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Population Dynamics of *Ludwigia Leptocarpa* (Onagraceae) and Some Factors Affecting Size Hierarchies in a Natural Population

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Summary

1. Germination cohorts of *Ludwigia leptocarpa*, a semi-aquatic annual plant were marked in the field at time of establishment and followed through the 1981 and 1982 growing seasons at a site in southern South Carolina.
2. Data from each cohort were pooled to determine demographic characteristics of the population as a whole, then analyzed separately to determine the effect of time on germination on survivorship, relative growth rate, and adult size.
3. Changes in numbers of *L. leptocarpa* fit a Deevey Type II survivorship curve. This and other characteristics of the species classify it as 'r-selected'. Aspects of the life history may reflect a 'bet-hedging' stratagem that ensures establishment.
4. Differences in the time of germination are not responsible for differences in adult size, even when early-germinating plants have as many as 35 days more for growth than late germinators. This, and the fact that differences occur even within single cohorts, implies that factors other than time of germination must influence plant size.

Introduction

In many natural and cultivated plant populations, there are usually many small plants and a few vey large plants (Harper 1977). This is particularly so in crops (Koyama & Kira 1956; Stern 1965; Obeid, Machin & Harper 1967; Naylor 1976) and plantation trees (Hozumi & Shinozuki 1970; Ford 1975; Mohler, Marks & Sprugel 1978). High density may accentuate the effect (Koyama & Kira 1956; Obeid, Machin & Harper 1967; White & Harper 1970). In natural populations, Ogden (1970) found the frequency distribution of individual weight to be skewed for the community both as a whole and for the individual species in a mixed annual herb community colonizing arable fields in Wales. Four of seven species studied had weight distributions which were log-normal. In a sagebrush community, Gottlieb (1977) found that 75% of the plants of the annual species *Stephanomeria exigua* were smaller than the population mean. Likewise, Leverich & Levin (1979) observed extreme differences in size and fecundity of individuals of the winter annual *Phlox drummondii*. Juvenile size was correlated with adult reproductive output. Extreme size differences which led to differences in survivorship and seed production have also been reported for *Viola sororia*, an herbaceous woodland perennial (Solbrig 1981).

Together with the hierarchy in size, there is often one in reproductive output. In *Phlox drummondii* (Leverich & Levin 1979), more than half of the annual seed crop was produced by

only 10% of the flowering individuals (2% of the original cohort). Plant size is often highly correlated with fecundity (Harper & White 1974; Wener 1975; Solbrig 1981) and is frequently a more important factor in determining seed production than is age (Harper & White 1974; Naylor 1976). Therefore, a few large plants often contribute the majority of offspring produced in any one growing season and will contribute disproportionately to the gene pool of the population.

Harper (1977) suggested four major factors that determine the position of an individual in a size hierarchy: (i) time of germination; (ii) starting capital; (iii) relative growth rate of the genotype; and (iv) environmental restrictions on growth. Environmental restrictions may be abiotic (e.g., soil fertility, water availability) or biotic (e.g., grazing, pathogens, or interactions with co-occurring species).

Within populations of annual plants, there may be an age structure resulting from different times of germination (Harper & White 1974). The earliest-germinating seedlings have longer to grow and thus may become larger. For species in which germination is spread over several weeks, however, seedlings which germinate at different times may be exposed to different environmental conditions. This may either increase or decrease survival, growth rate, and seed production. This study examines the role of time of germination in determining an individual's relative size in a population of the annual species *Ludwigia leptocarpa* as part of a larger study of size hierarchies in this species.

Materials and Methods

Ludwigia leptocarpa (Nutt.) Hara (Onagraceae), shows great variation in size of individuals (0.1-1.5m in height) at the end of the growing season. In South Carolina, near the northern edge of its distribution, it behaves as an annual. Germination begins in late April. Flowering begins in late August and continues indeterminately until the plants die in October. An average of 250 seeds, of mean weight 0.1mg are borne in slender, linear capsules. Although dehiscence may begin in late autumn, most seed shed occurs during mid-spring.

