

REPRODUCTIVE MORPHOLOGY, GENETIC CONTROL AND INCOMPATIBILITY RELATIONS IN TRISTYLOUS

Oxalis physocalyx (OXALIDACEAE)

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ABSTRACT

Oxalis physocalyx Zucc. ex Progel is shown to be tristylous. Pollen production was determined to be greatest in the short anther whorls, intermediate in the mid anther whorls and lowest in the long anther whorls. Pollen size is dimorphic, the lower anther whorl of each morph producing pollen grains 30 μm in diameter and the upper whorl 40 μm in diameter. The genetic control of style form is by two unlinked loci, one controlling short versus non-short, the other mid versus long. Short is epistatic to non-short, and mid is dominant to long. Legitimate pollinations were more successful than illegitimate, both in frequency and seed production per capsule. However, illegitimate other form crosses were successful when longs and mids were used as females, as were self and own-form crosses of longs. Despite these modifications of incompatibility relations, representation of style morphs in natural populations indicates isoplethy. It is suggested that isoplethy results from a competitive advantage of legitimate over illegitimate pollen when pollination is mixed and that incompatibility relations in *O. physocalyx* are essentially unmodified functionally.

INTRODUCTION

Heterostylous species have two (distylous) or three (tristylous) types of plants which differ from one another on the basis of style and anther lengths. In tristylous species three distinct groups of plants exist which are characterized by short-, mid- and long-styled flowers, each of the three floral forms bearing anthers at

two levels, neither of which corresponds to the level of the stigma. The flowers of Oxalidaceae have ten stamens disposed in two unequal whorls of five stamens each. Thus, short-styled plants (S) have one whorl of mid length (mS) and one whorl of long (1S) stamens, mid-styled plants (M) have one whorl of short (sM) and one whorl of long (1M) stamens and long-styled plants (L) have one whorl of short (sL) and one whorl of mid length (mL) stamens. The abbreviated designations follow Weller (1976a).

Several North American species of *Oxalis* have been well studied as regards heterostyly, most notably by Ornduff (1964, 1972, 1983 and 1987), Weller (1975, 1976a, 1976b, 1978, 1979, 1980 and 1981) and Mulcahy (1964). The purpose of the present paper is to report on the reproductive morphology, genetic control and incompatibility relations of a tristylous Brazilian species of *Oxalis*, *O. physocalyx* Zucc. ex Progel. *Oxalis physocalyx* is a weakly shrubby species which lacks vegetative means of reproduction and grows to about 2,5 m tall. It is distributed from southern (state of Paraná) to central (state of Mato Grosso do Sul) and northeastern (state of Piauí) Brazil and is mostly associated with open cerrado type vegetation or with areas which formerly supported such vegetation. *Oxalis physocalyx* belongs to section *Thamnoxys*, subsection *Stenophyllum*, series *Robustae* (Progel, 1877). Lourteig (1975) considered section *Thamnoxys* as composed of about thirty species which occur from Texas to Argentina, one of which is African.

MATERIALS AND METHODS

The crossing program involved an experimental garden population composed of 9 short-styled, 12 mid-styled and 9 long-styled plants transplanted from a natural population encountered in the município of São José do Rio Preto. Flowers about to enter anthesis were bagged to prevent insect pollination and unbagged only at the time of manual pollination, which was done using an eye loupe and a fine-pointed needle to transfer the pollen. Following pollination, the flowers were rebagged until flower fall or fruit initiation. Mature capsules were bagged to prevent seed loss. Mature seeds were sown directly into experimental plots to obtain the F1 generation. Measurements of reproductive whorls were made using a dissecting microscope and a millimetered slide. Style length was measured from the base of the ovary to the tip of the stigma and stamen length from the point where the stamens become free from the fused androecium base to the midpoint of the anthers. All stamen whorls of *Oxalis physocalyx* contained pollen grains, shown to be nonviable by tetrazolium chloride staining. Pollen grain measurements and counts were based exclusively on stainable grains. All measurements and observations were made using fresh material. Material or populations of *Oxalis physocalyx* were collected or studied in the following municipalities of the state of São Paulo: Nova Aliança, Pirassununga, Rancharia and São José do Rio Preto (Eldorado, Talhados and Sítio São Luís). Voucher material is

deposited in the herbarium of the Museo Nacional de Rio de Janeiro (R) and the herbarium of the Instituto de Botânica do Estado de São Paulo (SP). Standard root tip squash techniques were used for chromosome number determination.

