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Seasonal pollen flow and progeny diversity in *Amianthium muscaetoxicum*: ecological potential for multiple mating in a self-incompatible, hermaphroditic perennial

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Summary. The ecological potential for multiple mating is high in *Amianthium muscaetoxicum*. The percentage of long-distance pollinations (20–100 m) is greater than reported for most insect-pollinated systems. Estimations of neighborhood area are at least an order of magnitude larger than any previously reported for plant species. Seasonal effects on fluorescent dust dispersal indicate that neighborhood areas change during the flowering season. The number of flowers marked with fluorescent dust on an inflorescence increases with increasing inflorescence size, and the proportions of available inflorescences that are marked decrease with distance from the source. Allozyme analysis indicates that heterozygosity levels are typical of outcrossing plants. The diversity of seed genotypes is increased by increasing the size of the floral display. The present investigation is the first to consider the effects of floral display on seed diversity and adds to existing data indicating that inflorescence size is important to fecundity and/or pollen donation in some systems.

Key words: *Amianthium muscaetoxicum* – Inflorescence size – Pollen flow – Progeny diversity – Seasonal effects

Although the ecological potential for multiple mating has received wide attention for animal species (Emlen and Oring 1977), mating in plants is usually viewed in terms of outcrossing. The focus has not been on the factors determining the variety of mates, but on whether or not the mate is the self (Grant 1958). Whether a plant mates with one other plant, say its nearest neighbor, or whether it mates with many plants at random in the population, the outcome is still outcrossing.

In many instances plants that donate pollen to several recipients and that in turn are fertilized by pollen from two or more donors can have higher fitness than individuals that exchange pollen with only one other plant. The benefits of multiple mating should derive from two main sources. First, the genetic diversity of seed progeny should be enhanced. In a heterogeneous environment or under some conditions of frequency-dependent selection, production of genetically variable progeny should be advantageous (Ellstrand and Antonovics 1985). Second, in a self-incompatible plant, the probability of compatible crosses should increase. For instance, given a population with a single sterility locus with only three sterility alleles (the minimum possible number), a third of all possible crosses among genotypes will be prevented by sterility barriers. Plants that would "sample" the population more than once stand a better chance of hitting a plant that does not carry one of the same sterility alleles.

The ability to exchange pollen among genetically different plants will be controlled by several ecological components: the number of individuals in the population ready to reproduce at the same time, the distance to which available vectors carry pollen, and the seasonal and spatial patterns in the dispersal of pollen. We examine the first of these components in another paper (Palmer et al. manuscript). Here, we estimate the extent of pollen movement to plants at short (<30 m) and long (30–100 m) distances, and we estimate the neighborhood area, i.e. the area unit of random mating (Wright 1969), for two different times in the flowering season. In addition, we examine the effects of floral display and season on the estimated patterns of pollen dispersal: are large racemes pollinated differently from smaller ones, and does the proportion of flowers visited vary with distance and season? Finally, we use isozyme markers to analyze genetic diversity in progeny as it is affected by some of these ecologic factors.

The virtually self-incompatible (Travis 1984) perennial *Amianthium muscaetoxicum* is excellent for the study of spatial and temporal factors affecting pollen flow. It has a bracteate raceme with indeterminate flowering, and at our study site at Mountain Lake Biological Station (elevation 1220 m) in Giles County, Virginia, it displays a great deal of variation in flowering times and in inflorescence sizes. Furthermore, it is abundant and widespread at the site, and it has pollinators representing several orders (Coleoptera, Lepidoptera, Hymenoptera). These details and other aspects of the reproductive biology of the plant are discussed elsewhere (Travis 1984).

Material and methods

Estimation of short- and long-distance pollen dispersal

Tracking of fluorescent dusts was performed in two areas of an 80-m-radius study area. First, a 20-m-radius circle was used to follow short-distance dust dispersal. Second, four wedges that radiated 60 m in each compass direction from the edge of the 20-meter circle were used to investigate long-distance dispersal. Each wedge centered on a transect

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that was divided into 5-m distance intervals, and the area searched increased with distance. This increase was proportional to the increase in the area of a circle at each distance. The area of the wedges represents 17.6% of the total area (outside of the original 20-m-radius circle) of the 80-m-radius large circle. These wedges were used to standardize the area of search among the distance intervals; otherwise long-distance dispersal might have been severely undersearched relative to the intervals closer to the center.

