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Robert I. Bertin

*College of the Holy Cross*, [rbertin@holycross.edu](mailto:rbertin@holycross.edu)

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NONRANDOM FRUIT PRODUCTION IN *CAMPSIS RADICANS*:  
BETWEEN-YEAR CONSISTENCY AND EFFECTS  
OF PRIOR POLLINATION

ROBERT I. BERTIN

Department of Biology, College of the Holy Cross, Worcester, Massachusetts 01610

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Production of fruits on plants that receive pollen from several pollen parents is sometimes nonrandom with respect to donor (Bertin 1982*b*; Levin 1983; Bookman 1984). This fact has potentially important consequences for the evaluation of mating structure (Levin 1983) and sexual selection (Willson and Burley 1983) in plant populations. Before its significance can be adequately evaluated, however, it is important that the constancy of such nonrandom production of fruits be assessed. In particular, it would be useful to document the within- and between-year stability of these patterns and the extent to which they can be influenced by environmental factors.

An examination of the patterns of fruit maturation following hand pollination within a season is also of interest because such patterns provide insight into the factors limiting fruit production. In particular, the distinction between pollen limitation and resource limitation of fruit production is considered important in the evolutionary interpretation of many aspects of plant reproductive biology (Charnov 1979; Willson 1979; Bierzychudek 1981; Willson and Burley 1983). Previous work with *Campsis radicans* suggested seasonal shifts in the patterns of fruit production that obscured the distinction between pollen and resource limitation of fruit production, though the lack of an experimental approach prevented my distinguishing the effects of resource availability (as influenced by prior pollinations) and date (Bertin 1982*b*).

The goals of this study were to determine (1) the between-year stability in patterns of fruit production with respect to pollen donor, and (2) whether the extent of prior pollinations in an inflorescence or on a plant influences the patterns of fruit production with respect to pollen donor. The subject was *Campsis radicans* (L.) Seem. (Bignoniaceae), a self-incompatible climbing woody plant of the southeastern United States, whose floral biology has been described (Bertin 1982*a*). Individuals of this species are nonrandom in their production of fruit with respect to pollen donor (Bertin 1982*b*).

## STUDY SITE AND METHODS

Fieldwork was conducted at Trelease Prairie, 8 km northeast of Urbana, Illinois. All plants were growing along a fence separating a managed prairie from a field cultivated in corn/soybean rotation.

All pollinations were made by hand on flowers from inflorescences bagged with nylon netting. Pollen was collected from newly dehisced anthers, and pollinations were made 0–10 h after collection. The time after collection had no significant effect on pollen effectiveness (unpubl. data).

*Between-year variability.*—In 1982, flowers on two sets of plants were pollinated with pollen from several donors. Plants 1–10 each received pollen from 10 different donors, and plants 21, 22, 25, and 26 received pollen from 8 different donors. Each flower received pollen from a single donor selected from the donor group in random fashion, stratified according to date. For example, the first 10 flowers to open on plant 1 received pollen from the 10 donors in random order, the second 10 flowers received pollen from the same 10 donors, also in random order, etc. This was repeated as many times as possible over the blooming season. Flowers were marked individually with paper tags, and the plants were revisited in mid-August to score fruit production.

In 1983 the same two sets of plants were used for further pollinations. Plants 21, 22, 25, and 26 received pollen from the same 8 donors. Because plants 1–10 were also needed for another experiment, the pollination procedure was modified. Only 4 of the 10 original donors were used for each plant (#1–10 above). For each recipient, the 1982 donors were ranked from most to least successful in fruit production. The two least successful were dropped. The remaining eight were divided into four consecutive pairs (with respect to success in fruit siring), and one member of each pair was chosen randomly as a pollen donor. This procedure ensured inclusion in 1983 of donors representing a wide range of paternal success. Although this reduction in number of donors is undesirable, the results from these plants are consistent with those from plants 21–26 and similar to those obtained in 1982. Such consistency in spite of the modified pollination procedure helps document the year-to-year repeatability of the results.

*Prior pollinations.*—Three approaches were used. First, on plants pollinated throughout the season, the parentage of the first and second halves of the fruit crop of each plant was compared. Pollinations giving rise to the first and second halves of the fruit crop are preceded by few and many pollinations, respectively. Thus, differences in parentage between the first and second halves could reflect prior pollination history (though they might also reflect a correlated factor, such as date). Second, inflorescences on the same plant received different initial treatments: pollination or no pollination, followed by several test pollinations. Parentage of fruits resulting from test pollinations was compared between treatments. Third, whole plants received either pollination or no pollination treatments early in the season, followed by several test pollinations. The parentage of fruits resulting from test pollinations was compared between groups.

