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Abstract.—Both pollen and seed dispersal components of gene flow were examined in the annual plant *Chamaecrista fasciculata* (Leguminosae) and quantified in terms of Wright's neighborhood area. Pollen dispersal was estimated by measuring pollinator flight movement throughout the flowering season and the contribution of pollen carryover to pollen dispersal was determined by comparing pollinator flight movement with dispersal of electrophoretic markers in an experimental transect. Phenological effects on the probability of fruit set were measured to determine whether pollinations should be weighted differentially across the flowering season. The outcrossing rate, a major determinant of the role of pollen dispersal in gene flow, was estimated from electrophoretic analysis of progeny arrays and by measuring the proportion of nongeitonogamous pollinator flight movements. Seed dispersal was measured in a prairie habitat and in experimental plots without surrounding vegetation.

Seed dispersal was small in comparison to pollen dispersal in both environments. Fruit set was low at the beginning and end of the flowering season, periods when flower density is low and pollinator flight distances are large. Although the outcrossing rate was high (t = 80%) and pollen carryover substantial, pollen dispersal was limited. Averaged over 4 years, neighborhood area, based on both seed and pollen dispersal, was 17.6 m^2, and corresponds to a circle of radius 2.4 m. The observed limited gene dispersal suggests the population of *C. fasciculata* is genetically subdivided into small breeding units of related individuals.

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Gene flow, the movement of genes within and among populations and their subsequent establishment (Endler, 1977), is an important evolutionary parameter. It determines the extent to which individuals across the species range share a common gene pool (Mayr, 1970) and the amount of local genetic subdivision (Wright, 1946). Wright (1943, 1946, 1951) demonstrated that in the absence of selection the amount of genetic differentiation in a population is largely determined by the size of the basic breeding unit, the neighborhood. To understand the evolutionary processes that are responsible for the distribution of genetic variation in natural populations it is essential to have an accurate estimate of gene flow and neighborhood size.

Gene dispersal occurs in two stages: (1) a series of prefertilization events that are responsible for bringing together two uniting gametes and (2) the dispersal of the zygote. Gene establishment will depend on the fitness of the resultant zygote. These pre- and post-fertilization events can be broken down into a series of discrete and measurable stages of gene flow. In plants, gene dispersal will correspond to pollen and seed dispersal. Pollen dispersal will depend on (1) pollinator flight distance and (2) the amount of pollen carryover, which has been shown to increase pollen dispersal over that inferred from pollinator flight movement alone (Schaal, 1980; Thompson and Plowright, 1980; Levin, 1981; Handel, 1983; Waser and Price, 1982). The plant's breeding system can be a major determinant of the role of pollen dispersal in gene flow (Wright, 1969; Crawford, 1984). In plants with mixed mating systems the amount of gene dispersal through pollen dispersal is directly proportional to the amount of outcrossing. Seed dispersal is determined by both the primary dispersal event mediated by the maternal parent and secondary dispersal prior to germination. Gene establishment will depend on the probability of fertilization and offspring survivorship and reproduction.

Despite long recognition that gene flow depends on not only how far genes are dis-

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persed but also on the selective advantage or disadvantage they confer on individuals (Fisher, 1937; Endler, 1977; Levin, 1981), no study to date has estimated gene flow based on both gene dispersal and gene establishment. In a companion paper (Fenster, 1991*a*) the gene establishment phase of gene flow is linked to the gene dispersal data to give a complete description of gene flow in a natural plant population in terms of neighborhood area and the effective number of individuals within the neighborhood.

The objective of this study was to determine the relative contribution of pollen and seed dispersal to gene dispersal and neighborhood area in a natural population of *Chamaecrista fasciculata* (Leguminosae). This study departs from previous investigations of gene dispersal in plants by integrating information on the role of phenology on pollen dispersal with measurements of pollen carryover, the outcrossing rate, and seed dispersal.

METHODS

Study Site and Study Organism

The study site is located at Gooselake Prairie Nature Preserve (GLP), Grundy Co., Illinois, a 700-ha disturbed mesic prairie located in the floodplain of the Illinois River. Controlled burns are conducted on approximately one-third of the preserve each spring. The population of *C. fasciculata* at GLP is subdivided into discrete subpopulations consisting of 100s–1000s of adult flowering individuals. Each of the approximately 30 subpopulations is separated from its nearest neighbor by 50–200 m. From these, 14 subpopulations were chosen for study using stratified random sampling.

Chamaecrista fasciculata Michx., partridge pea (formerly known as *Cassia fasciculata* or *Cassia chamaecrista,* Irwin and Barneby, 1982), is a self-compatible annual legume of old field, disturbed prairie, and savanna. Seedlings emerge from late April through early May. Flowering begins in mid-to-late July and continues until first frost (early October). Flowers remain open for only 1 day and are developmentally enantiostylous, i.e., the style emerges from opposite sides of the flower in alternating flowers in an inflorescence. *Chamaecrista fasciculata* falls into the "buzz" pollination syndrome (Faegri and Van der Pijl, 1979): the large, yellow caesalpinoid flowers provide no nectar rewards and the pollen is released through terminal pores in the anthers following vibration by large bees. *Chamaecrista fasciculata* is exclusively bee pollinated (Lee and Bazzaz, 1982*a*), and most flower visits (>80%) in GLP are by *Bombus* ssp.; the remaining are by *Apis mellifera, Megachile* spp., and Anthophoridae. Seed dispersal is through explosive pod dehiscence. In Northern Illinois, seed dispersal begins in early September.

