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High Pollen Loads Can Cause Pistillate Flower Abscission in Walnut

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Abstract. **The role of pollen in abscission of pistillate flowers of Persian walnut (*Juglans regia* L.) cv. Serr was investigated over a 4-year period by controlled pollinations and pollen counts. Self-pollen, pollen from other walnut selections or cultivars, or dead pollen was applied at high and low doses to pistillate flowers enclosed in pollination bags. Unbagged, open-pollinated flowers and bagged, nonpollinated flowers served as controls. In all cases, presence of pollen significantly increased the probability of pistillate flower abscission (PFA). Dead pollen resulted in as much PFA as live pollen. Counts of pollen grains confirmed that PFA-type flowers had significantly more pollen than normal flowers. In the fourth year 'Serr' pollen was applied to unbagged flowers of 'Serr' and ten other Persian walnut cultivars, and the amount of PFA on the artificially pollinated flowers was significantly higher than on the open-pollinated flowers, while the control flowers dusted with talc or pine pollen had almost no PFA. These results clearly indicate that excess pollen is involved in pistillate flower abscission in 'Serr' walnut and suggests that other cultivars may also be sensitive to pollen load. This phenomenon may have implications in the biology of selfing and evolution.**

Juglans regia L. (Persian or English Walnut) is a monoecious, wind-pollinated species. The trees produce pistillate inflorescences of one to three flowers borne terminally on long shoots or lateral spurs, and staminate inflorescences (catkins), which are borne laterally on 1-year-old branches. The catkins are composed of many flowers and produce up to 4 million pollen grains per inflorescence (Westwood, 1993). The species has a heterodichogamous bloom habit: Individuals may be protandrous (staminate bloom begins before pistillate bloom) or protogynous (pistillate bloom begins before staminate bloom). This bloom habit encourages outcrossing but does not completely eliminate the possibility of self-fertilization because the temporal separation of male and female flowering is rarely complete. The extent of overlap between staminate and pistillate bloom varies considerably between cultivars and from year to year (Hendricks et al., 1985).

Commercial walnut production is based on clonally propagated cultivars grafted to seedling rootstocks. In California, where 99% of the commercial walnut crop of the United States is produced, pistillate flower abscission (PFA) has emerged as a serious non-pathogenic problem of some walnut cultivars (Catlin et al., 1987). PFA is characterized by cessation of pistillate flower growth when the ovary is ≈3 to 4 mm in diameter followed by flower abscission 1 to 2 weeks later (Catlin et al., 1987). Near the time of abscission, PFA-type flowers show signs of necrosis at the tips of the stigma, in the integument, and throughout the placental evaginations (Catlin and Polito, 1989). Flower abscission due to PFA is clearly distinguishable from abscission that results from lack of fertilization. Unfertilized flowers usually expand to ≥7 mm in diameter and remain attached for 3 weeks or longer (Polito, 1985). 'Serr', which can have flower losses due to PFA >90%, appears to be the most susceptible cultivar, but other cultivars are also affected, usually to a lesser extent (Catlin et al., 1987; Catlin and Olsson, 1990). Pistillate flower abscission has been investigated since it was first observed in 1978, but results have been limited and no definite causal factor(s) has been identified. Low nitrogen levels, competition for carbohydrates (Deng et al., 1991; Ryugo, 1982), and excessive shading (Ryugo, 1986; Ryugo et al., 1985) have been postulated as possible causes of PFA. However, several years of field measurements on 'Serr' and other cultivars failed to establish any connection between PFA and environmental or cultural factors, including competition between various parts of the plant, age, pruning system, shading, alternate bearing, or pests and diseases (Catlin and Ramos, 1985; Catlin et al., 1987).

McGranahan and Hansen (unpublished) observed flower abscission similar to PFA during controlled pollinations in the course of walnut breeding in 1987. On certain female parents there was more abscission in bags with pollinated flowers than in bags with unpollinated flowers when the bags were removed 2 weeks after pollination. This led to a preliminary study in 1988 in which 40 pollination bags were placed over 133 fruitful spurs of 'Serr' before anthesis. At peak pistil receptivity, 'Serr' pollen (≈1 cm^3/bag) was injected into half of the bags. Flower abscission was recorded 2 weeks later. Pistillate flower abscission occurred at a higher frequency in flowers in pollinated bags (44%) than in unpollinated bags (5%), but PFA was highest (83%) on open-pollinated flowers (G. McGranahan and P. B. Catlin, unpublished).

