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THE EFFECT OF SEED SIZE AND MATERNAL SOURCE ON INDIVIDUAL SIZE IN A POPULATION OF *LUDWIGIA LEPTOCARPA* (ONAGRACEAE)¹

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ABSTRACT

Seed size is normally distributed for many annual species, while mature plant size is frequently positively skewed. A study was conducted to determine the influence of seed size and the role of genetic differences in determining relative seedling size for *Ludwigia leptocarpa*. Seed size had a significant effect on percentage germination and time of seed germination but no effect on dry weight or leaf area of seedlings. Seed size and spacing had a significant effect on seedling dry weight for plants grown under competition, while relative day of emergence had no effect. Familial (genetic) differences were found in average seed weight between maternal plants, but not in average number of days to germination, average weight of seeds which germinated, or shoot dry weight. It is concluded that neither seed size alone nor genetic differences between plants are directly responsible for the development of size hierarchies in *Ludwigia leptocarpa* populations. Large seed size does convey an advantage in growth when plants from seeds of differing initial size interact.

POPULATIONS of *Ludwigia leptocarpa*, a member of the Onagraceae, characteristically develop a positively skewed distribution of individual plant biomass by the end of the growing season (Dolan and Sharitz, in press). This species behaves as an annual in South Carolina where this work was done. It is a colonizer of streambanks, mudflats, and other exposed semi-aquatic habitats. It is most likely modally out-crossing but is self compatible (Ormond, 1978; Raven, 1979). Seeds are produced in long slender capsules which usually bear several hundred seeds. Seeds average 0.1 mg in weight and are released from the capsules via longitudinal dehiscence prior to germination in the spring. *Ludwigia leptocarpa* has little or no seed bank for populations in South Carolina (Dolan and Sharitz, in press). Each year's seed production represents the pool from which the next season's plants will develop.

Size hierarchies, in which there are a few very large individuals and many small individuals, are characteristic of many plant populations under natural (Ogden, 1970; Gottlieb, 1977; Leverich and Levin, 1979; Solbrig, 1981) and cultivated conditions (Koyama and Kira,

1956; Obeid, Machin and Harper, 1967; Naylor, 1976; Ford, 1975). The causes of this skewed distribution of size structure have not been fully documented despite the fact that plant size is usually highly correlated with reproductive output (Harper and White, 1974; Werner, 1975; Solbrig, 1981) and is frequently a more important indicator of reproductive success than is age (Harper and White, 1974; Naylor, 1976; Werner and Caswell, 1977). Relatively few individuals contribute most of the offspring from which future generations will be drawn.

Seed size within a population is generally accepted to be nearly normally distributed (Williams, 1975; Naylor, 1976; Rabinowitz, 1979; Howell, 1981). Extremely skewed distributions of adult size are therefore probably not a direct reflection of starting capital. In some species, however, seed size has been demonstrated to have an effect on adult plant size: Larger seeds may maintain a size advantage and develop into larger plants (Black, 1956, 1957; Schaal, 1980; Gross and Soule, 1981; Weis, 1982). The direct relationship of variable performance of different sized seeds to the development of a size hierarchy is not known.

This study assesses the early seedling vigor of plants of the annual *Ludwigia leptocarpa* (Nutt.) Hara derived from seeds of different size and maternal source within a population and is part of a larger study of the causes and implications of size hierarchies in *L. leptocarpa*. The following questions are addressed:

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What is the distribution of individual plant biomass in a population at the end of the growing season for *L. leptocarpa* and how does this compare with the distribution of seed size from which the population developed? What is the effect of seed size on germination and seedling development for single plants and for plants grown under intraspecific competition? What is the effect of maternal source, or genetics, on early seedling vigor? How strong is genetic control of size? Do large plants tend to have more vigorous offspring?

MATERIALS AND METHODS— to determine the frequency distribution of plant size near the end of the growing season, 178 *Ludwigia leptocarpa* plants were sampled at time of flowering (Fig. 1(a)). Size was non-destructively estimated by measuring total length of stem and all branches. Total length and dry weight are highly correlated for *L. leptocarpa* ($r = 0.95$, $N = 42$, $P = 0.001$). Plants used in this study were located in 23 1-m² plots, located randomly along a transect parallel to the bank of Ellenton Bay, a shallow water-filled depression termed a "Carolina Bay," in Aiken County, South Carolina.

