Seed Dispersal in Erythronium grandiflorum (Liliaceae)

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ORIGINAL PAPER

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Abstract Primary and secondary seed dispersal was investigated for the glacier lily *Erythronium grandiflorum* in the Colorado Rocky Mountains. These heavy seeds have no obvious adaptations for biotic or abiotic dispersal, but can be thrown short distances when the dehiscent fruits are shaken by wind. We used sticky traps to measure primary transport of seeds up to 1 m away from individual plants. A seed cafeteria experiment examined the role of ants and rodents in secondary seed transport. Primary dispersal by wind was positively skewed and median transport distances were influenced by variation in plant height. Secondary dispersal was negligible compared to *Viola nuttallii*, an elaiosome-bearing species. Thus, seed dispersal was highly restricted in *E. grandiflorum*, and a 1 m radius encompassed the modal section of the seed dispersal curve. The seed dispersal component of gene flow was quantified and combined with previous measurements of pollen flow to yield a more complete estimate of Wright's neighborhood size, N_e, for *E. grandiflorum*. The lack of a special seed dispersal mechanism in *E. grandiflorum* is discussed in terms of a source-sink model for seedling establishment with respect to distance from the parental plants.

Key words Gene flow · Neighborhood size · Seed dispersal · Seed predation

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Introduction

Seed dispersal plays several important roles in maintaining plant populations, including the reduction of density-dependent mortality near the parent plant, the location of favorable microhabitats for establishment on a local scale, and the expansion of a species range on a regional scale (Howe and Smallwood 1982). Seed dispersal mechanisms also contribute to gene flow (Levin 1981; Levin and Kerster 1974) and the genetic structure of plant populations (Hamrick et al. 1993). Recent studies have focused on the dispersal mechanics of aerodynamic seeds by wind (Andersen 1993; Augspurger 1986; Burrows 1986), and the description of seed shadows (Portnoy and Willson 1993), and their contribution to estimates for gene flow (Eguiarte et al. 1993; Fenster 1991; Para et al. 1993).

Seed dispersal can be divided into primary and secondary phases (van der Pijl 1969). Primary dispersal from the fruit to the ground can occur by wind, via the removal of fruit by animals who void the seeds, or through the explosive dehiscence of fruits (Beattie and Lyons 1975; Levin and Kerster 1968, 1969). Secondary transport of seed along the ground prior to germination can occur through the movement of water or by seeds being gathered by animals (Hanzawa et al. 1985; Turnbull and Culver 1983). Estimates of dispersal and establishment have been inferred from seedling distribution patterns (Meagher and Thompson 1987). Burrows (1986) predicted seed dispersal distances based on trajectory analysis, and several experimental studies have measured primary dispersal distances under controlled conditions (Lee 1984; Levin and Kerster 1968, 1969). Only recently have researchers mapped seed shadows under natural conditions (Casper 1987; Eguiarte et al. 1993; Fenster 1991, Para et al. 1993). Our study examined both primary and secondary phases of seed dispersal within a single species. To our best knowledge, previous comparison

of the relative contributions of primary and secondary transport to gene flow is limited to *Astrocaryum* (Eguiarte et al. 1993), *Chamaecrista* (Fenster 1991), and *Viola* (Beattie and Culver 1979).

Gene flow within and among populations has the important consequence of limiting the amount of local differentiation, depending on the extent of selection and genetic drift. If local genetic differentiation is favored by natural selection, then disruption of adaptive genotypes can result from matings with individuals from outside the local deme. If gene flow is restricted, then the local population may experience genetic drift, and matings between close relatives can result in inbreeding depression. Wright (1979) defined the basic breeding unit of populations, the neighborhood, as the area around an individual plant within which mating is random. Wright's statistics for neighborhood area (A) and effective population size (N_e), as refined by Crawford (1984a,b) have been commonly discussed in relation to the roles of pollen and seed dispersal in gene flow (Levin and Kerster 1974). The effect of seed dispersal on gene flow is a function of: (1) the distribution of seeds around the parent (or seed shadow), and (2) recruitment patterns. Seed shadows are typically leptokurtic (Levin and Kerster 1969), with seed density declining exponentially as distance from the parent increases. The long tail of the seed dispersal curve has proved difficult to measure (Levin 1981), but may be as important as the modal section of the curve (Portnoy and Willson 1993). In this paper, we compare seed shadows from *Erythronium grandiflorum* Pursh (Liliaceae) to previous data on pollen shadows for this species.

