

WIND DISPERSAL DISTANCES IN DIMORPHIC ACHENES OF RAGWORT, *SENECIO JACOBAEA*¹

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Abstract. A mark–recapture study of wind-dispersed achenes of *Senecio jacobaea* conducted in western Oregon showed that the proportion of achenes dispersing a given distance varied significantly with changes in site (inland vs. coastal), surroundings (mown vs. unmown), height of release (0–50, 50–100, 100–150, 150–200 cm), time of release (early vs. late in the season), direction of dispersal, and achene type (disk vs. ray achenes). Influences of height of release, direction, achene type, and time of release were strongly conditioned by site and surroundings.

The majority of achenes dispersed very short distances. Of 53 301 achenes falling in the recapture area, 31% travelled only 1 m, 89% travelled 5 m or less, and none were collected >14 m from the source. Thus, while it is theoretically possible for these wind-dispersed achenes to travel long distances, actual dispersal distances are short due to local conditions of humidity, wind, and vegetation structure.

Key words: alien; biennial; colonization; demography; dispersal; fugitive; life history; population dynamics; seeds; *Senecio jacobaea*; somatic polymorphism.

INTRODUCTION

Seed dispersal can influence the population biology of higher plants by contributing to changes in population size (Harper 1977), to founding of new populations (Ridley 1930, van der Pijl 1969), and to gene flow between established populations (Levin and Kerster 1974, Levin 1981, 1984). Dispersal can, in theory, profoundly alter species interactions in a patchy environment, facilitating coexistence of competitors, of predator and prey, and of parasite and host, thereby increasing diversity (Levin 1974, 1976a, b). Evolutionary advantages of dispersal are colonizing new sites and avoiding unfavorable conditions at the home site. Mathematical models suggest dispersal is of special advantage to organisms that live in transient habitats (Gadgil 1971, Roff 1975, Comins et al. 1980, Levin 1980), yet it is also important to organisms that live in uniform and predictable environments (Hamilton and May 1977).

The measurement of dispersal in natural populations has lagged behind the theoretical studies. For plants, only a handful of studies has measured the distribution of seeds or juveniles around the parent (see reviews by Levin and Kerster 1974, Harper 1977, Cook 1980, Howe and Smallwood 1982). Most studies have focused on the evolutionary origins and ecological consequences of dispersal without measuring the frequency distribution of individual dispersal distances. We measured distances moved by individual wind-borne achenes (fruits) of ragwort *Senecio jacobaea* L. liberated from the parent under a variety of field conditions. We then used our results to interpret other aspects of

ragwort's population biology, including colonization of new areas, population dynamics, the spread and control of weed infestations, life history evolution, and plant–herbivore interactions.

Ragwort is a biennial or short-lived perennial herb native to Europe and introduced in North America, Australia, and New Zealand. The plant displaces forage species in pastures, is toxic to livestock, and is a target of biological, chemical, and cultural control programs (Cheeke 1979).

Ragwort fruits are heteromorphic: fruits with different morphologies and behaviors are produced on different parts of a flowering head (capitulum) (Green 1937, Baker-Kratz and Maguire 1984, McEvoy 1984). Central (disk) florets yield achenes that are lighter, more numerous, and bear a pappus that aids wind transport, and rows of trichomes that aid animal transport (Fig. 1a). Marginal (ray) florets yield achenes that are heavier, less numerous, and lack obvious dispersal structures (Fig. 1b). Whereas disk achenes are released shortly after they mature, ray achenes remain on the parent plant for a period of months following maturity. These differences should result in differential dispersal in nature. Earlier studies of ragwort dispersal (Poole and Cairns 1940) did not distinguish the two achene types.

Movement of seeds is influenced by a variety of factors including source height, source concentration, dispersability of the seed, activity of the dispersal agent, etc. (Harper 1977), and it is difficult to isolate the effect of each factor in a single field experiment. We used modified field environments, marking achenes on source plants and recapturing them in linear arrays of traps extending outward from the source. We analyzed the effect of differences in site (coast vs. inland) surrounding vegetation (mown vs. unmown), time of re-

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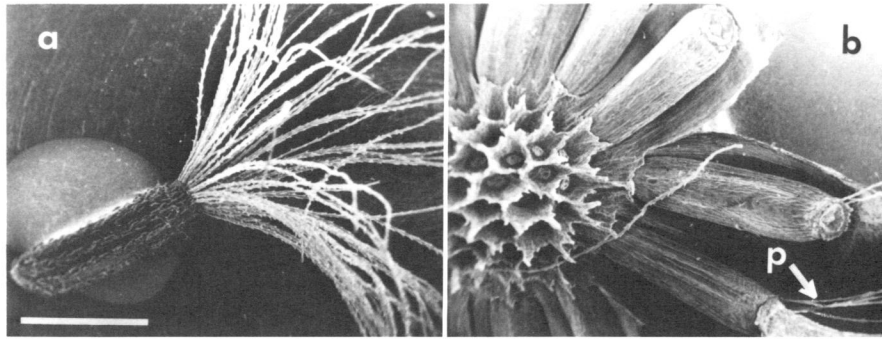