Near the center of the circle, four source plants with inflorescences that had 1/3 to 2/3 of their flowers open were brushed with dusts during the early (25 June–1 July), middle (4–10 July), and late (12–17 July) parts of the 1983 flowering season. Each plant was dusted with one color, red, orange, blue, or green. All flowers on the source plants were dusted daily, and the inflorescence was discarded upon completion of flowering. Dust movement was measured three times in the first week and four times in the second and third weeks; sampling intervals were not the same for each replicate because of variable weather conditions. Dust was detected on recipient plants at night with a hand-held ultraviolet lamp, and discovery of dust on stigma and/or petals of at least one flower was the criterion by which a plant was considered marked.

All plants in the circle and wedges were mapped, and every plant in these areas was examined at each search. Distances from the source plant were determined from the map and are presented in 5-m intervals from the source plants. Because source plants were at various locations near the center of the inner circle, distances searched could exceed 20 m for the short- and 80 m for the long-distance surveys.

Season and color effects on pollen dispersal

We performed G-tests to compare the effects of dust color, season, and their interaction on the number of dispersal events for the short-distance sample. The number of inflorescences in each distance interval could not be estimated for the beginning of the season, because the fraction of all inflorescences that were in flower at that time was not known. Also, because there was only one color per source plant, we could count the number of dust recipients by the number that were marked by each color.

Seasonal dispersal distances

Regression analysis was used to describe the number of inflorescences marked with dust as a function of the distance of dust dispersal in the short- and long-distance surveys.

Axial variance and kurtosis of dust transport data were used to estimate neighborhood areas in middle and late season as was done by Schmitt (1983). Estimates of axial variance (s_p^2) and kurtosis (γ^2) of distances of dispersed dust in middle and late season were based on centered data (Crawford 1984). dust transport distances were not normally distributed, and the neighborhood area A was estimated as: $A=\pi\, r(k_p\, s_p^2+k_s\, s_s^2)/4$, where $k=2^{2a}[\Gamma(2a+1)\,\Gamma(a)/\Gamma(3a)]$ and is estimated from the relationship: $\gamma^2+3=[\Gamma(a)\,\Gamma(5a)/\Gamma(3a)]^2$ (Wright 1969; Beattie and Culver 1979; Schmitt 1983--Γ denotes the gamma function). The value of r, the outcrossing rate, is considered to equal 1 because this plant is predominantly an outcrosser (Travis 1984). The variance of seed dispersial (s_s^2) was considered negligible relative to the variance of pollen dispersal and set equal to zero (Crawford 1984). The seeds of *Amianthium muscaetoxicum* are heavy and do not appear to be dispersed far beyond the length of the fallen plant.

Effects of distance on the proportion of flowers marked

In order to see how the proportion of flowers marked on an inflorescence relates to the distance of dispersal, we regressed the log of the proportion of flowers marked (i.e. log of number marked – log number of flowers open on an inflorescence) on the distance of the inflorescence from the source plant. We used this transformation of the proportion because both numerator (number of flowers marked) and denominator (number of open flowers) are random variables, and the log of the proportion thus becomes a linear combination of two random variables; the interpretation is that of a proportion, but without the troublesome distributional properties of ratios of random variables (cf. Mosimann and James 1979).

Effects of inflorescence size on pollen flow and flowering duration

Inflorescence size may influence pollinator service in several ways. To ascertain whether pollinators visit particular size classes of inflorescences preferentially, we compared the lengths (to the nearest 5 cm) of the 989 inflorescences available in the search area to the lengths of the 116 inflorescences marked by fluorescent dust. We compared these by means of a chi-squared analysis with 7 length categories and used data from the late season when flowering was the most full on inflorescences. Length of inflorescence is strongly correlated with number of flowers in the inflorescence ($r=0.90$, df$=94$, $P=0.0001$). To ascertain whether larger inflorescences, once visited, might obtain more pollinations, we regressed the number of flowers marked on an inflorescence on the size of the inflorescence.