Gene Dispersal

Pollinator Flight Distance.—To determine the relationship between interplant pollinator flight distance and the density of flowering individuals, plots ranging in area from 25 to 100 m^2 were set up in one subpopulation in 1983, four subpopulations in 1984, and three subpopulations in 1986 (one plot/subpopulation). Plot sizes were chosen to minimize extreme variation in plant density within the plots. In each plot the number of flowering individuals and the total number of *C. fasciculata* flowers were counted on the days pollinator flight distances were measured. Pollinator observations were conducted in each plot for 1–5 days from 0700 to 1000, the primary period of bee foraging on *C. fasciculata.* In each plot individual pollinators were followed from the time they were first observed until they left the plot. The flight distance between plants was determined by following the pollinators with a 1.5-m calibrated pole and the number of flowers visited on each plant were recorded. The mean flight distances of constant vs. inconstant (includes visits to other plant species) pollinators were measured to determine the effect of long interplant pollinator flights on pollen dispersal. If a pollinator flight between two flowers of *C. fasciculata* was interrupted by one or more visits to a flower of another plant species, then the flight was considered as inconstant but was included as a *C. fasciculata* interplant flight. A total of 2,550 interplant pollinator flight distances were recorded across the entire phenology (range = 60–295 observations/plot/day).

Floral Density and Phenology.—The density of flowers and flowering plants was de-

termined in four randomly placed, 1 m^2 quadrats, in 11 of the 14 subpopulations in 1983 and in each of the 14 from 1984 to 1986. To simplify comparisons among years the flowering season was divided into the following 5 periods (1) 7/20–7/30, (2) 7/31–8/12, (3) 8/13–8/23, (4) 8/24–9/10, and (5) >9/10, when the density of flowering plants was intermediate, high, intermediate, intermediate, and low, respectively.

Seasonal Variation in Pollinator Effectiveness.—Conspecific stigmatic pollen loads were measured throughout the flowering season in 1983, 1984, and 1985 at GLP as one indicator of pollinator activity. One undamaged flower/plant was collected and pistils were removed and fixed in FAA late in the same day in which they opened. The stigmas were stained with 1% aniline blue in lactophenol and the number of pollen grains counted under a microscope at 100×. Pollen grains were counted on an average of 400 stigmas for each of the five periods combined across the 3 years.

Bee/flower ratios were used as another measure of pollinator activity across the season. The number of bees foraging on *C. fasciculata* within the pollinator observations sites was recorded at 15-min intervals throughout the 1984 flowering season. Bees were observed in a average of 20 census intervals evenly distributed across the four subpopulations in each of the five periods.

To determine seasonal variation in fruit set, the probability of flowers becoming fruit was measured throughout the season. One open, undamaged flower/plant (62–349 flowers/period, $\bar{x} = 190$) was tagged and its survivorship to mature fruit was determined in 1983, 1984, and 1985. For interyear comparisons, the relative fruit set was calculated by dividing all periods in a given year by the period with the largest value, giving 100% as the upper bound of relative fruit set. Mean relative fruit set for each period in 1983, 1984, and 1985 was used to weight pollinator flights across the 1986 flowering season.

Pollen Carryover.—The contribution of pollen carryover to pollen dispersal was examined by comparing the actual dispersal distance of an electrophoretic marker, diaphorase (Dia), to the observed pollinator flight distribution in an experimental transect. The Dia locus is polymorphic for two alleles within natural populations of *C. fasciculata* and shows simple Mendelian inheritance (Fenster, 1988). In 1984, two genotypes homozygous for the alternative alleles were identified and self-pollinated. The following spring the seeds were germinated and the plants grown in the greenhouse. That summer an experimental transect of 13 genetically identified plants at the Dia locus was spaced 0.30 m apart in a line. The target plant in the middle of the line (position #7) was homozygous for the fast allele of Dia, and was flanked by plants (#1–6, 8–13) homozygous for the slow allele. Three target individuals were used on a rotational basis over the course of the experiment. Each plant was allowed to produce two flowers/day, within the range of daily flower production in GLP. *Bombus* spp. foraged freely on the plants for 6 days in a vacant lot close to the University of Chicago and pollinator flight distances between plants and the number of within-plant movements were recorded on five of these days. *Bombus* foraged in the transect with similar behaviors exhibited on *C. fasciculata* in GLP. Other bees were not present. After the experimental period, the plants were returned to the greenhouse and the fruit allowed to mature. In each of the seven distance classes (self, 1, 2, 3, 4, 5, and 6 plants away from the target), 67 seeds were assayed for a total of 469 genotypes. Parental and progeny genotypes were determined on the modified gel and electrode buffer system 8 (Soltis and Soltis, 1987). Staining methods followed Soltis et al. (1983). Gene dispersal was indicated by heterozygous F1 progeny. The outcrossing rate in this experiment was measured by the proportion of heterozygous progeny produced on the three target homozygotes.