FIG. 1. (a) Scanning electron micrograph of disk achene showing pappus and rows of trichomes on the achene surface; (b) Scanning electron micrograph of the ray achenes cradled in the bracts following dispersal of the disk achenes. Arrow denotes vestigial pappus p, which is shed prior to release of ray achenes. Reference bar: 1 mm.

lease (early vs. late in the season), height of release (0–50, 50–100, 100–150, 150–200 cm above the ground), direction of dispersal (N, E, S, W), and achene type (disk vs. ray). This encompasses most of the sources of variation in wind dispersal of seeds.

METHODS AND MATERIALS

We trapped dispersing ragwort achenes during the fall of 1981 at two sites in western Oregon, USA. The first site (45°2'22" N, 123°59'3" W) was located in the central coast of Oregon, south of Three Rocks Road in the Cascade Head Scenic Research Area, near Otis, Tillamook County. The second site (44°42'30" N, 123°12'30" W) was located 66 km inland in the central Willamette Valley at the Wilson Game Farm, 9 km north of Corvallis, Benton County. The vegetation at the coastal site was essentially a monoculture of ragwort with a mean density of 60 stems/m² (maximum density 104 stems/m²), whereas at the inland site a sparse stand of ragwort (maximum density 30 stems/m²) was interspersed with occasional stems of weedy forbs (*Cirsium arvense*, *Daucus carota*, *Chrysanthemum leucanthemum*) of stature similar to ragwort, rising above a lower, background vegetation composed predominantly of grasses. Stem height, capitula per stem, and capitulum height were all greater for the coastal site (Table 1). Weather conditions at both sites follow the typical western Oregon pattern of wet winters and dry summers (Fig. 2). From August through November, when ragwort achenes disperse, the coastal site has more rainfall (88.0 cm in 1981) than the inland site (39.0 cm). Rainfall is also more frequent at the coastal site (43 d with > 3 mm of rain in 1981) than at the inland site (32 d). Average wind speed is higher at the coastal site.

Each grid of traps consisted of ≈60 traps laid out in a cross pattern. Traps extended to 16 m on at least one leg of each grid and 15 m on most legs. Trap positions alternated left then right of lines extending from the center and were spaced 1 m on center to preserve some undisturbed vegetation between traps and the seed

source. For analysis, traps > 14 m from the source were excluded, as no seeds were trapped at those distances. The traps were aluminum offset printing plates covered with a thin layer of Stikem Special (Seabright Enterprises, Emeryville, California) adhesive applied with a rolling pin. Two sizes of traps were used, 50 × 70 and 40 × 70 cm, and each trap was marked with a grid of 10 × 10 cm cells to facilitate counting and collecting of seeds. We used nails (15 cm long) to secure the traps to the ground.

At each site we set out two grids with the centers separated by 50 m. One grid was established in an area that had been mown to remove all of the vegetation except the source plants. At the coastal site this area required periodic clipping to keep mown vegetation < 30 cm tall. The other grid was set out in undisturbed vegetation; we removed only plants that interfered with placement of the traps or access to them.

The source plants in each grid bore ≈1000 capitula (range 902–1367). Achenes in each capitulum were marked with fluorescent powders (Radiant Color, Richmond, California) applied from a plastic squirt bottle. We used four colors to indicate the height above the ground of each capitulum. Because of differences in the height of plants at the two sites, the distribution of marked heads differed between sites (Table 2). Preliminary tests showed that marking did not affect the

TABLE 1. Comparison of ragwort plants sampled at inland and coastal sites in December 1981.

	Stem height (cm)	Capitula per stem	Capitulum height (cm)
Inland site			
\bar{X}	77.7	70.7	71.2
SE	1.6	9.1	14.7
n	85	20	20
Coastal site			
\bar{X}	125.3	133.2	121.7
SE	1.7	21.1	16.3
n	70	20	20

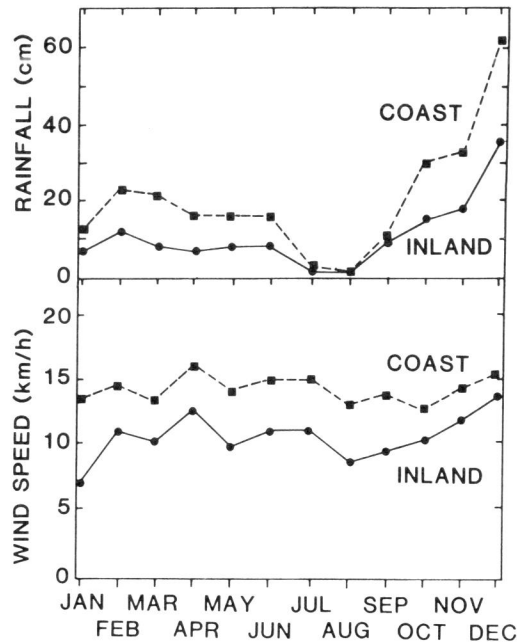


FIG. 2. Monthly rainfall and average wind speed during 1981 for inland and coastal sites. Rainfall data for the inland site are from the Oregon State University weather station, Corvallis, and from the Otis 2 NE station for the coastal site. Wind speed data are from the Salem Airport for the inland site and from Astoria Airport for the coastal site.

proportion of seeds dispersing a given distance under field conditions.