Ludwigia leptocarpa is a colonizer of exposed semi-aquatic habitats such as mudflats or stream banks. The sampled population occurred along the shore of Ellenton Bay (a shallow water-filled depression termed a 'Carolina Bay'; 33° 13'N, 81°45'W) on the Savannah River in southern South Carolina. Fluctuating water levels provided exposed soil for colonization. Associated species in the area, which spans habitats ranging from shallow water to surrounding old fields, included: *Cephalanthus occidentalis*, *Eupatorium compositifolium*, *Hypericum walteri*, *Ludigia decurrens*, *Nymphaea odorata*, *Panicum* spp., *Polygonum hirsutum*, *Salix nigra*, and *Utricularia subulata*. (Nomenclature follows that of Radford, Ahles & Bell (1968).)

In autumn 1980, *L. leptocarpa* plants were randomly sampled to determine the distribution of plant size and seed production. More than fifty plants were collected at the end of the growing season, oven-dried at 60°C to constant weight, weighed, and analysed for seed production. Since some of the plants were very fecund, a good estimator of seed number was sought. Capsule length was found to be highly correlated with seed number ($r = 0.89$, $n = 60$, $P = 0.001$). Seed production, therefore, was estimated from the total number and length of the capsules.

The following spring more than 800 seedlings were followed throughout the growing season in twenty-three randomly selected 1-m^2 plots along a 150-m transect running parallel to the bank of Ellention Bay. Individuals were permanently marked with flagged toothpicks once a plant had produced its first true pair of leaves. Weekly censuses were taken and any new plants establishing in the plots between censuses were grouped as the same germination cohort.

Survival, size, and seed production were recorded every 2-3 weeks for each individual. Size was estimated as the total length of plant stem and all branches. Laboratory analysis of a previous sample of plants had demonstrated a high correlation ($r > 0.98$, $n = 42$, $P = 0.001$) between total stem length and dry-weight biomass. This paper will refer to this estimated dry weight as plant size. Seed production was again estimated from the total number and length of capsules.

At the end of the growing season, the data from each sample period were pooled to determine demographic features and the final frequency distribution of size and seed number production for population in 1981. The data were also analysed by cohorts to determine the effect of time of establishment on survivorship, size at each observation date, seed production, and relative growth rate. Statistical analysis was performed using the Statistical Analysis System (Helwig & Council 1979).

The field censuses were repeated in 1982 to provide comparative demographic information in different weather. The 1981 study was repeated, except that only 250 plants were marked in twelve plots, only four germination cohorts were identified and, after establishment, censuses were taken approximately every 3 weeks.

Results

Population traits

The final frequency distributions for individual plant size and seed production in 1980 and 1981 were very similar. Only the 1981 data are presented here (Fig. 1). The distribution of size was similar to a log-normal distribution (Kolmogorov-Smirnov D-statistic for goodness of fit of log-transformed data to normal distribution = 0.099, $P < 0.05$). The skewness value (g) was 1.78 for the plant size distribution and 3.42 for seed production. Eighty-four per cent of the plants were smaller than the arithmetic mean size and 61% were smaller than half the mean size (Fig. 1a). Nine per cent of the plants accounted for 26% of the total biomass of *L. leptocarpa*.

Seed production varied greatly between individuals (Fig. 1b). Sixty-four per cent of the plants produced fewer than the mean number of seeds and 49% produced fewer than half the mean number. Five per cent of the 117 plants which flowered produced 39% of the seeds in 1981. Plant size was highly correlated with seed production in 1980 ($r > 0.95$, $n = 42$, $P = 0.001$) and in 1981 ($r > 0.63$, $n = 42$, $P = 0.001$).