Outcrossing Rate.—The multilocus estimation procedure of Ritland and Jain (1981) was used to estimate t for each subpopulation. I sampled 22–27 families from 5 × 5 to 10 × 10 m plots in each of seven subpopulations (total = 180 families): three subpopulations in 1983 and four different ones in 1985. The size of the plots was chosen to correspond roughly to neighborhood size based on pollinator flight movement so that inbreeding due to population subdivi-

sion would not confound estimates of the selfing rate (Ennos and Clegg, 1982). The subpopulations chosen spanned the range of flowers produced/plant/day observed at GLP. There was an a priori expectation based on pollinator flight behavior that subpopulations that produced larger plants with more than one flower/day (an estimate of the potential for geitonogamous pollinations) might have higher selfing rates compared to subpopulations with smaller plants producing at most one flower/day.

Outcrossing estimates were based on Mendelian codominant alleles at four loci, two isozymes of leucine-aminopeptidase (Lap1 and Lap2), one isozyme of phosphoglucomutase (Pgm), and one isozyme of 6-phosphoglucose dehydrogenase (6Pgd), in progeny arrays of seeds ranging from 6 to 10 individuals. Progeny genotypes were determined on system 11 of Soltis et al. (1983) and staining methods followed Soltis et al. (1983) for Pgm and 6Pgd and Soltis and Soltis (1987) for Lap. The estimate of the outcrossing rate was not confounded by differential germination or survivorship of outcrossed vs. selfed seedlings as progeny were assayed at the seed stage. For Lap1, Lap2, and Pgm, the rarest alleles were combined, resulting in three segregating alleles for all four loci. Whenever possible, seeds were sampled from more than one fruit/plant. Outcrossing rates were also estimated from pollinator observations conducted in seven subpopulations in 1983, 1984, and 1986 as the proportion of interplant pollinator movements.

Seed Dispersal.—Seed dispersal was measured in two environments: (1) a restoration prairie, similar in vegetation to GLP (representing natural conditions) and (2) an experimental garden plot, devoid of surrounding vegetation (where seed dispersal should be at a maximum).

Restoration Prairie. Seed collected from GLP were germinated in the Spring of 1985 and grown in a greenhouse through the following summer. In mid-September when *C. fasciculata* normally disperses its fruit 40 fruiting plants were transplanted into a restoration prairie adjacent to GLP where *C. fasciculata* was absent. The vegetation type, height, and density in the prairie approximated the natural community for *C. fasciculata* in GLP. The transplants were placed in a grid, spaced 20 m apart. Only 8 of the 40 transplants escaped damage by small rodents and dispersed seed. In early April 1986, 3 weeks before natural germination of *C. fasciculata,* a controlled prairie burn (a natural part of the life cycle of *C. fasciculata* in prairies and savannas) was conducted to remove the ground litter, encouraging germination and facilitating location of the seedlings. Germination of *C. fasciculata* occurred from late April through mid-May and the seedlings were easily located. The distance of the seedlings from their maternal parents was determined by searching a 10 × 10 m square area around each dispersing adult. The transplant closest to each seedling was assumed to be its seed parent.

Experimental garden plot. Four greenhouse-grown plants were each transplanted into the center of four 6 × 6 m barren plots (no surrounding vegetation) adjacent to the Univ. of Illinois at Chicago Greenhouse, in mid-September 1985. The locations of the emerged seedlings relative to the dispersing adults were determined the following spring.

Calculation of Neighborhood Area

The following general formula for neighborhood area based on pollen and seed dispersal was used (Crawford, 1984):

$$N_a = \frac{1}{2}\pi\left(\frac{tk_p\sigma_p^2}{2} + k_s\sigma_s^2\right) \qquad (1)$$

where k_p and k_s are the correction factors for kurtosis for pollen and seed dispersal, σ_p^2 and σ_s^2 are the variances of pollen and seed dispersal, respectively, measured as absolute distance and assuming a mean of zero. The factor of ½ at the beginning of the equation converts dispersal distances measured on an absolute scale to correspond to Wright's (1943) derivation of neighborhood area where measurements are assumed to be made on one axis. The correction factors for kurtosis (k) are equal to 4 when dispersal is normally distributed. Pollen dispersal was weighted by the outcrossing rate based on Ritland and Jain's (1981) multilocus estimate (t) and by ½ since total dispersal is the average of dispersal through male and female components (Crawford, 1984).

