The Fitness of Dispersed Progeny: Experimental Studies with Anthoxanthum odoratum

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ABSTRACT

To examine how dispersal distance, density, and genetic variation influence progeny fitness, tillers of Anthoxanthum odoratum (Sweet Vernal Grass) were transplanted into their natural habitat (a mown field) at different distances from their parents. Tillers were either cloned from the parent and genetically identical, or, from seed-derived progeny of single parents and genetically variable. In a simulated seed shadow, competition among sibs reduced the fitness of the progeny in the dense regions of the gradient, but the reduction was small (two-fold) relative to the forty-fold change in density. Genetic variance did not reduce competition at high densities, but at lower densities genetically variable sibs had a greater fitness than asexual sibs. Long distance dispersal was generally unfavourable for asexually derived tillers. In contrast, some seed-derived tillers had a high fitness far from the parents. Seed dispersal measurements showed that most seeds fell close to the parent. The individual advantages of long distance dispersal of genetically variable progeny are therefore likely to be small, except in a colonising situation. The results show that the ecological consequences of dispersal depend on genetic variation among the progeny.

INTRODUCTION

The ubiquity and elaborate nature of dispersal mechanisms unequivocally argues that there are often large evolutionary advantages associated with dispersal. These advantages fall into two general classes (Howe and Smallwood, 1982): escape

from the parent and colonisation of new areas. Advantages to escape from the parent include avoidance of competition with the parent or among sibs, avoidance of predators and pathogens concentrated around the parent, and avoidance of inbreeding. Advantages to colonisation include escape from deteriorating environments (as in a successional situation), and increased probability of finding new suitable habitats. In spite of a wealth of speculation, many of the hypothesised advantages to dispersal remain untested, particularly by direct studies of progeny experimentally dispersed to different distances around the parent plant (Howe and Smallwood, 1982; for exceptions see Janzen, 1972, Wilson and Janzen, 1972). In the present study we experimentally transplant tillers of <u>Anthoxanthum</u> <u>odoratum</u> (Sweet Vernal Grass) at different distances from the parent, to answer the following questions.

1. Does progeny fitness decrease as the density of progeny increases?

2. Does genetic variation among sib-progeny ameliorate the effects of density?

3. Does dispersal well away from the parent increase or decrease progeny fitness?

4. Does the outcome of long distance dispersal depend on the genetic variance of the progeny?

The experiments described here were part of a larger study of the evolutionary significance of sexual reproduction (Antonovics and Ellstrand, 1984; Ellstrand and Antonovics, 1985; Antonovics, 1984; Antonovics and Ellstrand, 1985). In these experiments, plantings were carried out with tillers rather than seeds so as to permit control of the genetic variance among the progeny: tillers cloned from the parent are genetically uniform, while tillers cloned from seed progeny of one parent provide a genetically variable family group. All experiments were carried out in a long-established mown field on the campus of Duke University, Durham, North Carolina. Tillers were planted without disturbing the surrounding vegetation. Initially, studies on seed dispersal are described as a context for the experimental work.

DISPERSAL IN ANTHOXANTHUM

<u>Anthoxanthum</u> posseses no obvious dispersal mechanisms. As in many other grasses, the caryopses ("seeds") plus associated glumes are shed when the inflorescence dries at maturity. The

seeds are small (c. 1 x 1.5 mm) and the glumes are somewhat hairy with a hygroscopic awn. Dispersal occurs by wind and when seeds plus inflorescence fragments are scattered by mowing: such mowing occurs regularly in the spring when seeds are mature and has been a regular feature of the study site for at least thirty years.

To assess wind dispersal, the vegetation around eight large individuals of Anthoxanthum was mowed, and dispersed seeds were trapped on three plastic sheets (1m x 2m) radiating around each individual and covered with sticky 'tanglefoot'. To assess mower dispersal, the mature panicles of ten large individuals of Anthoxanthum were lightly spray-painted different colours prior to mowing. After mowing, the distances of inflorescence fragments from each parent were measured; all fragments, regardless of size, were counted equally. Mowing was carried out, as at other times, with a rotary power-mower with an unprotected side discharge.