Despite numerous studies of its reproductive biology, there has been no study specifically addressing seed dispersal in *E. grandiflorum* (Cruzan 1990; Fritz-Sheridan 1988; Rigney et al. 1993; Thomson 1986; Thomson and Stratton 1985). In field experiments, we used fluorescent dyes to mark seeds, which allowed us to measure the distance and direction of primary dispersal from different fruits within individual plants of *E. grandiflorum*. This approach allowed us to investigate an often assumed relationship between plant height and dispersal distance (Fox 1993; Lee 1984; Levin and Kerster 1968). Secondary seed transport by ants and rodents was also examined. We combine direct measures of the seed shadow with pollen dispersal data (Thomson and Thomson 1989), to obtain a more complete estimate of N_e. In contrast to studies which emphasized the adaptive significance of long-distance seed dispersal in other species (Andersen 1993; Hanzawa et al. 1985; Turnbull and Culver 1983), we report no specialized dispersal strategy for *E. grandiflorum*.

Materials and methods

Study site and organisms

Our field sites were subalpine meadows between 2900 m and 3300 m elevation near the Rocky Mountain Biological Laboratory at Gothic, Gunnison County, Colorado. Measurements of primary seed dispersal in the glacier lily *E. grandiflorum* were made in 1990 near Forest Service Trail #403 (3230 m altitude) and in 1992 at Lake Irwin (3110 m altitude). Secondary seed dispersal by ants and rodents was investigated in 1990 along Forest Service Trail #401 (2990 m altitude). We chose meadows dominated by herbaceous perennials and with large flowering populations of *E. grandiflorum*. The higher altitude sites (Trail #403 and Irwin) are surrounded by subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) forest, and the lower altitude site (Trail #401) is contiguous with aspen woodland (*Populus tremuloides*).

E. grandiflorum is a perennial herb with 1–3 flowers appearing shortly after the spring recession of snow, in our study area between May and June. Fruits develop throughout June and July, releasing seeds during August and September. *E. grandiflorum* produces a three-sided capsule, typically containing from 20 to 60 seeds, that dehisces length-wise from the apical end. Three capsular walls recurve slightly as the fruit dries and seeds are released gradually from the apex when the erect peduncle is shaken by the wind. In *E. grandiflorum*, fruit heights within a plant range from approximately 25 to 45 cm. We expected to find that the distance seeds travel on the wind is small, but varies according to fruit height.

Primary dispersal experiments

Sticky traps were used to measure seed dispersal distances up to 1.0 m from individual plants. In August 1990, we selected ten plants at the Trail #403 site, each plant bearing two capsules ready to dehisce. After clearing vegetation to ground level within a 1.0 m radius of each plant, we placed a 3.14 m² polyethylene "apron" around each plant. Plastic sheets were staked to the ground and sprayed with aerosol Tanglefoot (Tanglefoot Co; Grand Rapids, MI). We used approximately 75 ml Tanglefoot per m², which effectively captured seeds where they landed on the sheet. Because rainwater pools interfered with the plastic sheets, we used "aprons" of window screen material, also sprayed with Tanglefoot, to capture seeds from 11 plants at the Irwin site in August 1992. Window screen permitted water to pass through the traps, resulting in greater trapping efficiency although the total trap area was reduced to 2.60 m² ($r = 0.91$ m).

We marked seeds in different capsules with different colors of fluorescent powdered dyes to distinguish the seeds from different fruits within a plant. Dyes were blown with drinking straws into the apical end of partially dehiscent capsules. Seeds were trapped over 2-week periods in 1990 and 1992. We mapped the locations of trapped seeds by measuring the distance (nearest centimeter) from each seed to the base of the parent plant. The angle of each seed from the base of the parent plant relative to magnetic north was obtained with a compass (nearest 5°), providing polar coordinates.

Cafeteria experiments

Frequencies of seed removal by rodents and ants were measured simultaneously using a "cafeteria" method modified from Turnbull and Culver (1983). We chose a 12 × 9 m grid at the Trail #401 site and marked 20 plots (0.4 × 0.4 m²) at regular 3 m intervals within the grid. Four cafeterias ("open ground", "ant exclusion", "rodent exclusion", and "control") were placed randomly at the corners of each plot. In the "open ground" treatment, seeds were placed directly on the ground, providing access to both rodents and

ants. The "ant exclusion" cafeteria presented seeds on top of golf tees protruding 3 cm from the ground. The bases of the tees were coated with a band of Tanglefoot to exclude ants while presumably allowing rodents to remove seeds. The "rodent exclusion" cafeteria presented seeds within hardware cloth cages (15 cm cubes; 1 cm mesh) that were staked to the ground to deter rodents while providing access to ants. As a control, ants and rodents were excluded from seeds on golf tees inside wire exclosures.

We placed 5 freshly collected seeds in each cafeteria ($5 \times 4 \times 20$ = 400 seeds) at 0900 hours and recorded the number of seeds remaining in each cafeteria after 3, 7 and 24 h. At 2400 hours, any remaining seeds were replaced with fresh seeds. The experiment was repeated for *E. grandiflorum* and for *Viola nuttallii* Pursh (Violaceae), each for 5 days (and nights). *V. nuttallii* was studied in comparison with *E. grandiflorum* since *V. nuttallii* seeds have an elaiosome and are thus attractive to ants and rodents (Beattie and Culver 1983).

