Age-Specific Survivorship and Reproduction in Phlox drummondii

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AGE-SPECIFIC SURVIVORSHIP AND REPRODUCTION IN
PHLOX DRUMMONDII

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The interest of ecologists in the demography of natural populations has developed greatly since Lotka (1925) used the Euler equation to describe population growth in terms of age-specific components. Theoreticians have demonstrated the significance of life-history strategies in determining reproductive performance and growth of populations (e.g., Cole 1954; Gadgil and Bossert 1970; Emlen 1970; Schaffer 1974a, 1974b; Schaffer and Gadgil 1975), and the influence of demographic characteristics upon the genetic structure and evolutionary potential of populations (e.g., MacArthur 1961, 1962; Anderson and King 1970; King and Anderson 1971; Charlesworth 1970, 1972). Although theory is well developed information on life-history parameters of natural populations is meager.

There are relatively few life tables for organisms other than man. The first complete tables for nonhuman organisms were those of Pearl and Parker (1921) for laboratory populations of Drosophila melanogaster. Deevey (1947) constructed life tables for natural populations of several animal species, including Dall mountain sheep (Murie 1944), a sessile rotifer (Edmondson 1945), a barnacle (Hatton 1938), and several bird taxa. Since then life-history data have been published for a variety of invertebrates (Birch 1948; Leslie and Park 1949; Evans and Smith 1952; Howe 1953; Lefkovitch 1963; etc.) and vertebrates (Zweifel and Lowe 1966; Lowe 1969; Spinage 1972; Wilbur 1975; etc.).

Only during the past decade has the study of plant life tables received due attention. Harper and White (1974) reviewed contemporary studies of survivorship in several Plantago species (Sagar 1959; Hawthorne 1973), Ranunculus species (Sarukhan and Harper 1973), Anthoxanthum odoratum (Antonovics 1972), and in several other perennial herbs. A few researchers have investigated survivorship in woody perennials (e.g., Hett and Loucks 1971, 1976; Guittet and Laberche 1974; Yarranton and Yarranton 1975; etc.). Other studies have revealed the age structures of perennial plant populations (e.g., Kerster 1968; Levin 1973; Schaal 1974; Van Andel 1975), which also add to our knowledge of survivorship in nature.

Formal life-table analyses of natural populations of annual plants have been reported only for Sedum smallii and Minuartia uniflora (Sharitz 1970). Except for this exemplary study, our knowledge of the demographic features of annual plant populations is fragmentary. Furthermore, there are essentially no data concerning the age-specific fecundities of plants in natural populations. It is the details of

age-specific survivorship and reproduction which best elucidate the dynamics of populations, and they are crucial to understanding the consequences of particular life histories. Complete measurements are needed from species of a variety of habits and habitats before the merits and liabilities of divergent life histories in plants may be fully assessed.

In this report a detailed life table is presented for a natural population of the annual herb *Phlox drummondii*. Life-history features derived from survivorship and fecundity data will be discussed, including the net reproductive rate, the intrinsic rate of increase, and age-specific reproductive values.

The winter annual *Phlox drummondii* Hook. (Polemoniaceae) is a conspicuous element of the spring flora of south central Texas. Within its range the species typically occurs in discontinuous populations of thousands of individuals. The plants of the population in this study are referred to variety *drummondii* (*sensu* Erbe and Turner 1962).

Seeds of *Phlox drummondii* germinate in late November or early December and exhibit slow vegetative growth through the winter months. Plants typically begin flowering profusely in March, although some few individuals may flower as early as late January. The plants show indeterminate growth and flowering, and given sufficient rainfall plants will continue to flower through May. The plants are almost completely self-incompatible. Individual flowers can remain open for as long as 8 days, providing abundant opportunity for cross-pollination. The primary pollen vector is the pipe-vine swallowtail butterfly, *Battus philenor* L. There are three ovules per flower, and although the average seed set is less than three, three seeds per mature capsule is common. The small seeds (ca. 1 × 3 mm) are disseminated by explosive dehiscence of the capsule, and can be scattered as far as 5 m (Levin and Kerster 1968). The seeds are readily distinguishable from seeds of ecological associates.

METHODS

The population examined in this study occupies approximately $\frac{1}{4}$ ha on an electric cooperative right-of-way on the northern edge of Nixon, Gonzales County, Texas. The site is protected from cattle grazing and human disturbance but not natural pests, providing optimal conditions for monitoring a natural population. This population is typical of those occurring in south central Texas.

A section of the population was divided into 50 permanently marked quadrats, each 3 × 3 m, arranged in an array of 10 rows and five columns. Within each quadrat specific areas were reserved for quadrat access, repeated soil sampling for seed, vegetative and reproductive mapping, and plant sample removal.

Soil samples for seed recovery were taken to a depth of approximately 8 cm, since examination revealed that most *Phlox* seed was in the detritus layer of the soil surface and none was found deeper than 5 cm. At each sampling episode, five samples totaling 929 cm^2 were taken from each of the 50 quadrats, thus yielding data periodically on number of seeds present from 250 samples totaling 4.65 m^2, or approximately 1% of the study area. Soil samples were taken for seed recovery on May 29, July 31, and September 30, 1974, and February 1, 1975. The samples were taken to the lab and processed through numbers 12 and 18 U.S.A. standard testing

sieves to recover the size class of material including *Phlox* seeds. This was sorted manually, and the *P. drummondii* seeds were removed and counted.

To measure the dynamics of the vegetative and reproductive phases of the population, individual seedlings were located, mapped, and censused at intervals for the duration of their lives. This was accomplished by placing a mapping frame in the reserved area withirl each quadrat, locating it with steel pins driven into the soil, and recording the coordinates of all seedling contained in an area of 929 cm², equivalent to the area sampled for the seed population. Individual plants could then be located from their coordinates during each subsequent census by replacing the frame on the steel pins. The first census of this sort was taken on November 29–30, 1974, a few days after seedlings were first detected. Subsequent censuses were taken as indicated in the life table, and they were made weekly during the period of flowering and reproduction. In total, 190 individual plants were located in the 50 quadrats and observed for their life durations. Observations recorded during the vegetative phase included numbers of nodes, numbers of branches, evidence of damage by herbivores, and date of first floral bud appearance. During the reproductive phase flower number was recorded at weekly intervals, since flower life is about 1 wk. Finally, the numbers of capsules maturing in a given week were determined (the calyx recurves after dehiscence and persists on the plant). Plants were recorded as dead when they were leafless, dry, and brittle, and when subsequent examination showed no sign of renewed growth.