Others have reported that excessively high pollen loads may lead to flower abscission in *J. regia* (Kavetskaya and Tokar, 1963; Por and Por, 1990; Szentivanyi, 1990) and *J. nigra* L. (Beineke and Masters, 1976). Romberg and Smith (1950) noted that high, single doses of pollen can reduce seed set in pecan, another species in the Juglandaceae. However, because the specific type of abscission was not described for these cases, it is not clear whether these phenomena are similar to PFA. Young and Young (1992) surveyed literature on the effect of pollen load on reproductive success. They analyzed published data from 99 experiments in which hand-pollination was compared to natural, insect-mediated pollination, and concluded that in 17 cases female reproductive success (determined by either numbers of fruits or numbers of seeds) was significantly reduced after hand-pollination. They proposed several possible mechanisms for this reduced fruit/seed production, including a direct effect of high pollen loads as well as possible experimental artifacts.

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We conducted the following experiments to evaluate the hypothesis that exposure to excessive pollen levels can cause pistillate flower abscission in *Juglans regia*, and our results indicate that this mechanism has the potential for causing the PFA problem observed in commercial orchards.

Materials and Methods

Flower isolation. These experiments were conducted on four 18- to 21-year-old 'Serr' trees growing in a walnut cultivar collection at the University of California, Davis. In the first year, three 17-year-old 'Chico' trees in close proximity were also used. 'Serr' and 'Chico' were used because they have had exceptionally high and moderate levels of PFA, respectively, over several years (Catlin et al., 1987). Before stigma receptivity, randomly selected individual branches bearing one or more flowering spurs, each with one to three pistillate flowers, were enclosed in white, non-woven, fiber bags (22.5 × 45.5 cm) with a plastic window on one side (PBS International, Scarborough). Nonabsorbent cotton was wrapped around the branch at the point of bag attachment. To ensure against contamination by self-pollen, all catkins and lateral unexpanded buds were removed from the portion of the branch that was inserted into the bag. Between 30 and 50 bags were used per treatment.

Pollen collection. 'Serr' pollen was used every year. In the first year (1990), O-20-1072 (a selection introduced from Iran and unrelated to 'Serr' and 'Chico') was also used. In the second year 'Tehama' pollen was used instead of O-20-1072 because it is the most common pollinizer in commercial plantings of 'Serr'. In the third year, the effect of live and dead 'Serr' pollen was compared on 'Serr' flowers. To obtain pollen, well-developed, healthy catkins, which had just started to shed pollen from their apical florets, were collected and spread on wire screens over butcher paper in the laboratory. After 24 h the pollen was collected from the paper, sieved, and stored over a saturated magnesium chloride solution at –20C until used (Luza and Polito, 1985). Dead pollen was obtained by exposing stored pollen to microwave radiation (1500-W microwave oven) for 2 min.

Controlled pollinations. Pistillate flowers inside the bags were pollinated at the stage of maximum receptivity, i.e., when the majority of stigmas were well expanded and their two lobes were visibly separated at an angle of ≈45° (Forde, 1975; Forde and Griggs, 1975). Bags received pollen at one of two levels (≈50 mg/bag and 800 mg/bag). Pollen was injected into the bag with a 12-cm^3 syringe bearing a 25- or 19-gauge needle for the two pollen levels, respectively. One injection with the 25-gauge needle averaged 51.2 mg pollen (SE = 6.6) in preliminary tests, whereas one injection with the 19-gauge needle averaged 198.5 mg pollen (SE = 9.2). Thus, four injections were used to obtain ≈800 mg pollen per bag for the high pollen load. The points of the needles were bent slightly to facilitate dispersion of the pollen inside the bag. An equal number of bagged branches were left unpollinated as controls, and a similar set of unbagged flowers on each tree was tagged for monitoring natural PFA of open-pollinated flowers.

Observations and assessment of PFA. The bags were removed 14 to 18 DAP. By this time growth of many of the open-pollinated flowers had stopped, and observations indicated that abscission was imminent. The total number of pistillate flowers, and the number of pistillate flowers showing PFA characteristics, either still attached to the spur, ready to drop, or already abscised and inside the bag, were recorded.

Statistical analysis. Analysis of variance (ANOVA) was performed on transformed (arcsin $\sqrt{}$ (%) abscission data using the Statistical Analysis System (SAS) and differences among means were tested with the Duncan's multiple range test.

