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Quantitative analysis of pollination diallels of two Australian species of *Pandorea* (Bignoniaceae)

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Summary. The genus *Pandorea,* family Bignoniaceae, occurs naturally in Australia. *Pandorea pandorana* and *P. jasminoides* were used in intraspecific diallel crosses in order to test for the presence of self-incompatibility and the effect of genotype. Both species were found to be highly self-incompatible. Only 2 out of 353 (0.6%) self-pollinations compared to 337 out of 485 (69.5%) of outcross-pollinations of *P. pandorana* set fruit. Similarly, for *P. jasminoides,* 4 out of 235 (1.7%) self-pollinations and 175 out of 296 (59.1%) of outcross pollinations set fruit. Both reciprocal and genotype effects were found in *P. pandorana.* Fruit-set differences occurred between two different genotypes of *P. jasminoides,* but reciprocal effects were not found. Data were analysed using generalized linear models with a logit-link function assuming a binomial error distribution. The relative merits of the various models are discussed.

Key words: Bignoniaceae – Diallel analysis – *Pandorea* – Self-incompatibility

Introduction

The genus *Pandorea,* family Bignoniaceae, contains six species, of which four occur in Australia (van Steenis 1977). Little is known of the breeding systems of *Pandorea* species. Three species, *P. jasminoides, P. nervosa* and *P. baileyana* are endemic with restricted ranges (van Steenis 1977). The fourth, *P. pandorana,* is widespread throughout Australia but also occurs in New Guinea and South East Asia. *Pandorea jasminoides* and *P. pandorana* are popular landscape plants in Australia because of their vigorous growth and spectacular floral display. *Pandorea pandorana* is particularly variable, often displaying strikingly different growth and foliage characteristics with flower colour varying between white, pink, yellow and brown. By contrast, *P. jasminoides* shows little variation but is highly valued for its display of large pink or white flowers. Variability between and within *Pandorea* species indicates a promising potential to produce novel hybrids from any breeding programme.

The presence of a self-incompatibility mechanism in related genera was first mentioned for Bignoniaceae by Muller (1868) who found that flowers of *Tecoma* sp. failed to set seed when self-pollinated. Examples of species within the family Bignoniaceae in which self-incompatibility has been demonstrated are shown in Table 1. Self-incompatibility is a genetically controlled mechanism that promotes outcrossing. Whilst usually considered to be a pre-fertilization barrier (de Nettancourt 1977), it can also affect post-zygotic development in some taxa (Seavey and Bawa 1986). This phenomenon is probably widespread throughout the family (Gentry 1990), but there is a single report of a species, *Tecomanthe speciosa,* which is apparently self-compatible (Hunter 1967).

In the study reported here, *P. jasminoides* and *P. pandorana* were used in intraspecific diallel crosses in order to test for the presence of a self-incompatibility system and for genotype and reciprocal effects.

Materials and methods

Plant material

The origin of all plant material, flowering characteristics and the coding system used are shown in Table 2. Clonal material of 3 genotypes each of *P. jasminoides* (HW, LD, AL) and *P. pan-*

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Table 1. Records of self-incompatibility in the family Bignoniaceae

Species	Nature of evidence	Reference
Bignonia venusta	Observation that "artificial pollination with pollen from the same plant was ineffective" during study of embryo-sac development suggesting that self-pollen did not result in fertilization	Duggar (1899)
Campsis radicans	(As *Tecoma radicans*) Controlled hand pollinations of plants outside native habitat	Elrod (1904)
	Controlled hand pollinations in field with bagged and unbagged controls	Bertin (1982)
Catalpa speciosa	Controlled self- and outcross-pollinations in field with comparisons between bagged and unbagged flowers	Stephenson and Thomas (1977)
Chilopsis linearis	Controlled self- and outcross-pollinations in field with comparisons between bagged and unbagged controls	Petersen et al. (1982)
Tabebuia neochrysantha	Flowers bagged for controlled self- and outcross-pollinations in field and compared to open-pollinated fruit set	Bawa (1974)
Tabebuia rosea	Controlled hand pollinations in field	Bawa (1974) Bawa and Webb (1984)
Tecoma spp.	Observation that flowers of *Tecoma* species were infertile to their own pollen	Muller (1868)

dorana (SCH, AF and GS) was obtained from commercial nurseries as rooted cuttings. The remaining genotypes were selected from wild populations or arboreta in New South Wales, Victoria and Queensland.