We first marked capitula on the source plants on 18 August at the inland site and 23 August at the coastal site. We censused, marked, and trapped achenes at six approximately biweekly intervals during the rest of the dispersal season, which ended in mid-November. We re-marked source capitula immediately following each census, except on 30 October, when marking was postponed for a week due to heavy rain. On each date after 15 September we collected all marked achenes for microscopic determination of achene type.

Trapping efficiency declined over time due to weathering of the adhesive and saturation by achenes. All traps were removed on 5 October (coastal site) and 16 October (inland site). New traps were set out on 11 October (coastal site) and 19 October (inland site).

Because the fraction of the total dispersal area that is trapped declines as the distance from the source plants increases, our trapping design underestimates the fraction of achenes that disperse long distances. To calculate the true proportion of achenes dispersing a given distance, we transformed trap catches to estimate the number of achenes that would have been trapped had trap area remained a constant fraction of potential dispersal area. The formula used to transform the data was:

$$X' = (X)(\pi/4)(1/A)(2wr + w^2),$$

where X = trap catch, A = trap area, r = distance of the front of the trap from the source, and w = trap width.

Distributions of dispersal distances were highly non-normal both before and after transformation, so we used nonparametric statistical tests, the Kolmogorov-Smirnov two-sample test and its K -sample analogue (Kiefer 1959), on untransformed data to test for significant differences between treatments. We summed trap catches over all four directions to determine the effect of release height, and summed catches from all release heights to determine the effect of dispersal direction. Catches were summed over both of these treatments to determine the effect of site, surrounding, and achene type. The effect of time of release was analyzed by comparing distance distributions for early (censuses 1–3, \approx August–September) and late (censuses 4–6, \approx October–November) dispersing achenes. Since these contrasts would not have been orthogonal had an analysis of variance been possible, significance levels were adjusted according to the Dunn-Sidak Method (Sokal and Rohlf 1981). We report the results of the tests either as D , the maximum difference between two relative cumulative frequency distributions, or as T , the K -sample test statistic. While tests were made on untransformed data, medians based on transformed data were used to summarize the data. We used medians instead of means due to the skewed nature of the distributions. The medians were calculated using methods for data collected as frequency distributions, assuming seed densities changed linearly between traps (Sokal and Rohlf 1981).

RESULTS

The most striking result of this study is that the majority of achenes dispersed very short distances. Of 312 000 achenes marked (Table 2), 53 501 (17%) fell in the trap area, while the rest remained on source plants or dispersed <1 m and did not reach the first trap. Of those dispersing into the trap area, 31% travelled only 1 m, 89% travelled 5 m or less, and none was collected >14 m from the source.

Effect of site

Achenes dispersed significantly farther at the inland site than at the coastal site, and the difference between

TABLE 2. Distribution of marked capitula. Assuming an average of 70 achenes per head, we marked ≈ 312 000 achenes.

Release heights (cm)	Inland site		Coastal site		Totals
	Mown grid	Un-mown grid	Mown grid	Un-mown grid	
>150	0	0	577	500	1077
101–150	186	215	567	513	1481
50–100	645	748	223	200	1816
<50	71	10	0	0	81
Totals	902	973	1367	1213	4455

sites was greater on unmown than on mown grids (Fig. 3, Table 3). The median dispersal distance at the inland site was $1.39 \times$ that of the coastal site comparing mown grids, and $2.29 \times$ that of the coastal site comparing unmown grids.

Effect of surrounding vegetation

At both sites, achenes dispersed farther when surrounding vegetation was mown than when natural vegetation remained (Fig. 3, Table 3). The medium dispersal distances on the mown grid were $2.57 \times$ that of the unmown grid at the coastal site, and $1.56 \times$ that of the unmown grid at the inland site. The taller and denser vegetation at the coastal site likely explains why the contrast in dispersal distances between mown and unmown surroundings was greater there than at the inland site, and why the contrast in dispersal distances between sites was greater in unmown surroundings than in mown surroundings.

Effect of release height

The height at which achenes were released affected dispersal distances on the mown but not on the unmown grids (Table 4). At the coastal site the median dispersal distance of seeds from the tallest plants was $1.92 \times$ that of the shortest plants. At the inland site the factor was 1.64.