Pistil sampling and pollen grain counts. In the first year open-pollinated flowers at maximum receptivity on both 'Serr' and 'Chico' were tagged. Ten and 12 days later, samples of PFA-type pistils (i.e., those that had stopped growing at 3 to 4 mm in ovary diameter) and normally developing pistils were collected, fixed in FAA, and their diameters were measured. In the second year, samples were collected from the bagged flowers in each pollination treatment as well.

Stigma squashes were prepared according to Martin (1958). Germinated and ungerminated pollen grains on each stigma were counted under ultraviolet light in a Leitz Diaplan microscope equipped with an incident light luminescence illuminator.

Other cultivars. To determine if other walnut cultivars are sensitive to excess pollen, 'Serr' pollen was applied with a paintbrush (#6) to 100 unbagged flowers of 'Serr' and ten other walnut cultivars at peak receptivity. Treated stigmas appeared yellow with pollen. An equal number of untreated flowers were tagged as normal controls and 100 'Serr' flowers were dusted with either talc or pine pollen (*Pinus eldarica* Medw.) as treated controls. Two weeks later, the number of abscised flowers was recorded.

Results

Effects of controlled pollinations on PFA. In both 'Serr' and 'Chico' , PFA was highest in unbagged, open-pollinated flowers (Table 1). In 'Serr', the next highest PFA occurred in bagged flowers exposed to the heavy pollen load, and there was significantly less PFA in flowers exposed to the light pollen load or to no pollen. The source of pollen did not influence PFA significantly. A similar trend occurred in 'Chico', but differences could be detected only between the light and heavy O-20-1072 pollen applications.

Data from the second year (Table 2) differed in that the open-pollinated flowers of 'Serr' had a low percent PFA (33%) compared to the previous year (93%). No differences could be detected between the high and low pollen loads, but the unpollinated control had no PFA. There was a significant difference in

Table 1. Percent pistillate flower abscission (PFA) of 'Serr' and 'Chico' in 1990 after pollination with pollen from two sources, at two levels.

	% PFA (SE)[z]	
Pollination treatment	'Serr'	'Chico'
Open pollination	93 (7.4) a	33 (6.2) a
High pollen load (800 mg/bag)		
'Serr'	48 (10.8) b	19 (6.6) bc
O-20-1072	64 (12.7) b	20 (8.6) b
Low pollen load (50 mg/bag)		
'Serr'	16 (4.4) c	11 (5.2) bc
O-20-1072	15 (8.7) c	6 (2.0) c
Unpollinated (bagged controls)	3(1.9) c	12 (8.8) bc
Source of variation in % PFA[y]		
Bag effect	**	*
Pollination effect	**	NS
Pollen source effect	NS	NS
Pollen load effect	**	NS
Source × load effect	NS	NS

[z]Mean separation within columns by Duncan's multiple range test, $\alpha \leq 0.05$.
[y]See Table 2 for source explanation.
NS,*,**Nonsignificant or significant at $P = 0.05$ and 0.01, respectively.

Table 2. Percent pistillate flower abscission (PFA) in 1991 of 'Serr' and pollen grain counts after pollination with pollen from two sources, at two levels.

Pollination treatment	% PFA (SE)[z]	Pollen grains/flower (SE)	
		PFA-type	Normal
Open pollination	33 (4.2) c	233 (13)	130 (6)
High pollen load (800 mg/bag)			
'Serr'	78 (4.2) a	3649 (268)	2291 (505)
'Tehama'	52 (6.8) b	3557 (116)	1253 (169)
Low pollen load (50 mg/bag)			
'Serr'	88 (4.4) a	3410 (354)	667 (265)
'Tehama'	35 (6.1) c	2924 (198)	1295 (324)
Unpollinated (bagged controls)	0 (0.3) d	---	---
Source of variation in % PFA			
Bag effect (open pollinated vs. bagged and pollinated)			**
Pollination effect (bagged and pollinated vs. bagged and not pollinated)			**
Pollen source effect (Serr vs. Tehama pollen)			**
Pollen load effect (high vs. low pollen load)			NS
Source × load effect			*

[z]Mean separation within columns by Duncan's multiple range test, $\alpha \leq 0.05$.
[NS,*,**]Nonsignificant or significant at $P = 0.05$ and 0.01, respectively.

Table 3. Percent pistillate flower abscission (PFA) in 1992 on 'Serr' pollinated with live and dead 'Serr' pollen at two levels.