The early stages in the life history of *L. leptocarpa* were the most critical for survival (Table 1). Life expectancy in days was highest for the pre-dispersal stage, then decreased greatly during dispersal. It increased again following establishment, reaching a maximum for juveniles and then gradually declining through maturity and senescence. Survivorship data have a similar trend (Table 1; Fig. 2). Very high loss occurred at the seed dispersal stage and a very small
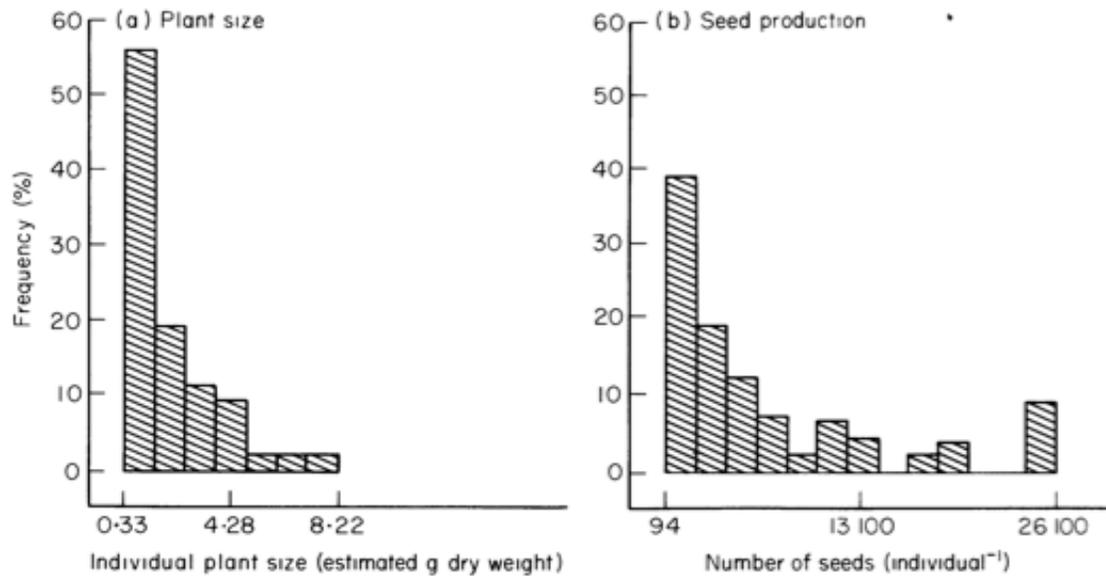
percentage of the seeds produced germinated within the plots. The causes for this loss have not been studied directly, but the seeds are equipped with a specialized endocarp (Eyde 1978) which remains attached and enables the seed to float. This means of dispersal may result in loss from Fig. 1. Percentage frequency distributions at the end of the growing season for (a) individual plant size ($n = 81$, $\dot{x} = 2.08$g) and (b) seed production per individual ($n = 117$, $\dot{x} = 2100$) for *Ludwigia leptocarpa* at a site in South Carolina in 1981.

Table 1. Life table for *Ludwigia leptocarpa* at Ellenton Bay, South Carolina in 1981. Format is adapted from Sharitz & McCormick (1974) and Leverich & Levin (1978). Time of senescence of the parent plant is considered the beginning of the life cycle.

Age of plant (days)	Life cycle stage	Length of interval (days)	Number surviving to end of interval	Survivorship§	Mean life expectancy (days) at end of interval
0-160	pre-dispersal*	160	236 255	1.0	148
161-176	dispersal	16	181 916	0.77	14
177-197	germination†	21	1301	0.005	55
198-212	establishment ‡	15	838	0.003	39
213-219	juvenile	7	801	0.003	47
220-238		19	685	0.003	47
239-252		14	513	0.002	40
253-272	mature	20	376	0.002	38
273-297		25	266	0.001	30
298-317		20	187	0.0008	24
318-333		16	116	0.0005	14
334-340		7	64	0.0003	3.5

