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Variation in Seed and Seedling Size in *Anthoxanthum odoratum*

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ABSTRACT: Success at the juvenile stage of the life cycle may have important consequences for the size-hierarchies and distribution patterns of adult plants. This study was designed to evaluate the factors contributing to variation in seed and seedling size in *Anthoxanthum odoratum*. In experiments in the greenhouse and within the natural habitat of this species, significant differences in seed weight were found among inflorescences and maternal half-sib families, and marginal differences were found among populations. Larger seeds had a higher probability of germinating and individuals from them had a longer leaf length as juveniles. Covariate analysis showed that differences among populations in leaf length were caused by population differences in seed weight. Root growth was studied using plexiglass root boxes. Individuals from larger seeds tended to produce longer roots, and there were no differences among populations, maternal families, or inflorescences for root length.

INTRODUCTION

The relative success of individuals at the earliest stages of the life cycle may have important consequences for their fitness. A number of studies have shown that early size hierarchies are important determinants of demographic patterns (*e.g.*, Black, 1958; Harper, 1977; Cook, 1979) and may, in some cases, affect adult reproductive output (Stanton, 1984; Roach, 1986). Variation in size at the earliest stages of the life cycle may be caused by microsite variation, differential performance of genotypes or maternal effects. Ecological studies have suggested that seed size is highly correlated with seedling size (Black, 1958; Harper, 1977; Schaal, 1980a, Stanton, 1984). Given the importance of size at the juvenile stage, and in order to understand the role of natural selection in determining variation in traits at this stage, it is essential to understand the relative contribution of factors determining variation in juvenile characters. This study was therefore designed to evaluate the factors contributing to variation in seed and seedling size in *Anthoxanthum odoratum*. Experiments were set up both in the greenhouse and the natural habitat of this species. The experiments were designed to examine the effects of population, maternal half-sib family and inflorescence, on seed weight and seedling size.

One aspect of this study which is unusual is that it considers the belowground parts of the plant. Most ecological studies have ignored belowground growth, because of the difficulties of measurement. But, variation in root development may be an important determinant of differential success of individuals. At the juvenile stage of the life cycle, rapid development of a root system may be particularly important in order to exploit critical resources. Moisture is one of the major environmental factors which has been identified in demographic studies as being limiting to seedling survival (Scharitz and McCormick, 1973; Mack, 1976), and individuals with longer roots may be able to use water from greater depths. For this study, seeds were germinated in root boxes and the effects of population, maternal half-sib family, inflorescence and seed weight on root length were evaluated.

METHODS

Seeds of *Anthoxanthum odoratum* were collected from three sites within a mown, but otherwise undisturbed field in Durham, N. C. (for description, *see* Fowler and Antonovics, 1981). The three sites were ecologically contrasting areas approximately 50 m apart, and were characterized by distinct vegetational associations (Ellstrand and An-

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tonovics 1985). Because of the contrasting nature of these sites, and because this distance is well beyond the pollen or seed dispersal distances known for this species (Antonovics and Ellstrand, 1985), the sites will hereafter be called "populations" with designations: D, J and L. The seed was collected from each population by common female parent ("family") in May, and was stored in paper bags at room temperature until sowing in October. Since *A. odoratum* is self-incompatible and wind-pollinated, these seeds most closely represent half-sib families. From each female parent, seeds were collected from different inflorescences, and the performance of seeds derived from different inflorescences was later evaluated. The overall experimental design was a nested design including: three populations within which 4-5 families were sampled; from each family 3-5 inflorescences were sampled; and from each inflorescence up to 10 seeds were collected. The term "seed" in this paper refers to the caryopsis (ovary wall plus the developed ovule or true seed), plus the closely appressed ensheathing bracts (the lemma and palea), plus two other hairy bracts (the sterile lemmas). This propagule is dispersed as a unit.

Field study.—An experiment was set up at the site from which Population D originated. Two hundred-seven seeds were weighed and sown at random, next to a color-coded toothpick for identification, at 5-cm spacings. The seeds were sown on 12 October, the same time at which natural emergence occurs. Emergence was recorded daily, and leaf length 23 days after sowing was used as a comparative growth measure.

Greenhouse study.—From the nested design 139 seeds were weighed and sown at random next to color-coded toothpicks in trays of soil in an unheated greenhouse. The trays were watered daily and kept under natural lighting. Leaf length at 23 days and total percentage emergence were recorded.

