |
| α Yakima · B ^A Castleberry A-1/1 | ⊙ 10, 2 pairs |
| albicans Grado · B ^A Castleberry A-1/2 | ⊙ 8, ⊙ 4, 1 pair |
| α Bestwater · B ^A Castleberry A-1/2 | ⊙ 12, 1 pair |
| α biennis 1 · B ^A Castleberry A-1/2 | ⊙ 12, 1 pair |
| ^h blandina · B ^A Castleberry A-1/2 | ⊙ 12, 1 pair |
| α Camas · B ^A Castleberry A-1/2 | ⊙ 8, ⊙ 4, 1 pair |
| α Forsberg · B ^A Castleberry A-1/2 | ⊙ 12, 1 pair |
| ^h hookeri deVries · B ^A Castleberry A-1/2 | ⊙ 12, 1 pair |
| ^h hookeri Johansen · B ^A Castleberry A-1/2 | ⊙ 10, 2 pairs |
| punctulans chicag. · B ^A Castleberry A-1/2 | ⊙ 12, 1 pair |
| gaudens lamarckiana · B ^A Castleberry A-4 | ⊙ 12, 1 pair |
| ^h hookeri deVries · B ^A Castleberry A-4 | ⊙ 12, 1 pair |
| ^h hookeri Johansen · B ^A Castleberry A-4 | ⊙ 10, 2 pairs |
| α Richmond · B ^A Castleberry A-4 | ⊙ 14 |
| velans lamarckiana · B ^A Castleberry A-4 | ⊙ 8, ⊙ 4, 1 pair |
| albicans Grado · B ^A Castleberry A-7 | ⊙ 12, 1 pair |
| α Bestwater · B ^A Castleberry A-7 | ⊙ 14 |
| α Buck Creek · B ^A Castleberry A-7 | ⊙ 14 |
| α Camp Peary · B ^A Castleberry A-7 | ⊙ 14 |
| elata Cholula · B ^A Castleberry A-7 | ⊙ 8, ⊙ 4, 1 pair |
| gaudens lamarckiana · B ^A Castleberry A-7 | ⊙ 10, 2 pairs |
| ^h hookeri deVries · B ^A Castleberry A-7 | ⊙ 14 |
| ^h hookeri Johansen · B ^A Castleberry A-7 | ⊙ 10, ⊙ 4 |
| α Indian River · B ^A Castleberry A-7 | ⊙ 12, 1 pair |

Table 6 (continued)

| Complex combination | Chromosome configuration |
|---|--------------------------|
| α Littleton · B ^A Castleberry A-7 | ⊙ 14 |
| β Wakefield · B ^A Castleberry A-7 | ⊙ 14 |
| α Williamsville · B ^A Castleberry A-7 | ⊙ 8, ⊙ 4, 1 pair |
| α angustissima · B ^A Chastang 1 | ⊙ 6, ⊙ 4, ⊙ 4 |
| α biennis 1 · B ^A Chastang 1 | ⊙ 12, 1 pair |
| ^h blandina · B ^A Chastang 1 | ⊙ 12, 1 pair |
| β Elma II · B ^A Chastang 1 | ⊙ 10, 2 pairs |
| α Forsberg · B ^A Chastang 1 | ⊙ 12, 1 pair |
| ^h hookeri deVries · B ^A Chastang 1 | ⊙ 12, 1 pair |
| ^h hookeri Johansen · B ^A Chastang 1 | ⊙ 10, 2 pairs |
| punctulans chicag. · B ^A Chastang 1 | ⊙ 12, 1 pair |
| albicans Grado · B ^A Chastang 7 | ⊙ 8, ⊙ 4, 1 pair |
| rubens · B ^A Chastang 7 | ⊙ 12, 1 pair |
| ^h blandina · B ^A Chastang 7 | ⊙ 12, 1 pair |
| α Birch tree II · B ^A Chastang 7 | ⊙ 12, 1 pair |
| α Fruitland · B ^A Chastang 7 | ⊙ 8, 3 pairs |
| ^h hookeri deVries · B ^A Chastang 7 | ⊙ 12, 1 pair |
| ^h hookeri Johansen · B ^A Chastang 7 | ⊙ 10, 2 pairs |
| α Indian River · B ^A Chastang 7 | ⊙ 10, 2 pairs |
| α Iowa II · B ^A Chastang 7 | ⊙ 8, ⊙ 6 |
| α Monett · B ^A Chastang 7 | ⊙ 14 |
| α Richmond · B ^A Chastang 7 | ⊙ 14 |
| rigens ammophila · B ^A Chastang 7 | ⊙ 10, ⊙ 4 |
| α Yakima · B ^A Chastang 7 | ⊙ 10, 2 pairs |
| α Williamston · B ^A Chastang 7 | ⊙ 12, 1 pair |
| α Lanoraie · B ^A Chastang 7 | ⊙ 12, 1 pair |

Table 7. Chromosome configurations of hybrids between B^A complexes confirming the identity of their chromosome formulae

| Cross | Chromosome configuration |
|-------------------------------------|--------------------------|
| Brewton × Castleberry A-1/1 | 7 pairs |
| Chastang 7 × Brewton | 7 pairs |
| Brewton × Castleberry A-4 | 7 pairs |
| Castleberry A-1/1 × Castleberry A-4 | 7 pairs |
| Castleberry A-9 × Castleberry A-4 | 7 pairs |
| Castleberry A-1/2 × Castleberry A-4 | 7 pairs |
| Castleberry A-1/2 × Castleberry A-9 | 7 pairs |