A greenhouse study accompanied the field work in order to obtain information on the growth and reproductive performance of plants under uniform conditions and free from constraints such as predation, drought, and disturbance encountered in natural situations. Plants were grown in individual containers from seed of the same cohort as that studied at Nixon. They were given adequate water and nutrients, and maintained until all had died. Plants were then dried, weighed, and the total number of flowers produced was determined by counting calyces.

RESULTS

The life table for the 1974–1975 generation of *Phlox drummondii* at Nixon is given in table 1. The basic form used by Pearl and Miner (1935), Deevey (1947), Sharitz (1970), and others has been adapted for this study. A glossary of the symbols used is provided in table 2. The data of the life table are summarized in the survivorship curve in figure 1.

The semilogarithmic plot of figure 1 indicates initial survivorship as unity. The curve declines fairly evenly during the period of seed dormancy, then levels off somewhat during the period of growth and reproduction. Finally, the curve falls sharply in the period of seed set as the surviving plants die.

The causes of mortality cannot be completely documented, but there is some indication of their nature. Decline in numbers in the seed pool is due to the removal of individuals, presumably by granivores. Seed stored for several seasons, both in the lab and in the field, shows no loss of viability. However, in the natural seed pool the number of individuals remaining declines at a fairly constant rate. At Nixon seed harvesting ants were observed to take Phlox seeds, but only if presented with them;

TABLE 1

LIFE TABLE FOR *Phlox drummondii* AT NIXON, TEXAS

Age Interval (days) $x - x'$	Length of Interval (days) D_x	No. Surviving to Day x N_x	Survivor-ship l_x	No. Dying During Interval d_x	Average Mortality Rate Per Day q_x	Mean Expectation of Life (days) E_x
0– 63	63	996	1.0000	328	.0052	122.87
63–124	61	668	.6707	373	.0092	104.73
124–184	60	295	.2962	105	.0059	137.59
184–215	31	190	.1908	14	.0024	137.05
215–231	16	176	.1767	2	.0007	115.72
231–247	16	174	.1747	1	.0004	100.96
247–264	17	173	.1737	1	.0003	85.49
264–271	7	172	.1727	2	.0017	68.94
271–278	7	170	.1707	3	.0025	62.71
278–285	7	167	.1677	2	.0017	56.78
285–292	7	165	.1657	6	.0052	50.42
292–299	7	159	.1596	1	.0009	45.19
299–306	7	158	.1586	4	.0036	38.46
306–313	7	154	.1546	3	.0028	32.36
313–320	7	151	.1516	4	.0038	25.94
320–327	7	147	.1476	11	.0107	19.55
327–334	7	136	.1365	31	.0325	13.85
334–341	7	105	.1054	31	.0422	9.90
341–348	7	74	.0743	52	.1004	5.58
348–355	7	22	.0221	22	.1428	3.50
355–362	7	0	.0000			

TABLE 2

GLOSSARY OF SYMBOLS

|	
x	Age in days. (This designates the first day of an interval.)
x'	The first day of the interval following the interval of x.
D_x	Length in days of the interval beginning with day x.
N_x	Number of individuals surviving to day x.
l_x	Survivorship: the probability an individual age zero will survive to day x.
d_x	Number of individuals dying during the interval beginning with day x.
q_x	Average mortality rate per day during the interval beginning with day x.
E_x	Mean expectation of life on day x, in days.
B_x	Total number of progeny produced during the interval beginning with day x. Superscripts indicate the basis of measurement, e.g., B_x^{ovule} or B_x^{seed}.
b_x	Average number of progeny per individual during the interval beginning with day x. Superscripts are as above.
$l_x b_x$	Contribution to R_0 during the interval beginning with day x.
R_0	Net reproductive rate. $R_0 = \sum l_x b_x$.
r	The intrinsic rate of increase, from $1 = \sum l_x b_x e^{-rx}$.
T	Generation length.
e	The base of natural logarithms; $e = 2.71828....$
$\ln x$	The natural logarithm of x.
v_x	The average reproductive value per individual alive on day x.
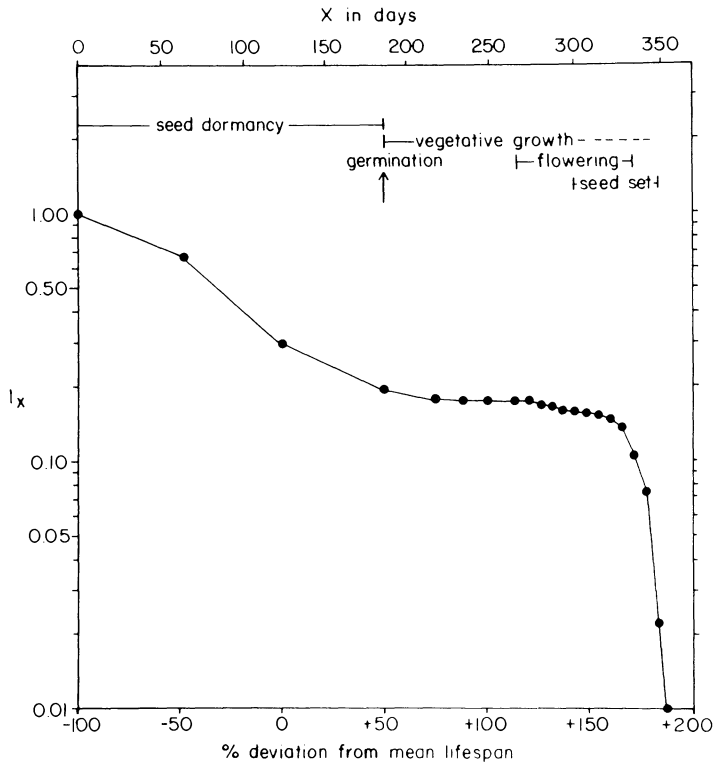
FIG. 1.—Survivorship curve for *Phlox drummondii* at Nixon, Texas, 1974–1975. Age is indicated both in days (day 0 = May 29, 1974) and as percent deviation from mean life span (= 122.87 days).

other invertebrates and birds may take them also. Because of their small size and infrequency compared to the seeds of other members of the community, it is unlikely that they are selectively removed.

Seedlings show a lower mortality rate than do individuals in the seed pool; this lower rate continues until final senescence of the population. During the period of growth and reproduction, almost all damage to *P. drummondii* individuals is due to feeding by larvae and adults of a Chrysomelid beetle, *Disonycha alabamae*. Most, if not all, of the plants at Nixon suffered some degree of damage. Although completely defoliated plants often recover, show renewed growth, and subsequently flower, about 37% of all plants ultimately failed to recover following extensive beetle damage.