The first approach used three sets of plants and was carried out in 1982. These sets contained 10 (#1–10), 8 (#21–28), and 5 (#11–15) individuals, and received

pollen from 10, 8, and 16 donors, respectively. (These numbers were determined by other uses of these data; their variation does not detract from the present design.) Each flower received pollen from a single donor, and donors were selected in stratified random fashion, as described above. Fruit production was monitored in August. The fruit crop of each plant was divided into equal early and late halves according to the date of pollination, and the number of pollen donors contributing to each half was compared.

Second, on each of eight plants (#21–28) 8–14 inflorescences were selected in 1982, and each inflorescence was randomly assigned to one of two groups. All flowers in group-A inflorescences were pollinated as their stigmas became receptive, with pollen from one of eight donors, selected in stratified random fashion. No flowers in group-B inflorescences were pollinated until near the end of the blooming period (when the ratio of dropped flowers to buds was more than 2:1). Thus the group-A inflorescences had many prior pollinations and developing fruits by the time the last pollinations were made; the group-B inflorescences had none. Selectivity following pollinations of the group-B flowers was compared with selectivity in a similar number of group-A flowers at the end of the pollination sequence.

Plants 21–28 were also used to evaluate changes in selectivity on a whole-plant basis. The 1982 pollinations of group-A inflorescences indicated the expected patterns of selectivity on plants that received pollinations throughout the blooming season. In 1983 these plants were randomly assigned to two groups of four. Group-A plants were pollinated throughout the year, as in 1982. Group-B plants received no pollinations until the end of the blooming period. The selectivity in fruit production following these pollinations was then compared with that following a similar number of pollinations at the end of the 1982 season. The group-A plants served as between-year controls.

#### RESULTS

*Between-year variability.*—Selectivity in fruit production with respect to pollen donor was consistent between years. Correlation coefficients between donor acceptability in the years 1982 and 1983 were above 0.82 for 11 of 12 recipient plants (tables 1, 2).

*Effect of prior pollinations.*—Hand-pollinated plants accepted pollen from fewer donors for the second halves of their fruit crops than for the first halves (table 3). The pollen donors for each recipient plant can be placed into two groups, favored and nonfavored, according to whether they give rise to more or less fruit production than the mean. In such a classification the pollen of the nonfavored donors becomes less acceptable (by a factor of 2) between the first and second halves of the fruit crop (table 4).

Similar results were obtained on plants whose inflorescences were divided into groups with and without prior pollination. The number of donors whose pollen was accepted for the fruit crop was lower in inflorescences that had received prior pollinations and in which fruits were already developing than in those inflores-

TABLE 1

PROPORTION OF POLLINATIONS FROM EIGHT DONORS CAUSING FRUIT PRODUCTION IN 1982 AND 1983

PLANT #		POLLEN DONOR								<i>N</i> *	<i>r</i>	<i>r</i> <sub>1</sub> †
		21	22	23	24	25	26	27	28			
21	1982	.00	.65	.10	.15	.00	.10	.70	.20	20	.96	.96
	1983	.00	.81	.15	.19	.19	.15	.69	.19	26		
22	1982	.73	.00	.09	.27	.45	.36	.00	.55	11	.88	.85
	1983	.75	.00	.20	.25	.15	.20	.00	.65	20		
25	1982	.00	.00	.69	.00	.00	.00	.00	.62	13	.83	.82
	1983	.23	.08	.38	.23	.00	.00	.00	.69	13		
26	1982	.46	.23	.23	.62	.38	.00	.38	.69	13	.91	.90
	1983	.39	.09	.17	.87	.52	.00	.22	.70	23		

\**N*, the number of flowers pollinated using pollen from each donor.†*r*<sub>1</sub> excludes self-pollinations.