Effect of direction

Dispersal distances also varied with the dispersal direction (Table 4), but there was little association between direction of dispersal and direction of prevailing winds. At the coastal site distances varied with direction only on the mown grid. Achenes dispersing to the south and east dispersed farther than those dispersing to the west. Dispersal distances to the north were intermediate. A continuously recording mechanical weather station (Weathermeasure) at the coastal site

TABLE 3. Effect of site and surroundings on median dispersal distances (m). Ranges in parentheses and sample sizes in brackets.

Inland site	Coastal site	D^\dagger (between sites)
Mown grid		
2.5 (1-14) [8229]	1.8 (1-14) [10 242]	0.13*
Unmown grid		
1.6 (1-12) [5878]	0.7 (1-13) [2230]	0.34*
D (between grids)		
0.41*	0.16*	

* Adjusted $P < .05$ (corresponds to unadjusted $P < .0015$). Adjustment of significance levels was according to the Dunn-Sidak Method (Sokal and Rohlf 1981).

† The maximum distance between two relative cumulative frequency distributions.

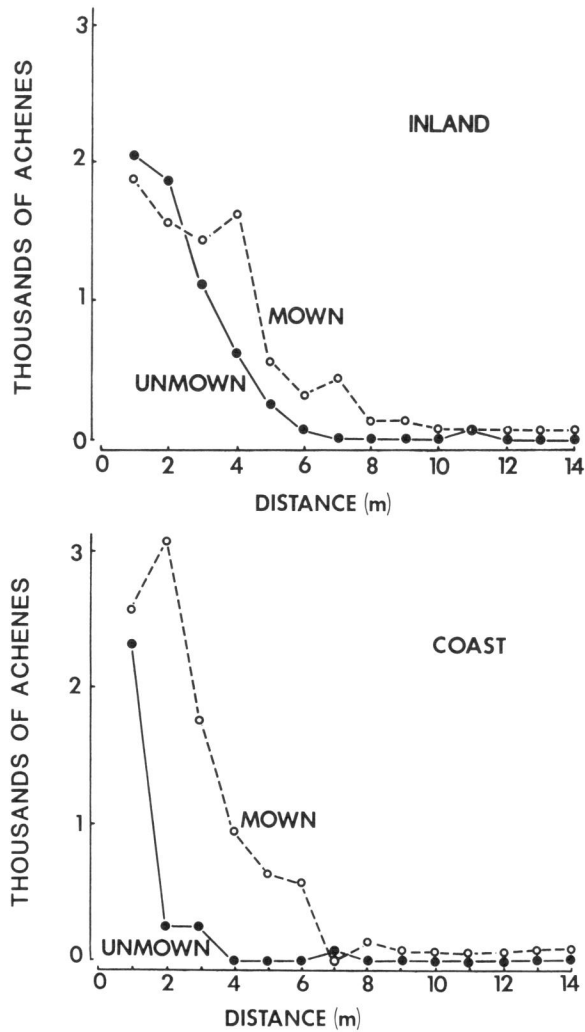


FIG. 3. Numbers of achenes dispersing a given distance at the inland and coastal sites with natural and mown surroundings. Data plotted are transformed trap catches.

indicated that winds > 8 km/h were from the southeast 79% of the time, including a violent storm 14 November 1981. The direction of light winds was highly variable. At the inland site, on the mown grid, seeds dispersed farthest to the east and south. On the unmown grid, dispersal distances were greatest to the north.

Effect of achene type

Disk and ray achenes had different distributions in space and time. Disk achenes dispersed farther than ray achenes on the mown grid of the inland site, but achene differences were not significant on the other three grids (Table 5). However, on all grids the range of dispersal distances of disk achenes was about twice that of ray achenes. Ray achenes appear to be concentrated near the source on mown grids, and the fraction of dispersing achenes that were the ray type increased

TABLE 4. Effect of release height and dispersal direction on median dispersal distances (m). † Ranges in parentheses and sample sizes in brackets.

	Inland site		Coastal site	
	Mown grid	Unmown grid	Mown grid	Unmown grid
Release height (cm)				
> 150	2.1 a (1-14) [4592]	0.8 a (1-8) [1401]
101-150	3.6 a (1-10) [716]	0.9 a (1-3) [279]	1.8 b (1-13) [3663]	0.6 a (1-8) [1080]
50-100	2.6 b (1-14) [7056]	1.6 a (1-12) [5921]	1.1 c (1-12) [1909]	0.6 a (1-13) [742]
< 50	2.2 c (1-6) [774]	1.9 a (1-3) [62]
T_{\ddagger}	5.15*	1.75	5.73*	1.84
Dispersal direction				
N	1.8 b (1-8) [1887]	1.8 a (1-11) [1775]	1.7 ac§ (1-6) [978]	0.6 a (1-11) [587]
E	3.0 a (1-13) [4180]	1.4 b (1-7) [1298]	2.1 b (1-9) [1144]	0.9 a (1-4) [446]
S	3.0 a (1-14) [1579]	1.7 ab (1-12) [2784]	2.7 a (1-14) [1667]	0.6 a (1-3) [282]
W	1.2 b (1-12) [584]	1.0 b (1-3) [502]	1.8 c (1-13) [6570]	0.7 a (1-13) [1570]
T_{\ddagger}	4.20*	2.61*	3.20*	1.78

† Within a column, medians followed by the same letter summarize distributions that are not significantly different (adjusted $P > .05$, corresponding to an unadjusted $P > .0168$ for release height data and $P > .0085$ for direction data).