Table 8. Chromosomal end arrangements found among *Oenothera grandiflora* strains from Alabama, Florida, and Tennessee

| End arrangement | | | | | | | Designation |
|-----------------|-----|------|------|------|-------|-------|-------------|
| 1·2 | 3·4 | 5·6 | 7·10 | 9·8 | 11·12 | 13·14 | A |
| 1·4 | 3·2 | 5·6 | 7·10 | 9·8 | 11·12 | 13·14 | B |
| 1·2 | 3·4 | 5·14 | 7·10 | 9·8 | 11·12 | 13·6 | C |
| 1·2 | 3·4 | 5·13 | 7·10 | 9·8 | 11·12 | 6·14 | D |
| 1·4 | 3·2 | 5·14 | 7·10 | 9·8 | 11·12 | 13·6 | E |
| 1·2 | 3·4 | 5·6 | 7·10 | 9·14 | 11·12 | 13·8 | F |
| 1·3 | 2·4 | 5·14 | 7·10 | 9·8 | 11·12 | 13·6 | G |
| 1·2 | 3·5 | 4·14 | 7·10 | 9·8 | 11·12 | 13·6 | H |
| 1·4 | 3·2 | 5·6 | 7·10 | 9·8 | 11·13 | 12·14 | I |
| 1·2 | 3·4 | 5·6 | 7·10 | 9·8 | 11·13 | 12·14 | K |
| 1·3 | 2·4 | 5·6 | 7·10 | 9·8 | 11·12 | 13·14 | L |

Crosses among the B^A complexes (Table 7) show that the B^A complexes of Castleberry A-1/1, A-1/2, A-4, A-9, and Chastang 7 are identical in segmental arrangement.

Discussion

The various segmental arrangements (designated A–E) of typical ^h*grandiflora* (B type) complexes previously reported by STEINER & STUBBE (1984) are here supplemented by six new formulae shown in Table 8. All eleven formulae have the 7·10 in common, ten of the eleven have the 9·8 and nine of the eleven the 11·12 chromosome. The remaining chromosomes show more variability; the reason for this difference is unknown.

The Castleberry and Chastang strains showing circles of 10, 12 or 14 chromosomes at meiosis are clearly composed of two different complexes, one a B type typical of *O. grandiflora*, and the second a B type that has been modified in the direction of the A type found in *O. villosa* as well as in the beta complexes of the *biennis* group 1 of *O. biennis*. The latter species is sympatric with *O. grandiflora* in Alabama and hybrids between the two have been found (STEINER & STUBBE 1986). Nevertheless, the large-circled strains that carry a B^A complex cannot be simple hybrids between *O. grandiflora* and *O. biennis*, as already pointed out by STEINER & STUBBE (1986). It is likely that the B^A complex has been derived from unstable hybrids between *O. grandiflora* as seed parent and *O. biennis* as pollen parent. The integration of some of the beta *biennis* 1 chromosomes into a ^h*grandiflora* complex could have occurred in such a hybrid. For example, if a hybrid forms a circle of 10 and a circle of 4 and the latter is free of lethals, a ^h*grandiflora* complex carrying two beta *biennis* 1 chromosomes is a possible segregate. Other mechanisms of integration are also possible, e.g., a translocation between the two complexes of a hybrid after the interlocking of chromosomes. The question remains as to which

chromosomes, or parts of chromosomes, of the B^A complex are B or A type chromosomes.

A comparison of the most common B^A arrangement (1·6 3·2 5·11 7·10 9·4 8·12 13·14) with the arrangements of the beta complexes of *O. biennis* growing in association with the complex-heterozygotes of *O. grandiflora* would be instructive; unfortunately at the time of *O. grandiflora* collections were made, a parallel collection of *O. biennis* strains from the same range did not seem likely to yield new information and was not made. Of the few arrangements determined for *biennis* 1 strains from Alabama earlier (STEINER 1952), most carry the 5·11, 8·12, and 13·14 chromosomes. The 13·14 is regularly present in the B complexes, but the remaining two may be the A chromosomes (or modifications thereof) of the B^A arrangement. The 3·2 and 7·10 are most likely B chromosomes. In the complex-heterozygotes with a circle of 10 and 2 pairs the pairs are formed by the 7·10 and 13·14 and are in all probability homozygous. The 1·6 and 9·4 chromosomes cannot be classified because of their absence in closely related or associated strains. They may be of hybrid origin, arising from a translocation between an A and a B complex.

Ultimately the analysis of the gene content of single chromosomes may be necessary in order to confirm the presumed hybrid origin of the newly discovered complex-heterozygotes of *O. grandiflora*.

Whether or not the complex-heterozygotes of *O. grandiflora* will play a role in the further evolution of the species is difficult to say. Presumably the hybridity might confer a selective advantage, thus favoring a gradual spread of the B^A genome with an ultimate shift to populations which are predominantly complex-heterozygous rather than structurally homozygous. At present they are no true breeding when selfed. Their flower structure favors cross pollination. Nevertheless, the B^A genome appears to have become established in a number of different local populations in southern Alabama; since it seems unlikely that its distribution can be explained through a multiple origin of the genotype, one is led to conclude that its spread is already in progress.

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