In order to determine how duration of flowering (in days) varied with inflorescence size (number of flowers), we followed the flowering phenologies of 102 inflorescences over calendar time. The relationship between the two variables was evaluated by regression of duration of flowering on size of inflorescence.

Estimation of genetic variability and progeny diversity

To estimate the genetic variability in the population, we conducted starch gel electrophoresis on 70 individuals contained within and in the vicinity of a high-density plot (5×8 m with 3.68 plants/m^2). Leaf tissue was extracted (Soltis et al. 1983), and gels were run anodally in LiOH electrode buffers. The gels were stained for esterase (EST), phosphoglucomutase (PGM), leucine amino peptidase (LAP), and shikimate dehydrogenase (SKDH). Superoxide dismutase (SOD) activity was checked on gels stained for SKDH and PGM. *Amianthium muscaetoxicum* is a diploid, and segregation proceeds according to expectation.

The actual diversity of seed progeny was examined for plants whose inflorescences were categorized according to their time of flowering and size. Early-flowering inflorescences are considered to be those that began flowering before the median date of flowering in the sample of phenologies, whereas late-flowering inflorescences are those that

began flowering on the day after this date or later. Small inflorescences ranged from 45 to 70 mm in length ($x=47.1$ mm, s.d. $=0.62$ mm) and large inflorescences from 80 to 140 mm ($x=107.1$ mm, s.d. $=18.5$ mm).

Among inflorescences in these size and season categories we chose only inflorescences from plants homozygous at each locus in order to control for maternal genotype effects on diversity of the seeds. From each plant we collected 10 seeds from the topmost and ten from the bottommost flowers with seed.

Seed coat tissue was removed from each seed so that only the products of fertilization, i.e. endosperm and embryo tissues, would be tested. The seed extractions (Soltis et al. 1983) were run anodally in LiOH buffer. In order to sample genotype diversity of the progeny, we used SKDH, LAP1, and LAP2 as marker enzymes.

Diversity consists of two components, evenness and richness (Peet 1974). Evenness is the equitability of proportions of seed genotypes, and richness is the number of genotypes. Evenness of the 10 genotypes from each season-size-location category was analyzed as the sum of the squared deviations from the value of perfect evenness. For example, if there are three possible genotypes at a locus, the value of perfect evenness in a collection of individuals is 0.33, and the index is:

$$\sum_{i=1}^{N=3} (\text{dev})^2 = \sum_{i=1}^{N=3} (0.33-f_i)^2$$

where f_i is the proportion of seeds in the ith genotype class. Values of this index inversely proportional in magnitude to evenness. This index is asymptotically normally distributed, and a three-way analysis of variance was used to compare the effects of season, size, and location upon it. Richness of genotypes is measured as the number of genotypes for each season-size-locality category. These data were analyzed with a log linear fit to a three-way contingency table (Bishop et al. 1975).

Results

Season and color effects on pollen dispersal

In the short-distance sample, the time of the flowering season has a significant effect on the number of dispersal events (Table 1). Fluorescent dusts were dispersed more frequently in the late part of the flowering season ($n=86$ events) than in the middle part ($n=44$ events). This greater dust movement in the late season also occurred in the long-distance samples (Table 2). In addition, there was a statistically significant difference in the effects of different fluorescent colors on pollinator activity (Table 1). Blue and especially green dusts were either distributed, transferred from pollinators' bodies, or detected less often than the other colors. Season and color effects did not interact.

Each source plant dispersed its colored dust to many different individuals (range 3 to 28).

Seasonal dispersal distances

Dust flow was detected in all distance intervals of the short-distance sample and in 11 out of 17 intervals in the long-distance sample, including the farthest distance interval sampled, 95–100 m away from the source plants (Table 2).