* Adjusted $P < .05$ (corresponds to unadjusted $P < .0015$).

‡ T is the K -sample test statistic (see Methods and Materials).

§ Differences in medians based on transformed data (transformation according to the equation in Methods and Materials) do not necessarily reflect differences in dispersal distances identified by tests on untransformed data.

progressively through time (Fig. 4). These differences are less clear if the surrounding vegetation is not removed (Fig. 4). This is probably because movement was so restricted in the unmown grid that many ray achenes dispersed < 1 m and failed to reach the first trap.

Disk achenes dispersed earlier than ray achenes; overall 63% of disk achenes were early dispersers compared to 6% of ray achenes (Table 6). Early dispersers accounted for 68–86% of disk achenes on inland grids but only 44–48% on coastal grids. Among disk achenes, early dispersal was associated with longer dispersal distances on the inland mown and the two coastal grids (Fig. 5, Table 6). Early dispersers were in the majority only at the inland site. A clear majority of ray achenes were late dispersers at the inland site (85–96%) and coastal site (87–94%), and dispersal distances of early

and late dispersers were not significantly different (Table 6, Fig. 5).

DISCUSSION

We found dispersal distances were far shorter than previously thought; for example, Begon and Mortimer (1981) speculate that ragwort seeds travel at least 15 m, a figure that exceeds the maximum dispersal distance observed in our study. Our study showed that the effects of height of release, wind direction, achene type, and time of release may be greatly modified by the site and its characteristics (Table 7).

Both the site and surroundings influenced dispersal distances. The coastal site experiences more rainfall and higher wind speeds than the inland site (Table 2). We expected these factors to have opposite effects on dispersal distances, the former to decrease dispersal distances, and the latter to increase them (Sheldon and Burrows 1973). Since dispersal distances at the coastal site were 44–77% of those at the inland site, differences in humidity due to greater rainfall appear to override differences in wind speed. High atmospheric humidity reduces dispersal distances by causing the pappi to become matted and the phyllaries to close around the achenes (Poole and Cairns 1940). The vegetation surrounding the source plants reduced dispersal distances, particularly at the coastal site where the surrounding vegetation was both taller and denser. Surrounding vegetation reduces dispersal distances by reducing wind speed and by obstructing the path of the dispersing achene (Sheldon and Burrows 1973).

The height of release in relation to the canopy affected dispersal distance. The chance of a diaspore being picked up by local rising air currents and carried long

TABLE 5. Median dispersal distances (m) for disk and ray achenes under different sites and surroundings. Ranges in parentheses and sample sizes in brackets.

	Disk achenes	Ray achenes	D_{\dagger}
Inland site			
Mown grid	3.3 (1-14) [7729]	0.9 (1-7) [531]	0.32*
Unmown grid	1.6 (1-12) [5720]	0.9 (1-3) [127]	0.18
Coastal site			
Mown grid	1.7 (1-14) [8422]	1.4 (1-6) [1101]	0.08
Unmown grid	0.6 (1-13) [2837]	0.6 (1-2) [91]	0.06

* Adjusted $P < .05$ (corresponds to unadjusted $P < .0015$). Adjustment of significance levels was according to the Dunn-Sidak Method (Sokal and Rohlf 1981).

† The maximum distance between two relative cumulative frequency distributions.