Root boxes.—Root boxes were constructed of two pieces of 15 x 25 cm plexiglass, separated by 2 cm of colored sand, and held together by rubber bands. Each box was wrapped with foil and was placed at a 45-degree angle in a pan of water. By removing the foil, root growth of the seedlings could be measured through the Plexiglas. A total of 120 seeds were planted in the root boxes. The depth of the root boxes was 15 cm. The length of the longest root was measured 14 days after sowing.

For all parts of the study, a nested analysis of covariance was used to evaluate the effects of seed weight, population, family, and inflorescence.

RESULTS

There were highly significant differences in seed weight among inflorescences and among families, and marginal differences among populations (Table 1). Approximately one-quarter of the variation in seed weight could be attributed to differences among maternal half-sib families. The mean seed weight for Population L was greater than Population J, which was greater than Population D, but these population differences were not significant (Table 2).

The mean weight of seeds in both experiments was significantly higher for seeds which emerged vs. the weight of seeds which did not emerge ($P < .01$, Table 3). Seed weight therefore had a significant effect on emergence in both the field and the greenhouse. The frequency distribution of the weight of emerging and nonemerging seeds shows that the differences in these means may be largely explained by the fact that a large percentage of the lightest seeds did not emerge (Fig. 1). The variance of the distribution of weights of the nonemerging seeds was significantly greater than the variance for the emerging seeds (F_{max} -test, $P < .01$). In the field, there were no differences among populations, families or inflorescences for percentage emergence (G-tests, all $P > .10$); and in the greenhouse, there were no differences among populations or families, and only marginal differences among seeds from different inflorescences (G-test, $.05 < P < .10$). Between the time of emergence and when the leaf length was measured at 23 days, all seedlings survived.

In the field, leaf length differed among populations (Table 4). A multiple comparisons test showed that Population L had significantly longer leaf length than Populations D and J, and Populations D and J did not have means significantly different from each other (Table 2). When leaf length differences are adjusted for initial differences in seed weight, using a covariate analysis, there are no significant differences in leaf length among populations (Table 4). In other words, the major effect of population differences on leaf length is an indirect effect due to seed weight differences among populations. Analysis with or without a covariate showed no differences in leaf length among families or inflorescences for the field data. In the greenhouse there were no significant differences among populations, families or inflorescences for leaf length (Table 4). The general trend however was that the F value for populations was again reduced in the covariate analysis. The covariate analysis shows a significant effect of seed weight on leaf length in the field, and a marginally significant effect in the greenhouse. This effect is further illustrated by a significant regression of leaf length on seed weight (greenhouse: $y = 6.17x + 1.72$, $P < .0005$, field: $y = 2.59x + 0.86$, $P < .0001$).

In the root boxes, the mean length of the longest root was 5.16 ± 0.27 cm ($n = 74$). Similar to the effects of seed weight on leaf length, individuals from larger seeds produced longer roots, although the effects were marginal ($y = 3.17x + 2.54$, $P < .08$). The means for each population are given in Table 1. There was no significant effect of population, family, or inflorescence on the length of the longest root (all $P > .10$).

DISCUSSION

The results of this study demonstrate the influence of seed weight on early life history traits. Seed weight is an important determinant of whether an individual will germinate, and it also has a significant effect on aboveground leaf length. Some previous studies have shown that seed weight can influence the probability of germination (Schaal, 1980a, 1980b; Cideciyan and Malloch, 1982; Gross, 1984; Stanton, 1984;

TABLE 1. — Nested analysis of variance for seed weight

Variance source	df	sum of squares	percent variance explained
Population	2	2.15	11.11 +
Family	11	4.21	23.15 ***
Inflorescence	39	2.66	14.15 ***
Error	410	8.50	51.59

+ $P < .10$, *** $P < .001$

TABLE 2. — Mean seed weight (mg), leaf length (cm) and root length (cm) for each population (\pm SE). Sample sizes are in parentheses. All population means are statistically similar to each other according to the Bonferroni simultaneous confidence test at the .05 level except leaf length in the field for Population L

	Population		
	D	J	L
Seed weight	0.71 \pm .01 (165)	0.81 \pm .01 (134)	0.87 \pm .02 (164)
Leaf length - field	2.46 \pm .14 (46)	2.81 \pm .14 (39)	3.59 \pm .17 (52)
Leaf length - greenhouse	5.79 \pm .60 (27)	7.11 \pm .47 (25)	7.55 \pm .50 (36)
Root length	5.10 \pm .39 (28)	5.37 \pm .39 (26)	4.98 \pm .69 (20)