Results

Statistical analysis

Primary dispersal was analyzed with reference to both the direction and distance of seed transport. First, we tested for directionality by comparing actual seed captures in NE, NW, SE, and SW quadrants around the parent, against an expectation of equal numbers of captures among the quadrants using replicated goodness-of-fit tests. Plants that dispersed less than 20 seeds were pooled within the field sites, since the expected frequencies in each of the four quadrants could not be less than five for the G-test (Sokal and Rohlf 1981). Second, we calculated median transport distance, the

distance from the parent at which one-half of the seeds recovered from a given fruit were deposited. We regressed median transport distance on fruit height. Nonparametric analyses compared median dispersal distances within two-fruited plants (Mann-Whitney U-test), within three-fruited plants (Kruskal-Wallis test), and between upper and lower fruits from all plants combined (Wilcoxon's signed-ranks test). We performed an analysis of variance on results from the secondary dispersal experiment, examining the effects of variation in timing, treatment type, seed species, and plot location on seed removals by ants and rodents.

Primary seed dispersal

Collective seed shadows for plants at Trail #403 and Irwin field sites are plotted in Fig. 1.1 and 1.2, respectively. Statistical analyses do not include one aberrant incident caused by a dog straying across the trap for plant 14 (see Fig. 1.3). Replicated tests of goodness-of-fit (Table 1) suggested that dispersal by wind was directional for many of the plants, but that directional trends were highly variable among plants from the same population. Seed distribution patterns for most plants deviated significantly from the expectation of equal numbers among NE, NW, SE, and SW quadrants. There was an overall NW-SE trend for plants at Trail #403, despite high heterogeneity among plants. At Irwin, there was no overall trend, and a high G_H indicated that trends for individual plants were

Table 1 Directionality of primary seed dispersal at Trail #403 and Irwin study sites. Replicated G-tests for goodness-of-fit compared actual seed captures against the expectation of equal captures among NE, NW, SE, and SW quadrants. Directional trends at Trail #403 and Irwin were tested for independence using a G-test with William's correction. (*ns* = not significant)

	NE	NW	SE	SW	G-test	df	G-value	P-value
#403 site								
Plants 1, 3, 4, 6, 7 & 8	21	13	15	8		3	6.20	n.s.
2	10	2	7	2		3	9.19	< 0.05
5	18	2	15	26		3	25.09	< 0.001
9	12	10	35	17		3	19.06	< 0.001
10	3	17	6	2		3	18.22	< 0.001
	64	44	78	55	Pooled	3	10.32	< 0.05
					Heterogeneity	12	67.46	< 0.001
					Total	15	77.78	< 0.001
Irwin site								
12, 13, 14, 16, 17 & 21	16	19	19	10		3	3.66	n.s.
11	9	4	4	5		3	2.82	n.s.
15	10	8	4	4		3	4.17	n.s.
18	18	6	8	7		3	8.44	< 0.05
19	4	4	9	8		3	3.37	n.s.
20	4	1	14	13		3	18.59	< 0.001
	61	42	58	47	Pooled	3	4.70	n.s.
					Heterogeneity	15	36.34	< 0.005
					Total	18	41.04	< 0.005
#403 and Irwin	125	86	136	102	Pooled	3	13.75	< 0.001
					Heterogeneity	30	72.38	< 0.001
					Total	33	86.13	< 0.001
#403 versus Irwin (G-test for independence)							2.169	n.s.