Fecundity schedules for *P. drummondii* were constructed from two different data bases, seed production and ovule production. The fecundity schedule based on seed output is given in table 3, and that based on ovule production is in table 4. The seed production estimates are based on total capsules matured multiplied by 2.787, the average number of seeds per capsule (see table 5). Ovule production is based on three ovules per ovary. From the estimates of age-specific fecundity in tables 3 and 4, the

TABLE 3

FECUNDITY SCHEDULE FOR *Phlox drummondii* AT NIXON, TEXAS, BASED ON SEED PRODUCTION

$x - x'$	B_x^{seed}	N_x	b_x^{seed}	l_x	$l_x b_x$
0–299	.000	996	.0000	1.0000	.0000
299–306	52.954	158	.3394	.1586	.0532
306–313	122.630	154	.7963	.1546	.1231
313–320	362.317	151	2.3995	.1516	.3638
320–327	457.077	147	3.1904	.1476	.4589
327–334	345.594	136	2.5411	.1365	.3470
334–341	331.659	105	3.1589	.1054	.3330
341–348	641.023	74	8.6625	.0743	.6436
348–355	94.760	22	4.3072	.0221	.0951
355–362	.000	0	.0000	.0000	.0000
					$\sum = \overline{2.4177}$

$R_0 = \sum l_x b_x = 2.42$ (per capita)

$r = \dfrac{\ln R_0}{365} = 0.0024$ (per capita per day)

NOTE.—$x - x'$ = age interval; B_x^{seed} = total no. of seeds produced during interval; N_x = no. surviving to day x; b_x^{seed} = average no. of seeds per individual during interval; l_x = survivorship; $l_x b_x$ = contribution to net reproductive rate during interval.

TABLE 4

FECUNDITY SCHEDULE FOR *Phlox drummondii* AT NIXON, TEXAS, BASED ON OVULE PRODUCTION

$x - x'$	B_x^{ovule}	N_x	b_x^{ovule}	l_x	$l_x b_x$
0–264	0	996	.0000	1.0000	.0000
264–271	123	172	.7151	.1727	.1235
271–278	573	170	3.3706	.1707	.5753
278–285	696	167	4.1678	.1677	.6988
285–292	729	165	4.4182	.1657	.7319
292–299	663	159	4.1698	.1596	.6657
299–306	756	158	4.7848	.1586	.7590
306–313	609	154	3.9545	.1546	.6114
313–320	579	151	3.8344	.1516	.5813
320–327	369	147	2.5102	.1476	.3704
327–334	285	136	2.0956	.1365	.2861
334–341	177	105	1.6857	.1054	.1777
341–348	0	74	.0000	.0743	.0000
348–355	0	22	.0000	.0221	.0000
355–362	0	0	.0000	.0000	.0000
					$\sum = \overline{5.5813}$

$R_0 = \sum l_x b_x = 5.58$ (per capita)

$r = \dfrac{\ln R_0}{365} = 0.0047$ (per capita per day)

NOTE.—$x - x'$ = age interval; B_x^{ovule} = total no. of ovules produced during interval; N_x = no. surviving to day x; b_x^{ovule} = average no. of ovules per individual during interval; l_x = survivorship, $l_x b_x$ = contribution to net reproductive rate during interval.

TABLE 5

SEED PRODUCTION PER CAPSULE

SEEDS PER CAPSULE	CAPSULES		SEEDS	
	No.	Proportion	No.	Proportion
April 16, 1975				
0	7	.033	0	.000
1	1	.005	1	.002
2	24	.114	48	.082
3	177	.839	531	.903
4	2	.009	8	.013
Total	211	1.000	588	1.000
Mean no. seeds per capsule = 2.7867				
May 5, 1975				
0	7	.026	0	.000
1	2	.007	2	.003
2	33	.123	66	.088
3	225	.840	675	.904
4	1	.004	4	.005
Total	268	1.000	747	1.000
Mean no. of seeds per capsule = 2.7873				

Pooled
No. of capsules = 479
No. of seeds = 1,335
Mean no. seeds per capsule = 2.787

fecundity curves in figure 2 have been drawn. These graphically show the relation between the estimates of age-specific fecundity and survivorship.

The net reproductive rate R_0 is the average number of offspring produced per individual alive on day 0. This is given by the expression

$$R_0 = \sum l_x b_x,$$

and estimates of R_0 based on both seed production and ovule production are given below the fecundity schedules in tables 3 and 4. The actual replacement rate in this study is based on seed production (since seeds are the individuals which enter age class zero of the next generation), and $R_0^{seed} = 2.42$. This value would indicate that the population was increasing in numbers during the 1974–1975 generation. Calculating the net reproductive rate from ovule production gives $R_0^{ovule} = 5.58$, which is of course greater than realized population growth.