Genotypes other than those bought from nurseries were propagated from 10-cm cuttings with the basal leaves removed. Fresh cutting material was first dipped in the fungicide Rovral, the base of each cutting was then dipped in 2,000 mg l^{-1} IBA for 5 s, inserted into individual propagation tubes containing 1 peat:2 sand (v/v) and finally placed under intermittent mist until rooting occurred (after about 6 weeks).

Rooted cuttings were potted into growing media comprising 2 pine bark:2 coarse washed river sand: 1 brown coal (v/v) and fertilized with 3 kg N:P:K: Osmocote, 1 kg Micromax, 0.5 kg coated Fe and 2 kg dolomite per m^3 at the time of media preparation. Plants were grown in a glasshouse and transferred to an insect-proof house for experimentation. Pots were watered automatically once each day with a drip-feed system that ensured that the flowers were kept dry.

Pollinations and fruit set

Experimental pollination involved removing the pollen from the anthers of the desired male parent with the tip of forceps, then applying it by gentle brushing directly onto the open stigma lobes of the female parent either on the day of anthesis or the following day. Once pollinated, the stigma lobes closed.

Table 2. Description and source of genotypes of *P. pandorana (P.p)* and *P. jasminoides (P.j.)* used in diallel pollinations

Species	Genotype	Description of flowers	Source
P. p.	TS3 TS4 TS6	Cream flowers, maroon centres, unscented	Single population near Merimbula, New South Wales
	VC	Cream flowers, maroon centres, unscented	Valencia Creek, Gippsland, Victoria
	TH	Cream flowers, maroon centres, unscented	Thorpdale, Gippsland, Victoria
	SCH	Pale yellow, scented	Schubert's Nursery, Victoria
	AF	Pale yellow, scented	Austraflora Nursery, Victoria
	GS	Narrow tubed, yellow, unscented	Austraflora Nursery, Victoria
P. j.	HW	Pink flowers, faintly scented	Hardwick's Nursery, Victoria
	LD	White flowers, faintly scented	Austraflora Nursery, Victoria
	AL	White flowers, faintly scented	Banksia Nursery, Victoria

Fruit set was recorded 2 weeks after pollination. At this stage the corolla tube had fallen off, and the swollen ovary was clearly visible above the level of the calyx. Each flower has only one ovary producing a single fruit.

Statistical analyses

All diallel crosses were analysed by fitting one or more generalized linear models using a logit-link function (McCullagh and Nelder 1989) and assuming a binomial error distribution. Data were processed using a Genstat 5 statistical package (Lawes Agricultural Trust, Rothamsted, UK).