Dispersal distances were relatively short, with 95 % of the seed dispersed less than 1.6 m by wind and less than 3.0 m by the mower (Fig. 1). The furthest dispersal recorded was an
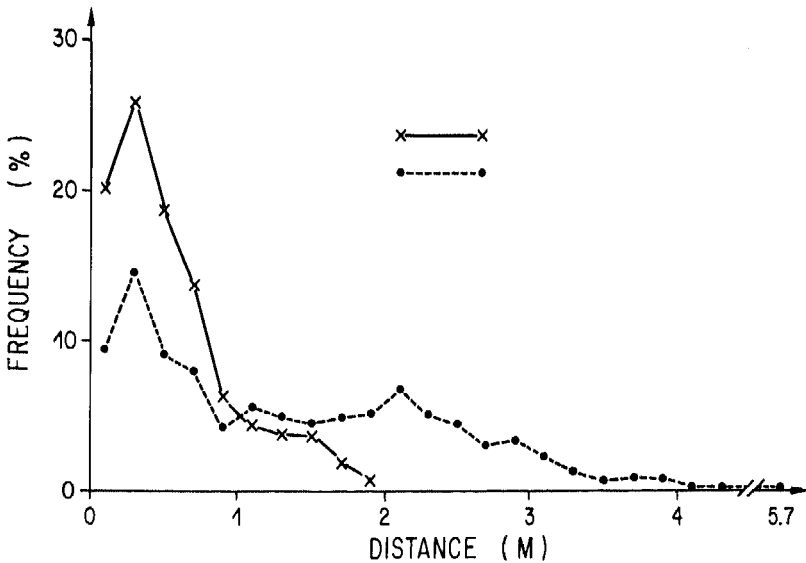

Fig. 1. Seed dispersal by wind (x---x) or mower (o---o). Graph shows frequency falling at a given distance from the parent, within a fixed arc angle. Totals: 572 for wind and 1313 for mower dispersal. Data from Kelley (unpublished results).

inflorescence fragment which was mower-dispersed 5.7 m from the parent.

SHORT DISTANCE DISPERSAL EXPERIMENTS

Methods. As part of a study to examine the effects of density on performance of variable and uniform progeny (Ellstrand and Antonovics, 1985), adult- and seed-derived tillers were grown in hexagonal fan arrays resembling seed dispersal patterns (Fig. 2). Arrays were planted into the natural community within three meters of the parents. The density within these arrays varied from 43 plants to 1 plant per 100 sq cm. There were eight replicates of variable (half-sib family) and non-variable (clonal) arrays within each of two sites. Tillers were planted in the autumn of 1979, and followed through two flowering seasons, by which time most individuals had died. Fitness was estimated as total inflorescence production over two years.
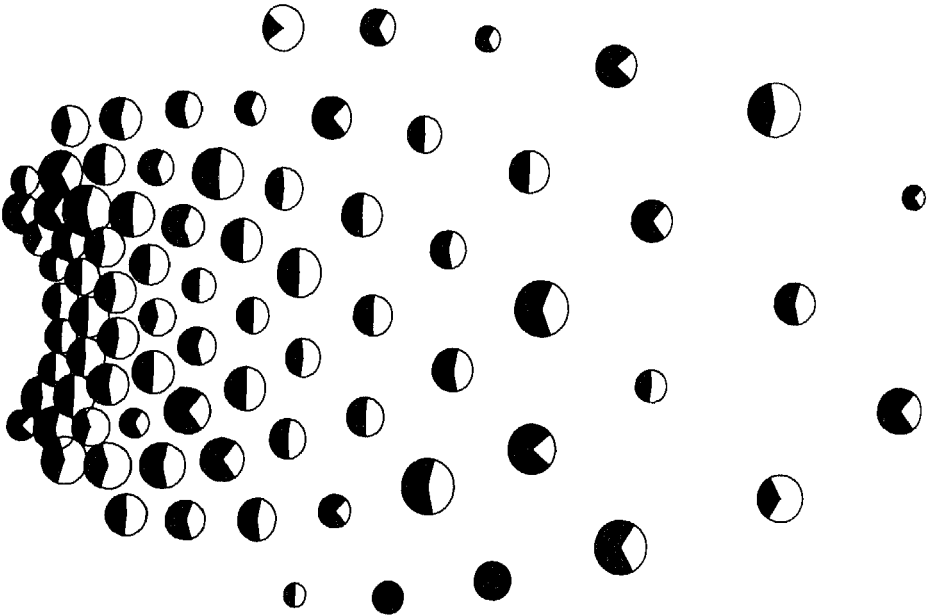
Fig. 2. Fitness of genetically variable and uniform progeny at each position in the density gradient. The center of each pie-chart indicates plant position in the hexagonal fan design (closest spacing is 1cm). Shaded segment is fitness of variable progeny, unshaded segment is fitness of uniform progeny, while area of each pie-chart is proportional to overall fitness at each position.