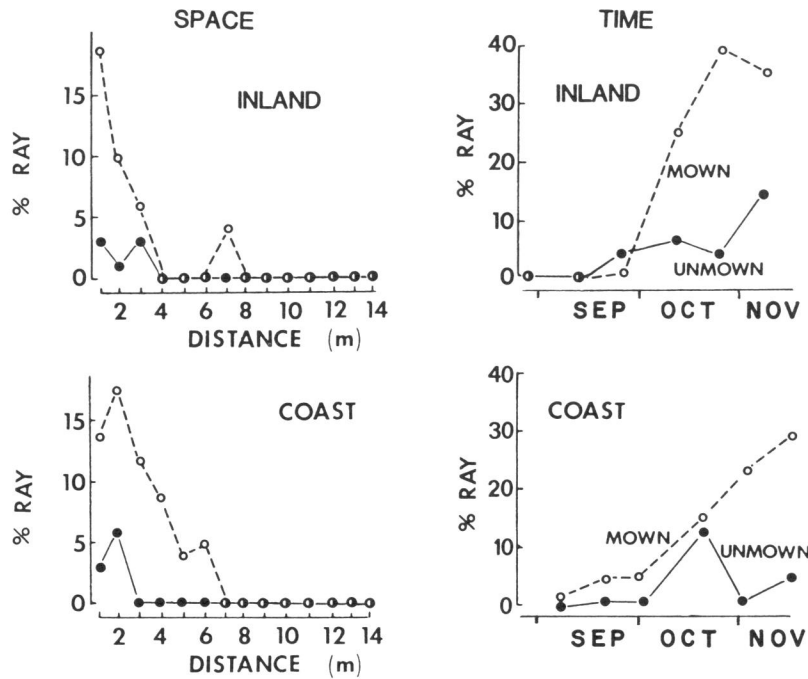


FIG. 4. Distribution of ray achenes (as a percentage of total achenes trapped) in space and time for inland and coastal sites with natural (●—●) and mown (○—○) surroundings. For temporal distributions, the time plotted is the midpoint of the biweekly trapping interval.

distances should increase with an increase in height of release (Sheldon and Burrows 1973). At our study sites, longer dispersal distances were associated with increased height of release only on mown grids. Sheldon and Burrows (1973) reported that maximum dispersal distances increased in direct proportion to release height. Under our field conditions the increase was less.

On the mown grid at the coastal site, ragwort achenes did not travel farthest in the direction of the prevailing winds, although this relationship had been observed earlier by Poole and Cairns (1940). There were no significant direction effects on the unmown grid at the coastal site. At our inland site, local conditions determined the effect of direction, as maximum dispersal occurred in different directions on the two grids.

Differences in the morphology of disk and ray achenes (McEvoy 1984) led us to predict that disk achenes would disperse farther than ray achenes. The pappus and the lighter mass of disk achenes decrease their terminal velocity, prolong their time of fall and increase the chance of the fruit being carried by wind currents. The ray achenes fall more quickly because they are heavier and shed their vestigial pappus prior to dispersal. Secondary dispersal and animal dispersal may increase differential dispersal of disk and ray achenes under some conditions. Since achenes were held where they landed in our experiments, secondary dispersal was impossible. We assume that the dense, low vegetation characteristic of our sites would lead to negligible secondary dispersal. In a dry, open habitat,

however, disk achenes may be moved along the ground or swept into the air by wind, and thus secondary dispersal may increase the differential dispersal by the two achene types. The rows of trichomes on disk achenes may increase their dispersability by increasing the resistance to the air or by aiding attachment to passing animals. Ray achenes lack the surface trichomes.

The differences in dispersability due to achene morphology were affected by site and surroundings. At the coastal site, disk and ray achenes dispersed similar distances, probably because dispersal of disk achenes was sharply reduced by wet weather and tall vegetation. At the inland site, disk achenes dispersed farther than ray achenes on the mown grid, but on the unmown grid the surrounding vegetation reduced the dispersal distances of disk achenes, and differences between achene types were not significant. Thus achene differences appear to yield dispersal differences only in dry, open habitats. Nevertheless, on all four trapping grids the range in dispersal distances of disk achenes was greater than that of the ray achenes.

Differences in the morphology and behavior of disk and ray achenes led us to expect disk achenes would disperse earlier than ray achenes. The temporal differences in dispersal of disk and ray achenes derive not from difference in time of ripening, but from difference in time of retention of ripe seed before dispersal (Baker-Kratz and Maguire 1984). Under environmental conditions favoring dispersal, the disk achenes are blown away as they ripen, leaving ray achenes in the invo-