Morse and Schmitt, 1985). Other studies however have shown no relationship between seed size and percentage germination (Bentley, *et. al.*, 1980; Cideciyan and Malloch, 1982; Gross, 1984). Even within *Anthoxanthum odoratum*, another study showed no relationship between seed weight and germination percentage (Schmitt and Antonovics, 1986). These conflicting results suggest that the relationship between seed size and germination success may be environment-dependent. An environment-dependent germination response was found in a study on sowing depth, seed size and time of emergence with *Linum usitatissimum*. In that study it was found that small seeds were the first to emerge from shallow sowings, but larger seeds emerged first from deeper sowings (Harper and Obeid, 1967). The seed of *A. odoratum* is largely endosperm with only a small embryo (Antonovics and Schmitt, 1986). Thus, variation in seed weight largely reflects differences in the quantity of endosperm. The results of the two studies with this species suggest that the quantity of endosperm may be more critical in determining germination success, but this may be environment- or year-dependent.

A positive correlation between seed size and seedling size can confer size advantages which may have important consequences for life history patterns. Demographic studies have shown that there is often high mortality at the earliest stages of the life cycle (Harper, 1977; Cook 1979). These studies have also shown that under severe environmental conditions, or dense competition, larger individuals have a higher probability of surviving through this critical period. In this study there was 100% survival of all emerging individuals through the earliest seedling stages. In another study with *A. odoratum* which carried through later in the life cycle, there was also relatively high survivorship during the 1st few months of growth, with an increased risk of death occurring during the winter and summer months. Only 1.4% of the seedlings survived through 2 years (Schmitt and Antonovics, 1986). Thus, although the correlation between seedling size and survivorship cannot be calculated from this study, there does appear to be high

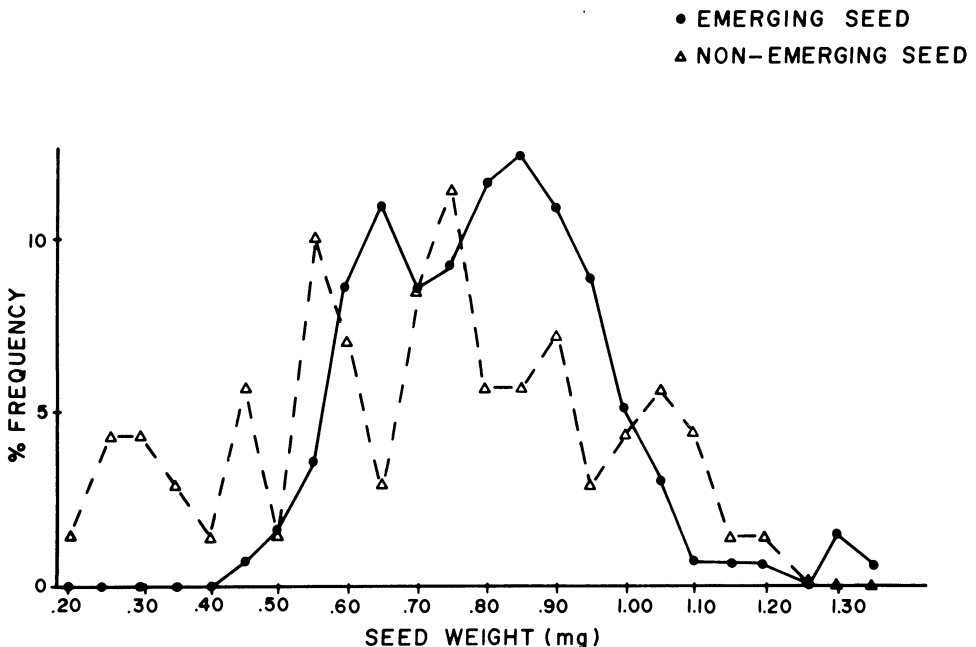


Fig. 1.—Frequency distribution of seed weight of emerged and nonemerged individuals in the field

mortality during the juvenile stage in this species. In some cases, the size hierarchies established during the earliest stages of the life cycle carryover to affect reproductive output of an individual (Edwards and Emara, 1969; Stanton, 1984; Roach, 1986). In other cases however, the correlation between seed size and seedling size does not carry over to later stages (Lewis and Garcia, 1979; Kotecha, 1981; Cideciyan and Malloch, 1982). For example, in a study with *Linum usitatissimum*, seedling growth 2 weeks after sowing was linearly related to seed weight, but when grown to full size, differences between varieties in terms of yield components could not be explained by differences in initial seed size (Harper and Obeid, 1967).