In the fall of 1980 the distribution of seed weights for the individuals in this population was estimated from the weights of 1,000 seeds (100 seeds from each of 10 plants collected randomly) from the site. Each plant was air-dried, weighed, and the total number of seeds produced on each plant estimated from the sum of the lengths of all capsules ($r = 0.89$, $N = 60$, $P = 0.001$ for total length of all capsules and actual seed number). Seeds were then removed from the capsules and pooled for each plant, and those which appeared inviable or misshapen were rejected. One hundred seeds were selected at random and weighed individually on a Cahn Electrobalance to an accuracy of 0.001 mg, and a frequency distribution of seed size was then generated. The term "seed" in this study refers to the entire propagule of *L. leptocarpa*, which includes the seed and a horseshoe-shaped endocarp that may aid in flotation dispersal (Eyde, 1978). Weighing of a subsample of seeds with the endocarp attached and then removed showed a high correlation between seed and seed + endocarp weights ($r = 0.95$, $N = 75$, $P < 0.001$). Because they were easier to handle, entire propagules were used throughout this study.

To study the effects of seed size on early seedling vigor, five plants were again randomly collected from the Ellenton Bay site in the spring of 1982. Seeds from each plant were pooled and sieved into three size classes using standard

soil sieves. Seeds were designated as small (diam < 0.85 mm), medium (diam > 0.85 and < 1.00 mm), or large (diam > 1.00 mm). Individual weighting of 45 seeds from each size class showed a significant difference in weight between each class ($\bar{x} \pm 1$ SE: small = 0.088 mg \pm 0.002; medium = 0.143 mg \pm 0.006; large = 0.225 mg \pm 0.006; $F = 178.50$, $P < 0.001$). Three replicates of 50 seeds of each size class were selected randomly from each parent plant and tested for germination on moist filter paper in 9-cm diam petri dishes in a growth chamber at 16/8 hr light/dark at 22 C. These conditions are known to be favorable for germination of *L. leptocarpa* (Christy and Sharitz, 1980). Dishes were monitored for germination which was determined by emergence of the radicle.

Germinated seeds were transferred to individual pots filled with vermiculite and placed in a greenhouse under uniform conditions. Seedlings were watered daily and received weekly applications of complete nutrient solution. After 65 days, when the plants had 3 to 4 pairs of true leaves, the aboveground biomass of the seedlings was harvested. *Ludwigia leptocarpa* typically has a 7-month growing season in South Carolina. The harvested material was oven dried at 60 C to constant weight, and weighed. Aboveground biomass was sampled because the small roots could not be accurately separated from the vermiculite. Leaf area was measured with a Li-Cor leaf area meter. It was assumed that any differences in growth rate expressed in these 65-day-old plants would continue to be expressed as differences in adult size had the plants been grown to maturity. Factors which influence rank in the size hierarchy are believed to operate early in development (Harper, 1977).

The effect of intraspecific competition on growth of *Ludwigia leptocarpa* seedlings was studied using ten seeds from a random sample of 1,000 seeds collected following after-ripening at the Ellenton Bay site. Seeds were sown randomly in each of five 10 \times 10-cm plastic pots filled with vermiculite. Pots were watered daily and received weekly applications of one-half strength Hoagland's solution. Pots were monitored daily for emergence of cotyledons. Seedlings were marked, and their locations in the 100-cm² area of the pot were mapped. Seed size from which the cotyledons developed was estimated by measurement of cotyledon length. Cotyledon length is highly correlated with seed weight in *L. leptocarpa* (Dolan, unpublished). The plants were grown for 55 days at which time the above ground biomass was harvested, oven-dried, and weighed. The Statistical Anal-