The role of ecological factors as determinants of pollen dispersal variance was taken into account by estimating the contribution of pollen to the dispersal variance

$$N_a = C \sum_{i=1}^{n} A_i p_i t_i m_i$$

(Schmitt, 1983) where A_i is neighborhood area estimated from pollinator movement on date i, p_i is the proportion of flowers open on date i, t_i is the proportion of outcrossing on date i, m_i is the relative proportion of flowers pollinated on date i that mature seed, and C is a factor that accounts for the difference between N_a based on pollinator flight movement and N_a estimated from pollen dispersal, including pollen carryover. Mean interparent distance is inversely proportional to the square root of plant density, assuming a Poisson distribution of interplant distances (Clark and Evans, 1954). Neighborhood area, based on pollinator flight distance, was regressed on the reciprocal square root of flowering plant density. From this regression, a predicted average neighborhood area was calculated for each period, based on the average density of *C. fasciculata* at GLP (A_i). This predicted neighborhood area was weighted by the proportion of flowers produced during that period (p_i). Seasonal variation in the outcrossing rate was measured (t_i). The contribution of pollinator flight distances to neighborhood area in a given period was further weighted according to the differential probability of fruit set across the flowering season (m_i). Average neighborhood area based on pollen dispersal was calculated by multiplying neighborhood area based on pollinator flight distance by the increase in neighborhood area due to pollen carryover (C).

Neighborhood area based on seed dispersal alone was calculated from the variance and kurtosis of the restoration prairie and greenhouse plots separately. By using each plot as a replicate, an unweighted average σ_S^2, and kurtosis were calculated, resulting in less bias in the estimate of the dispersal curve. The calculated neighborhood ares thus reflect the average seed dispersal distribution in the two contrasting environments.

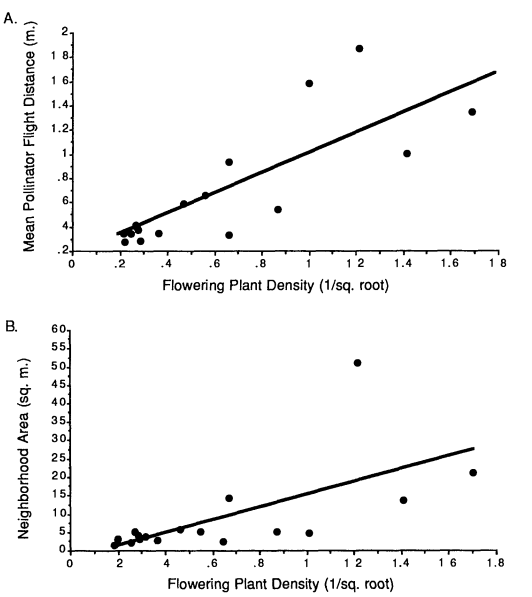

FIG. 1. Regression of mean pollinator flight distance (A) and regression of neighborhood area (B) on the inverse square root of flowering plant density.

RESULTS

Pollen Dispersal.—Pollinator flight distances were inversely related to the density of flowering individuals (mean flight distance = 0.874[1/(density of flowering individuals)]½ + 0.128, $r^2 = 0.66$, $P < 0.001$) (Fig. 1A), resulting in a negative relationship between neighborhood area and density of flowering individuals (N_a = 17.1[1/(density of flowering individuals)]½ − 2.9, $r^2 = 0.41$, $P < 0.01$) (Fig. 1B). Pollinator constancy was strongly associated with pollinator flight distance. The mean flight distance of uninterrupted flights was 43 cm (n = 2,848, 1 SE = 4 cm) vs. 192 cm (n = 39, 1 SE = 32 cm) for inconstant or interrupted flights and 37 cm (n = 2,631, 1 SE = 3 cm) for flights not interrupted one flight later vs. 135 cm (n = 58, 1 SE = 21 cm) for flights interrupted one flight later.

Phenology.—The phenology of *C. fasciculata* at GLP from 1983 to 1986, based on the proportion of flowers (Fig. 2A) and the density of flowering individuals (Fig. 2B), was very similar. The density of flowers and flowering plants peaked in period 2 (7/31–8/14) and then gradually declined until the onset of frost during period 5 (late Septem-

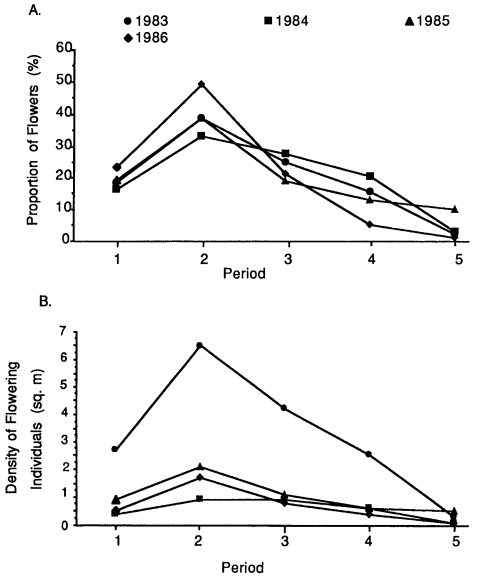

FIG. 2. The phenology of *C. fasciculata* at GLP estimated from the proportion of flowers open during each period (A) and from the density of flowering individuals during a period (B).

ber–early October). The shape of the phenology curve differed among years (X^2 = 90.1, $P < 0.001$), due to greater than average flowering in period 5 for 1986 and lower than expected flowering during period 4 in 1986 ($P < 0.05$, Bonferroni multiple comparison). The absolute density of flowering individuals also varied among years ($F = 4.135$, $P < 0.025$), probably reflecting differences in rainfall and time since disturbance (fire). The higher density of individuals in 1983 (Fig. 2B) was associated with greater flower production per individual (Fenster, 1988). However, daily individual mean flower production did not vary seasonally or between years, ranging from 1.0 to 1.6 flowers per individual per day.