1.1 Trail #403 site

1.2 Irwin site
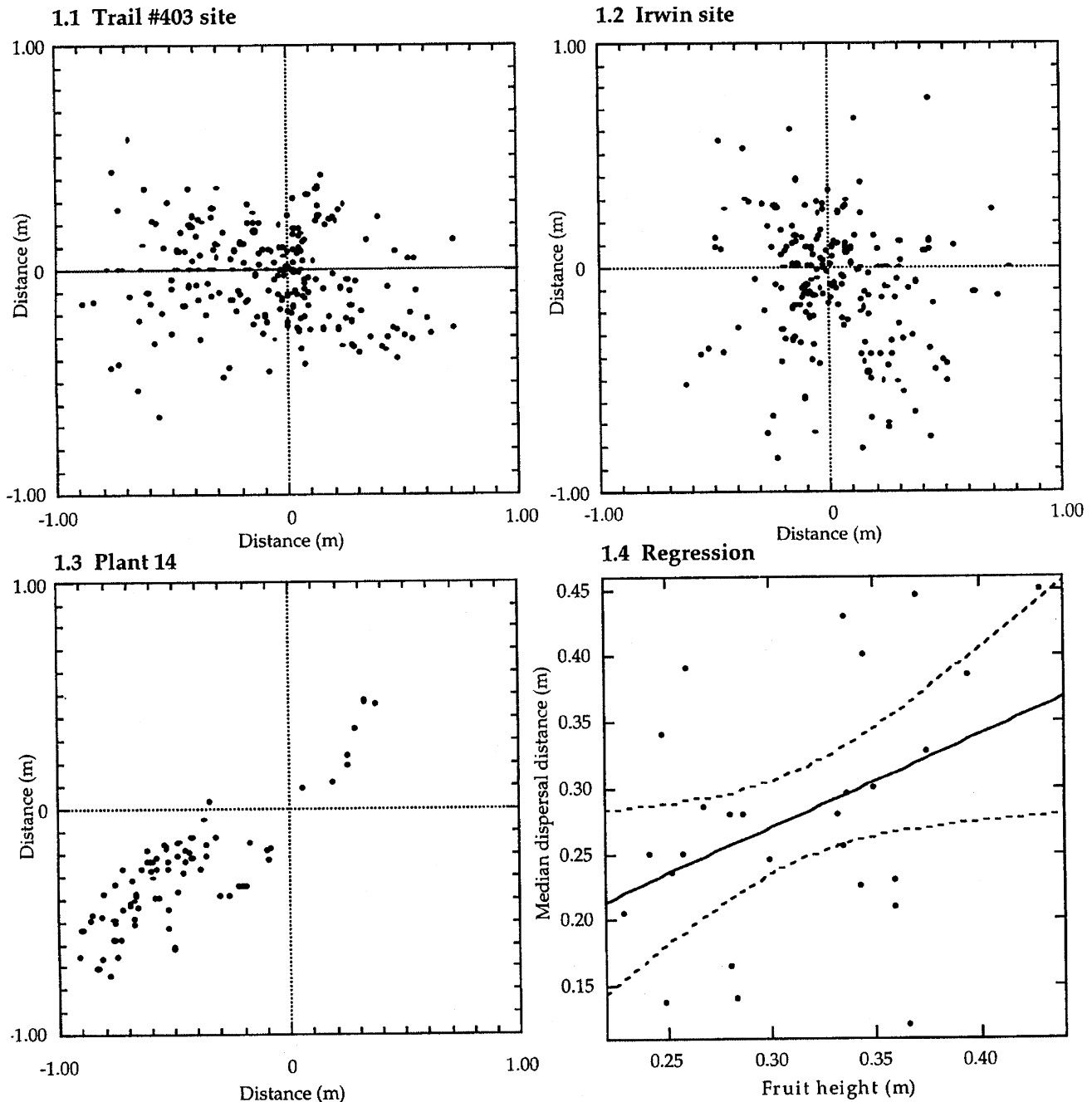

1.3 Plant 14

1.4 Regression

Fig. 1 "Seed shadows" for (*1*) Trail #403 and (*2*) Irwin study sites. Points reflect the positions of seeds on sticky traps relative to their maternal parents (located at the origin). (*3*) From plant 14, 77 seeds were dispersed when a dog strayed across our trap, and these are not included in our analyses. Note the linear, bidirectional pattern. We infer that the dog bent the infructescence toward the NE, spilling some seeds, and then released it. The rebound catapulted many seeds to the SW. (*4*) Linear regression (with 95% confidence intervals) for median dispersal distance as a function of height for 27 fruits. The regression (*y*-intercept = 5.947, coefficient = 0.704, $r^2 = 0.161$, $P < 0.05$) excludes fruits that dispersed fewer than five seeds

heterogeneous. A comparison between Irwin and Trail #403 of total captures in each quadrant indicated that the sites were not independent (Table 1).

Median seed dispersal distances at Trail #403 and Irwin were 0.32 m and 0.26 m, respectively (Table 2). There was overall a roughly linear relationship between dispersal distance and fruit height, although the regression of median transport distance on fruit height was significant at Irwin but not at Trail #403 (Table 2). The line for the regression of the pooled data is plotted in Fig. 1.4. We also tested for the effect of fruit position (and height) on median distance within individual plants (Table 3). Seeds from upper fruits dispersed statistically greater distances than seeds

Table 2 Regressions for seed transport distance as a function of fruit height. Median transport distance is the distance away from the parent at which one half of the seeds are deposited (see Thomson et al. 1986). Mean transport distance is the average distance a seed traveled away from the parent plant prior to striking the ground.