*Estimated from 1982 seed production
† Estimated from seedling germination in sub-plots
‡ Based upon census of marked individuals
§ Survivorship — the probability that an individual of age zero will survive to the end of an interval
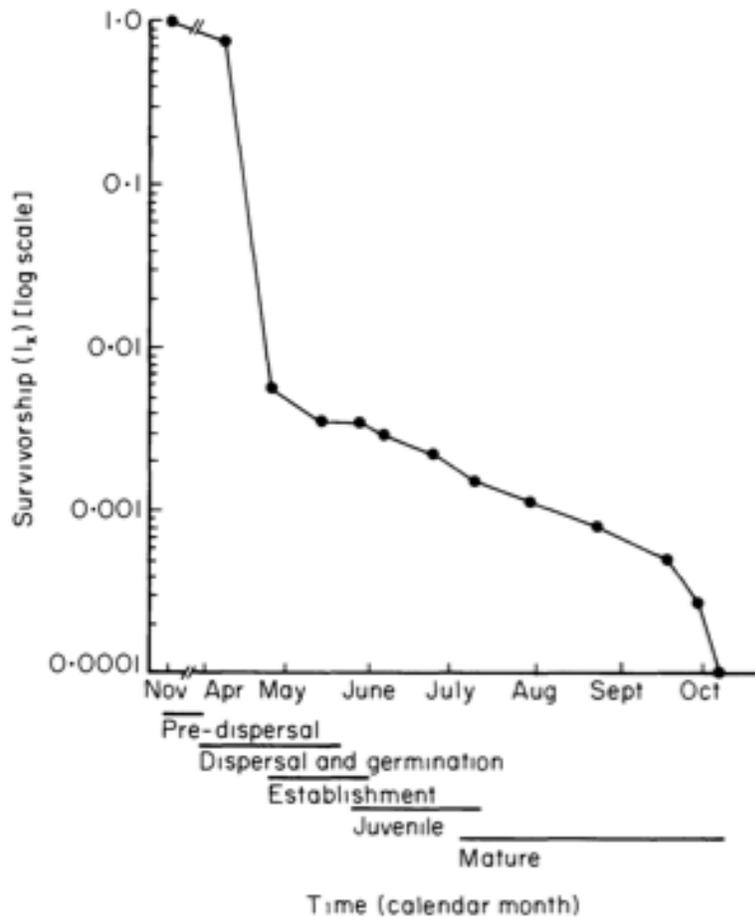
Fig. 2. Survivorship curve for *Ludwigia leptocarpa* at Ellention Bay, South Carolina, 1980-1981.

the population when the water level is high. Also, seeds that germinate while floating may establish on available stumps and sediments but perish if no permanent substratum is found. No animals were seen to eat the fruits or seeds. Analysis of the seed bank through soil-sieving to reclaim seeds and through greenhouse and field germination experiments showed that few or no viable seeds remain from year to year. The small size of the seeds made chemical testing for viability impractical.

The rate of mortality was constant through the seedling establishment, juvenile, and early mature stages (Fig. 2). Mortality was again high at the end of the growing season when mature plants completed their annual cycle and senesced (Fig. 2).

Cohort study

In 1981, five cohorts of germinating seedlings were marked over 6 weeks (23 April, 30 April, 12 May, 21 May and 28 May). There were no significant differences in the traits studied for plants that established at different times. Individuals of the five cohorts showed similar patterns of

survivorship, average size at each observation date, and relative growth rate (Fig. 3). However, slight differences between them may be correlated with rainfall and subsequent soil moisture availability during the early seedling stage. Drought occurred from 15 April to 1 June 1981 (Fig. 3d), during which cohorts 1-4 became established. No mortality was observed for cohorts 1 and 2 until the third week of the drought. Total mortality was greatest for cohort 4, which became established near the end of the drought when the soil was most depleted of surface moisture. Survivorship was essentially linear for all of the cohorts; all had similar slopes (Fig. 3a). A decreasing relative growth rate for each cohort was evident from April to the end of May, followed by an increase in growth rate after more than 75mm of rain fell on 1 June (Fig. 3b). The most recently established plants grew best following this rainfall. Thereafter, the five cohorts had similar relative growth rates with no significant differences in average size at each observation date (Table 2 and Fig. 3c).

Seed production per individual was also unaffected by the date of establishment (Table 3). Although plants that established early (cohorts 1 and 2) produced greater absolute numbers of seeds, the average number of seeds per individual was not significantly larger ($F = 0.88$, $N = 73$, $P > 0.48$, for an analysis of variance performed on log-transformed data).