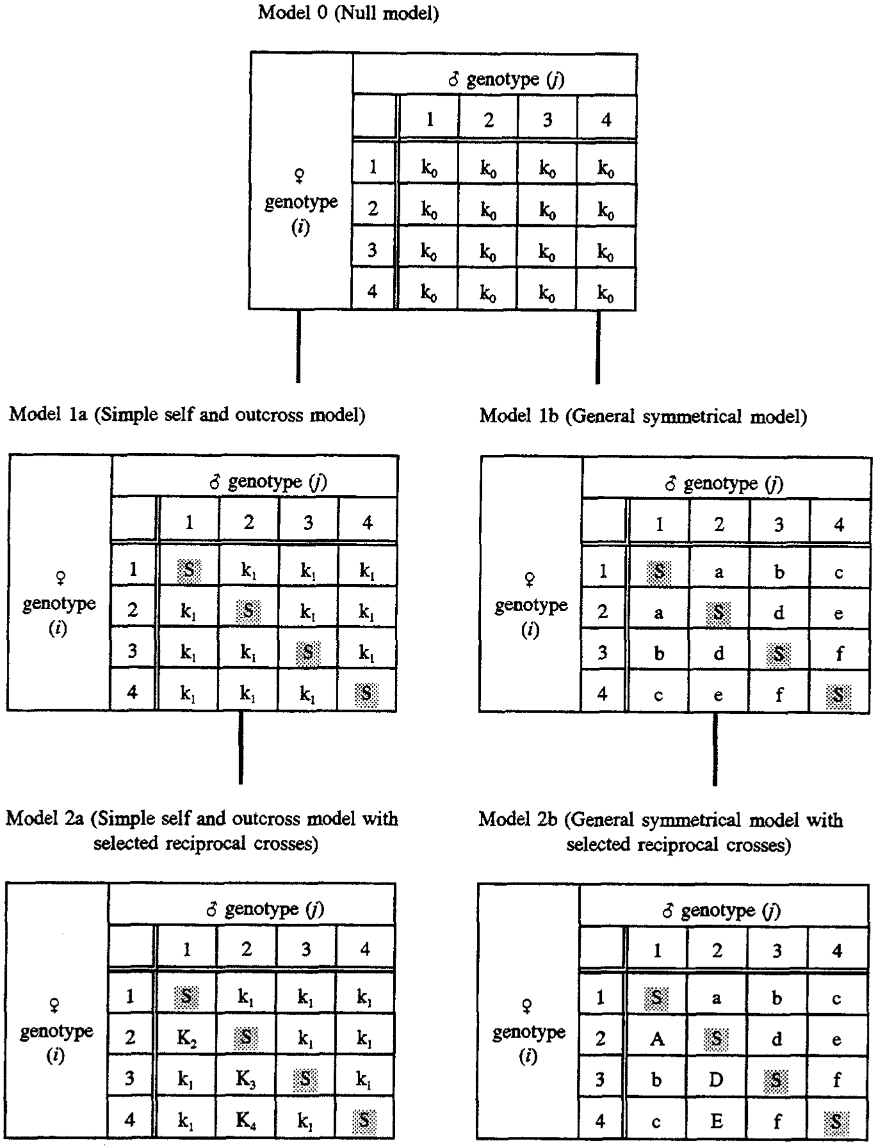
A series of hierarchical models was devised to test, in turn, for the influence of self-pollinations, genotype combinations and reciprocal effects. Figure 1 represents two pathways of sequential models that can be used to fit the data from a 4 × 4 diallel. A full explanation of this figure is given below when the different models are described. The suitability of any model to describe and fit the experimental data was judged on the significance of the residual deviance ("lack-of-fit") and, where appropriate, on the significance of the change in residual deviance when two models were compared.

The simplest model that can be used to explain any diallel data is one where the probability of fruit set is the same for all crosses (Null Model, Fig. 1). In this case, the logit-link model can be expressed as:

$$\log\left(\frac{P_{ij}}{1-P_{ij}}\right)=k_0 \qquad \text{(Model 0)}$$

where P_{ij} is the probability of fruit set from a cross of a female plant of genotype (i) and a male plant of genotype (j) and k_0, a constant, is the log-odds ratio of fruit set.

All subsequent models were derived to allow for different probabilities of fruit set between-self-pollinations (geitonogamous) and outcross-pollinations (xenogamous). If it is assumed that within these pollination categories the probabilities of fruit



Model 0 (Null model)

♀ genotype (*i*)		♂ genotype (*j*)			
		1	2	3	4
	1	k_0	k_0	k_0	k_0
	2	k_0	k_0	k_0	k_0
	3	k_0	k_0	k_0	k_0
	4	k_0	k_0	k_0	k_0

Model 1a (Simple self and outcross model)

♀ genotype (*i*)		♂ genotype (*j*)			
		1	2	3	4
	1	S	k_1	k_1	k_1
	2	k_1	S	k_1	k_1
	3	k_1	k_1	S	k_1
	4	k_1	k_1	k_1	S

Model 1b (General symmetrical model)

♀ genotype (*i*)		♂ genotype (*j*)			
		1	2	3	4
	1	S	a	b	c
	2	a	S	d	e
	3	b	d	S	f
	4	c	e	f	S

Model 2a (Simple self and outcross model with selected reciprocal crosses)

♀ genotype (*i*)		♂ genotype (*j*)			
		1	2	3	4
	1	S	k_1	k_1	k_1
	2	K_2	S	k_1	k_1
	3	k_1	K_3	S	k_1
	4	k_1	K_4	k_1	S

Model 2b (General symmetrical model with selected reciprocal crosses)

♀ genotype (*i*)		♂ genotype (*j*)			
		1	2	3	4
	1	S	a	b	c
	2	A	S	d	e
	3	b	D	S	f
	4	c	E	f	S

Fig. 1. Flow diagram showing alternative model pathways depending on whether the bulk of outcrosses are considered to result in a common outcome or in discrete and varied results

set are constant, then the appropriate model has two parameters and is of the form:

$$\log\left(\frac{P_{ij}}{1-P_{ij}}\right)=\begin{bmatrix} S \text{ for } i=j \\ k_1 \text{ for } i\neq j \end{bmatrix} \qquad \text{(Model 1 a)}$$

where S, a constant, is the log-odds ratio of fruit set for self-pollinations (i.e. $i=j$), and k_1, another constant, is the log-odds ratio for outcross-pollinations (i.e. $i\neq j$).