The probability of fruit set varied between periods and years (Table 1) but the relative probability of fruit set was consistent for periods across years (Friedman rank statistic $S = 8.4$, $P < 0.05$). The mean relative fruit set (Fig. 3B) across the 3 years was lowest for periods 1 and 5. Stigmatic pollen load (Fig. 3C) and bees/flowers ratio (Fig. 3D) lagged behind the flowering season (Fig. 3A) and were lowest during periods 1 and 5 and highest during period 3 and 4, while floral density was highest during period 2.

Gene Dispersal.—Most of the pollinator flights and gene dispersal events in the experimental line of marked plants were <1 m (Fig. 4). However, the actual movement of genes was greater than pollinator flight distances ($X^2 = 47.0$, $P < 0.001$). Mean gene dispersal distance in this experiment (0.57 m) was almost twice as great as the mean pollinator flight distance (0.30 m). The shapes of the distributions of gene dispersal and pollinator flight distance were very different. Pollinator flight distance in the experimental population followed a leptokurtic distribution ($g_2 = 2.90$, $P < 0.05$), whereas gene dispersal was normal ($g_2 = 0.15$). Linear neighborhood area for the experimental population was 3.4 times greater based on gene dispersal (9.6 m^2) vs. pollinator flight distance (2.8 m^2).

Outcrossing Rate.—In GLP the population of *C. fasciculata* is, on average, highly outcrossing. The mean outcrossing rate estimated from the electrophoretic data was 0.80 (range = 0.65–0.92) and 0.86 for pollinator observations (range = 0.68–0.98). The proportion of nongeitonogamous pollinations (0.66) was very similar to the outcrossing rate (0.68) estimated from gene dispersal in the pollen carryover experiment (Fig. 4). No association between outcrossing

TABLE 1. Probability of fruit set of *C. fasciculata* in GLP across the flowering season for 3 years. Sample size of the flowers marked is given in parentheses.

	Probability of fruit set (%)				
Year	Period 1 (7/20–7/30)	Period 2 (7/31–8/12)	Period 3 (8/13–8/23)	Period 4 (8/24–9/10)	Period 5 (>9/10)
1983	7 (118)	41 (126)	41 (37)	56 (61)	0 (16)
1984	8 (60)	14 (57)	4 (54)	10 (59)	0 (21)
1985	13 (60)	40 (166)	54 (65)	31 (39)	0 (25)
Mean	9	32	33	22	0

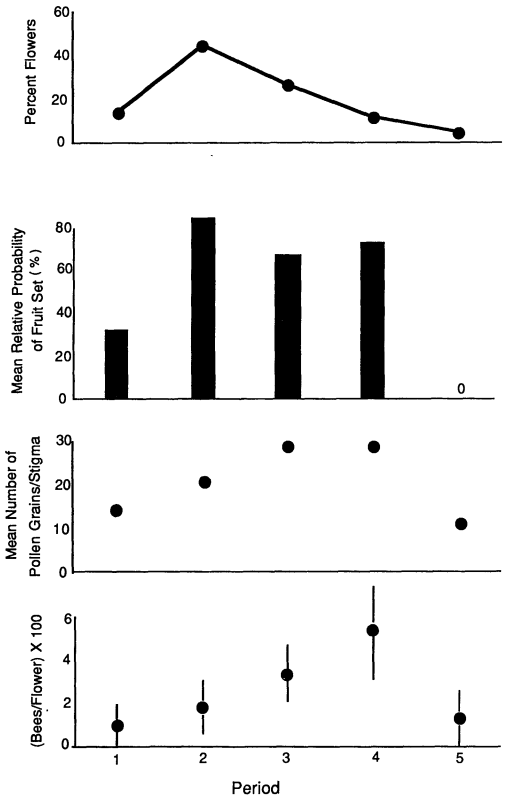

FIG. 3. Variation in fruit set across the phenology. (A) The mean phenology curve from 1983 to 1986, estimated from the proportion of flowers open in each period. (B) The mean relative probability of fruit set from 1983 to 1985. Two indices of pollinator effectiveness throughout the phenology are presented: the stigmatic pollen load (C), 95% confidence intervals smaller than the data points, and the bees/flower ratio with 95% confidence intervals (D).

rate estimates and the average number of flowers produced/plant/day across subpopulations was observed. The outcrossing rate, estimated from pollinator observations, was independent of phenology.