RESULTS AND DISCUSSION

Reproductive morphology

Measurements of representatives of five natural populations of *Oxalis physocalyx* revealed that stigmas and anthers occur at three distinct levels in each of the three floral morphs as well as the existence of a reciprocal correspondance in style and stamen lengths among the morphs (Table I). Greatest mean pollen production was determined to occur in the sM and sL whorls, intermediate production in the mS and mL whorls and lowest production in the 1S and 1M whorls (Table II). These observations agree with those which Weller (1976a) reported for *O. alpina*, although in that species considerably more plant to plant variation was detected. Difference in pollen production between stamen whorls of a given floral form was invariably statistically significant ($P < 0.05$) (1S x mS: $t_{38} = 8.22$, 1M x sM: $t_{42} = 5.44$ and mL x sL: $t_{38} = 4.51$). Difference in pollen production by corresponding stamen whorls of different floral morphs was statistically insignificant for mL x mS ($t_{38} = 1.42$) and 1S x 1M ($t_{40} = 0.30$) but significant for sL x sM ($t_{40} = 2.36$).

Pollen grain diameter in *Oxalis physocalyx* was highly uniform for given stamen whorls, but notable size differences were observed among grains from different whorls (Table II). The 1S, 1M and mL whorls each produce pollen grains 40 μm in diameter, whereas the sM, sL and mS whorls produce grains 30 μm in diameter. Thus, in *O. physocalyx* pollen size is dimorphic, the lowermost stamen whorl of each morph producing pollen grains 30 μm in diameter and the uppermost whorl producing grains 40 μm in diameter. A consequence of this situation is that the corresponding stamen whorls mS and mL have different size pollen, 30 μm and 40 μm in diameter, respectively.

Weller (1976a, 1979) reported pollen size to be trimorphic in tristylous *Oxalis alpina* and also observed a significant size difference between the pollen produced by the mS and mL whorls. However, in *O. alpina* it is the mS whorl, instead of the mL whorl, which produces the larger pollen grains. It could be expected that pollen production by the mS whorl of *O. physocalyx* would be greater than that of the mL whorl since the pollen grains formed by the latter whorl are 1/3 larger than those formed by the former whorl; however, pollen production does not vary significantly between the two whorls.

Table I - Means lengths in mm, $\pm$ standard error of reproductive whorls of representatives of six natural populations of *Oxalis physocalyx*.

Locality	Short-styled flowers	Mid-styled flowers	Long-styled flowers
Sítio São Luís	1S 7.68 ± 0.05	1M 7.84 ± 0.05	L 8.00 ± 0.09
	mS 5.21 ± 0.03	M 5.31 ± 0.05	mL 5.31 ± 0.05
	S 3.50 ± 0.04	sM 3.34 ± 0.05	sL 3.39 ± 0.02
	N = 130	N = 141	N = 157
Talhados	1S 7.95 ± 0.12	1M 7.87 ± 0.14	L 7.72 ± 0.13
	mS 5.69 ± 0.11	M 5.06 ± 0.13	mL 5.45 ± 0.08
	S 3.63 ± 0.11	sM 3.32 ± 0.09	sL 3.53 ± 0.06
	N = 20	N = 29	N = 20
Rancharia	1S 7.81 ± 0.08	1M 7.66 ± 0.08	L 7.62 ± 0.08
	mS 5.47 ± 0.06	M 5.52 ± 0.08	mL 5.33 ± 0.06
	S 3.73 ± 0.09	sM 3.77 ± 0.09	sL 3.69 ± 0.09
	N = 27	N = 25	N = 24
Eldorado	1S 8.84 ± 0.09	1M 8.82 ± 0.13	L 8.33 ± 0.15
	mS 5.80 ± 0.07	M 6.08 ± 0.08	mL 5.79 ± 0.10
	S 3.75 ± 0.06	sM 3.79 ± 0.06	sL 3.80 ± 0.06
	N = 29	N = 31	N = 29
Nova Aliança	1S 8.00 ± 0.12	1M 7.56 ± 0.09	L 8.00 ± 0.11
	mS 5.58 ± 0.11	M 5.06 ± 0.12	mL 5.58 ± 0.10
	S 3.70 ± 0.10	sM 3.32 ± 0.09	sL 3.85 ± 0.11
	N = 30	N = 29	N = 30
Pirassununga	1S 7.97 ± 0.11	1M 7.61 ± 0.09	L 7.96 ± 0.11
	mS 5.57 ± 0.09	M 5.06 ± 0.11	mL 5.34 ± 0.09
	S 3.76 ± 0.10	sM 3.42 ± 0.08	sL 3.60 ± 0.08
	N = 30	N = 30	N = 30