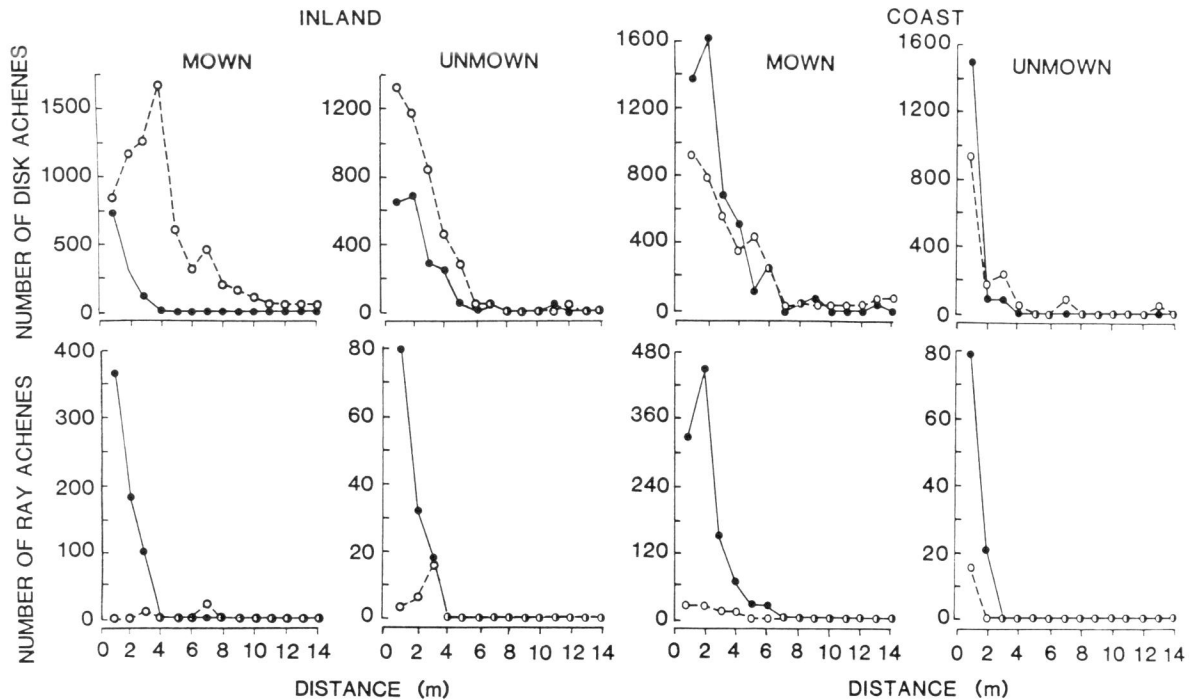


FIG. 5. Numbers of seeds dispersing a given distance for early (O--O) and late (●—●) dispersing achenes for different achenes types, sites, and surroundings. Early dispersers were those recorded in censuses 1–3 (\approx August–September) and late dispersers were recorded in censuses 4–6 (\approx October–November).

lucral cup from which they are eventually shaken out (Green 1937). Under the prevailing climate of dry summers and wet autumns, the early release of disk achenes should increase dispersal distances by increasing the chance achenes will meet with the dry weather that is required for effective functioning of the pappus.

Disk achenes dispersed earlier than ray achenes under all experimental conditions in our study. Among disk achenes, the association between early release and long-distance dispersal was partially obscured by effects of site and surrounding. Early release of disk achenes enhanced their dispersal on the mown inland grid and both coastal grids, yet a majority were early dispersers on only the inland grids. Conversely, early release of disk achenes failed to increase dispersal distances on the unmown inland grid, yet a clear majority of early disk achenes were early dispersers on that grid. Among ray achenes (1) the majority dispersed late, and (2) early and late dispersers travelled similar distances. Since ray achenes lack specialized mechanisms for dispersal, their dispersal distances were short and independent of seasonal changes in the weather.

Effect of dispersal on distribution

Classical surveys of seed dispersal (Ridley 1930, van der Pijl 1969) stress the association between widespread distribution and specialized modifications of the diaspore that aid dispersal. Our findings force a re-examination of mechanisms underlying this associa-

tion. First, diaspore geometry is but one of many factors influencing dispersal distances, and measurements of subtle differences in geometry cannot substitute for direct measurement of dispersal distances. Second, few species disperse exclusively by a single mechanism. Our study suggests wind dispersal is too feeble to account for the widespread and increasing distribution of ragwort. Dispersal may be by humans, animals, or water (Poole and Cairns 1940). Two other features of ragwort's life history, extremely high fecundity (Harper and Wood 1957) and moderately long-term dormancy (Poole and Cairns 1940), increase the probability of successful colonization.

Effect of dispersal on population dynamics

Exchange of migrants between habitats. — The landscape surrounding our study area is a mosaic of habitats with boundaries set by waterbodies, hedgerows, forest margins, and highways. Short dispersal distances measured in our study should lead to very little exchange of migrants between these habitats. At the very least, migrants are at an extreme numerical disadvantage relative to locally produced seed, and we should look to changes in birth and death rates, rather than migration rates, to explain changes in local population size. Restricted dispersal will tend to uncouple the dynamics of one local population from another; local uniqueness (site-specific characteristics such as soils, land use pattern) and phase difference (differences in maturity of

TABLE 6. Median dispersal distances for early (≈August–September) and late (≈October–November) dispersing achenes for different achene types, sites, and surroundings. Ranges in parentheses and sample sizes in brackets.

	Mown			Unmown		
	Early	Late	<i>D</i> †	Early	Late	<i>D</i>
Inland						
Disk	3.2 (1–14) [6827]	0.8 (1–5) [1115]	0.46*	1.7 (1–12) [4161]	1.5 (1–11) [1914]	0.06
Ray	4.0 (3–7) [24]	0.9 (1–3) [627]	0.93	2.3 (1–3) [23]	0.8 (1–3) [129]	0.52
Coast						
Disk	2.3 (1–14) [3724]	1.6 (1–13) [4712]	0.10*	0.8 (1–11) [1515]	0.6 (1–5) [1659]	0.14*
Ray	1.5 (1–4) [67]	1.4 (1–6) [1037]	0.07	0.5 (1) [14]	0.6 (1–2) [96]	0.08

* Adjusted *P* < .05 (corresponds to unadjusted *P* < .0015). Adjustment of significance levels was according to the Dunn-Sidak Method (Sokal and Rohlf 1981).