Given the demonstrated correlation of seed size with percentage emergence and seedling size, it is important to identify the factors influencing variation in seed size. In *Anthoxanthum odoratum*, maternal half-sib families explain the largest percentage of the variation in seed size. Variation in seed size among families can be caused by genetic differences among progeny or maternal effects which may be either genetic or environmental in origin. In another study with *A. odoratum*, it was found that maternal effects on propagule weight were large, and there was also some weak effect of the individual's own genotype on propagule size (Antonovics and Schmitt, 1986). Studies with other species have also demonstrated a strong maternal effect on seed size (e.g., Connolly, 1978; Williams and McGibbon, 1980; Roach, 1984). These types of results emphasize the problems of using maternal half-sib families in studies designed to examine variation in early life history characters. Without experiments using particular crossing de-

TABLE 3.—Mean seed weight and percentage emergence of seeds in the field and greenhouse experiments

	Field	Greenhouse
Weight of nonemerged seed	0.73 ± .03 (70)	0.73 ± .03 (53)
Weight of emerged seed	0.82 ± .01 (137)	0.84 ± .02 (87)
Percentage emergence	66	62

TABLE 4.—F-values for leaf length in the field and in the greenhouse unadjusted (Type I SS) and adjusted (Type III SS) for the covariate seed weight

	df	Unadjusted	Adjusted for covariate
Field			
Population	2	14.22 ***	2.38
Family (population)	11	1.29	1.89
Inflorescence (family)	16	0.84	0.85
Seed Weight	1	7.28 **	7.28 **
Greenhouse			
Population	2	2.40	0.37
Family (population)	11	1.10	0.87
Inflorescence (family)	11	1.28	1.22
Seed weight	1	3.73 +	3.73 +

+ P < .10, ** P < .01, *** P < .001

signs, it is not possible to identify the source of among-family variance for seed weight. Except for agronomic species, however, there have been few studies of this kind (Roach, 1984; Antonovics and Schmitt, 1986).

Even without a complete analysis of the causes of within-family variation in seed weight, a study of the frequency distribution of seed weights for emerging and non-emerging seeds reveals an interesting pattern. Individuals with seed weights at the extremes of the distribution, particularly the smallest seeds, have a lower probability of emerging. The lower variance in seed weight for the emerging seeds compared to the total seed population, along with the significantly greater mean weight of emerging compared to nonemerging seeds, suggests that directional selection may be acting on seed weight. In other words, individuals with slightly larger than intermediate seed weight will have the highest fitness at this early stage of the life cycle. A change in the mean and variance in seed weight should be expected through time unless there are constraints on the response to selection (Roach, 1985).

Despite the fact that only a small percentage of the variation in seed weight could be explained by differences among populations, the effect of populations had a significant influence on seedling leaf length. The populations were chosen from ecologically contrasting areas. They were only 50 m apart, but this was far enough to result in differences in juvenile leaf length in the field from small differences in seed weight. It is not possible to determine whether the population differences in leaf length are genetic or environmental. Usually in a common garden experiment, when population differences persist, one can conclude that there are genetic differences among populations. When maternal half-sib families are used, however, differences among populations may be caused by maternal carry-over effects (Baskin and Baskin, 1973). This is probably the situation in this study with *Anthoxanthum odoratum*, because population differences in leaf length were no longer significant after adjustments were made for differences in initial seed size. In this case, population differences were most likely caused by environmental differences among the populations, and were transmitted through environmental maternal effects on seed size. It was surprising to note that these differences among populations were only observed in the field and not in the greenhouse. In other words, it was only under natural conditions, surrounded by competitors, pathogens and other natural biotic and abiotic environmental pressures that the differences were apparent. Such results emphasize that in order to understand the amount and type of variation in natural populations, it is important to conduct experiments under as natural conditions as possible.

Except for the population differences in leaf length, which appear to be caused by maternal effects, there is no evidence for genetic differentiation among populations for the traits expressed at the earliest stages of the life cycle. The common garden experiment was set up at the site from which Population D originated. There is no evidence that selection has acted at this stage to favor the "home" population. In fact, although not significant, the general trend was that the home population had the lowest percentage emergence and the shortest leaf length. As discussed earlier, both of these traits are correlated with seed size, also, population D had the lightest seeds. In either case, if genetic differentiation has occurred between these populations, it is for traits expressed at some later stage of the life cycle.

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