With a discrete generation organism, R_0 may be obtained directly from the total number of offspring divided by the number of individuals in the original cohort (in this case $R_0 = 2408/996 = 2.42$). However, this shortcut obscures information about the distribution of reproduction within the generation; it is not obvious how many individuals produced how many seeds or when. Figure 3 is a plot of $l_x b_x$ values, the contributions to R_0 from each age class. The area under each curve shows the magnitude of the corresponding R_0 estimate. The $l_x b_x$ curve from seed output data
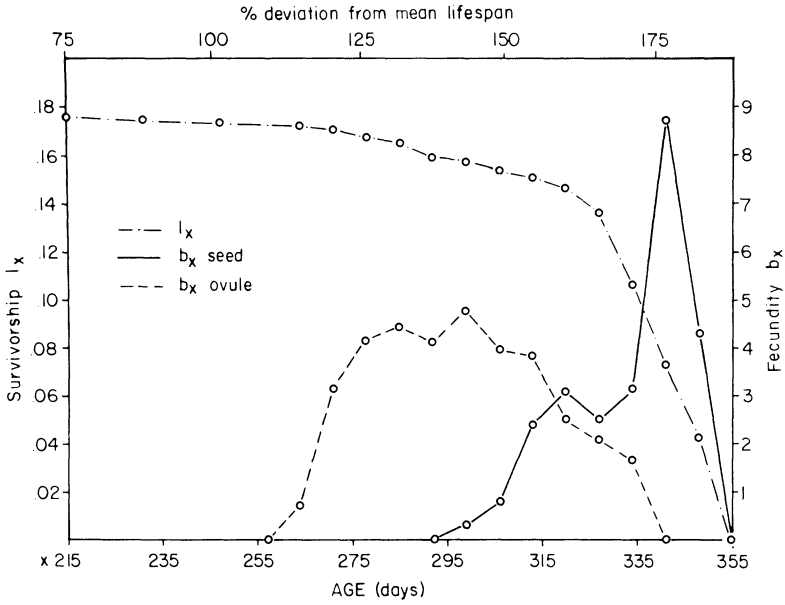
FIG. 2.—Fecundity curves for *Phlox drummondii* at Nixon, Texas, 1975. The solid line = average no. of seeds produced per individual during an interval (b_x^{seed}); the broken line = average no. of ovules produced per individual during an interval (b_x^{ovule}). A portion of the survivorship curve (l_x), on an arithmetic axis, is shown for reference.
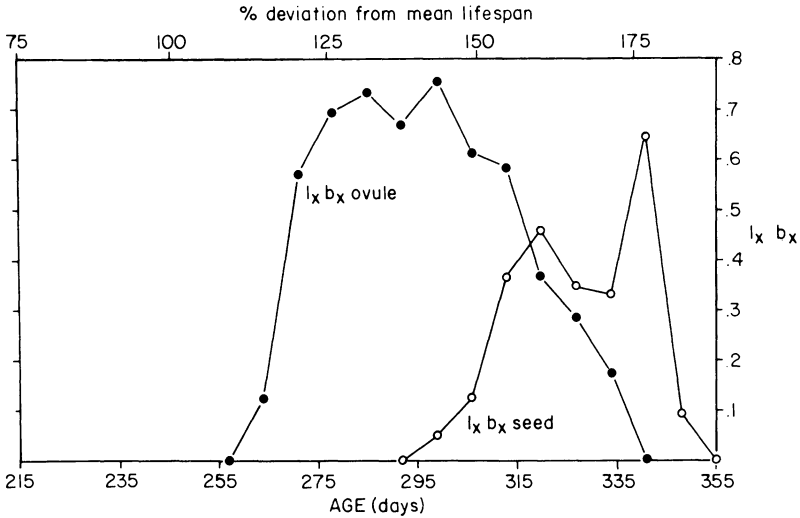

FIG. 3.—Distribution of the contributions to net reproductive rate during age intervals ($l_x b_x$ values). Open circles = $l_x b_x$ values based on seed production; closed circles = $l_x b_x$ values based on ovule production.

shows that actual reproduction is not at all evenly distributed, but that a larger portion of the total value of R_0 accrues late in the generation.

The intrinsic rate of increase, r, can be determined by solving the Euler equation, $1 = \int_0^\infty l_x b_x e^{-rx} dx$, for r (Lotka 1925). However, in this study the measurements of l_x and b_x are from within the generation of a single cohort, and there is no current growth of the population during the one generation span; therefore the approximation $1 = \sum l_x b_x e^{-rx}$ is more appropriate. If T is the length of generation, then, since $R_0 = \sum l_x b_x$ is the net reproductive rate for one generation, the above expression can be rewritten $r = (\ln R_0)/T$.

The difficulties involved in ascertaining an appropriate measure for T, such that $R_0 = e^{rT}$ is satisfied in general, have been discussed by Laughlin (1965), Leslie (1966), and Caughley (1967). In this study we are dealing with a case like Caughley's birth-pulse model, and have adopted a measure for T that reflects the mean interval between birth of parent and offspring (after Andrewartha and Birch 1954; Laughlin 1965). This has been called cohort generation length (T_c) by Laughlin (1965) and is appropriate in this single cohort study.

Among annual plants generation length is commonly taken to be 1 yr, but extended dormancy can give rise to age-structured seed pools and mean generation lengths of greater than 1 yr. But, if extended dormancy is infrequent and germination of the seed pool is essentially complete, generation length may be taken as 1 yr without introducing serious error. In this study only about 3% of the original cohort of seed remained ungerminated and under a survivorship regime like that described above only a fraction of these could contribute to successive generations. Therefore, a generation length of 1 yr has been used in calculating r; this is the cohort generation length. A slightly greater value for T would decrease the value of r only negligibly.

Using actual seed production for the 1974–1975 generation of P. drumondii, r^{seed} is 0.0024 per day (see table 3). Using ovule production as an index of reproductive capacity for the generation, r^{ovule} is 0.0047 per day (see table 4). These values both show the population to be in a period of growth during the measured generation. Values of r must have a time unit specified (in this case, per day) or they have no use in comparison; $r = 0.0024$ was established over an entire year, but it is reported as a daily rate.

The concept of reproductive value was developed by Fisher (1930) to measure the average contribution by an individual at a given age to the ancestry of future generations. Fisher's reproductive value is given by

$$v_x = \frac{e^{rx}}{l_x} \int_{t=x}^\infty e^{-rt} l_t b_t,$$

where v_x is reproductive value at age x, and x and t are both age indices.

The above expression for reproductive value is based on a model of continuous growth, and the exponential functions e^{rx} and e^{-rt} weight the value for changing population size. However, because the data in this study are from a single discrete generation which is not experiencing current growth the exponentials may be omitted (their values would be zero). It is thus appropriate to examine the distribution of absolute reproductive value at each age, which is given by $v_x = 1/l_x \sum_{t=x} l_t b_t$. The values for v_x (based on actual seed production) are plotted in figure 4.
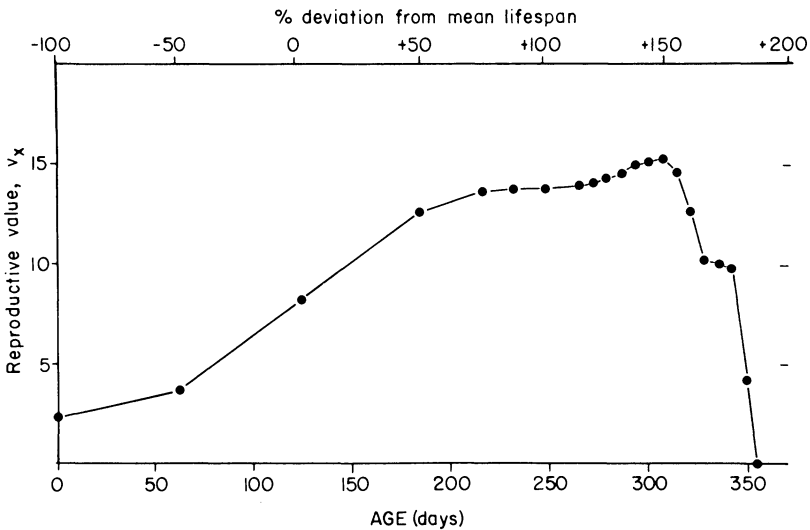
FIG. 4.—Reproductive values v_x for *Phlox drummondii* at Nixon, Texas, 1974–1975.