In 1982, four germination cohorts were marked (17 May, 1 June, 14 June and 28 June). As in 1981, there were no significant differences in survivorship between the cohorts. However, some differences were seen between the cohorts in average plant size on each observation date (Fig. 4). Members of the earlier cohorts were, on average, larger throughout the growing season than members of later ones. Rainfall and the availability of soil moisture, especially in the early stages, may have affected the growth of the cohorts. During the period 18 May to 31 June 1982, when cohorts 1-3 were being established, rainfalls of more than 12.5mm occurred on five separate occasions, and no more than 5 days passed without any precipitation. Plants of cohort 4 were significantly smaller on each observation date than those in the other three cohorts; the mean biomass for this group never exceeded 0.32g. Rainfall events were more widely spaced and less intense following the establishment of this cohort. Few plants died in any cohort prior to 1-10 July 1982, during which period there was no rainfall. There was some overlap in size among individuals of different cohorts, which also varied greatly within themselves, in both 1981 and 1982 (Fig. 5).
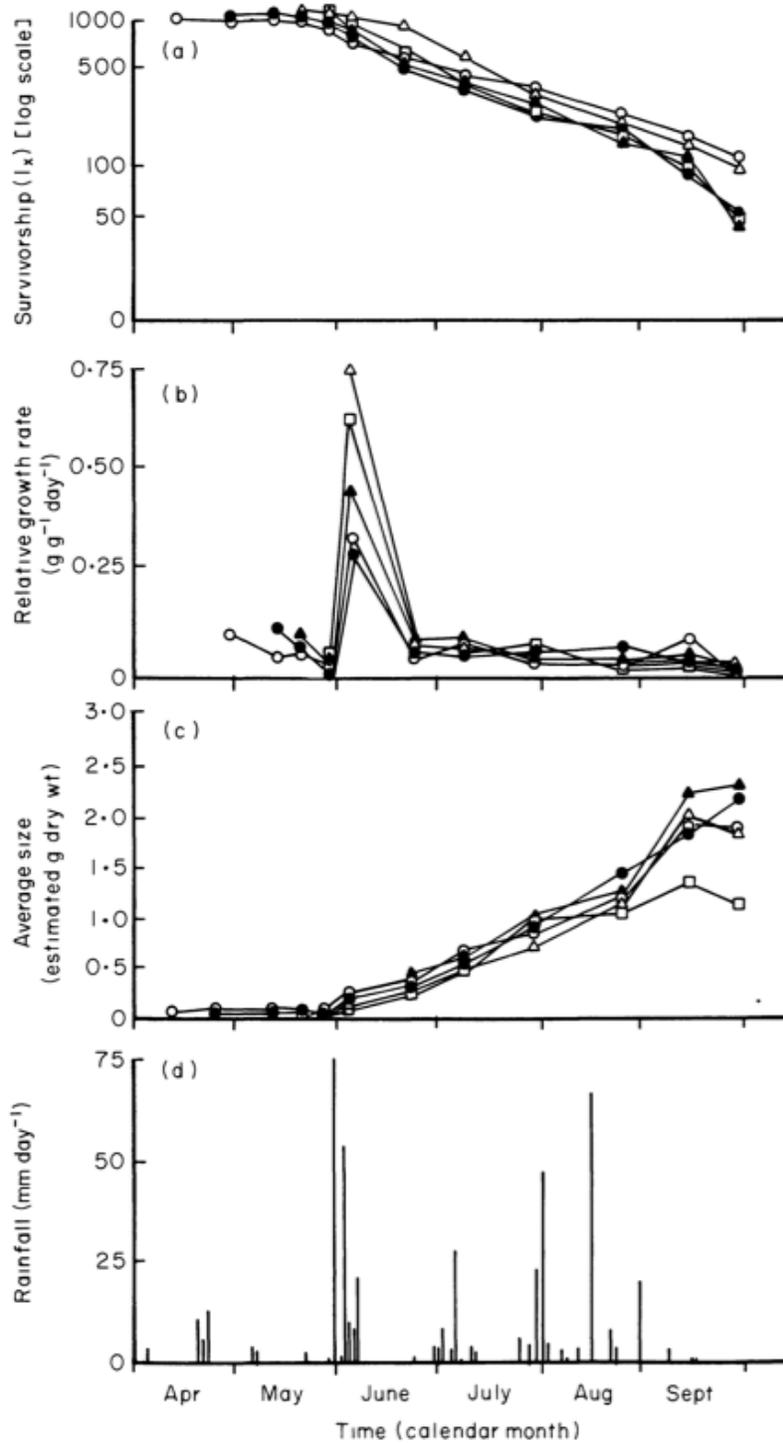
Fig. 3. Growth characteristics of five germination cohorts of *Ludwigia leptocarpa* during the 1981 growing season: (a) survivorship, (b) relative growth rate, (c) average size, (d) rainfall at Ellention Bay. Life of each cohort begins when plants were marked at establishment. Symbols:

(◯), cohort 1; (⬤), cohort 2; (▲), cohort 3; (□), cohort 4; (△), cohort 5. Overlapping points are slightly offset for clarity.

Table 2. Average size (estimated in g) of cohorts of *Ludwigia leptocarpa* from a site in South Carolina in 1981. *F* values presented are for analysis of variance performed on log-transformed data.

Date	1	2	3	4	5	*F*-value
30 April	0.04	0.02	—	—	—	384.02*
12 May	0.05	0.05	0.02	—	—	344.26*
21 May	0.07	0.06	0.04	0.02	—	113.67*
28 May	0.07	0.07	0.04	0.03	0.03	82.67*
5 June	0.24	0.21	0.17	0.15	0.16	4.74*
24 June	0.40	0.36	0.37	0.33	0.30	1.03
10 July	0.71	0.54	0.63	0.52	0.53	2.18
30 July	0.93	1.00	1.00	1.00	0.76	0.16
26 August	1.30	1.60	1.30	1.20	1.20	0.33
15 Sept	3.40	2.00	2.40	1.50	2.20	0.42
1 Oct	2.00	2.40	2.50	1.20	2.00	0.27

* $P < 0.001$; all other *F*-values insignificant.

Table 3. Fecundity data for germination cohorts of *Ludwigia leptocarpa* at a site in South Carolina in 1981.

Cohort	1	2	3	4	5
Date of initiation	23 April	30 April	12 May	21 May	28 May
Total number of individuals	197	264	290	91	73
Number of plants flowering	30	24	24	10	13
Plants flowering (%)	15.2	9.1	8.3	10.1	17.8
Total seeds per cohort	95 400	63 000	44 500	12 000	21 300
Seeds per individual flowering*	3180	2630	1860	1200	1640