Genetic control

Von Ubisch (1921) proposed that the genetic control of tristylly is by two

Table II - Pollen production per theca expressed as mean with standard error and pollen grain diameter, μm , in the three floral forms of *Oxalis physocalyx*.

Floral form	No. of anthers examined per whorl	Long-whorl		Mid-whorl		Short-whorl	
		No. of pollen grains counted	Pollen grain diameter	No. of pollen grains counted	Pollen grain diameter	No. of pollen grains counted	Pollen grain diameter
Short-styled	20	481 $\pm$ 21	40	683 $\pm$ 13	30	—	—
Mid-styled	22	490 $\pm$ 20	40	—	—	717 $\pm$ 20	30
Long-styled	20	—	—	648 $\pm$ 21	40	785 $\pm$ 22	30

loci, S and M, each with two alleles, the S locus being epistatic to the M locus. The S locus was proposed as controlling the expression of short versus non-short and the M locus as controlling the expression of mid versus long. In most tristylous plants, including *Lythrum salicaria* (Fisher and Mather, 1943) *Oxalis* section *Laxae* (Fyfe, 1950), section *Corniculatae* (Mulcahy, 1964; Ornduff, 1972) and section *Ionoxalis* (Weller, 1976b), short style is dominant to non-short. However, von Ubisch (1926) considered short style to be recessive in *O. rosea*, as did Fyfe (1956) for *O. articulata*. Bennett *et al.* (1986) in a restudy of style length inheritance in *O. rosea*, concluded that three gene pairs control style length in that species and that short style dominance or recessiveness varies from plant to plant.

In the present study of the genetic control of style length in *Oxalis physocalyx*, each of the three possible intermorph crosses, L $\times$ S, L $\times$ M and M $\times$ S, and the reciprocals were successfully made, as was the intramorph cross L $\times$ L. The crosses are summarized in Table III, which also presents the phenotypes of the progeny and the proposed genotypes of the parent plants.

The recessiveness of long style and the homozygosity of long parents were clearly demonstrated by the appearance of only longs in the progeny resulting from the self and own form crosses $L_1 \times L_1$ and $L_{42} \times L_1$. Also, the uniform heterozygosity of short parents at the S locus was indicated by the production of both short and non-short plants in the progeny of all crosses involving a short parent. The appearance of mids in the progeny of several crosses between short and long parents demonstrates that the S allele is epistatic to the M allele. The dominance of the M (mid) allele to the m (long) allele is demonstrated by the occurrence of only mids in the progeny of the crosses $L_{13} \times M_{17}$ (and the reciprocal), $M_{17} \times L_{42}$ and $M_{17} \times L_3$.

Table III - Style forms of progeny of crosses in *Oxalis physocalyx* and proposed genotypes of parent plants.