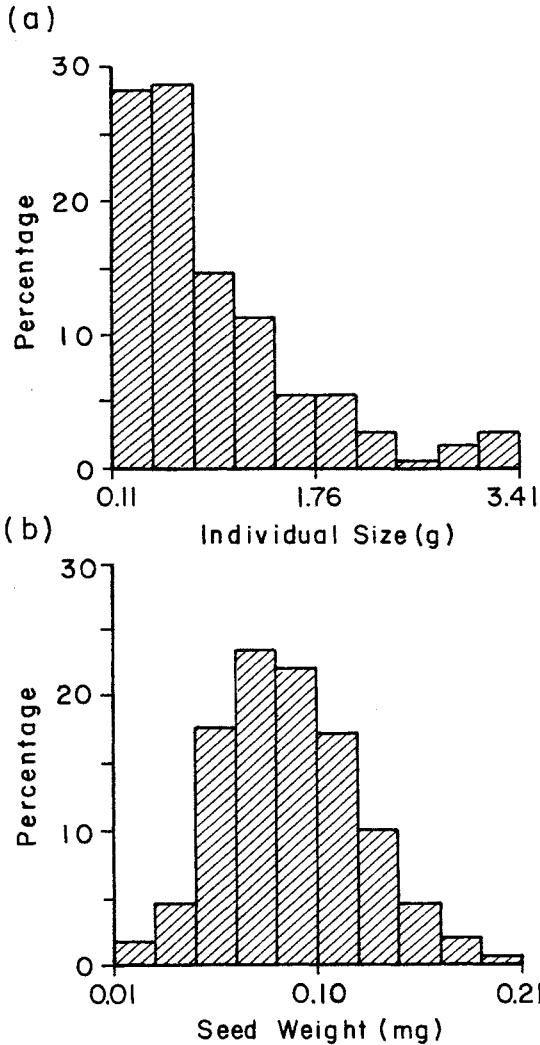


Fig. 1. Frequency distributions of (a) estimated individual plant size for *Ludwigia leptocarpa* at time of flowering (July 30) at Ellenton Bay in 1981 ($\bar{x} = 0.96$, g, $N = 178$) and (b) individual seed weights from the population produced in 1980 ($\bar{x} = 0.096$ mg, $N = 1,000$).

ysis System (Helwig and Council, 1979) was used to carry out a 3-way analysis of variance to determine the influence of seed size, emergence date of cotyledons, and average distance to three closest neighbors on plant dry weight.

TABLE 1. Relationship between maternal plant and seed characteristics for *Ludwigia leptocarpa* in the 1980 growing season

Plant no.	Maternal dry wt. (gm)	Estimated no. seeds	Avg. seed wt. (mg \pm 1 SE)
1	24.2	59,556	.1045 \pm .0028
2	22.0	39,710	.1118 \pm .0039
3	8.0	19,209	.0996 \pm .0032
4	3.4	3,031	.1083 \pm .0035
5	3.4	14,440	.0869 \pm .0027
6	0.5	960	.1205 \pm .0027
7	0.4	513	.0980 \pm .0030
8	0.4	2,214	.0758 \pm .0030
9	0.3	599	.0782 \pm .0021
10	0.1	475	.0804 \pm .0021

An additional ten plants were selected at random in the spring of 1982 for a common garden analysis of the role of genetic differences in determining early seedling vigor. For each plant maternal dry weight was recorded and the seeds removed and pooled. Thirty seeds were selected from each plant, weighed individually on a Cahn Electrobalance, and individually monitored for germination and seedling growth to an age of 65 days as described above. All seeds from the same mother are siblings and the group is referred to as a family. Only four families yielded sufficient seedlings for useful analysis.

RESULTS—The frequency distribution of individual plant size for *Ludwigia leptocarpa* at time of flowering in 1981 at Ellenton Bay is positively skewed leptokurtic ($g_2 = 7.94$) and skewed ($g_1 = 2.02$; Fig. 1(a)). This skewed distribution does not simply reflect a skewed input of starting capital. The seed size for the population is much closer to a normal distribution (Fig. 1(b)) with skewness and kurtosis values of only 0.344 and -0.033 respectively. The seeds are very small, with an average weight of only 0.096 mg. For the 1,000 seeds weighed here, there are significant differences in average seed weight between maternal plants ($F = 27.47$, $P < 0.001$). There is also a significant positive relationship between maternal dry weight and seed size ($F = 40.06$, $P < 0.001$).