The survivorship and reproduction data thus far described are measurements of the average performance of the entire population sample. Since the data were collected for individual plants the distribution of survivorship and reproduction may be more fully examined. Of those individuals which germinated, the greatest proportion (about 45%) produced no capsules at all. A small proportion produced relatively many capsules; the greatest number of capsules produced by any plant was 45. The distribution of actual reproduction by individuals is given in figure 5, where the percentage of individuals that eventually produced a given number of capsules is shown. Only those individuals which germinated are included here; inclusion of all members of the original seed cohort would greatly expand the zero class.

Vigor of plants was estimated by the number of nodes on the day of census. To examine the relation between early vigor and eventual reproduction, the number of nodes on a plant at the December 30 census (approximately 1 mo after germination) was correlated with the number of capsules subsequently matured, and the correlation ($r = .491$) was very significant ($P \ll .01$, 174 df). Figure 6 shows the average number of capsules produced by plants with the given number of nodes. It is clear that the plants more vigorous at this early stage tended to produce more capsules on the average. The data allow determining whether this difference in average capsule production is a consequence of different longevities among the plants or a consequence of different reproductive outputs.

The plants were grouped in two classes, small plants with five or fewer nodes ($N = 126$), and large plants with six or more nodes ($N = 50$). Using the individual mortality and seed-set data, survivorship and fecundity schedules were constructed separately for the two classes, assuming a common survivorship schedule prior to December 30. The resulting l_x and b_x curves are shown in figure 7, and the $l_x b_x$ curves are plotted in figure 8. The net reproductive rates for the two classes are $R_0^{small} = 1.34$ and $R_0^{large} = 5.13$; the intrinsic rates of increase are $r^{small} = 0.0008$ and $r^{large} = 0.0045$
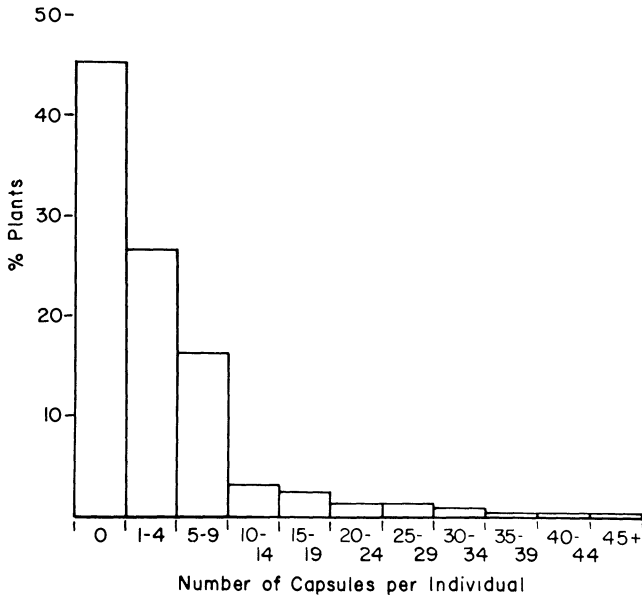
FIG. 5.—Distribution of individual reproductive outputs at Nixon, Texas, 1975. The height of a column shows the percentage of all plants that make up the given class.
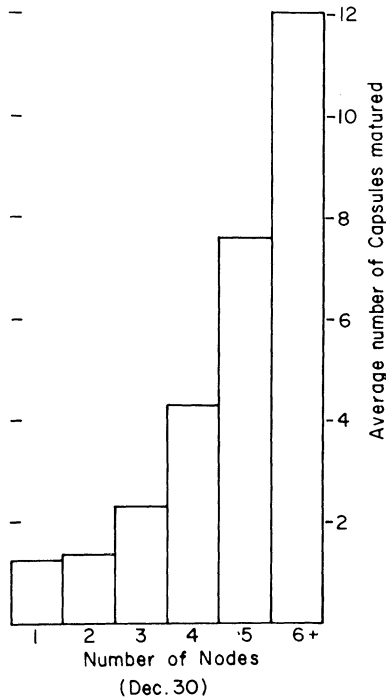

FIG. 6.—Reproductive output vs. no. of nodes on Dec. 30, 1974. The height of a given column shows the average number of capsules matured by the individuals making up the given class.
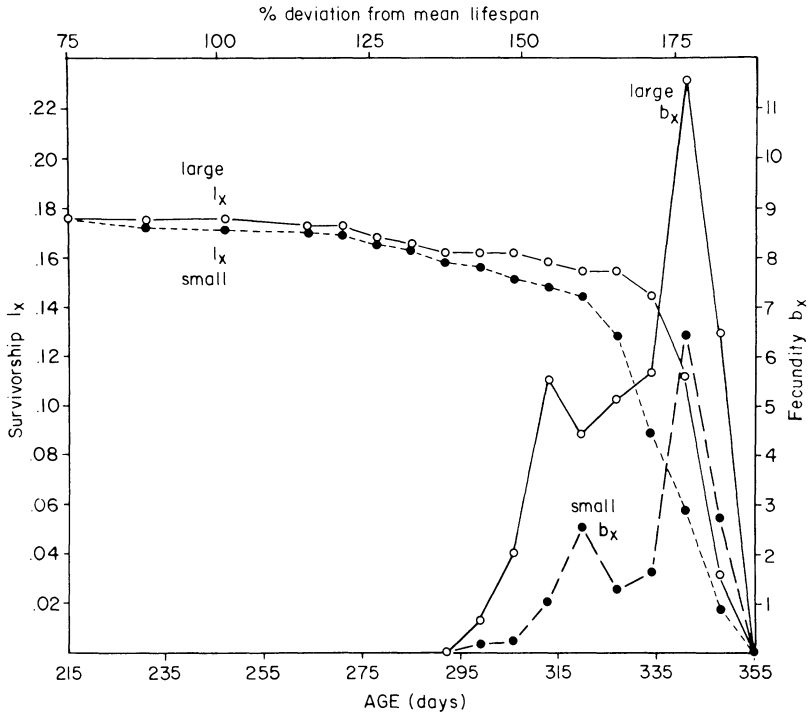
FIG. 7.—Survivorship curves (l_x) and fecundity curves (b_x) for the large and small classes of plants. The large class is made up of plants with six or more nodes on Dec. 30, 1974; the small class is made up of plants with five or fewer nodes. Common survivorship schedules prior to Dec. 30 are assumed.

per day. Finally, reproductive values were calculated for each class and the distributions of v_x^{small} and v_x^{large} are given in figure 9.