Results. Density had relatively little effect on reproductive output. A ten-fold difference in space available per plant produced only a two-fold difference in fitness (Fig. 2). The genetically variable progeny groups had a greater reproductive output than the genetically uniform groups. This effect was most apparent at the intermediate densities and at the edges of the fan designs, but was not seen at very high densities (Fig. 2).

LONG DISTANCE DISPERSAL EXPERIMENTS

Methods. Two experiments were carried out in successive years. In the first experiment single tillers from 22 genotypes were sampled from a limited area (c. 10 x 15 m) of the study site and cloned in the greenhouse for a year. One tiller of each genotype was then planted out along three transects spanning the field and intersecting the site from which the genotypes were originally sampled (see Fig. 3a). There were fifty transect positions and plants were arranged linearly within each transect position at 20 cm spacing. Tillers were planted in autumn 1978; survival and fecundity (inflorescence number) was measured over three years (for details, see Antonovics and Ellstrand, 1985). Since the position of "parental" individuals was known, the distances of cloned tillers from their parent could be determined.

The second experiment differed from the first in two ways. First, the genotypes were sampled from several diverse sub-habitats within the field rather than from a single area (Fig. 3b). Second, the individuals were sampled both as tillers and as seeds. The seeds were grown in the greenhouse to produce large individuals, from which tillers were cloned in a manner equivalent to that used in obtaining tillers from the parent individual. It was thus again possible to obtain seed-derived tillers, representing variable progeny (half-sib family) arrays, and adult-derived tillers representing uniform progeny (clonal) arrays. These tillers were planted in fall 1979 along transects parallel to the transects used in the first experiment, but separated from them by 20 cm. Again, genotypes were randomised within transect positions. Separate transects were used for the adult and seed derived transplants. About two weeks separated the time of planting of these transects. The experiment was followed through two flowering seasons.