TABLE 2

PROPORTION OF POLLINATIONS FROM FOUR DONORS CAUSING FRUIT PRODUCTION IN 1982 AND 1983

PLANT #	POLLEN DONOR*										<i>r</i>
	A		B		C		D		<i>N</i> †		
	'82	'83	'82	'83	'82	'83	'82	'83	'82	'83	
1	.55	.49	.05	.14	.15	.16	.45	.49	20	51	.98
2	.00	.00	.40	.11	.00	.02	.60	.68	10	63	.86
3	.30	.28	.35	.28	.45	.30	.30	.20	20	54	.64
5	.10	.11	.55	.48	.60	.53	.10	.19	20	75	.99
6	.88	.52	.62	.45	.69	.42	.25	.11	16	66	.97
8	.05	.28	.25	.29	.75	.64	.35	.32	20	69	.94
9	.77	.52	.45	.48	.05	.03	.77	.51	22	69	.93
10	.58	.30	.88	.75	.25	.19	.46	.26	24	69	.93

\*Donors A, B, C, and D were the same in 1982 and 1983 but differed among recipient plants.

†*N*, the number of flowers pollinated using pollen from each donor.

cences that had received no prior pollinations (table 5). The acceptability of pollen from nonfavored donors was much lower in inflorescences that had received prior pollinations than in those that had not (table 5).

In the four (group-B) plants whose early-season flowers were not pollinated in 1983, selectivity in fruit production was less than for the same plants in 1982 (33% more donors accepted), although the difference was not significant (paired-comparisons tests,  $P = .11$ ; table 6). Control (group-A) plants also became less selective (19% more donors accepted), although this change was also not significant ( $P = .25$ ; table 6). Both experimental and control plants matured more fruits sired by nonfavored donors in 1983 than in 1982, though the differences were not significant (table 6).

TABLE 3  
 NUMBER OF POLLEN DONORS SIRING AT LEAST ONE FRUIT IN FIRST (1) AND LAST (2)  
 HALVES OF FRUIT CROPS OF 23 PLANTS

PLANT #	CROP HALF		PLANT #	CROP HALF		PLANT #	CROP HALF	
	1	2		1	2		1	2
1	8	4	11	12	14	21	5	4
2	3	3	12	11	9	22	6	5
3	9	8	13	16	14	23	5	5
4	8	6	14	11	6	24	6	5
5	8	5	15	16	14	25	2	2
6	9	8				26	7	6
7	8	8				27	5	3
8	8	7				28	4	4
9	7	7						
10	8	8						
Mean	7.6	* 6.4		13.2	11.4		5.0	* 4.2

NOTE.—Crop halves determined by dividing a plant's fruit crop into equal early and late halves based on date of pollination.

\*Significant difference in paired-comparisons test.

TABLE 4  
 PERCENT CONTRIBUTION OF NONFAVORED POLLEN DONORS TO FIRST (1) AND LAST (2)  
 HALVES OF FRUIT CROPS OF 23 PLANTS

PLANT #	CROP HALF		PLANT #	CROP HALF		PLANT #	CROP HALF	
	1	2		1	2		1	2
1	26	0	11	12	20	21	37	21
2	0	0	12	16	5	22	23	8
3	43	43	13	49	22	23	54	23
4	57	16	14	44	6	24	43	29
5	46	8	15	56	22	25	0	0
6	28	8				26	47	32
7	57	35				27	30	0
8	47	25				28	0	0
9	16	11						
10	45	28						
Mean	37	* 18		35	* 15		29	* 14

\*Significant difference in paired-comparisons test, based on arcsin square-root transformation of data.

#### DISCUSSION

*Between-year variability.*—Patterns of fruit production with respect to pollen donor were similar between years despite slight differences in the pollination regimens. This is significant because previous demonstrations of nonrandom fruit production in natural populations (e.g., Bertin 1982*b*; Bookman 1984) were each based on one year of data, and therefore the patterns found could simply have reflected environmental events specific to that year. Although this study does not

TABLE 5

EFFECT OF PRIOR POLLINATION IN AN INFLORESCENCE ON PATTERNS OF FRUIT PRODUCTION

PLANT #	NO. OF DONORS ACCEPTED		N†	CONTRIBUTION OF NONFAVORED DONORS (%)*	
	With Prior Pollination	No Prior Pollination		With Prior Pollination	No Prior Pollination
21	4	6	14	14	57
22	3	6	10	0	20
23	1	4	4	0	25
24	5	6	10	30	70
25	2	4	4	0	50
26	6	6	11	36	36
27	1	1	1	0	100
28	4	4	10	0	0
Average	3.2	‡ 4.6		10	‡ 45

\*Which donors were favored and which were not was determined on the basis of all pollinations on group-A inflorescences. Comparisons were based on arcsin square-root transformation of data.