The flowering performance of plants under uniform conditions in the greenhouse is compared with flowering performance of plants in the field in figure 10. The ranges of flower number are similar, but among greenhouse plants there is a lesser proportion with zero flowers. Furthermore, plants in the field show a more extended tail of distribution in the upper range; the greatest number of flowers produced in the greenhouse was 50 by one plant, while in the field one plant produced 79 and another extraordinary individual had 104 flowers. The mean number of flowers on the 196 greenhouse plants was 14.12, and the mean on the field plants was 9.75.

The flowering performance by greenhouse plants may be used to obtain an estimate of the upper limits of R_0 and r (the r_{max} of some authors). If survivorship prior to germination is neglected (or assumed to be unity), the total reproductive output per individual can be equated to the net reproductive rate R_0. Basing this estimate on the mean number of flowers per individual in the greenhouse, R_0 is $3 \times 14.1224 = 42.3672$, and r would be 0.0102.

An even more liberal estimate might be based on the single most floriferous individual in the greenhouse ($R_0 = 150.0$, $r = 0.0137$), or in the field ($R_0 = 312.0$,
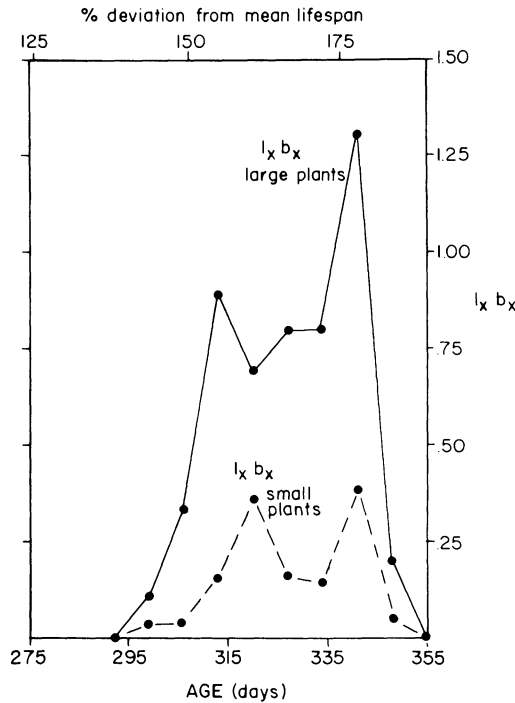
FIG. 8.—Distribution of the contributions to net reproductive rate during age intervals $(l_x b_x$ values) for the large and small classes of plants.

TABLE 6

ESTIMATES OF R_0 AND r FOR *Phlox drummondii*

Measurement Upon Which Estimate Based	R_0	r
Seed set at Nixon	2.42	.0024
Ovule production at Nixon	5.58	.0047
Mean no. flowers per plant, Nixon	29.26	.0092
Mean no. flowers per plant, greenhouse	42.37	.0102

$r = 0.0157$). However, since R_0 and r are statistics, these estimates based on single individuals have no meaning. Hairston et al. (1970) point out the distinction between Fisher's (1930) use of the Malthusian parameter (m) for individual genotypes and the use of r as a measure of population rate of increase. So, although individual plants in this study may be very fecund, population measures are the estimates of rate of increase. The various estimates of R_0 and r are summarized in table 6.

DISCUSSION

There are two distinct phases to the survivorship curve for *Phlox drummondii* (figure 1) which coincide with the major divisions of its life cycle. During the period
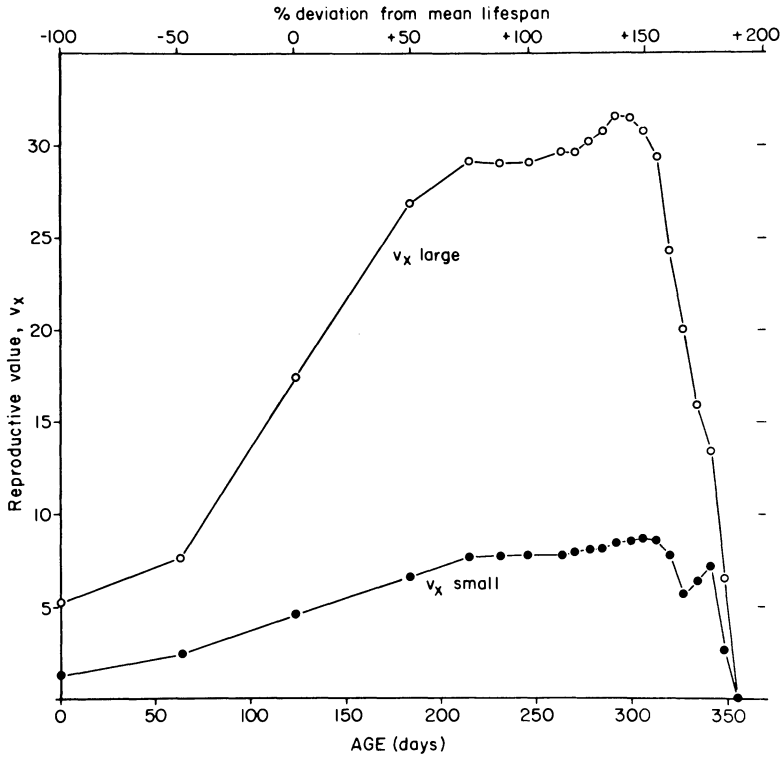
FIG. 9.—Reproductive values v_x for the large and small classes of plants.

of seed dormancy, the survivorship curve is approximately linear (on a semi-logarithmic plot) indicating a fairly constant mortality rate. This is best described as a type II curve (Deevey 1947). After germination through the vegetative and reproductive phase of the life cycle there is a relatively low mortality rate until late in the growing season, when the number of survivors plummets. This is best described as a type I curve.