Since multiple seeds were captured from each fruit, we tested for the significance of relationships between dispersal distance and fruit height by performing analyses of variance using the mean square values from each regression (ns = not significant)

	Median (mean) distance	Regressions			Analyses of variance			
		y-intercept	coefficient	r^2	df	MS	F	P
#403	0.32 (0.33)	13.006	0.425	0.042	1	82.0	0.740	n.s.
Irwin	0.26 (0.32)	−1.083	0.982	0.300	1	647.0	8.152	< 0.05
Pooled	0.28 (0.325)	3.355	0.784	0.163	1	678.4	7.225	< 0.05

Table 3 Summaries of seed transport for 20 plants. Fruit height and median dispersal distance are listed separately for upper and lower fruits (middle fruits in parentheses). Mann-Whitney U tests compared medians within two-fruited plants. We used Kruskal-Wallis (K-W) tests for three-fruited plants and for the pool of all individuals. A Wilcoxon's signed-ranks test examined median differences between upper and lower fruits in two-fruited plants and upper and middle fruits in three-fruited plants. (ns = not significant)

Plant	Lower fruit		Upper fruit		Test statistic		P-value	Difference
	Height (m)	Distance (m)	Height (m)	Distance (m)				
1	0.258	0.250	0.335	0.255		19.5	n.s.	+ 0.005
2	0.281	0.280	0.360	0.230		48.0	n.s.	−0.050
3	0.305	0.140	0.366	0.120		13.0	n.s.	−0.020
5	0.281	0.165	0.370	0.445		132.0	< 0.05	+ 0.280
6	0.196	0.250	0.275	0.190		2.0	n.s.	+ 0.060
7	0.268	0.285	0.337	0.295		26.0	n.s.	+ 0.010
8	0.249	0.137	0.343	0.225		28.5	n.s.	+ 0.087
9	0.248	0.340	0.336	0.430		483.5	< 0.05	+ 0.090
10	0.274	0.110	0.375	0.327		17.5	n.s.	+ 0.217
11	0.335	0.515	0.429	0.450		37.0	n.s.	−0.065
12	0.234 (0.288)	0.200 (0.182)	0.350	0.300	K-W =	0.646	n.s.	+ 0.117
14	0.336	0.192	0.395	0.385		0.77	n.s.	+ 0.192
15	0.260 (0.300)	0.390 (0.245)	0.332	0.280	K-W =	0.696	n.s.	+ 0.035
16	0.229	0.205	0.287	0.280		28.0	n.s.	+ 0.075
17	0.250	0.260	0.295	0.370		1.0	n.s.	+ 0.110
18	0.253	0.235	0.345	0.400		129.0	= 0.05	+ 0.165
20	0.284	0.140	0.360	0.210		67.5	< 0.05	+ 0.070
Total	0.266	0.272	0.358	0.362	K-W =	157.5	< 0.05	Σ signed-ranks:
Wilcoxon's signed-ranks test							< 0.005	−15; + 138

Fig. 2 Frequency distribution of seed captures with respect to distance from maternal parents. We fitted an exponential function ($x \cdot e^{1.923-0.0545x}$) to our observations. The integral of the function is plotted as a percentage of the total area under the curve, predicting the percentage of seed captures up to dispersal distances of 1.5 m
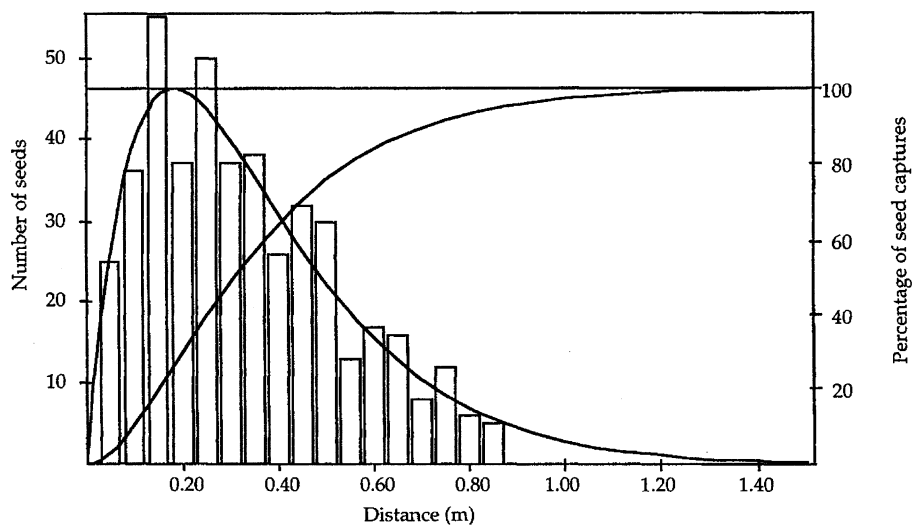
from lower fruits in 4 plants, while the remaining 13 within-plant comparisons were not significant. Mann-Whitney and Wilcoxon's signed ranks tests including all plants indicated that upper fruits tended to have significantly greater median dispersal distances than lower fruits.