Because reproductive output showed a highly skewed
distribution, regular regression analysis of fitness on
dispersal distance was not possible; instead contingency chi-
square tests were carried out on five distance classes (10m
intervals and distances >40m), and on 5 fitness classes (0, 1,
2-9, 10-49, and >49 inflorescences; the latter two were pooled
in Experiment 2). Analysis was also done on the zero vs. other
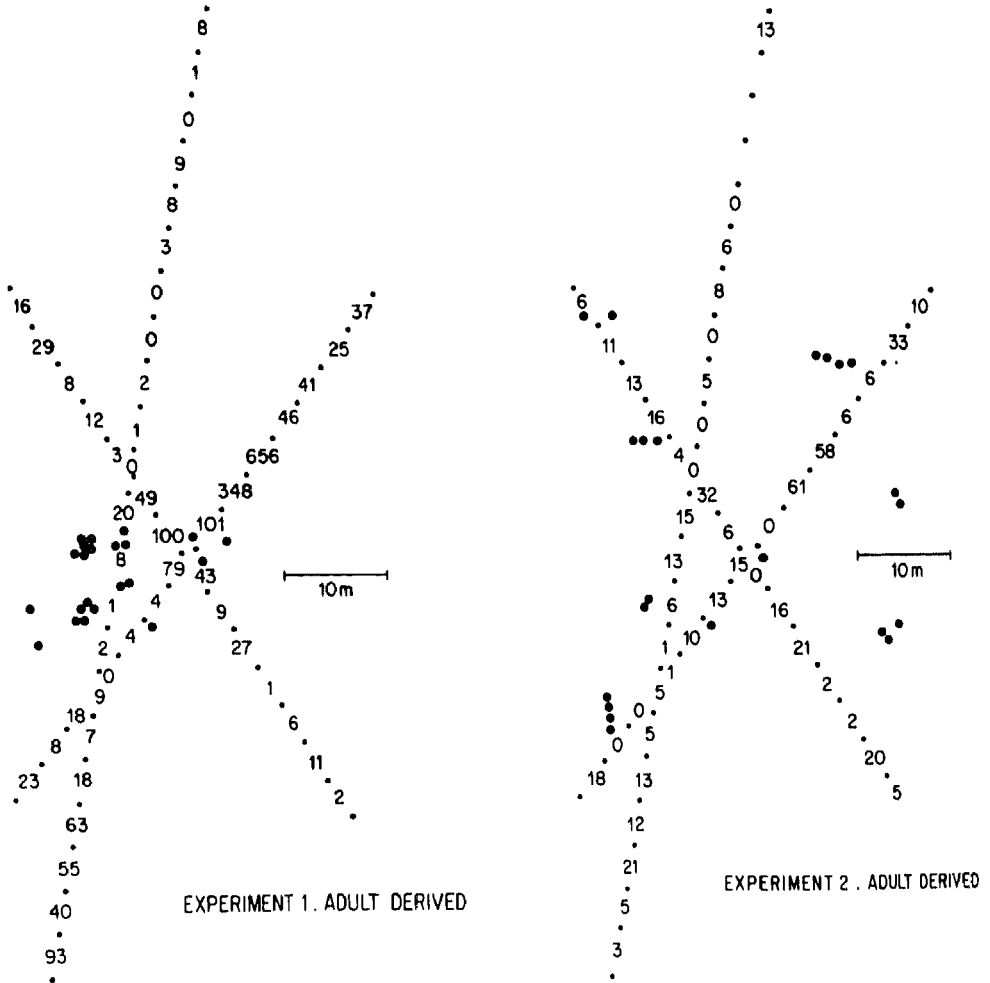classes, and separately on classes with fitness >0.

Fig. 3. Average fitness of 22 genotypes at each transect
position for adult derived tillers of (a) Experiment 1, and
(b) Experiment 2. The larger solid points indicate positions
of the parent individuals used in the two experiments.

Results. In Experiment 1, with cloned progeny, reproductive output increased at moderate distances from each parent (to about 20m) and thereafter declined (Fig. 4a). The interaction of fitness class and distance class was highly significant (x^2 = 39.0, d.f.=16, P<0.005). Distance had a nearly significant effect on whether individuals flowered or not (x^2=8.8, d.f.=4, P<0.10), but the main effect was on individuals that flowered (x^2 = 30.1, d.f.=12, P<0.005). The higher fitness at intermediate distances could be attributed to an area in the field where fecundity was particularly high, located about 20m to the east of where adults were sampled (Fig. 3).