In the short-distance samples, the number of dispersal events decreased with distance. The regressions of number of dispersal events on distance were similar for middle season and late season (slopes of -0.041 and -0.043 respectively; intercepts of 1.387 and 1.699 respectively), and both regressions were significant at the 0.005 level. Note that the number of inflorescences available for dust reception increased slightly with distance from the source (Table 2). This relationship cannot be due to a steadly decreasing density of plants, but must be due to patterns of pollinator movement.

Table 1. Number of fluorescent dust detections by season and color in the short-distance sample

Season	Color				
	Red	Orange	Blue	Green	
Middle season	21	12	8	3	44
Late season	28	26	24	8	86
	49	38	32	11	130

Tests	d.f.	G value	P
Color effects	3	27.293	0.005
Season effects	1	13.816	0.005
Color-by-season interaction	3	3.202	NS
	7		

For the long-distance samples, there were only four dispersal events in the middle season, so middle and late season data were pooled. These data revealed no significant relationship between the number of dispersal events and distance from the source ($\log (y+1)=0.005\,x+0.117$, $P=0.50$). Thus, there appeared to be a strong decrease in dispersal events with distance up to a distance of 30 meters, beyond which the number of dispersal events appeared to be independent of distance. Over all distances, neighborhood area increased dramatically from middle to late season. In the middle season, the area was 262.2 m^2 (corresponding to a circle of radius 9.1 m) whereas in the late season, the neighborhood area increased an order of magnitude to 1743.9 m^2 (circle of radius 23.6 m). Two outliers (at 73.3 m and 73.6 m) were deleted from the middle season estimation procedures, because they were unduly influential. We did not calculate neighborhood size, because the plants were not distributed uniformly in space.

Effects of distance on the proportion of flowers marked

Among inflorescences that received dust, distance from the source influenced the proportion of flowers on the inflorescence that were visited. However, the direction of this relationship changed between seasons. During the middle season, the proportion increased with distance ($F_{1,45}=7.68$, $P<0.01$, slope $=0.008$), but during the late season, the proportion decreased ($F_{1,114}=7.92$, $P<0.01$, slope $=-0.004$). Neither relationship is very strong (coefficients of determination were 0.14 and 0.06 in middle and late season respectively). The change in sign of slope could have been an artifact of the denominators' (number of flowers on the inflorescence) decreasing with distance in mid-season but increasing with distance in the late season. We regressed

Table 2. The number of detections of fluorescence dust dispersal in 5-m distance categories for three segments of the flower season. Parentheses contain the number of inflorescences available at each distance from the source plants. The number of inflorescences available during the early oat of the season are not included

Distance	Short-distance Sample			Distance	Long-distance Sample		
Category	Early	Middle	Late	Category	Early	Middle	Late
0– 5 m	4	21 (88)	31 (88)	10– 15 m	0	0 (19)	4 (37)
5–10 m	3	11 (209)	20 (218)	15– 20 m	0	0 (63)	0 (76)
10–15 m	0	5 (314)	18 (315)	25– 30 m	0	0 (157)	4 (151)
15–20 m	0	4 (338)	9 (337)	30– 35 m	0	1 (214)	4 (180)
20–25 m	4	2 (200)	7 (205)	35– 40 m	0	0 (240)	5 (203)
35–30 m	0	1 (59)	1 (87)	40– 45 m	0	1 (218)	3 (201)
				45– 50 m	0	0 (145)	0 (192)
	11	44	86	50– 55 m	0	0 (200)	3 (194)
				55– 60 m	0	0 (232)	0 (223)
				60– 65 m	0	0 (347)	3 (262)
				65– 70 m	0	0 (376)	0 (435)
				70– 75 m	0	2 (430)	3 (380)
				75– 80 m	0	0 (453)	1 (445)
				80– 85 m	0	0 (378)	0 (414)
				85– 90 m	0	0 (281)	0 (407)
				90– 95 m	0	0 (266)	0 (250)
				95–100 m	0	0 (86)	1 (121)
					0	4	33

these denominators on distance for both middle and late season data but found no significant relationship.