† The maximum distance between two relative cumulative frequency distributions.

successional habitats or time since last disturbance) are additional ways in which each local population can come to have its own distinctive dynamics (Levin 1976a). The applied significance of our results is that control of ragwort can be successful on a local scale, even when adjacent landowners are not involved.

Shifting occupancy within habitats.—Even in closed habitats, the dynamics of ragwort will be affected by the distribution of safe sites and the speed with which they are colonized. At a scale the size of a seed, the environment can be very heterogeneous and unpredictable (although there may be underlying periodicities). Success lies in chance colonization of safe sites unpredictable in space and time.

Disk and ray achenes have different distributions in space and time, particularly in dry, open habitats. The fruit syndrome in ragwort resembles that of other heteromorphic composites, combining reduced dispersal-delayed germination in the outer achenes and distance dispersal-quick germination in the central achenes (Venable and Lawlor 1980, McEvoy 1984). Disk achenes provide the chance of immediately retaining

the home site and colonizing new sites. Ray achenes provide the chance of gaining suitable local sites that become available in the future. Thus, the dimorphism averages out unpredictable environmental variation by spreading the distribution of achenes out in space and time, thereby increasing the probability of finding a safe site. However, at our sites spatial averaging tends to be over very short distances, particularly in a closed stand, and germination sites a few metres from the mother plant often go uncolonized.

Effect of dispersal on plant-herbivore dynamics

Dispersal may provide the key to coexistence of plants with their herbivores either through spatio-temporal fugitive strategies or by time-independent spatial ones. The former is more familiar, with fugitives being maintained globally despite ecological interactions which doom them locally (Dodd 1940, 1959, Huffaker 1958, Hutchinson 1959). For coexistence to be maintained by this mechanism, the dispersal rate of the plant must exceed that of the herbivore.

TABLE 7. Summary of significant influences on seed dispersal in *Senecio jacobaea*. Symbols indicate whether statements to the left are supported (+) or contradicted (–) by evidence from a given dispersal grid.

	Inland		Coastal	
	Mown	Unmown	Mown	Unmown
Dispersal distances increase with height of release	+	–	+	–
Dispersal distances vary among directions	+	+	+	–
Disk disperse farther than ray	+	–	–	–
Disk disperse earlier than ray	+	+	+	+
Among disk achenes, early dispersers travel farther than late dispersers	+	–	+	+
Majority of disk achenes disperse early	+	+	–	–
Among ray achenes, no difference in dispersal distances of early and late dispersers	+	+	+	+
Majority of ray achenes disperse late	+	+	+	+

The seed dispersal distances we observed appear to be far shorter than dispersal distances measured for ragwort's principal herbivore, the cinnabar moth *Tyria jacobaeae*, although we lack comparable data for insects. In a mark-release-recapture study of adults in a 60 × 90 m area, Dempster (1971) found one-fifth of the recaptured moths were caught in 20 × 30 m subplots other than those in which they were released. In a similar study N. T. Rudd (*personal communication*) measured 191 displacements for 175 moths on 1.2 ha. The median displacement per day was 18 m; 29% of the recaptured moths travelled >30 m per day, while 4% travelled >100 m per day. Van der Meijden (1973) found the median displacement of fifth-instar larvae from a release point to the pupation site was 10–12 m. However, larvae are capable of moving several hundred metres when food is in short supply (van der Meijden 1971, Dempster 1982). Where the insect dispersal rates exceed the plant dispersal rates, seed dispersal cannot facilitate coexistence except when it carries the plant to time-independent spatial refuges. For example, ragwort may persist in shady forest margins avoided by ovipositing cinnabar moth females (Frick and Holloway 1964, Harris et al. 1971, Rose 1978). Ragwort is an effective fugitive in time, eluding herbivores by seed dormancy (McEvoy 1985), and by shifting from a biennial, semelparous life history to a perennial and iteroparous one when attacked by herbivores (Cameron 1935, Poole and Cairns 1940, Green 1974, Cox and McEvoy 1983, Islam and Crawley 1983).

Improving the reliability of dispersal estimates

Two modifications in our trapping technique might improve estimation of the frequency of dispersal distances in plant populations. First, some traps should be placed directly beneath the parent to estimate the frequency of very short dispersal distances. Second, trap area should be increased with distance from the source to improve estimates of the frequency of long-distance dispersal. Long-range dispersal outside of the study area remains virtually impossible to measure, except indirectly by observing changes in the distribution of the species over time.

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