Pollination treatment	% PFA (se)[z]
Open pollination	88 (2.3) a
High pollen load (800 mg/bag)	
Live	25 (5.5) b
Dead	23 (5.1) bc
Low pollen load (50 mg/bag)	
Live	12 (4.2) bcd
Dead	8 (3.6) cd
Unpollinated (bagged controls)	0 (0) d
Source of variation in % PFA	
Bag effect (open pollinated vs. bagged and pollinated)	**
Pollination effect (bagged and pollinated vs. bagged and not pollinated)	**
Pollen source effect (live vs. dead pollen)	NS
Pollen load effect (high vs. low)	**
Source × load effect	NS

[z]Mean separation within columns by Duncan's multiple range test, 0.05.
[NS,*,**]Nonsignificant or significant at $P = 0.05$ and 0.01, respectively.

amount of PFA resulting from pollen source; 'Serr' pollen at both high and low levels resulted in more PFA than did 'Tehama' pollen.

In the third year (Table 3), pistillate flower abscission on open-pollinated flowers was high (86%) again. PFA was lower on bagged flowers, but the high pollen load resulted in significantly more PFA than the low load and unpollinated bagged flowers had no PFA. Pollen viability did not significantly affect PFA.

Pollen counts. Normal and PFA-type pistils were identified based on size and external appearance at time of collection and were measured before storage. In both years there was a significant negative correlation between pistil size and number of pollen grains in 'Serr' ($r = –70$ and –53, respectively). No correlation between number of pollen grains/stigma and size was found for 'Chico' . PFA-type pistils of 'Serr' had significantly more germinated, ungerminated, and total pollen grains/stigma than normal pistils (Tables 2 and 4). The pollen grain numbers averaged 179 and 130 on normal open-pollinated pistils in years 1 and 2, respectively, while the pollen grain number on PFA-type pistils averaged 322 and 233, respectively. With 'Chico', although fewer pollen grains failed to germinate on PFA-type pistils than on normal ones, the total number (germinated plus ungerminated) was significantly higher on the PFA-type pistils.

The number of pollen grains on bagged and pollinated flowers was substantially higher than on open-pollinated flowers (Table 2), but again there was a highly significant, negative correlation between pistil size and number of pollen grains ($r = –36$).

Comparison among other cultivars. In all cultivars tested, PFA was higher in the heavily pollinated flowers than in the open-pollinated flowers (Table 5). Flowers dusted with pine pollen and talc had very low PFA.

Discussion

Pistillate flower abscission was consistently higher in flowers exposed to walnut pollen than in flowers not exposed to pollen. Bagging flowers also affected PFA, but in years 1 and 3 there was less abscission in the bagged and pollinated flowers, while in the second year there was less abscission in the open-pollinated flowers. Pollen source did not significantly influence PFA except in the second year when 'Serr' pollen resulted in more PFA than did 'Tehama' pollen. It is notable that pollen viability did not

Table 4. Mean number of pollen grains/stigma of open-pollinated PFA-type and normal pistils of 'Serr' and 'Chico'.

Cultivar, pistil type and size (mm)	No. of pollen grains (SE)			
	No.	Germinated	Ungerminated	Total
'Serr'				
Normal (4.8–7.9)	15	131 (19)	48 (7)	179 (25)
PFA (2.7–3.5)	60	238 (11)	83 (5)	322 (24)
'Chico'				
Normal (5.2–7.4)	21	207 (20)	75 (5)	282 (22)
PFA (2.9–4.9)	35	353 (32)	42 (3)	395 (32)

Table 5. Pistillate flower abscission of open-pollinated (untreated) and heavily pollinated flowers in Persian walnut cultivars.

Cultivar	% PFA (SE)	
	Open pollinated	Artificially pollinated[z]
Serr	21	99
Payne	46	94
PI 159568	70	100
Sunland	18	88
Vina	15	100
Tulare	14	91
UC 76–80	1	86
Hartley	35	76
Chandler	33	99
Howard	9	92
Franquette	2	78
Mean	24	91

[z]Serr pollen dusted on with paint brush at peak fertility. Control flowers, dusted with talc or *Pinus eldarica* pollen (50 flowers each), had 8% and 4% PFA, respectively.

influence PFA, i.e., killed pollen caused the same amount of PFA as live pollen. Pollen load on the flowers significantly affected PFA in years 1 and 3, with high pollen loads causing more PFA than low pollen loads. These results are consistent with counts of the number of pollen grains per stigma; more pollen was found on stigmas of PFA-type flowers than on normally developing stigmas.