Seed Dispersal.—Seed dispersal was much greater in the garden plots than in the restoration prairie (Fig. 5). Although both dispersal distributions are leptokurtic ($P < 0.05$), they are significantly different from one another ($X^2 = 97.2$, $P < 0.001$). In the garden plots seed dispersal had reduced kurtosis ($g_2 = 1.9$) and a larger mean seed dispersal ($\bar{x} = 0.65$ m, $n = 192$ seedlings) compared to seed dispersal in the restoration prairie ($g_2 = 4.3$, $\bar{x} = 0.32$ m, $n = 534$ seedlings). Since no seedlings were found at intermediate distances in the prairie plots, it seems unlikely that serious bias was introduced by assigning seedlings to the nearest adults. Seed dispersal in both environments is limited, 2 m in the restoration prairie and 3 m in the garden. Neighborhood area estimated from seed dispersal alone ranges from 1.2 m^2 in the prairie to 4.6 m^2 in the garden.

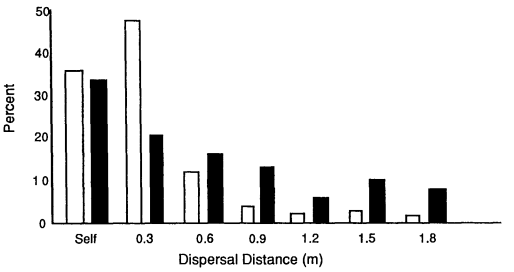

FIG. 4. Gene dispersal (solid bars) vs. pollinator flight movement (open bars) in a linear population of plants of known genotype.

Neighborhood Area Based on Pollen and Seed Dispersal.—The contribution of pollinator flight movement to neighborhood area in GLP was determined by the regression of neighborhood area on density of flowering individuals. Predicted neighborhood areas were then calculated throughout the flowering season for 1983–1986. Neighborhood area based on pollinator flight movement ranged from 2.8–9.0 m^2 and averaged 6.5 m^2 (Table 2). Neighborhood areas were slightly reduced, ranging from 2.7 to 8.4 m^2 and averaging 6.1 m^2 across the 4 years (Table 2) when weighted by the probability of fruit set. Further weighting

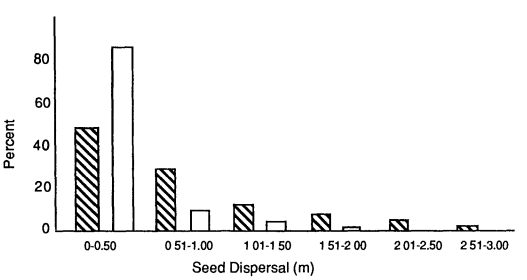

FIG. 5. Seed dispersal in a restoration prairie (with surrounding vegetation; open bars; $n = 534$), and garden plots (no surrounding vegetation; striped bars; $n = 192$).

TABLE 2. Breakdown of contribution of pollen (p) and seed (s) dispersal to neighborhood area (N_a) in square meters from 1983 to 1986 for *C. fasciculata* at GLP. N_a based on pollinator flights and weighted by the relative survivorship of fruit throughout the phenology, was weighted by the outcrossing rate (×0.8) and pollen carryover (×3.4) to produce an estimate of N_a for pollen dispersal. The arithmetic mean is presented.

Year	N_a (pollinator flight distance throughout the season)	N_a (pollinator flights weighted by the relative survivorship of fruit)	$N_{a(p)}$	$N_{a(s)}$	$N_{a(p+s)}$
1983	2.8	2.7	7.3	1.2	8.5
1984	9.0	8.4	22.8	1.2	24.0
1985	6.2	5.9	16.0	1.2	17.2
1986	7.9	7.2	19.6	1.2	20.8
Mean	6.5	6.1	16.4		17.6

by the outcrossing rate (0.8) decreased the mean neighborhood area to 4.8 m^2. When pollen carryover was included neighborhood area increased 3.4-fold to 16.4 m^2. Adding estimated seed dispersal from the prairie increased neighborhood area by 1.2 m^2 (Table 2).

DISCUSSION

Phenology and Pollen Dispersal.—The density-dependent relations of pollinator flight movement and pollen dispersal result in a density-dependent relation of neighborhood area that has been observed elsewhere (Bateman, 1947; Nieuwhof, 1963; Levin and Kerster, 1969*a*, 1969*b*; Kerster and Levin, 1968; Beattie, 1976; Schmitt, 1983). Neighborhood areas are site specific; larger during years of low flowering density or in sites with reduced flowering. From the negative relation between pollinator flight movement and density of flowering individuals it appears flight distances are much greater during periods with low floral density early and late in the season (periods 1 and 5). For example, in 1983, N_a estimated from pollen dispersal was 40.5 and 48.1 m^2 in periods 1 and 5 when the density of flowering individuals was 0.4 and 0.3 individuals/m^2, respectively, compared to 7.2 m^2 during period 2 when density of flowering individuals was 7.9 individuals/m^2. However, in 1983 fruit set was 6 times greater in period 2 than in period 1 and fruit set during period 5 was zero. From 1983 to 1985 the contribution of pollinator flights to reproduction was consistently low during periods 1 and 5. These large contributions of phenology to fruit set may be fairly common (Schemske, 1977; Schemske et al., 1978; Stephenson, 1981). For *C. fasciculata* at GLP the lower probability of pollen dispersal and fruit set during periods of lower floral density at the beginning and end of the floral season strongly limits long gene flow events.