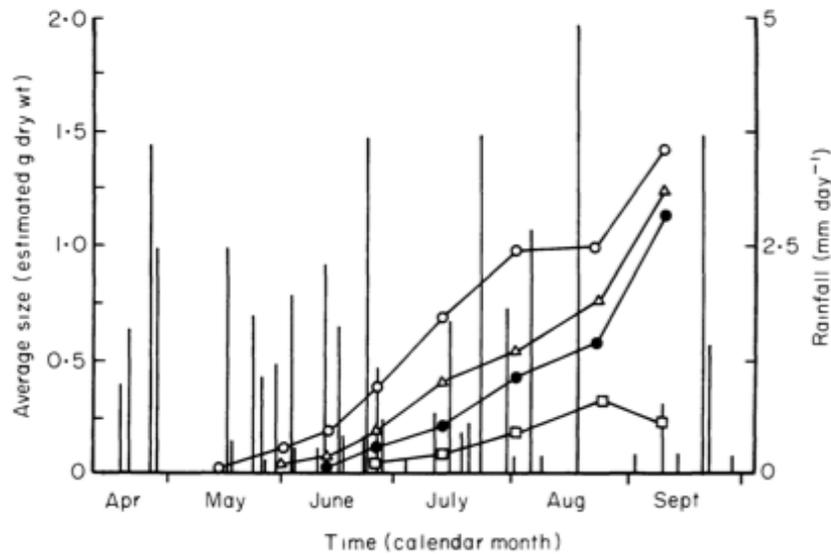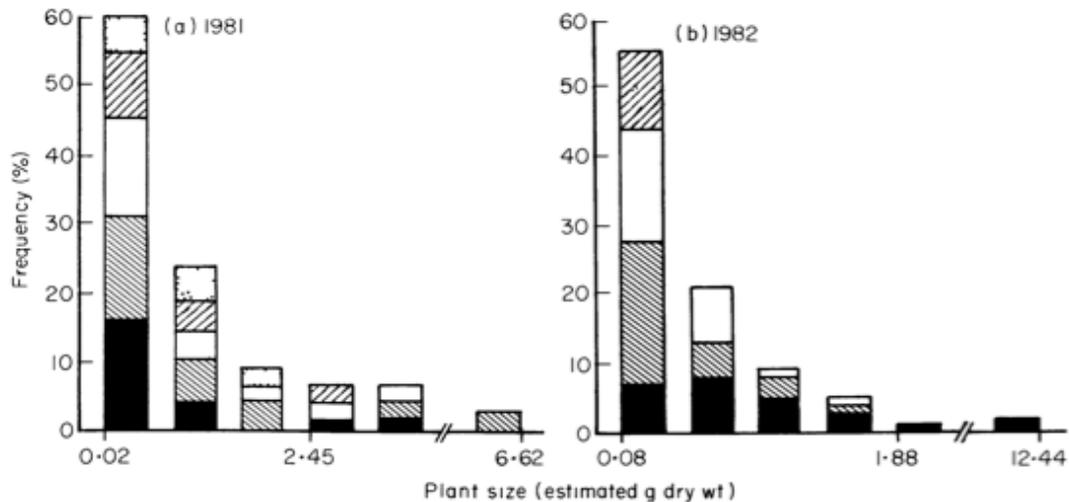* Means are not significantly different

Fig. 4. Average size at each census date for four germination cohorts of *Ludwigia leptocarpa* marked in 1982 at a site in South Carolina. Rainfall at the site is indicated by vertical lines.

Symbols: (○), cohort 1; (△), cohort 2; (●), cohort 3; (□), cohort 4.

Fig. 5. Percentage frequency distribution of individual size of *Ludwigia leptocarpa* at time of flowering in South Carolina for the population as a whole in (a) 1981 and (b) 1982. Percentage of plants belonging to each germinate cohort is indicated. Symbols: (■), cohort 1; (■), cohort 2; (□), cohort 3; (⊞), cohort 4; (□), cohort 5; $n = 184$ (in 1981); $n = 72$ (in 1982).

Discussion

The sample frequency distribution for *Ludwigia leptocarpa* at the ends of the 1980 and 1981 growing seasons show that a size hierarchy develops during the growing season. A few individuals become very large, while the majority are smaller than the population mean. Size is highly correlated with seed production, which follows the same trend; very few individuals contribute most of the potential offspring. These plants serve as the chief seed source for the next year's population, since *L. leptocarpa* has little or no seed bank.

The population of *L. leptocarpa* as a whole (Fig. 2) exhibits aspects of all three generalized survivorship curves described by Deevey (1947). There is high mortality in the early stages (Type III) from seed dispersal to establishment. After establishment, mortality rates are relatively constant (Type II). Finally, at the end of the growing season, there is a sharp increase in the mortality of adults (Type I), perhaps brought on by colder, drier weather.

Nevertheless, the overall shape of the survivorship curve is concave, showing mortality to be most concentrated in the early stages. Although most plant species for which date are available exhibit Type II curves, a Type III curve has been reported for *Danthonia caespitosa* (Williams 1970) a perennial range grass and for the winter annuals *Minuartia uniflora* and *Sedum smallii* (Sharitz & McCormick 1974). *Danthonia caespitosa* is an invader of sites under-going secondary succession for which some populations show high early mortality, presumably due to heavy grazing pressure. The *Minuartia* and *Sedum* species are inhabitants of rock outcrops, where they are subjected to alternating periods of drought and flooding. Spring rains carry seeds away and drying of the shallow soils results in a high mortality of early seedlings. Type III curves are also characteristic of animal species such as oysters or other shellfish which experience high mortality in their free-swimming larval stages (Odum 1971). The Type III survivorship curve might be more commonly observed in both plants and animals if studies of life-history traits concentrated more on the early stages (Watkinson & Harper 1978).