A histogram of seed transport distances (Fig. 2) indicated that the seed dispersal curve was positively skewed ($G_1 = 0.72$, student's $t = 6.2$, $P < 0.001$). Kurtosis ($G_2 = -0.18$) did not deviate significantly from normality (student's $t = 0.23$, not significant). We feel that a 1 m radius was sufficient to describe a significant portion of the seed dispersal curve. We fitted an exponential function to the frequency distribution and plotted the integral of the function as a percentage of the total area under the curve. Extrapolation from the probability curve predicts that more than 95% of the seeds fall within 0.9 m of the parent plant. The percentage of seeds traveling more than 1.5 m would be extremely low.

Secondary seed transport

Cafeteria experiments suggested that secondary seed transport in *E. grandiflorum* was negligible compared to *V. nuttallii*, an ant-dispersed species common in the same habitats. The analysis of variance summarized in Table 4 indicates that significant components of variation in seed removals were explained by the time of removal, type of treatment, and species of seed, but not by the location of cafeterias within the grid. Numbers of *E. grandiflorum* seeds removed from the grid during the day (0900–1600 hours) and during the night (1600–0900 hours) were minimal compared to *V. nuttallii* (Table 5). During the daytime, most seeds were probably removed from the "open ground" cafeterias by ants, as evidenced by high seed removals from the "rodent exclusion" cafeteria for *V. nuttallii*. Greater numbers of *V. nuttallii* seeds were removed from the "ant exclusion" cafeteria between 1600 and 0900 hours than from other cafeterias, suggesting that rodents were more active at night in our study area. *E. grandiflorum* seed removals from the "open ground", "rodent exclusion", and "ant exclusion" cafeterias did not differ statistically from the control cafeteria, whereas *V. nuttallii* removals from the same cafeterias were highly significant compared to their control. Significantly more *V. nuttallii* seeds were removed from the cafeterias than seeds of *E. grandiflorum* in all treatments except the control, where there was no difference.

Table 4. Analysis of variance of seed removal from our cafeteria experiment. Plot location was not significant, so we present a simplified ANOVA with only the effects of variation in treatment type (open ground, rodent exclusion, ant exclusion, or control), seed species (*Erythronium* or *Viola*), and location of cafeteria plot within the grid (1–20) (ns = not significant)

Source	df	SS	MS	F-value	P-value
Time of removal	1	123.84	123.84	76.89	< 0.001
Seed species	1	969.53	969.53	601.95	< 0.001
Treatment type	3	550.53	183.51	113.94	< 0.001
Plot location	19	46.99	2.47	1.54	n.s.
Residual	1255	2021.346	1.611		

Table 5 Secondary seed transport in *Erythronium grandiflorum* and *Viola nuttallii*. Seeds removed from the cafeteria grid during the daytime (0900–1600 hours) and night time (1600–0900 hours) are listed separately by species and treatment type. Five seeds per treatment in each of 20 plots within the grid yielded a total of 100 seeds per treatment ($n = 5$ days for each species). Removals were compared between *E. grandiflorum* and *V nuttallii* using Fisher's protected LSD for ANOVA. (ns = not significant)

	Mean seeds removed (SD)		
Day (0900–1600 hours)	*E. grandiflorum*	*V. nuttallii*	P-value
Open ground	7.0 (5.6)	56.8 (14.5)	< 0.001
Rodent exclusion	6.0 (4.2)	56.4 (9.2)	< 0.001
Ant exclusion	2.5 (2.1)	15.0 (7.9)	< 0.01
Control	0.6 (0.5)	3.0 (3.1)	n.s.
Night (1600–0900 hours)			
Open ground	2.7 (2.3)	32.0 (15.0)	< 0.005
Rodent exclusion	2.0 (2.0)	22.7 (11.9)	< 0.01
Ant exclusion	1.0 (1.0)	33.3 (16.2)	< 0.001
Control	1.3 (1.5)	9.7 (5.5)	n.s.

Neighbourhood parameters

The calculation of Wright's genetic neighborhood statistics was simplified in our case because we did not need to correct for leptokurtosis (Crawford 1984b). We estimated neighborhood area (A) and neighborhood size (N_e) based on seed shadows, and combined these with previous estimates (Thomson and Thomson 1989) from pollen shadows. The axial variance of seed dispersal distance (σ_s^2) was calculated as one-half of $\sigma_{s\text{ absolute}} = \Sigma x^2/n$, where x equals dispersal distance, assuming a mean value of zero, and n equals the number of samples. Neighborhood area was computed from the formulae: $A_s = 4\pi\sigma_{s^2}$ for seed only, and $A_{p+s} = 4\pi(1/2\sigma_{p^2} + \sigma_{s^2})$ for pollen and seed combined. The contribution of pollen to neighborhood area is half that of seed since pollen is haploid (Crawford 1984a). We calculated the effective neighborhood size as $N_e = Ad$, where d is the local flowering plant density. Flower density was obtained by counting the number of flowering individuals within belt transects (0.5 × 50 m² at Trail #403 and 2 × 110 m² at Irwin).