Seasonal variations in the probability of fruit set are due to a combination of ecological factors. In the greenhouse, flowers pollinated early in the season have higher fruit set than those pollinated later (Fenster, 1991*b*). Therefore the low probability of fruit set early in the flowering season observed at GLP may reflect seasonal variation in pollinator service throughout the season at GLP. Two indices of pollinator effectiveness, pollen load/stigma and the bee/flower ratio, both lag behind the flowering season, suggesting that 1–2 weeks are required for the major pollinator, *Bombus* spp., to recognize and begin to exploit *C. fasciculata*. Later in the season, when the density of *C. fasciculata* has dropped below some threshold, pollinator limitation may again occur. Resource limitation and onset of frost limited fruit set in period 5 (Lee and Bazzaz, 1982*a*; Fenster, 1988). Lee and Bazzaz (1982*b*) observed a similar phenological effect on fruit maturation in one of the three populations of *C. fasciculata* they studied. In the other two, fruit maturation was highest early in the season. Seasonal variation in pollinator limitation has also been observed in other natural populations (Schemske, 1977; Galen et al., 1985; Campbell, 1985*a*) and corresponds to fluctuations in the bee/flower ratio in cotton (Stephens and Finkner, 1953). However, in no year is the estimate of neighborhood area changed by more than 3% when the weighting factor of fruit set is used, reflecting the low proportion of flowers produced during periods 1 and 5. Although *C. fasciculata* requires pollinator visitation for seed set, the bee/flower ratio may be an important determinant of outcrossing rates in facultatively autogamous species.

Bee foraging behavior in mixed species stands further constrains the frequency of long distance pollen dispersal events. At low

densities of *C. fasciculata,* the likelihood of a bee switching to another species increased, as reflected in both a higher mean distance of interrupted flights and flights one sequence before the interrupted flight. This observation suggests that bees were following an optimal foraging rule, i.e., foraging only on *C. fasciculata* at GLP beyond a threshold floral density. Campbell (1985*b*) quantified the effects of competition between species for pollinator service and observed reduced pollen dispersal in mixed species stands vs. pure stands through a reduction of the outcrossing rate and pollen carryover following heterospecific visits. Pollinator constancy may vary within and between taxa. *Bombus* spp. have long been known to show less constancy than *Apis mellifera* (Grant, 1950), and different *Bombus* species may vary in their floral constancy (Free, 1970). Thus the opportunity for long distance pollen dispersal may be limited by temporal and spatial structure of the flowering plant community and the composition and density of species with overlapping phenologies and the composition of the pollinator fauna. In addition the division of the population of *C. fasciculata* into discrete subpopulations, with intervening patches of other species of flowering plants, suggests that the opportunity for gene flow events between subpopulations is limited.

Pollen Carryover and Pollen Dispersal.— The 3.4-fold increase in estimated neighborhood area is similar to Schaal's (1980) observation of a 2.3-fold increase in neighborhood area when gene dispersal was used to estimate neighborhood area in another legume, *Lupinus texensis.* The increase of N_a based on gene dispersal is most likely due to the contribution of pollen carryover since no effect of pollen source on pollen tube growth was observed (Fenster and Sork, 1988) and bees made few flight reversals while visiting the array. Direct measurements of pollen carryover using pollen color dimorphisms have found most pollen to be deposited on the first 10 flowers in a sequence with occasional long carryover events (Thomson and Plowright, 1989; Thomson et al., 1986). Similar results have been observed using fluorescent dye as a marker for pollen dispersal (Waser and Price, 1982). Other studies (Schlising and Turpin, 1971; Gaudreau and Hardin, 1974; Handel, 1983) using pollen-labeling techniques have found limited pollen dispersal in natural populations of animal-pollinated species. The limited size of the array may have led to an underestimate of the contribution of pollen carryover to pollen dispersal. However, it seems unlikely, since the distribution of gene dispersal so closely approximates a normal distribution. Kurtosis can result as a consequence of unequal contributions of two normal distributions of equal mean and unequal variance to a compound distribution (Wright, 1968; Crawford, 1984). Pollen dispersal kurtosis was reduced compared to pollinator flight distances since the detection of longer pollen dispersal events increased with pollen carryover. Schaal (1980) observed a similar phenomenon, with g_2 estimated from pollinator flights four times as great as that estimated from gene dispersal (11.7 vs. 3.0). Therefore, the assumption of a normal distribution of pollen dispersal may be robust for models of gene flow for bee pollinated plants.