It is informative to compare survivorship in *P. drummondii* with what is known about other plants. Harper and White (1974) reviewed the patterns of survivorship known from some perennial species. Their analysis of Tamm's data for several perennial herbs showed type II curves for *Sanicula europaea, Anemone hepatica,* and *Centaurea jacea.* Three perennial buttercups, *Ranunculus bulbosus, R. acris,* and *R. repens* also show type II survivorship (Sarukhan and Harper 1973). Antonovics' (1972) study of *Anthoxanthum odoratum* showed type II survivorship of cohorts. Harper and White (1974) point out that although survivorship in perennials may be linear over years, there can be seasonal fluctuations in the mortality rate, with the risk of death being greatest during periods of vigorous growth and reproduction. There is in fact seasonal fluctuation in the mortality rate for *P. drummondii,* but this is largely a consequence of the annual habit. However, there is certainly less fluctuation in the mortality rate for the seed population.
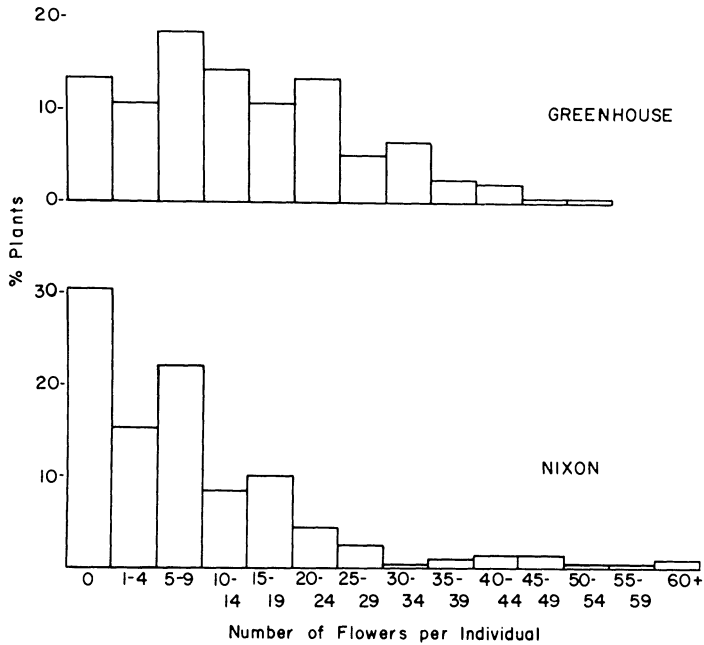
FIG. 10.—Flowering performance by individuals in the greenhouse (above) and at Nixon (below). The height of a column shows the percentage of all plants making up a given class.

Other patterns of survivorship are known from perennial herbs. Some primary and secondary range grasses (e.g., *Trichachne californica* and *Bouteloua chondrosioides*) exhibit type I curves (Canfield 1957; discussed by Sarukhan and Harper 1973) whereas the Australian grassland species *Danthonia caespitosa* shows a tendency toward a type III survivorship curve (Williams 1970). Sarukhan and Harper (1973) note that the grass populations whose survivorships depart sharply from type II curves are composed of clumps (genets) of tillers (ramets), and that the ramet rather than the genet might be the more appropriate unit of measure in survivorship studies. They show that in the mostly vegetatively propagating *R. repens* that the ramet is the effective unit in population regulation. Harper and White (1974) point out a potential bias in studies which yield type I survivorship curves for perennial herbs (e.g., certain orchids, Tamm 1972); when observations are relatively infrequent entire populations of seedlings may be neglected, and the resultant curves will show no hint of heavy mortality early in life. With *P. drummondii* this bias is unlikely, since observations were frequent and detailed. At Nixon in 1974–1975 seedling mortality was not heavy at all.

In the annual species *Sedum smallii* and *Minuartia uniflora* Sharitz (1970) found survivorship curves tending toward type III. These concave curves are in accordance with the plants' behavior as colonizing or *r*-selected species (MacArthur and Wilson 1967). Such species are generally noted for disseminating large numbers of seeds but suffering high early mortality (Harper and White 1974). Sharitz (1970) points out a number of characteristics, such as their winter annual habit, their high reproductive

potential, and high juvenile mortality, which correspond with the plants' roles as colonizers of granite outcrops.

Phlox drummondii, also a winter annual, differs quite sharply in its survivorship characteristics from the above species in that its survivorship curve is decidedly not type III. After germination, *P. drummondii* clearly tends toward type I survivorship with population collapse following peak reproduction. Its survivorship curve reflects the more stable nature of its habitat. The differing survivorship patterns of colonizing versus noncolonizing annuals underscore the adaptive nature of life-history phenomena.

The survivorship of phlox seed in the soil seems to follow a type II survivorship pattern, like that shown by the standing crop of perennial herbs over a number of years. Among annual plants the only means of perrenation is the seed pool; that viable seed which fails to germinate in 1 yr may, with some probability of survival, be carried over to subsequent years. However, germination removes an individual from the seed population permanently yielding a situation much like an age-structured population of a perennial monocarpic species. It seems that the probability of death remains fairly constant (at least for large portions of the year), indicating that mortality is largely exogenously controlled. Seeds may remain viable for several seasons, a period long enough that their fate is almost certain to be germination or removal by a granivore. On the other hand, the marked tendency toward a type I survivorship pattern for individuals once germinated and committed to the repro- duction sequence indicates the strength of viability selection in shaping survivorship curves.

Reproduction.—Consider now the distribution of fecundity during the life history of *P. drummondii*. A few individuals begin to flower about late February; flowering builds to a maximum by the beginning of April, and finally ceases in early May. Maturation of seed begins in late March, builds to a sharp peak in early May, and ceases shortly thereafter. As can be seen in figure 2, there is a marked increase in seed set immediately before the decline of the population. The temporal relation between flowering and seed set reflects the period for which developing seeds are borne on the parent.

Not all flowers produce capsules; this is the first manifestation of a reduction in reproductive capacity from its theoretical maximum. Lack of pollination and embryo abortion account for some reduction, as does the feeding of an hemipteran on the contents of some developing capsules. Nevertheless, the potential maximum of three seeds per capsule only slightly exceeds the observed average seed set of 2.78 seeds per capsule.

The net reproductive rate R_0 for a given generation describes the growth potential for a population. Figure 3 illustrates the distribution of the average contribution to R_0 from each age interval during this study, and it clearly shows that reproduction is greatest just prior to the demise of the population. The value of R_0 for the complete generation is 2.42 per individual, indicating more than enough seed for replacement in a generation of similar survivorship. By April 14, R_0 for the population had barely reached a value of 1, and total collapse of the population prior to that time (due to drought, disease, herbivores, etc.) would have meant failure to completely replace the current population. There are undoubtedly both good and bad years for various

populations of *P. drummondii* in which the value of R_0 far exceeds or fails to reach unity. But if this population in 1974–1975 is typical, as few as 3 wk of seed set can yield $R_0 = 0.5$. Although the bulk of reproduction occurs later in the season, enough offspring are produced early in the season that the seed pool is at least in part replenished, regardless of the subsequent fate of the adults. The R_0 value of 2.42 for the 1975 Nixon phlox population is a strong confirmation of the subjective assessment of 1975 as a good year for *P. drummondii*.