Cross	Style forms of progeny			Proposed genotypes of parent plants
	S	M	L	
L1 x L1	0	0	10	ssmm x ssmm
L42 x L1	0	0	8	ssmm x ssmm
L2 x M1	0	7	7	ssmm x ssMm
L13 x M17	0	13	0	ssmm x ssMM
L13 x M32	0	5	4	ssmm x ssMm
L1 x S1	17	10	12	ssmm x SsMm
L1 x S16	4	5	3	ssmm x SsMm
L13 x S16	3	3	2	ssmm x SsMm
L3 x S19	12	0	4	ssmm x Ssmm
L14 x S15	3	0	5	ssmm x Ssmm
L13 x S23	12	0	1	ssmm x Ssmm
M17 x L42	0	9	0	ssMM x ssmm
M17 x L3	0	18	0	ssMM x ssmm
M1 x L14	0	8	10	ssMm x ssmm
M17 x L13	0	6	0	ssMM x ssmm
M32 x S1	1	1	1	ssMm x SsMm
M17 x S19	5	3	0	ssMM x Ssmm
M1 x S16	16	14	15	ssMm x SsMm
M32 x S16	6	5	4	ssMm x SsMm
M12 x S30	2	2	2	ssMm x SsMm
S1 x L1	2	4	3	SsMm x ssmm
S16 x L13	3	2	2	SsMm x ssmm
S30 x L6	2	2	2	SsMm x ssmm
S31 x L13	5	8	0	SsMM x ssmm
S31 x L50	14	12	0	SsMM x ssmm
S15 x L6	7	0	5	Ssmm x ssmm
S23 x L6	3	0	6	Ssmm x ssmm
S30 x M32	5	6	4	SsMm x ssMm
S15 x M32	2	1	1	Ssmm x ssMM
S30 x M37	8	9	0	SsMm x ssMM
S19 x M17	3	3	0	Ssmm x ssMM
S31 x M17	4	4	0	SsMM x ssMM

The possibility of linkage between the S and M loci can be tested by the analysis of the progeny obtained from crosses between long and short individuals. If a short heterozygous at the M locus (SsMm) is crossed with a long (ssmm), the progeny expected would be, for linkage in repulsion (Sm/sm), only mid and long, for linkage in coupling (SM/sm), only short and long, and in the case of unlinked loci, short, mid and long in a 2:1:1 ratio. In the case of crosses between short homozygous for mid (SsMM) and long (ssmm), a progeny of short and long in a 1:1 ratio would be expected for unlinked loci.

In *Oxalis physocalyx* short heterozygous at the M locus, when crossed with long, invariably resulted in progeny composed of short, mid and long. Because of the small sizes of the individual progenies, a 2:1:1 ratio was not evident. However, the pooled results of the six pertinent crosses (31:26:24), although showing a better fit to a 1:1:1 ratio ($\chi^2 = 0.962$, $df = 2$, $P > 0.20$), do not differ significantly from a 2:1:1 ratio ($\chi^2 = 4.55$, $df = 2$, $P > 0.10$). The two crosses of short homozygous dominant at the M locus with long ($S_{31} \times L_{13}$ and $S_{31} \times L_{50}$) resulted in progenies which did not differ significantly from a 1:1 ratio of short and long (respectively, $\chi^2 = 0.692$, $df = 1$, $P > 0.20$ and $\chi^2 = 0.154$, $df = 1$, $P > 0.20$). These results clearly indicate the S and M loci to be unlinked.

The genetic control of style form in *Oxalis physocalyx* is consistent with disomic inheritance, which agrees with our determination of this species as being diploid ($2n=12$), and is basically similar to the model proposed by von Ubisch (1921) and already determined to exist in several other species of the genus. The most notable characteristics of the system as seen in *O. physocalyx* are the dominance of short style and, especially, the non-linkage of the S and M loci, until now reported in the genus only in *O. rosea*, and that for a three locus model (Bennett *et al.*, 1986).

Oxalis has major centers of diversity in south Africa and South America, and Weller (1980) suggests the invasion of North America by species of *Oxalis* migrating from the south to be a relatively recent event, as did Eiten (1963) specifically for section Corniculatae. These considerations strongly suggest the neotropical species of *Oxalis* to be ancestral to the northern temperate species. The occurrence of unlinked S and M loci in the South American *O. physocalyx* is of interest since it possibly represents the ancestral condition, in contrast with the invariably linked loci in those North American species thus far reported. It is further of interest that the only other species of the genus reported to have unlinked S and M loci is *O. rosea*, which is also South American.

Incompatibility relations

The floral polymorphism of heterostyly is characteristically associated with a diallelic system of incompatibility which prevents successful crosses between identical

morphs. Thus, nearly all heterostylous species are self-incompatible; however, the strength of incompatibility reactions vary and in some cases is very weak. Modification of incompatibility relations can lead to increased inbreeding and the derivation of distyly from tristyly, as Ornduff (1964) reported for *Oxalis* section Corniculatae and Weller (1976a, 1979) for section Ionoxalis.