Even accounting for pollen carryover, the arithmetic mean N_a from 1983 to 1986 is still small, corresponding to a circle with radius 2.8 m^2. Using paternity exclusion analysis, Ellstrand and Marshall (1985) observed pollen dispersal distances between populations of *Raphanus sativus* separated by 0.6–1.0 k. However, their populations were small (45–49 flowering individuals), *R. sativus* is self-incompatible, and the primary pollinators were hesperids and syrphids, Lepidoptera and Diptera, respectively, which are not known to forage by making short distance plant to nearest neighbor plant moves (Schmitt, 1980). In a paternity study of the dioecious understory herb, *Chamaelirium luteum,* Meagher (1986) observed a greater likelihood of mating events between neighboring plants within 5 m, but gene flow via pollen dispersal still reached distances of 30 m. Small population sizes, incompatibility or dioecism, and nonspecialist pollinators increase the likelihood of long distance gene flow events since interpopulation pollinator flights may be more common and there is no opportunity for self-pollination. Therefore, these studies may not reflect opportunities for long pollen dispersal in large

populations of bee-pollinated, self-compatible plants like *C. fasciculata.*

Outcrossing Rate and Pollen Dispersal.—The high observed outcrossing rate indicates pollen dispersal plays a predominant role in gene dispersal. The similarity of outcrossing rates, estimated from allozymes and pollinator observations, suggests that pollinator behavior is a good indicator of the potential for selfing in *C. fasciculata.* Outcrossing estimated from the proportion of nongeitonogamous pollinations and the proportion of heterozygotes observed in the pollen carryover experiment were also similar. The results correspond to the observation of no difference in pollen tube growth between self and outcross pollen in *C. fasciculata* (Fenster and Sork, 1988) and of only small differences in the allocation of resources to developing ovules following self and outcross pollinations (Fenster, 1991*b*).

The number of open flowers on a plant may determine the potential for selfing through geitonogamy. However, in GLP, the outcrossing rate is independent of plant size, and does not vary seasonally due to variation in flower production. In this population of *C. fasciculata,* there is also little seasonal variation in the number of flowers simultaneously open per plant. The enantiostylous morphology of the flower, a classic adaptation promoting outcrossing (Faegri and Van Der Pijl, 1979, but see Duhlberger 1981), may uncouple any relation between plant size and geitonogamy, given the low number of flowers on plants in GLP. Thus outcrossing rates estimated from pollinator observations appear to be independent of date. Crawford (1984) observed a negative relationship between plant floral production and outcrossing rate in *Malva moschata*; Stephenson (1982) found most of the between-plant pollinator movements occurred either early or late in the season for the mass flowering tree *Catalpa speciosa.* Therefore, temporal and spatial variation in the outcrossing rate due to environmental conditions affecting plant size in other species or even other populations of *C. fasciculata* (where conditions allow for a greater range in the number of flowers open on a plant) may be more common.

Seed Dispersal.—Seed dispersal in *C. fasciculata* is extremely limited as demonstrated for a number of other herbs (Levin and Kerster, 1969*a*; Beattie and Culver, 1979; Schaal and Levin, 1978; Rai and Jain, 1982). However, Meagher and Thompson (1987) observed much higher seed dispersal distances using parentage analysis in *Chamaelirium luteum,* which lacks any specialized seed dispersal mechanism ($\bar{x}$ seed dispersal = 10 m, $\sigma^2_s = 49.0$). The long distances may reflect limited and scattered suitable germination sites of *C. luteum* in its understory habitat, which reduce the tendency of progeny to occur in clumps near the maternal plant.

Both the average distance and shape of the seed dispersal curve may be affected by the habitat. In the experimental plots with no surrounding vegetation, neighborhood area based on seed dispersal increases 4-fold but the contribution of seed dispersal to neighborhood size is still small. Lee (1984) observed an approximate 2-fold increase in the σ^2_s seed dispersal of *C. fasciculata* under laboratory conditions compared to seed dispersal observed in the garden plots, suggesting that seed dispersal distributions studied outside of the native habitat probably give upper-bound estimates. The increased kurtosis and shorter distance of seed dispersal in the restoration prairie suggest that extreme clumping of sibs may occur for *C. fasciculata* in GLP, increasing the opportunity for consanguineous matings and the likelihood of sib competition.

The Role of Pollen and Seed Dispersal in Gene Flow.—Most of the gene dispersal in *C. fasciculata* is through pollen dispersal. Although pollen dispersal is much greater than seed dispersal, it is still very limited even when pollen carryover is included. Pollen dispersal varies seasonally, but the potential for long distance dispersal events during periods of low floral density early and late in the season appears to be limited by pollinator behavior and early frost. Neighborhood area estimated from the gene dispersal phase of gene flow is quite small, averaging only 17.6 m^2, corresponding to a circle of radius 2.4 m. These results correspond to a general pattern of limited pollen and seed dispersal observed in animal pollinated plants (Levin and Kerster, 1969*a,* 1969*b*; Kerster and Levin, 1968; Richards and Ibrahim, 1978; Beattie and Culver,

1979; Schaal, 1980; Schmitt, 1980, 1983; Antlfinger, 1982). Limited gene dispersal suggests that the population of *C. fasciculata* at GLP is genetically subdivided into small breeding units of related individuals.

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