TABLE 2. Effect of seed size on seed and seedling characteristics in *Ludwigia leptocarpa*. Each class started with 450 seeds. All means are ± 1 SE. Size classes S, M, L are described in the text. Means within a column with different letter designations are significantly different ($P < 0.001$)

Seed size class	% germination	Days to germinate	Shoot dry wt (gm)*	Leaf area (cm ²)*
S	6.40 (± 2.12)a	6.45 ($\pm .28$)a	.011 ($\pm .003$)	5.61 (± 1.23)
M	38.67 (± 6.57)b	6.82 ($\pm .16$)a	.008 ($\pm .001$)	4.29 (± 0.56)
L	68.53 (± 5.77)c	7.92 ($\pm .14$)b	.007 ($\pm .001$)	4.33 (± 0.50)

* For size class S, $N = 15$; M, $N = 43$; L, $N = 48$ seedlings.

TABLE 3. Three-way analysis of variance of the effect of estimated seed size, average distance to three nearest neighbors, and day of emergence on seedling dry weight for *Ludwigia leptocarpa* plants grown in the same pot

Source	df	F-value	Significance of F
Seed size	1	41.15	0.001
Distance	1	4.38	0.043
Emergence date	1	0.79	n.s.
Seed size × distance	1	9.04	0.005
Seed size × emergence date	1	0.53	n.s.
Distance × emergence date	1	2.25	n.s.
Seed size × emergence date × distance	1	0.00	n.s.
Error	38		

but the relationship explains only twenty percent of the variation in seed weight. The large sample size probably contributes to the large *F* value. Seed production is highly correlated with maternal plant dry weight ($r = 0.97$, $N = 10$, $P = 0.001$; Table 1).

Percentage germination and days to germination are strongly affected by seed size in this species (Table 2). Germination of the large size class of seeds was nearly twice that of medium sized seeds and over ten times that of small seeds. Those smaller seeds which did germinate, however, did so more quickly than larger seeds. Shoot dry weight and leaf area were not strongly influenced by seed size for plants grown in separate pots (Table 2).

When plants of *Ludwigia leptocarpa* are grown in the same pot, plant size is significantly influenced by seed size and by average distance to three nearest neighbors (Table 3). All plants in this study emerged within a period of 3 days and relative emergence time did not contribute significantly to variation in plant size. The only significant interaction was between seed size and distance to neighbors.

The common garden experiment showed

significant differences between the families in average weight of all seeds, but there was no significant relationship between maternal size and the seed and seedling traits studied. There were also no significant differences between weights of seeds which germinated, days to germination, or shoot dry weight after 65 days of growth (Table 4), indicating that these traits are not under strong genetic control.

DISCUSSION—Data presented for *Ludwigia leptocarpa* show that the skewed distribution of plant sizes characteristic of mature plants does not simply reflect a skewed distribution of original seed sizes. These findings support other studies for which species which normally distributed seed size develop a negatively skewed frequency distribution of adult plant size (Koyama and Kira, 1956; Howell, 1981) and indicate that starting capital alone cannot explain the development of size differences within a population.

Seed size, however, does influence germination percentage and days to germination in *L. leptocarpa*. Small-sized seeds with low germination (less than seven percent) may be due to the location of capsules on the parent plant or to the location of the seeds within a capsule. *Ludwigia leptocarpa* has an indeterminate inflorescence and small seeds may be produced in capsules that are still immature when the plant senesces, although an effort was made to select only fully developed fruits for this study. Ormond (1978) has reported that self-pollination of *L. leptocarpa* can result in narrow fruit bases caused by lack of development of ovules due to insufficient pollination. Position within the fruit has been shown to have a significant influence on seed size in legumes (Schaal, 1980). Smaller *L. leptocarpa* seeds may germinate more quickly because they have thinner seed coats for the embryos to penetrate. These particular seed sizes were chosen for ease

TABLE 4. Effect of family origin on seed and seedling traits for *Ludwigia leptocarpa*. $N = 30$ except where indicated in parentheses. \pm indicates ± 1 SE

Character	Family				F-value
	A	B	C	D	
Maternal plant dry wt. (g)	4.51	17.08	21.57	3.21	
Avg. seed wt (mg)*	0.178a \pm 0.012	0.148a,b \pm 0.010	0.140b \pm 0.011	0.138b \pm 0.011	2.70
Avg. wt. of seeds which germinated (mg)	0.224 (17) \pm 0.011	0.188 (16) \pm 0.010	0.181 (16) \pm 0.36	0.180 (10) \pm 0.012	1.69
% germination	53.3	53.3	23.3	33.3	
Avg. no. days to germination	7.8 \pm 0.4	6.4 \pm 0.5	7.5 \pm 1.0	6.0 \pm 0.5	1.17
Shoot dry wt. (gm)	0.011 (14) \pm 0.002	0.010 (11) \pm 0.002	0.016 (6) \pm 0.002	0.007 (6) \pm 0.002	2.26

* Means in a row with different letter designations are significantly different ($P < 0.05$).

of separation by use of sieves and do not necessarily reflect any biologically significant size distinctions.