Table IV summarizes the results of legitimate pollinations (stigma pollinated with pollen from anther of same level from other form flower), illegitimate other form pollinations (stigma pollinated with pollen from anther of different level from other form flower) and illegitimate self and own form pollinations realized in *Oxalis physocalyx*.

Legitimate pollinations: All six legitimate pollinations were successful; however, crosses using longs as females were more successful than those using mids which in turn were more successful than those using shorts. Nevertheless, all crosses resulted in approximately the same mean number of seeds per capsule.

Illegitimate other form pollinations: Those crosses using mids as the female plant were slightly more successful than those using longs and also resulted in a greater mean seed production per capsule. Crosses using shorts as the female plant were uniformly unsuccessful.

Illegitimate self and own form pollinations: This class of crosses was unsuccessful when mids and shorts were used and also when longs were pollinated with pollen from the sL whorl. However, when longs were pollinated with pollen from the mL whorl the crosses were successful at about the same frequency as when crossed with pollen from the mS whorl, and mean seed production per capsule approached that observed in legitimate pollinations of longs.

In a condition of equilibrium, the three morphs of a tristylous species are expected to be equally represented in a population (Finney, 1952; Spieth, 1971), and a disturbance of equilibrium is an expected consequence of a modification of incompatibility relations. The incompatibility relations of *Oxalis physocalyx* clearly deviate from the expected, since all illegitimate pollinations are expected to be unsuccessful.

Style morph representation was determined for five populations of *Oxalis physocalyx* (Table V). In two of these populations, Nova Aliança and Pirassununga, isoplethy was observed. A third population, Sítio São Luís, was initially anisoplethic in January, 1983, but was isoplethic in January of 1984 and 1985. The two remaining populations, Talhados and Eldorado, were anisoplethic in March, 1984, and their subsequent destruction prohibited their re-examination. It is possibly significant that the two anisoplethic populations were also the smallest populations studied and that they deviated from isoplethy in independent manners. These results suggest that under normal conditions well developed populations of *Oxalis physocalyx* can be expected to be isoplethic or to be moving toward isoplethy.

Table IV - Results of legitimate and illegitimate pollinations in *Oxalis physocalyx*.

Cross	Number of flowers pollinated	Successful crosses		Total seeds	Mean no. seeds per capsule	Mean no. seeds per pollination
		No.	%			
<i>Legitimate pollinations</i>						
L x 1M	188	108	57.45	799	7.40	4.25
L x 1S	148	100	67.57	712	7.12	4.81
Totals	336	208	61.90	1511	7.26	4.50
M x mL	161	76	47.20	555	7.30	3.45
M x mS	136	69	50.74	505	7.32	3.71
Totals	297	145	48.82	1060	7.31	3.57
S x sL	107	28	26.17	190	6.79	1.78
S x sM	105	25	23.81	165	6.60	1.57
Totals	212	53	25.00	355	6.70	1.67
Combined totals	845	406	48.05	2926	7.21	3.46
<i>Illegitimate other-form pollinations</i>						
L x sM	94	17	18.09	87	5.12	0.93
L x mS	59	10	16.95	26	2.60	0.44
Totals	153	27	17.65	113	4.19	0.74
M x sL	90	18	20.00	112	6.22	1.24
M x 1S	84	17	20.24	106	6.24	1.26
Totals	174	35	20.11	218	6.23	1.25
S x mL	60	0	0	0	0	0
S x 1M	60	0	0	0	0	0
Totals	120	0	0	0	0	0
Combined totals	447	62	13.87	331	5.34	0.74
<i>Illegitimate self and own-form pollinations</i>						
L x mL	169	27	15.98	178	6.59	1.05
L x sL	130	0	0	0	0	0
Totals	299	27	9.03	178	6.59	0.60
M x 1M	164	0	0	0	0	0
M x sM	165	0	0	0	0	0
Totals	329	0	0	0	0	0
S x 1S	110	0	0	0	0	0
S x mS	120	0	0	0	0	0
Totals	230	0	0	0	0	0
Combined totals	858	27	3.15	178	6.59	0.21

Table V - Representation of style forms in natural populations of *Oxalis physocalyx* in the state of São Paulo.