Departure from a Type II curve implies that selection is being concentrated at specific life cycle stages. For *L. leptocarpa*, the most critical stage is that between dispersal and establishment (Fig. 2). Assuming a seed lost to the observed population is not successfully recruited in another site, the chance of survival depends on landing in a moist exposed site with sufficient substratum to support growth.

To maximize the chance of establishment, large numbers of seeds are produced (mean production = 2100 seeds per flowering individual in 1981) and dispersal takes place over many weeks. The mean seed production of over 2×10^4 seeds per plant is characteristic of species of intermittently available habitats such as wood clearings, exposed mudflats, and shingle banks (Salisbury 1942). Species common in permanent, unshaded habitats characteristically produce about $5\text{-}6 \times 10^3$ seeds per plant. By the end of the growing season, some newly-produced *L leptocarpa* capsules may dehisce, but by March, fewer than 20% of the capsules will have she their seeds. The seeds are released gradually from March until July with maximum dispersal

from late April to June. The seeds germinate soon after dispersal with little or no germination occurring after June.

This prolonged time for dispersal may be a 'bet-hedging' stratagem (Stearns 1976) to help ensure that fresh seed will be available to germinate and take advantage of favorable conditions, such as heavy rainfall, as they occur, and to minimize the chances of all seeds being lost from the site. Sharitz & McCormick (1974) showed that seed retention until conditions were appropriate for immediate germination enhanced the survivorship of *Sedum smallii* over that of a non-seed-holding associated species of similar life history. *Ludwigia leptocarpa* thus appears well suited to colonization of temporary exposed habitats. It exhibits the characteristics of an '*r*-selected' species (MacArthur & Wilson 1967).

The absolute time of germination does not appear to determine an individual's rank in the size hierarchy of the population. This is true even though early-germinating plants may have as many as 35 days more growth than later-germinating plants. This, along with the observation that size hierarchies exist even within germination cohorts (Fig. 5), indicates that the time of germination is not the major factor affecting plant size in this species. Also, the time of germination has little effect on survivorship or seed production. In 1981, a drought during the establishment period may have been responsible for retarding the growth rate of the early-germinating cohorts. Cohorts 4 and 5, which established at the end of the drought period, experienced less severe early-mortality. Similarly, in 1982, individuals of cohort 4 which established during a period of drought were consistently smaller than the population mean (Fig. 4).

Small differences in the time of emergence of seedlings have been shown to have extremely large effects on survival, growth, and reproduction in glasshouse experiments with annual species (Ross & Harper 1972). Similar effects have not been so well established in natural populations. Howell (1981) followed six emergence classes of the annual *Impatiens capensis* which were separated by a total of 13 days. The time of emergence had substantial effects on survival and fecundity in stands dense enough to be experiencing self-thinning. Not all demographic variance between the classes, however, could be explained by emergence class. Unexplained variance was attributed to complex environmental factors affecting later stages of development. For *Verbascum thapsus*, a biennial, the probability of becoming established, overwintering, and having high reproductive success was greatest for individuals belonging to the earliest of three emergence classes which established in May, June, and August, respectively (Gross 1980). However, there was overlap of size among individuals in the May and June classes. Differences in survival and plant development were attributed to climatic factors in the spring and summer cohorts of the biennial *Melilotus alba* (Klemow & Raynal 1981) and in he perennial *Plantago lancelota* (Hawthorn & Cavers 1976), but the frequency distributions of individual size between and within cohorts were not presented.

If the time of germination is not solely responsible for the development of a size-hierarchy for *Ludwigia leptocarpa* and other species, and if the earliest germinating plants do not consistently develop into the largest individuals, then what factors are responsible? Harper (1977) has stated that factors which influence relative growth rate, especially at the early seedling stage, are likely to be important. An understanding of the role that differences in genetics, seed size, and microsite characteristics play in determining the position an individual of

L. leptocarpa occupies in the size-hierarchy of a population is needed before this question can be answered.

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