When plants derived from different sized seeds are grown in separate pots for sixty-five days, no significant differences in dry weight are seen. Design of the experiment allowed for only one harvest date but visual observation indicated seed size effect disappeared within the first few weeks after emergence. Seed size and early seedling vigor show conflicting trends in a variety of species. In some species, large seeds develop into more vigorous seedlings and adults (Black, 1956, 1958; Austenson and Walton, 1970; Haskins and Gorz, 1975; Gross and Soule, 1981; Weis, 1982). On the other hand, in fiber flax (*Linum usitatissimum*; Harper and Obeid, 1967), cocksfoot (*Dactylis glomerata*; Ross and Harper, 1972), barley (*Hordeum sativum*; Naylor, 1976), and *Rumex* spp. (Cideciyan and Malloch, 1982), there is no correlation between seed size and seedling growth when plants are grown in separate pots. In nature, where biotic and abiotic interactions are possible, the situation is more complex. There may be limitations and trade-offs to the production and effectiveness of large seeds, such as limited resources or space within a fruit, dispersal ability, or predator size preference.

When *L. leptocarpa* plants are grown together in pots, plants from larger seeds develop into larger plants. This is presumably due to an advantage in resource capture given by larger cotyledon size. This advantage is best expressed under conditions of competition. The same is true for *Trifolium subterraneum* and some species of *Rumex* but not others (Cideciyan and Malloch, 1982). For *L. leptocarpa*, seedling size was also significantly influenced by distance to neighbors. Relative emergence time was of greater importance than seed size or spatial distribution of neighbors in determining the size an individual attained for some grass species (Ross and Harper, 1972) and for *Impatiens capensis* (Howell, 1981). Black and Wilkinson (1963) showed that a delay of 5 days in time of emergence relative to other plants resulted in a 50% reduction in dry weight for *Trifolium subterraneum*. They attributed this reduction to severity of competition with plants already emerged. Variation due to seed size, however, was not controlled. This trend was not seen for *L. leptocarpa*.

For *Ludwigia leptocarpa*, growth rate of plants showed little genetic variability. Two lines of evidence support this claim. First, there is no consistent relationship between maternal plant size and size of offspring; large plants do not produce larger seeds or more vigorous

seedlings. Second, family analysis of the performance of seeds in a common garden showed no significant differences between families in seedling dry weight.

Studies addressing the role of genetic differences in the establishment of size hierarchies in natural populations are rare. Family analysis of seedling traits in *Viola sororia*, a perennial woodland herb, showed no genetic differences between large and small plants (Solbrig, 1981). Gottlieb (1977) studied the relatedness of plants of the annual *Stephanomeria exigua* using electrophoresis. Offspring of extremely large- and small-sized adult plants of this species were not significantly different from each other or the population as a whole in the isozyme patterns of four enzyme systems. Common garden studies showed that offspring from large- and small-sized plants had similar sizes and growth rates.

The experimental design employed for *Ludwigia leptocarpa* did not address the possibility of genotype-environment interactions which might be manifest under more stressful conditions than those used in the greenhouse. It also did not eliminate the possibility of non-genetic maternal effects exerting an influence on seed performance. Use of seeds from plants grown for one generation under uniform conditions has been suggested to help control this factor (Quinn and Colosi, 1977). Maternal effects may not be a significant concern in work with *Ludwigia leptocarpa* since no consistent differences in seed size or seedling vigor were evident for seeds from different maternal sources. Seed sizes were different, but were not related to maternal size or condition in any consistent manner.

The size hierarchy of *Ludwigia leptocarpa* does not simply reflect a hierarchy of seed size. Seed size in isolation does not influence early seedling vigor. When interaction between individuals is allowed, larger seed size and greater distance from neighbors do convey advantages in growth. The availability of nutrients, light, moisture and other environmental factors are also likely to influence growth rate and the distribution of individual plant size.

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