†N, the number of fruits in each treatment.

‡Significant difference in paired-comparisons test.

TABLE 6

COMPARISONS OF SELECTIVITY IN FRUIT PRODUCTION ON PLANTS THAT HAVE AND HAVE NOT RECEIVED PRIOR POLLINATION

PLANT #	NO. OF DONORS ACCEPTED		CONTRIBUTION OF NONFAVORED DONORS (%)*		N†
	1982	1983	1982	1983	
Group A (with prior pollinations)					
21	6	7	29	50	38
22	6	6	15	26	27
25	2	5	0	35	17
26	7	7	41	38	39
Mean	5.2	6.2	21	37	
Group B (no prior pollinations)					
23	4	7	17	58	12
24	6	7	32	50	22
27	4	6	12	44	16
28	4	4	0	0	8
Mean	4.5	6.0	15	38	

\*Comparisons based on arcsin square-root transformation of data. No differences were significant at the 5% level.

†N, the number of fruits in each treatment.

eliminate longer-term environmental effects, it does suggest a genetic determination of the crossing patterns, as observed in various cultivated species (e.g., Gutierrez and Sprague 1959; Crowe 1971; Dane and Melton 1973).

In a few species the variation in the success of different crosses has been attributed to the degree of genetic relatedness between parents (Price and Waser 1979; Levin 1984; Schemske and Pautler 1984). Genetic relatedness was not quantified, but it was thought to be inversely correlated with the physical distance between parents, as a result of restricted seed dispersal. In the Trelease *Campsis* population there was no relationship between crossing success and interplant distance ( $r = .00, -.06, -.09$  for three sets of plants with 9, 10, and 8 individuals, respectively). Maximum interplant distances were 190 m. This lack of significant correlation is not surprising because *Campsis* seeds are dispersed by the wind and therefore probably move much larger distances than *Phlox* or *Delphinium* seeds. Lee and Bazzaz (1982) and Bawa and Webb (1984) also found no significant effect of interparent distance on the fecundity of *Cassia fasciculata* and *Tabebuia rosea*, respectively.

The between-year consistency in the patterns of parentage demonstrated in *Campsis* suggests that the mating structure of the *Campsis* population is highly nonrandom and that natural selection acts strongly during the gametophytic generation (e.g., Mulcahy 1979) or shortly after zygote formation. If the basis for such selectivity is genetic relatedness between parents, such selectivity has much importance for ecological and evolutionary genetics (e.g., Levin 1983). In particular, if crosses between distantly related individuals are most successful, then inbreeding is reduced and the levels of heterozygosity and inter-individual variability will be greater than expected under models of random mating. Neighborhood size may increase, or more fundamentally, the neighborhood concept may have to be modified to reflect the absence of random mating in the population. Finally, local differentiation of populations would be less than with random mating as a result of reduced inbreeding.

*Selectivity and past pollinations.*—Comparisons of the paternity of the first and second halves of *Campsis* fruit crops, and the experimental comparisons of group-A and group-B inflorescences, show that prior pollination history (probably influencing fruit initiation and, therefore, resource availability in the inflorescence) affects pollen and/or zygote acceptability. Comparisons of fruit production between whole plants subjected to different treatments produced results consistent with the above interpretation, though differences were not significant.

The observed patterns of fruit production may reflect several factors including pollen-pistil compatibility, levels of fertilization, and seed abortion. Pollen-pistil compatibility can be at most a partial explanation because of the occurrence of pistil/fruit abortion at a wide range of developmental stages, some of which involved fruits at half or more of their mature size.

These results pertain to the ideas of selectivity and female choice in plants (e.g., Janzen 1977; Stephenson and Bertin 1983; Willson and Burley 1983), ideas that imply maternal influences on which paternal genomes are represented in the seed crop. These results indicate a non-male component to the interaction between pistil and either pollen or zygote. This is shown by the different behavior, with



respect to pollen from a single flower, of pistils in flowers of similar age blooming simultaneously in nearby inflorescences on the same plant. This eliminates the pollen per se as the cause of the observed patterns of fruit production; but it does not greatly clarify the maternal role, which might be passive, involving a regulation of the availability of resources for which young fruits and/or zygotes compete, or active (for some possible mechanisms, see Willson and Burley 1983).