Seed dispersal variance was nearly identical at the Trail #403 and Irwin field sites ($\sigma_{s^2} = 0.022$ m²) and yielded similar estimates of neighborhood area ($A_{\#403} = 0.28$ m² and $A_{\text{Irwin}} = 0.27$ m²). Differences in flower density among the sites ($d_{\#403} = 3.90$ m^{-2} and $d_{\text{Irwin}} = 3.04$ m^{-2}) yielded neighborhood sizes that were close to unity ($N_{e(403)} = 1.11$ and $N_{e(\text{Irwin})} = 0.83$). N_e based solely on seed dispersal is negligible when compared to N_e based on pollen shadows (50–2500 plants; see Thomson and Thomson 1989). Estimates of A and N_e combining pollen and seed shadows were computed using average values of σ_{p^2} (13.18 m²) and σ_{s^2} (0.022 m²). $A_{\text{seed+pollen}}$ was only 86 m², compared to 83 m² for A_{pollen} only. Assuming a mean flower density of 3.50 m², $N_{e(\text{seed + pollen})}$ was 302 plants, compared to 290 plants for $N_{e\ (\text{pollen})}$. The addition of seed dispersal data did not

dramatically increase our estimates of N_e for *E. grandiflorum*.

Discussion

Mean seed dispersal distance for *Erythronium grandiflorum* (0.325 m) was less than the averages reported in the literature for various perennial herbs, including *Echeveria* (1.1 m; Para et al. 1993), *Liatris* (2.5 m; Levin and Kerster 1969), *Phlox* (1.1 m; Levin and Kerster 1968), and *Viola* (0.8–2.1 m; Beattie and Lyons 1975). Although our data suggest that seed dispersal in *Erythronium grandiflorum* is highly restricted, the primary limitation of our method should be considered before accepting such a statement. The outer tail of the seed distribution was beyond our measurement since we captured seeds only within a 1 m radius of individual plants. The tail of the seed dispersal curve may be important to gene flow and population structure (Portnoy and Willson 1993), but it is a very difficult phenomenon to measure in the field (Levin 1981). Based on our extrapolation from the curve in Fig. 2, the probability of a seed traveling more than 1 m away from its parent would be less than 0.05. A 1 m radius was therefore adequate to describe a substantial portion of the seed dispersal curve in *E. grandiflorum*. The seed shadow was skewed to the right and had nearly zero kurtosis. A leptokurtic distribution has often been observed in studies of seed dispersal (Beattie and Culver 1979; Eguiarte et al. 1993; Fenster 1991; Levin and Kerster 1969; Meagher and Thompson 1987; Para et al. 1993). There is no a priori reason to expect a leptokurtic seed shadow for *E. grandiflorum*, although we might have encountered significant kurtosis had we sampled a wider radius. Slow rates of seed release from some fruits resulted in failure to obtain complete seed captures from all plants during our experiment. Heavy rain in 1990 also interfered with the original seed traps deployed at Trail #403.

Despite these sampling limitations, we found that variability in the height of fruits can affect the average distance of seed transport. The relationship between height and distance has been assumed in some studies (Fox 1993; Lee 1984), and has proved difficult to establish in others (Para et al. 1993). Our method of dyeing seeds from different fruits permitted us to test the height-distance relationship within individual plants. Not surprisingly, we found that seeds from higher fruits tended to travel greater distances than seeds from lower fruits. While there was an overall trend, the effect was not detectable across all individual comparisons, largely due to small seed numbers from some fruits. It is worth noting, however, that our estimates do not take into account the surrounding vegetation, which could have a damping effect on dispersal distances.

Seed shadows for most individual plants showed directionality (six out of nine plants where analysis was possible). Directionality has also been demonstrated for *E. grandiflorum* pollen shadows resulting from the foraging movements of bumblebees (Thomson and Thomson 1989). Seed shadows for ballistically dispersed species such as *Viola* (Beattie and Culver 1979) and *Cassia* (Lee 1984) are also directional, but no specialized launch mechanism is present in *E. grandiflorum*. Seed shadows were highly heterogeneous with respect to direction, but there was an overall NW-SE trend at Trail #403. We believe that the trend may have been a function of the prevailing wind direction at the site, although we did not measure wind speed or direction in the field.

E. grandiflorum seeds lack aerodynamic adaptations, although wind may be the most significant dispersal vector. Wind-dispersed seeds often have aerodynamic structures that increase dispersal distances by reducing the settling velocity of falling propagules (Andersen 1993; Augspurger 1986; Levin and Kerster 1968). Adaptive features such as plumes, beaks, and wings are absent in *E. grandiflorum*, but the mechanism of seed release from the fruits is dynamic. Seeds are launched when mechanical vibrations induced by wind or other disturbance exceed the oscillatory mode of the erect peduncle (Burrows 1986). This type of release mechanism should impart directionality to the seed shadow, which we did observe from a number of individual plants, including the dog-dispersed plant in Fig. 1.3.