These results agree with observations that high pollen levels are responsible for unsatisfactory nut set in *J. nigra* (Beineke and Masters, 1976) and *J. regia* (Kavetskaya and Tokar, 1963; Por and Por, 1990; Szentivanyi, 1990). Although these earlier reports did not clearly describe the developmental stages at which abscission occurs (Kavetskaya and Tokar, 1963; Szentivanyi, 1990) or included only differences in nut set or yield (Beineke and Masters, 1976, Por and Por, 1990), it appears that a similar phenomenon, flower abscission associated with excess pollen, is occurring in all cases. In addition to these reports of adverse effects of high pollen loads on nut set in *Juglans* spp., Romberg and Smith (1950) noted, without providing supporting data or additional comment, that high, single doses of pollen can result in heavy nutlet drop in pecan (*Carya illinoensis* (Wangenh.) K. Koch), another Juglandaceae. Apparently in *Juglans*, there are at least two distinct periods of abscission of female reproductive organs, both related to pollination. They can be lost soon after anthesis due to excessive pollen (PFA) or later due to a lack of pollen. The abscission of unpollinated flowers occurs after considerable growth of the ovary; in our experiments, for example, pistils in bags without pollen enlarged to more than 10 mm in diameter before abscising.

These results may also explain the reported beneficial effect of catkin removal, either by hand (Ryugo, 1982) or due to frost damage (Por and Por, 1990), which can be attributed to a decrease in the pollen-producing capacity of the tree, and hence to the lower amount of pollen available for pollination, rather than to elimination of competition as previously proposed.

The significant effect of the pollination bags suggests that the environment inside the bag (high relative humidity, no wind, and possibly more gradual and less significant temperature fluctuations) may have played a role in reducing PFA. A drying effect of pollen on corn stigma has been described by Stanley and Kirby (1973). Water deficits in the pistils, created by an imbalance between transpiration and water uptake by the roots (Catlin et al., 1987) may also be implicated. Alternatively, bagged flowers were pollinated when the majority of the flowers were receptive. A portion of the pistils may have been pre- or post-receptive and not exposed to excess pollen at the sensitive development period. In addition, the bagged flowers were only exposed to pollen from selected sources. The open-pollinated flowers were exposed to pollen from other cultivars as well as self-pollen.

Young and Young (1992) reviewed the literature on 99 experiments in which investigators hand-pollinated flowers of insect-pollinated species. They found that in 17 cases the hand-pollinations adversely affected either fruit or seed set. They offer several possible explanations for this phenomenon, several of which are related to activity of the biotic pollinators or experimental conditions that do not apply to our experiments with walnut. Among the points they consider is that at high densities pollen tubes may interfere with each other, thereby reducing fertilization. This would seem not to apply to walnut as unfertilized flowers continue to grow normally, but flowers receiving a heavy dose of pollen show early signs of abortion. In addition, dead pollen was as effective at inducing flower abortion as live pollen. Young and Young also consider the possibility that hand-pollinations using pollen from a single donor may swamp more varied natural pollen diversity, and that this factor may be implicated in the reduced reproductive success. This may apply to the situation in *J. regia*. In our experiments a single pollen source was used: either self-pollen or pollen from a single donor. Also, PFA was first observed in commercial walnut orchards, where one would expect low pollen diversity, typically self-pollen from incomplete dichogamy and non-self-pollen from a single pollinizer cultivar.

Based on the results presented here, we conclude that pistillate flower abscission can be caused by the presence of excess pollen on the stigma. In walnuts the most likely source of excess pollen is self-pollen from male flowers that shed pollen at the beginning (in protandrous genotypes) or end (in protogynous genotypes) of female receptivity. This phenomenon, early sacrifice of the ovum to avoid selfing, has not been reported in other plant genera; however, we suspect that it may be widespread, particularly in plants with energy-rich seeds like walnut, whose only mechanism to avoid selfing is incomplete dichogamy (some dichogamous plants are also self incompatible).

This phenomenon may also have a role in the evolution of dichogamy because trees that have overlapping male and female blooms would be at a reproductive disadvantage, and thus dichogamy would be favored. In forest tree competition, this phenomenon would tend to discourage walnut trees crowded by other walnuts from producing a heavy nut set, instead they could put their energy into vegetative growth. The impact of this phenomenon in orchard yields is clearly important since PFA is the reason for low yield in Serr walnut. In plant breeding it could be responsible for reduced seed set because plant breeders usually do not control the amount of pollen which lands on a stigma in making controlled crosses.

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