In Experiment 2 the adult-derived tillers showed a consistent decline in reproductive output with increasing distance from the parent (Fig. 4b). The effect of distance was nearly significant (x^2=18.3, d.f.=12, P<0.10). Distance had no effect on the proportion of individuals with greater than zero fitness (x^2=1.3, d.f.=4, n.s.), but had a significant negative effect on fitness of individuals that flowered (x^2 =17.0, d.f.=8, P<0.05). The seed derived tillers showed no clear relationship between distance and reproductive output (Fig. 4c); however, some individuals had a high fitness at considerable distances (40m or more) from the parent. No such high fecundity individuals were found that far from the parent when the tillers were adult-derived . The interaction of fitness class and distance for seed-derived tillers was significant (x^2=23.5, d.f.=12, P<0.05); this effect was largely the result of more individuals with greater than zero fitness at long distances (x^2=13.3, d.f.=4, P=0.01) rather than effects of distance on individuals that flowered (x^2 =10.2, d.f.=8, n.s.) . The three way interaction of tiller type (seed- or adult-derived), fitness class, and distance class was highly significant (x^2 =28.0, d.f.=12. P<0.01), showing that seed-derived and adult-derived tillers performed differently when transplanted at different distances from the parent. To examine this relationship more closely, the average fitness of adult- and seed-derived tillers was standardised to 1, and their relative fitness determined at each 5 m distance class (Fig. 5). With increasing distances the relative fitness of the seed-derived transplants increased significantly (Spearman's rank correlation = 0.54, P<0.01).

To examine if transplants had a higher fitness when near the parental genotype, the fitness of the eleven transplants nearest their respective parents and that of the eleven
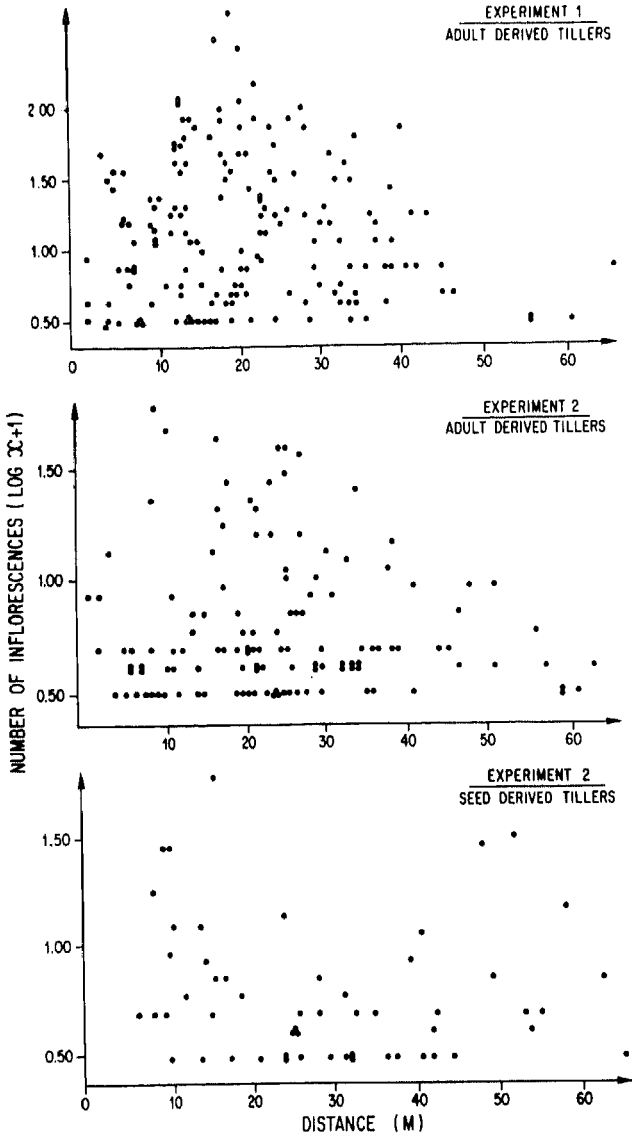
Fig. 4. Relationship between fitness and distance from the parent plant for (a) adult-derived tillers of Experiment 1, (b) adult-derived tillers of Experiment 2, and (c) seed-derived tillers of Experiment 2. Each point represents one individual. Individuals with zero inflorescences are not shown: numbers in each 10m distance class were as follows: (a) 174, 242, 207, 118, 51, 30, 2; (b) 127, 213, 233, 148, 77, 27, 12; (c) 133, 269, 279, 156, 96, 42, 14.