Effects of inflorescence size on pollen flow and flowering duration

Marked inflorescences of various size classes reflected their overall representation in the entire population (Table 3: $\chi^2 = 4.73$, df = 6, $P < 0.50$). inflorescence size did affect the number of flowers marked with dust in the late season: larger inflorescences displayed a weak tendency to have more of their flowers marked than smaller inflorescences (regression significant at the 0.01 level with sample size of 116, but a coefficient of determination of only 6%).

We examined 102 inflorescences and recorded the duration of their flowering in days. The inflorescences contained from 14 to 145 flowers ($\bar{x} = 12.88$, S.D. = 3.319). The length that an inflorescence was in flower increased as a function of inflorescence size ($r^2 = 41.62$, $F_{1,101} = 71.29$, $P < 0.001$; $y = 0.062x + 8.152$). Large inflorescences were in flower longer than small ones.

Estimation of genetic variability and progeny diversity

In the sample of 70 plants, seven of the 8 loci tested were polymorphic: EST1, EST2, LAP1, LAP2, SKDH, PGM, and SOD. The heterozygosity index at 0.262 is about average for an outcrosser (H = 0.29; Hamrick 1982). The frequencies of heterozygotes at each polymorphic locus used in the seed analysis were 0.208 for LAP1 ($n = 50$), 0.061 for LAP2 ($n = 49$), and 0.405 for SKDH ($n = 42$). Inflorescence size significantly affected the evenness of genotypes in seed progeny at the LAP1 locus (Table 4). Large inflorescences have smaller evenness values ($\bar{x} = 2.884$, i.e. greater mean diversity) than small inflorescences ($\bar{x} = 4.844$), and this difference accounts for 32% of the variance among plants. No other effects on evenness were significant. No significant effects were detected for genotype richness at any locus.

Table 3. Dispersal events as a function of inflorescence size class

Size class	Observed	Expected
≤ 39 mm	18	14.72
40– 49 mm	16	22.156
50– 59 mm	31	26.796
60– 69 mm	21	24.360
70– 79 mm	14	15.428
80– 89 mm	8	6.148
90–100 mm	8	6.246

Discussion

Levels of potential multiple mating in this population of *Amianthium muscaetoxicum* appear to be high but seasonally restricted. Fluorescent dust from one source travels to a number of plants over a wide range of distances; however, the high frequency and wide-ranging dust movement was largely restricted to the late part of the season. In the later part of the season, when there are fewer inflorescences with nectar to choose from, pollinators may move more frequently and/or to greater distances in search of adequate resources. Once there, pollinators appear to stay for shorter periods of time, because they mark a smaller proportion of flowers.

Restriction of distant flow patterns to the late season probably occurs because pollinators may restrict their movements to near neighbors at peak flowering in the middle season. The composition of the pollinator community probably changes over the season, and the late season community may be characterized by wider-ranging foraging habits than was the earlier community. It is interesting to note that this pattern of gene flow and phenology appears to be the reverse of that in wind-pollinated *Plantago lanceolata* (Tonsor 1985).

Representatives of at least three orders (Coleoptera, Le-

Table 4. Analysis of variance for genotype evenness of seed progeny

Source	d.f.	S.S. $\times 10^3$	M.S.	F	P
a Analysis of variance for SKDH					
Season	1	176.817	176.817	2.64	NS
Size	1	14.017	14.017	0.21	NS
Season × Size	1	58.017	58.017	0.87	NS
Plants (Season and Size)	8	535.600	66.950		
Location	1	30.817	30.817	1.39	NS
Location × Season	1	12.150	12.150	0.55	NS
Location × Size	1	18.150	18.150	0.82	NS
Location × Size × Season	1	0.150	0.150	0.01	NS
Residual	8	176.933	22.117		
	23	1022.651			
b Analysis of variance for LAP_1					
Season	1	0.67	0.067	0.00	NS
Size	1	160.067	160.067	8.70	<0.05
Season × Size	1	3.267	3.267	0.18	NS
Plants (Season and Size)	8	147.200	147.200		
Location	1	0.267	0.267	0.02	NS
Location × Season	1	21.600	21.600	1.64	NS
Location × Size	1	1.067	1.067	0.08	NS
Location × Size × Season	1	60.000	60.000	4.57	NS
Residual	8	105.067	13.133		
	23	498.602			
c Analysis of variance for LAP_2					
Season	1	0.067	0.067	0.01	NS
Size	1	19.267	19.267	2.24	NS
Season × Size	1	24.067	24.067	2.80	NS
Plants (Season and Size)	8	68.867	8.608		
Location	1	0.067	0.067	0.01	NS
Location × Season	1	0.067	0.067	0.01	NS
Location × Size	1	19.267	19.267	2.40	NS
Location × Size × Season	1	19.267	19.267	NS	
Residual	8	67.197	8.025		
	25	215.133			