If the probabilities of fruit set in the various outcross-pollinations are allowed to have independent values, then the log-odds ratios for these outcrosses can be represented as pairs of parameters (aa–ff in Model 1 b, Fig. 1).

Models 1 a and 1 b are symmetrical, in that no terms are introduced to allow for any reciprocal effects that depend on the direction in which the cross was performed. Terms to allow for these reciprocal effects can be added to the models, if justified by the "lack-of-fit" test. In Fig. 1, Model 2 a is an extension of Model 1 a, where one genotype displays certain reciprocal effects. In this example, the majority of outcross-pollinations produce the same probability for fruit set, but the reciprocal pairs for genotype number 2 have different log-odds ratios (i.e. $K_2\,k_1$, $K_3\,k_1$, $K_4\,k_1$). Similarly, Model 2 b is an extension of Model 1 b, with genotype number 2 displaying reciprocal effects (i.e. Aa, Dd, Ee) and all other outcross-pollinations having independent but paired values (i.e. bb, cc, ff).

Results

Floral morphology

Pandorea flowers are tubular with four stamens arranged in two pairs lying dorsally in the corolla tube and an elongated style that terminates in a stigma comprising two lobes. The stigma lobes are sensitive to touch and close permanently if a flower has been pollinated. The stigma lies in front of and close to the anthers, but mechanical self-pollination has not been observed.

Table 3. Proportion of fruit set and fitted values [ ] resulting from various numbers of pollinations ( ) carried out in the diallel crosses for *P. pandorana*. Shading refers to self-pollinations

2 × 2 diallel: 2 genotypes

		♂ genotype (*j*)	
		ATH	TS4
♀ genotype (*i*)	ATH	0 (13) [0]	0.30 (10) [0.30]
	TS4	0.30 (10) [0.30]	0 (10) [0]

3 × 3 diallel: 3 genotypes

		♂ genotype (*j*)		
		GS	TS6	TS3
♀ genotype (*i*)	GS	0.03 (40) [0.01]	0.40 (5) [0.38]	0.30 (30) [0.38]
	TS6	* (*) [0.38]	0 (10) [0.01]	0.60 (5) [0.38]
	TS3	0.90 (30) [0.90]	0.60 (5) [0.38]	0 (40) [0.01]

4 × 4 diallel: 4 genotypes

		♂ genotype (*j*)			
		SCH	GS	TH	VC
♀ genotype (*i*)	SCH	0 (30) [0]	0.87 (15) [0.81]	0.97 (30) [0.81]	0.77 (30) [0.81]
	GS	0.47 (15) [0.47]	0 (30) [0]	0.70 (30) [0.81]	0.73 (30) [0.81]
	TH	0.90 (30) [0.81]	0.47 (30) [0.47]	0 (90) [0]	0.80 (30) [0.81]
	VC	0.90 (30) [0.81]	0.47 (30) [0.47]	0.75 (60) [0.81]	0.01 (90) [0]

Table 4. Residual deviance, residual degrees of freedom and significance of lack-of-fit between fruit set resulting from pollinations between four genotypes of *P. pandorana* (Table 3), and fitted values

Model		Residual deviance	Residual degrees of freedom	Significance of "lack-of-fit"
Null	0	436.95	15	$P<0.001$
Simple	1a	51.23	14	$P<0.001$
Simple + reciprocal	2a	17.59	11	ns
Null	0	436.95	15	$P<0.001$
General	1b	19.07	9	$0.05>P>0.01$
General + reciprocal	2b	5.48	6	ns

Pandorea pandorana pollinations

Table 3 shows the proportion of fruit set resulting from various numbers of pollinations carried out in three diallel crosses for *P. pandorana*. Combining the data for all three diallels, self-pollination produced extremely low fruit set (1 fruit from 353 pollinations). As a consequence, the Null Model, which predicts that all crosses will result in a constant fruit set, is not applicable to describe the data and is, therefore, not considered further.

For the 2 × 2 diallel, no fruit formed from self-pollinations, but a similar number of fruit developed in both crosses between the two genotypes. When the data were fitted to the simplest extension of the Null Model, Model 1a, the resultant residual deviance was 0.0006, and the probabilities of fruit set for self- and outcross-pollinations were zero and 0.3, respectively (Table 3).