Locality	Style form representation number and frequency			Sample size	G value
	Short	Mid	Long		
<i>Nova Aliança</i>					
March, 1984	40 (0.31)	47 (0.38)	40 (0.31)	127	0.962
<i>Pirassununga</i>					
March, 1985	44 (0.33)	50 (0.37)	40 (0.30)	134	1.169
<i>Sítio São Luís</i>					
January, 1983	37 (0.34)	46 (0.43)	25 (0.23)	108	6.346*
January, 1984	40 (0.40)	40 (0.40)	31 (0.31)	101	0.263
January, 1985	39 (0.33)	42 (0.36)	37 (0.31)	118	1.838
<i>Talhados</i>					
March, 1984	24 (0.33)	36 (0.50)	12 (0.17)	72	12.558*
<i>Eldorado</i>					
March, 1984	7 (0.17)	14 (0.33)	21 (0.50)	42	7.347*

*Representation differs significantly ($P < 0.05$) from equality.

In *Oxalis physocalyx* modification of incompatibility relations evidently is not associated with the formation of anisoplethic populations, as would be expected. This can not be attributed to genetic depression resulting in the premature death, non-flowering or otherwise impaired reproductive capacity of plants resulting from illegitimate crosses, since all such plants obtained experimentally were normal. One possible factor contributing to the maintenance of isoplethic populations is that modification of incompatibility relations in *O. physocalyx* is not accompanied by morphological convergence of reproductive whorls as occurs, for example, in *O. alpina* (Weller, 1979). Convergence of stamen whorls could result in pollen from two whorls being deposited essentially together on a pollinating insect's body and the transference of both legitimate and illegitimate pollen in nearly equal amounts to a stigma. Thus, the function of stamen-style polymorphism in promoting legitimate pollinations, as proposed by Darwin (1877), would be circumvented.

A considerably more effective factor in maintaining isoplethy in populations

of *Oxalis physocalyx* would be the existence of a competitive advantage of legitimate over illegitimate pollen when pollinations are mixed. Numerous studies have shown that mixed stigmatic pollen loads are usual in heterostylous species (see Ganders, 1979 and Richards, 1986). Weller and Ornduff (1977) demonstrated a competitive advantage of legitimate over illegitimate pollen in cryptically self-incompatible distylous *Amsinckia grandiflora* which, despite being self-compatible when exclusively self-pollinated, forms isoplethic populations. The isoplethy observed in populations of *O. physocalyx* suggests the incompatibility relations of that species to be essentially unmodified functionally, conceivably as a result of a competitive advantage of legitimate pollinations.

RESUMO

O presente trabalho demonstrou que *Oxalis physocalyx* Zucc. ex Progel é trístila. A produção de pólen foi determinada como sendo maior nos verticilos curtos de anteras, intermediária nos verticilos médios e menor nos verticilos longos de anteras. O tamanho do pólen é dimórfico, o verticilo inferior de antera de cada forma produzindo grãos de pólen de 30 μm de diâmetro e o verticilo superior de 40 μm de diâmetro. O controle genético da forma floral é determinado por dois locos independentes, um controlando brevistila *versus* não-brevistila, o outro medistila *versus* longistila. Brevistila é epistático sobre não-brevistila e medistila é dominante sobre longistila.

As polinizações legítimas foram mais bem sucedidas que as ilegítimas tanto na frequência como na produção de semente por cápsula. Entretanto, cruzamentos ilegítimos entre formas diferentes foram bem sucedidos quando plantas logistilas e medistilas foram usadas como femininas e também nas autopolinizações e nos cruzamentos entre plantas longistilas. Apesar dessas modificações nas relações de incompatibilidade, a representação das formas em populações naturais indica isopletia. É sugerido que a isopletia resulta de uma vantagem competitiva de pólen legítimo sobre ilegítimo quando os grãos estão associados na polinização e que, as relações de incompatibilidade em *O. physocalyx* não estão essencialmente modificadas na função.

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