farthest was measured within each transect position. In Experiment 1, averaged over transect positions, genotypes near their parents surprisingly had a significantly lower reproductive output than those farther away (3.18 vs. 5.54; $P<0.027$). In Experiment 2, tillers near their parents performed better than tillers far away, nearly significantly so for adult-derived (1.15 vs. 0.94, $P<0.066$) but not for seed-derived tillers (0.46 vs. 0.34, $P<0.47$). Within each transect position, the individuals were ranked according to their fitness and their distance from the parent. A regression of rank fitness on rank distance, over all transects positions, was not significant in Experiment 1 ($0.068x -0.0020x^2$, $P<0.45$ & $P<0.80$ for linear and quadratic coefficients, respectively). It approached significance in the adult-derived transplants of Experiment 2, where there was a negative relationship ($-0.164x+ 0.0059x^2$, $P<0.07$ & $P<0.11$ for the coefficients) but was non-significant in the
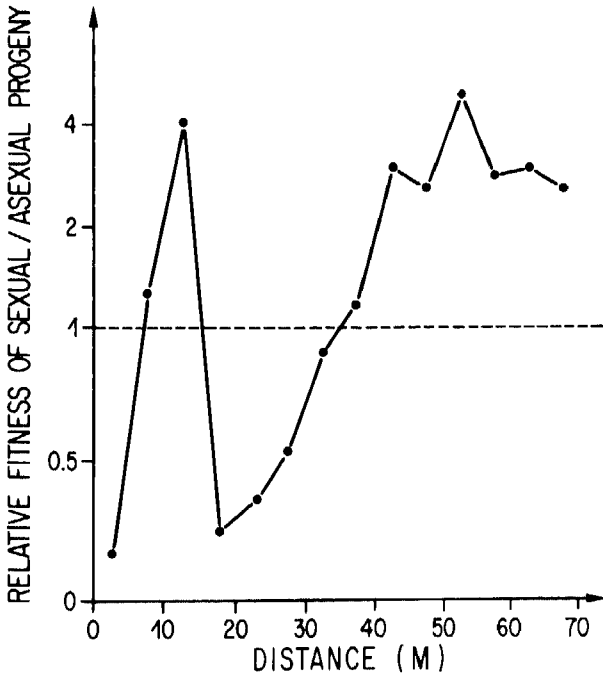

Fig. 5. Relationship between relative fitness of seed-derived vs. adult-derived tiller transplants and distance from the parent. The overall fitness of sexual and asexual transplants was standardised to 1; actual fitnesses were 0.412 and 1.086 inflorescences per plant, respectively.

seed-derived transplants (-0.042x +0.0023x , P<0.56 & P<0.44, for the coefficients).