For the 3 × 3 diallel, a high proportion of fruit set occurred in outcrosses, but only a single fruit formed from the 90 self-pollinations. Consequently, when Model 1a was fitted rather than Model 0, the change in residual deviance was 80.67 using 1 degree of freedom (d*f*), which represented a highly significant ($P<0.001$) difference in fruit set between self-pollinations and outcrosses. However, Model 1a did not fit the observed data closely, and the residual deviance of 27.00 with 6 d*f* was significant at $P<0.001$. The "lack-of-fit" appeared largely to be due to the cross of TS3♀ × GS♂, which had a much higher percentage fruit set than the other outcrosses (Table 3). When a model akin to Model 2a was used (Fig. 1), which allowed for a reciprocal effect for that particular cross, the fit improved substantially, and the residual deviance of 4.46 with 5 d*f* was no longer significant ($0.25<P<0.5$). The fitted model was, therefore, of the form:

$$\log\left(\frac{P_{ij}}{1-P_{ij}}\right)=\begin{bmatrix} S \ \text{ for } i=j \\ K_2 \ \text{ for } i=3,\ j=1 \ (\text{i.e. TS3}♀+\text{GS}♂) \\ K_1 \ \text{ for } i\neq j \text{ except } i=3, j=1 \end{bmatrix}$$

where the estimated values of the log-odds parameters, S, k_1, and K_2 were significantly different from zero ($P<0.001$) and corresponded to estimated probabilities for fruit set of 0.01, 0.38, and 0.90, respectively (Table 3).

For the 4 × 4 diallel, the average effect of outcross-pollinations again resulted in a much higher percentage of fruit set (68%) compared to self-pollinations (0.7%). In addition, reciprocal effects were evident in some of the primary data presented in Table 3. The two pathways of sequential models (Fig. 1) that allow for reciprocal effects depend on whether the outcross-pollinations generally have a similar outcome (Model 2a) or are independent (Model 2b). Table 4 shows a comparison of the residual deviance, d*f* and significance when the data were sequentially fitted to the two alternative model pathways. Significant "lack-of-fit" was eliminated for both Model 2a and

Table 5. Proportion of fruit set and fitted values [ ] resulting from various numbers of pollinations ( ) between three genotypes of *P. jasminoides*. Shading refers to self-pollinations

		♂ genotype (*j*)		
		HW	LD	AL
♀ genotype (*i*)	HW	0.00 (150) [0.02]	0.71 (104) [0.69]	0.57 (49) [0.62]
	LD	0.66 (67) [0.69]	0.06 (64) [0.02]	0.25 (36) [0.24]
	AL	0.73 (22) [0.62]	0.22 (18) [0.24]	0.05 (21) [0.02]

2b when reciprocal terms accounting for the crosses GS♀ × SCH♂, TH♀ × GS♂ and VC♀ × GS♂ were included.

In this study, no statistical analysis to compare the models across the two pathways has been devised. Thus, for the present 4 × 4 diallel, either Model 2a or 2b could be used to describe the data. The predicted values from Model 2a, the simpler model, have been chosen for presentation in Table 3.

Pandorea jasminoides pollinations

Table 5 shows the proportion of fruit set resulting from various numbers of pollinations carried out in a 3 × 3 diallel for *P. jasminoides*.

As for *P. pandorana* a higher proportion of fruit set occurred in outcross-pollinations than in self-pollinations, which only yielded 4 fruit from 235 pollinations. The model best suited to explain the experimental data was akin to Model 1b, which accounted for both the differences between self- and outcross-pollinations and for the observed genotype differences. The resultant model had a residual deviance of 10.49 with 5 df and a "lack-of-fit" that was not significant ($P > 0.05$). The predicted probability for fruit set in self-pollinations was close to zero. No reciprocal effects were apparent, but when genotype AL was crossed with LD the probability of fruit set was more than halved in comparison to AL × HW or LD × HW crosses (Table 5).