pidoptera, and Hymenoptera) and nine families pollinate *Amianthium* flowers (Travis 1984), and this diversity (especially in pollinator phenology) must play a significant role in determining dispersal distances and consequent neighborhood areas. Literature on insect pollination is dominated by reports concerned only with bee pollination, and most reports suggest that the majority of insect-mediated pollen movement occurs within 10 m (reviewed by Levin and Kerster 1974; Hamrick 1982). Otherwise, only a few studies have sought or found evidence of insect pollen flow beyond 30 m, but these are usually in agricultural studies. For instance, Bateman (1947) observed 60% seed contamination at 20 ft, 13% at 80 ft, and 6% at 140 ft, whereas 1% seed contamination remained constant from 160 through 580 ft away from contaminating varieties of turnips and radishes planted at 20-ft distance intervals. This pattern is similar to our results but on a different scale.

Schmitt (1980) infers that small amounts of pollination by lepidopteran species can significantly increase the size of the neighborhood area when added to pollination by density-dependent bee species in *Senecio*. Hence, annual and seasonal variation in species composition, sensitivity to floral density, and phenology of pollinators may cause the neighborhood area to fluctuate. Our estimations of neighborhood area reflect the seasonal effects of pollination by multiple vectors to variable distances. In the middle part of the season, the area is 262 m^2 (radius of 9.1 m), whereas in the late season it increases to 1743 m^2 (radius of 23.6 m). These estimations of neighborhood areas are one to three orders of magnitude greater than other estimations (references in Crawford 1984). Furthermore, our estimates of neighborhood area are conservative. Long-distance sampling involved only 17.6% of the total area 20–80 m from the center of our circle, and thus we may have undersampled. Although little is known about the correspondence of dust dispersal to pollen dispersal, the "dust method" appears suitable for estimating minimum pollen dispersal rates (Handel 1983; but see Thomson and Plowright 1980 and Waser and Price 1982).

These results suggest that plants with small inflorescences, which have short flowering durations, can experience very different neighborhood areas than those plants with large inflorescences, which flower for longer periods. This effect would be particularly marked for plants in flower during the middle part of the season. Thus, closely adjacent individuals could conceivably experience dramatically different neighborhood areas. On the other hand, the long-lived, iteroparous lifestyle of *Amianthium* may override all of these sources of variation and generate very large "effective neighborhood areas."

We also found an effect of inflorescence size that operated on a spatial scale. Larger inflorescences were no more likely to receive at least one visit than expected on the basis of their numbers. However, late in the season, larger inflorescences had more of their flowers marked with dust. This finding suggests that a visiting pollinator lingered longer and covered more flowers with dust.

As a result of the effects of inflorescence size that operate on both temporal and spatial scales, large inflorescences had a greater evenness of genotypic diversity in their seed progeny at the LAP1 locus than did small inflorescences. Despite our crude categorization of inflorescence size, the effect was a strong one, accounting for 32% of the variance in evenness. This demonstration of the effect of the size of the floral display on the genotypic diversity of progeny is the first that we are aware of for a natural population. We suggest that the effect occurs predominantly through the longer flowering duration of larger inflorescences, enabling their ovules to "sample" a larger fraction of the genetic diversity of pollen in the population.

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