If we assume the more passive maternal role (as did Bookman 1984), the following model is consistent with the results of this and a previous study (Bertin 1982*b*). I assume that fruit abscission is hormonally mediated and that more than some threshold level of hormone must be produced to prevent abscission. The threshold level depends at least partly on the resource status of an inflorescence, which would be determined by such factors as the amount of photosynthesis in leaves near the inflorescence and the number of fruits already developing in that inflorescence. The hormone could be produced by pollen grains, growing pollen tubes, zygotes, a combination of these, or gynoeical tissues responding to their presence. The quantity of hormone produced is determined by the number of pollen grains, pollen tubes, and/or zygotes and by their quality (e.g., genetic congruity, compatibility, heterosis). This model accounts for the observed patterns of fruit production in *Campsis* and may well be applicable to other plants. Essential features of the model are that the thresholds for fruit production vary in space and time and that hormone production is influenced by the quality (as well as quantity) of gametes or zygotes. The former feature accounts for the observed spatial and temporal differences in response to pollination; the latter accounts for nonrandomness of fruit production with respect to paternity. Westoby and Rice (1982) and Willson and Burley (1983) provided detailed discussions of some mechanisms potentially relevant to this model.

*Limitation of female reproductive success.*—Determining the factors limiting fruit production is of theoretical interest because attempts to explain patterns of resource allocation or reproductive adaptations often assume that fruit production is limited by pollen availability or by resources such as energy and mineral nutrients (e.g., Bierzychudek 1981; Stephenson and Bertin 1983; Willson and Burley 1983). For example, sexual-selection explanations of reproductive behavior assume that the reproductive success of one sex (usually females) is limited by resources (Willson 1979; Willson and Burley 1983).

The current results support a previous suggestion (Bertin 1982*b*) that pollen and resource availability interact in determining whether a particular ovary yields a fruit. This is shown by how dependent on the resource status of an inflorescence is the success of pollinations using pollen from particular donors. The fewer the number of resources committed to fruit production, the greater the variety of pollen donors that is effective at siring fruit. Therefore, in a particular inflorescence the production of a fruit is determined both by resource availability and by paternity.

This finding supports the notion that both resources and pollen can determine fruit production (Wyatt 1981; Willson and Burley 1983; McDade and Davidar 1984; Stephenson, pers. comm.). It may sometimes be inappropriate to specify only one of these as the factor limiting fruit production, unless we know both how

levels of fruit production in one year affect fruit production in subsequent years and how fruit production on one part of a plant affects fruit production elsewhere on the plant (Janzen et al. 1980; Willson and Burley 1983; Bawa and Webb 1984). Only in the (perhaps exceptional) case in which stigmatic pollen loads are consistently below the minimum ever needed for fruit production could one confidently conclude that fruit production is limited by pollen availability.

The practical consequences of this result are at least threefold. First, the amount of pollen, even nonself pollen, on a stigma may not be a good indicator of pollination adequacy (Shore and Barrett 1984) unless it is below the minimum ever needed for fruit production, and therefore clearly inadequate. Second, assessing pollinator limitation of reproduction by comparing fruit production following hand pollination with that following natural pollination must be done in a carefully controlled manner. Pollen from several individuals in the population should be used to increase the likelihood of including some superior pollen donors; and it may be necessary to monitor entire plants for several years to ensure that an increase in fruit production following hand pollination is not achieved at the expense of decreased flower or fruit production in other years or on other parts of the plant. Finally, statements in the literature about whether pollen or resources limit fruit production should be examined critically in light of the above information, as Bawa and Webb (1984) have emphasized.

#### SUMMARY

The tendency in *Campsis radicans* for fruits to be produced from certain crosses was consistent between years. This increases the likelihood that observed patterns are genetically based. Early in a season, plants were more selective about which donor they accepted pollen from, as measured by the parentage of mature fruits. Field experiments indicated that this increase in selectivity was related not to date, but to the number of prior pollinations and developing fruits in an inflorescence, and therefore presumably to the availability of resources. These differences in fruiting indicate a non-male component to selectivity (since pollen source was controlled). That the acceptability of pollen from particular donors depends on the resource status of the inflorescence means that the distinction between pollen limitation and resource limitation of fruit production is not a sharp one. A model is proposed to account for patterns of fruit production with respect to paternity in *Campsis radicans*.

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