We might expect wind-dispersal strategies in subalpine plants such as *E. grandiflorum*, since their habitat is subject to turbulent winds and is depauperate in biotic dispersal agents. *E. grandiflorum* seeds are too heavy (0.16 ± 0.04 mg, $n = 50$) to respond to turbulence, and are therefore unlikely to be dispersed long distances by wind. *E. grandiflorum* also lacks adaptations for animal-mediated dispersal, in contrast to *E. americanum* seeds, which bear eliaosomes and are ant-dispersed in eastern North American deciduous forests (Handel et al. 1981). Although we did not measure secondary dispersal distances directly, we found that rates of seed removal by the two most likely animal vectors, ants and rodents, were negligible. It would be instructive to know if the eliaosome is an ancestral or derived character in *Erythronium*. If eliaosomes were present in the ancestral *Erythronium* species, then *E. grandiflorum* may have lost an ant-dispersal strategy in its subalpine environment.

We suggest that the selective advantages often invoked to explain adaptive strategies for long-distance dispersal may not be important for *E. grandiflorum*. Hypotheses for long-distance dispersal include: (1) escape from density-dependent predation, (2) transport to favorable microsites for establishment, and (3) increased gene flow (Howe and Smallwood 1982). Although it is beyond the scope of our study to infer whether ants or rodents are seed dispersers or

predators, our cafeteria results suggest that neither ants nor rodents show much interest in *E. grandiflorum* seed. Post-dispersal seed predation at our study site appears to be minimal, especially when compared to pre-dispersal predation by deer and elk that we have repeatedly observed in the field. We feel that in our research area corm predation by pocket gophers may have an even greater impact on the spatial structure of *E. grandiflorum* populations than predation at any other life history stage.

If seed predation near the parental plants is minimal, and seed dispersal is localized, we might expect heavy seedling establishment within 0.5 m of the parents. In a seedling census of 256 quadrats measuring 2 × 2 m (J. D. Thomson and G. D. Weiblen, unpublished data), we found that seedlings were not positively associated with flowering plants; in fact, the data suggest a negative relationship. A negative spatial correlation between seedlings and adults may not be unusual in subalpine meadows, where the distributions of microsites favoring seed germination and survival to maturity are patchy. From our population census, it appears that the optimal sites for seed germination are not necessarily the optimal sites for seedling recruitment. Flowering plants occurred in rocky sites with dry soil, but seeds tended to germinate in deep and moist soil. We hypothesize that seeds fail to germinate in rocky sites due to desiccation, and that flowering plants are rare in rock-free soil due to corm predation by gophers, who avoid rocky areas. Flowering populations are thus the "source" for a "sink" population of seedlings that seldom attain maturity. In this scenario, any selective advantage of dispersal away from the parent would be small, since the probability of locating a microsite suitable for both germination and survival to maturity would be extremely low.

Genetic neighborhood calculations assume that pollen and seed distribution patterns adequately reflect patterns of gene dispersal and establishment (Crawford 1984b), which may not be the case in *E. grandiflorum* for reasons discussed below. Previous measures of A_p were not corrected for leptokurtosis or for the rate of self-pollination (see Thomson and Thomson 1989 for explanation). Our estimates are therefore not accurate measures of gene flow, but rather indicators of the relative contribution of pollen and seed to gene flow.

Neighborhood estimates indicate that seed dispersal makes a relatively small contribution to gene flow, compared to pollen dispersal by bumblebees. Studies comparing pollen and seed dispersal have generally concluded that pollen accounts for most of the gene dispersal in natural populations (Beattie and Culver 1979; Eguiarte et al. 1993; Fenster 1991; Levin and Kerster 1968; Meagher and Thompson 1987; Para et al. 1993). The addition of *E. grandiflorum* seed dispersal data to previous neighborhood estimates based solely on pollen shadows (Thomson and Thomson 1989) only increased N_e from 290 to 302 plants. This was due to the fact that pollen dispersal variance (σ_{p^2}) exceeded seed dispersal variance (σ_{s^2}) by several orders of magnitude. Wright (1979) suggested that a neighborhood of this approximate size would permit a moderate degree of local genetic differentiation and drift.

We hypothesize that selection for long-distance seed dispersal mechanisms yielding increased gene flow is unlikely to occur in *E. grandiflorum*. Long-distance seed dispersal does not automatically increase gene flow, as this ultimately depends on establishment and survival to reproductive maturity. Since seed dispersal is not likely to result in seedling establishment outside of the immediate genetic neighborhood, gene flow among *E. grandiflorum* populations may be accomplished more readily through pollen dispersal by bumblebees. A further step toward determining the effects of pollination and seed dispersal on genetic structure will require a close look at patterns of realized gene flow, possibly using genetic markers.

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