DISCUSSION

The present study shows that the fate of progeny dispersed to different distances from the parents depends both on the distance and on the genetic variance of these progeny. The short distance dispersal experiment tested for the presence of sib-competition among the descendants of one individual. Such competition is an obvious expectation given the skewed dispersal distributions typical of higher plants, where, as was the case with <u>Anthoxanthum</u>, most of the seeds fall around the maternal plant (Levin and Kerster, 1974). However, in spite of the large range of densities within the artificial 'seed shadow' of the present study, such competition was relatively weak. Because the community studied here is a dense sward of many different species, the dense arrays of <u>Anthoxanthum</u> may have been subjected to more inter- and intra-specific than intra-family competition. Moreover, the high rate of density-independent mortality precluded strong interactions among the transplants. Also, the experiment was started with tillers rather than seeds: tillers contain more initial resources, and probably grew relatively little prior to floral induction in the winter. These results therefore suggest that sib-competition in natural populations may be reduced by three major ecological factors, namely, density of associated species, level of density independent mortality , and initial size or starting capital. Genetic variance did not appear to alleviate sib-competition, since the effects of genetic varability were most evident at the lower densities and at the edges of the plots. A possible explanation (see Ellstrand and Antonovics, 1985) is that genetic variance is advantageous in the face of predators or pathogens, but that this advantage is not evident at high densities where the plants are resource-limited.

In the first of the long-distance dispersal experiments some unexpected results were obtained. When the parents came from a single small section of the field, there appeared to be an "optimum" dispersal distance. However, this optimum was not the result of any complex ecological process (cf Janzen, 1970), but the simple consequence of the most favourable habitat for <u>Anthoxanthum</u> in this field being at an

intermediate distance from where the parents were sampled. These results indicate that plant populations are by no means uniform in their demography (see also Fowler and Antonovics, 1981; Antonovics and Primack, 1982), but contain regions of high population growth and reproduction ("fountainhead regions" or "hotspots" of Gill, 1978) as well as regions where population growth is negative ("reproductive sinks") and the numbers are maintained largely by immigrants from fountainhead areas. Such areas with intrinsically negative population growth can be considered demographically marginal, and the plants there may be subject to ecological and evolutionary forces which are quite different from those in the demographically central fountainhead areas (Antonovics,1978).

In the second experiment, where the parents were from different parts of the field, fitness of asexual progeny declined with increasing distance, partly because of a decline in the suitability of more distant habitats for Anthoxanthum, and partly because genotypes had been locally selected for high performance in their own region of the field; this latter explanation was supported by the observation that transplants performed better when they were nearer their own parental genotype, than when they were further away.

Only the seed-derived transplants gave individuals with high fitness at considerable distances from the parents. This observation is consistent with the classical view that sexual reproduction is favoured because it provides new and different genotypes that are adapted to a new environment (Williams, 1975). However, although this seems to be the first experimental demonstration of the commonplace assertion that genetically variable progeny are favoured in changing environments, whether such change provides a sufficient force for the maintenance of sexual reproduction is more problematical, especially since there was almost no natural dispersal beyond 5m. The effect of this on relative fitness of sexual and asexual types can be illustrated as follows. If there is a stable population where the average absolute fitness of each individual is one, and if 1% of a sexual progeny group are dispersed to a distance where they have a 5-fold advantage, then the relative fitness of this group (compared to an asexual progeny group) will be only $(0.99 \times 1) + (0.01 \times 5) = 1.04$. If however long distance dispersal involves a colonisation event, such that after dispersal the average absolute fitness is high (say 100) then the fitness of

the sexuals will be (0.99 x 1) + (0.01 x 500) = 5.99, and that of the asexuals will be (0.99 x 1) + (0.01 x 100) = 1.99. The relative fitness of sexual vs. asexual in this second case is approximately 3:1. The plant community within which the present experiments were carried out is relatively stable (Fowler and Antonovics 1983), and probably sexual reproduction is not being maintained by the advantage of producing variable progeny in long distance dispersal events. However, if within the larger metapopulation (the interconnected populations of Anthoxanthum within its general area of distribution), colonisation was frequent, and if colonisation success depended on novel genotypes then sexuality could be maintained. We unfortunately have no data on colonisation and extinction rates of Anthoxanthum in the Durham area.

The experiments carried out here were not designed specifically to examine dispersal. They have been reinterpreted in this context as a stimulus to further experimental research on dispersal biology. The results demonstrate that studies of fitness at the individual level need to take dispersal into consideration, and that the ecological consequences of dispersal are often modified by genetic events.

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