Discussion

Pollination effects

Self-pollination in *P. pandorana* and *P. jasminoides* always resulted in a highly significant reduction in, or absence of, fruit set. This observation is consistent with the responses found for other members of the Bignoniaceae, including: *Campsis radicans* (Elrod 1904; Bertin 1982), *Catalpa speciosa* (Stephenson and Thomas 1977), *Chilopsis linearis* (Petersen et al. 1982), *Tabebuia neochrysantha* (Bawa 1974) and *Tabebuia rosea* (Bawa 1974; Bawa and Webb 1984). The demonstration of this self-incompatibility, however, depended on comparisons of fruit set resulting from pollinations involving only self-pollen with those involving only outcross-pollen. Bertin and Sullivan (1988) and Bertin et al. (1989) whilst confirming self incompatibility in *Campsis radicans* when using only self-pollen also showed a degree of self-fertility when using a mixture of self- and outcross-pollen. Selfed progeny ranging from 2–30% of seeds in individual fruits were recorded after pollination with mixed pollen, and this percentage was found to vary with the genotype of the outcross-pollen donor.

Whilst no data were obtained in the present study on the site of the barrier to fruit set in *P. pandorana*, self- and outcross-pollen tubes were observed in the style tissue and ovary. Similar observations in *Campsis radicans* led to the conclusion by Bertin and Sullivan (1988) that there was no self-incompatibility operating in the stigma or style. Rather, a late-acting self-incompatibility mechanism, found also in other woody plants (Seavey and Bawa, 1986), is indicated. Further studies with that species (Bertin et al. 1989) showed sporadic abortion of embryos and reduced seedling vigour following self-pollinations, suggesting the occurrence of inbreeding depression. As a result the self-sterility observed in *C. radicans* has been interpreted as a partial self-incompatibility with inbreeding depression reducing embryo and seedling viability of selfed progeny, which bypass the self-incompatibility barrier (Bertin et al. 1989). Elucidation of the exact site of self-pollen tube arrest or the premature termination of zygotic development, which could explain the very low fruit set observed, awaits further microscopy studies for both *Pandorea* and *Campsis*.

In some of the *P. pandorana* crosses, fruit set for a pair of genotypes varied according to the direction in which the cross was performed. Notably, these reciprocal effects always involved the GS genotype, but there was no consistent pattern between either the magnitude or direction of the reciprocal effect and whether GS was used as the ♂ or ♀ parent. Reciprocal effects have been reported for *Macadamia* (Sedgley et al. 1990) and for *Banksia coccinea* (Fuss and Sedgley 1991). Within Bignoniaceae, *Campsis radicans* also appeared to exhibit reciprocal effects (Bertin 1985). The present reciprocal effects with GS are difficult to explain without further study and a knowledge of the geographical origin and distribution of this popular nursery selection. Whilst no reciprocal effects were observed in *P. jasminoides*, crosses involving genotypes LD and AL showed a reduced fruit set compared to outcrosses genotype HW with either genotype LD or AL. Both AL and LD are nursery selections with white flowers and may be more closely related to each other than to the pink-flowered genotype HW.

Suitability of models

The development of the generalized linear models proved a useful approach in fitting diallel data that had a binomial distribution. The progression of models allowed for factors such as the influence of self-pollination (as distinct from outcrosses), the effect of different genotypes and the effect of reciprocal crosses to be added and evaluated in turn. By fitting several models of increasing complexity we were able to determine when the residual deviance ("lack-of-fit") first became insignificant ($P > 0.05$). It is possible to extend the number of models further to allow for any, or all, differences in the diallel cells to be fitted. However, continued extension of the model will lead to a point where data are overfitted. Such overfitted complex models may not be helpful in describing the underlying general trends in breeding behaviour. Thus, the use of the models requires a certain subjective balance between oversimplification of the trends and overfitting of the actual data.

Another shortcoming of the present statistical approach is the need to subjectively decide between the model pathways 1a/2a and 1b/2b. This decision depends on whether the bulk of the outcrosses are considered to result in a common outcome or in discrete and varied results. Fruit set for outcross pollinations where no reciprocal effects are evident, varies from 0.3 to 0.81 (Table 3) for *P. pandorana* and 0.24 to 0.69 for *P. jasminoides*, making pathway 1b/2b the appropriate pathway for the data presented here. No statistical basis for this choice has been devised here. Moreover, no statistical method to compare models across these two pathways was developed.

Despite the constraints mentioned, the present approach allowed an adequate description of the breeding behaviour of *P. pandorana* and *P. jasminoides*. However, improvements on the model approach used here are warranted. In particular, a statistically based algorithm that allows comparisons between and within paired diallel cells and addresses the concerns of overfitting data will be needed if this approach is to be widely adopted as an analytical tool.

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