The actual rate of increase, r, can be estimated for annual plants from data of the type in this study as described earlier. This is an instantaneous measure, which of course might not be applicable to organisms such as annual plants whose population growth is not currently realized. Nevertheless, it is most useful to have estimates for r and its theoretically maximal value r_{max} for purposes of comparison with other organisms. An estimate for actual r for the generation is best based on seed set; computed from seed set data, the value for r is 0.0024 per individual per day.

However, the choice of a basis for estimating a maximal value for r is less clear; ideally it would represent performance in an ecological vacuum. The performance of the single most productive individual could be measured, as pointed out by Andrewartha and Birch (1954), but their r_m (the "innate capacity for increase") is a statistic which is an estimate for the mean value for a population. We have used mean ovule production by plants in the greenhouse to estimate r_{max} as 0.0102. This is a quite generous estimate, particularly with the assumptions of complete seed survivorship and germination and no extended dormancy. For various organisms estimates of r_{max} range from 0.0003 per individual per day for man and 0.001 for the 17-yr cicada to as high as 0.12 for some beetles and much higher for bacteria. A value for $r_{max} = 0.0102$ for *P. drummondii* is of the same order of magnitude as that for some rodents and insects. Figure 11 has been adapted from Pianka (1970) and replotted using estimates of r_{max} and T from various sources to illustrate the position of *P. drummondii* relative to a number of organisms. It should be noted here that this phlox falls near the corner of the inverse hyperbola of distribution, between short-generation high r_{max} and long-generation low r_{max} organisms. The use of any of the other estimates of r in table 6 would not greatly alter its relative position.

It is difficult to compare *P. drummondii*'s r and r_{max} values with those of other plants, because the necessary age-specific data have not been collected. More readily available are data of total seed production such as the compilation by Salisbury (1942) for a variety of British plants. Salisbury lists average seed output per plant, and for some taxa the reproductive output, which he defines as the average seed output weighted by average germinability. His calculations include only plants which survive to produce seed. The average seed output per plant for *P. drummondii* at Nixon measured in this manner is 22.72 per plant. In Salisbury's study, herbaceous species with seed outputs of less than 50 per plant were common only among those of shaded habitats and were very infrequently found among species of permanent open or semiopen habitats. The average outputs of herbaceous species of open and semiopen habitats were 2,904 and 2,379 seeds per plant, respectively, and the average for shade species 280 seeds per plant. Sharitz (1970) gives values of 114.4 seeds per plant for *Sedum smallii* and 305.2 seeds per plant for *M. uniflora*, both being colonizing annual plants of granite outcrops. To the extent that data of this type are
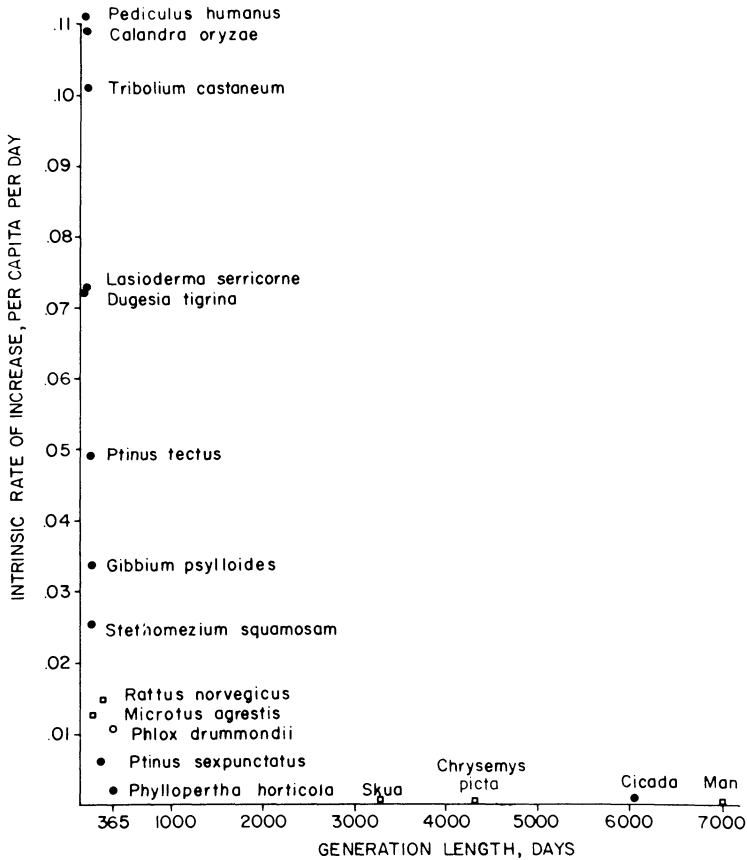
FIG. 11.—Intrinsic rate of increase r_{max} vs. generation length T. The values for r_{max} are all per capita per day and T values are in days. Closed circles = invertebrates; open squares = vertebrates; open circle = the plant *Phlox drummondii* (after Pianka 1970, using data from Leslie and Ranson 1940; Birch 1948; Leslie and Park 1949; Evans and Smith 1952; Howe 1953; Root 1960; Lefkovitch 1963; Laughlin 1965; Pianka 1974; Wilbur 1975; O'Donald and Davis 1975).

comparable, these also have low seed outputs, but not so low as the nonpioneering *P. drummondii*.

The significance and consequences of the distribution of reproduction during the life cycle of organisms has been dealt with extensively (e.g., Cole 1954; Slobodkin 1962; Gadgil and Bossert 1970; Schaffer 1972; Taylor et al. 1974; Pianka and Parker 1975). Reproductive values measure average reproductive contributions at given ages, but there are comparatively few records of the actual distributions of reproductive values in natural populations (see Pianka and Parker 1975). There are no detailed data of this sort for natural plant populations.

In *P. drummondii* the average reproductive value of an individual reaches its maximum very nearly at the age of first reproduction. This is in accordance with expectation, since survivorship decreases with age prior to reproduction and this is characteristic of the organisms for which there are data. The v_x curves plotted by

Pianka (1974) for several animals and by Fisher (1930) for humans show the same initial increase to maximum and gradual diminishing thereafter. An interesting aspect of the distribution of reproductive values in *P. drummondii* is that although v_x begins to decline soon after the maximal value is reached, it is maintained at a moderately high level throughout the remainder of the reproductive period and falls sharply only as the remaining individuals enter final senescence. This reflects the greater fecundity of individuals which survive to a greater age. Plants like *P. drummondii* with indeterminate growth and flowering may exhibit a b_x curve which increases at later ages, thereby maintaining their reproductive values.

While reproductive value is a measure of the average contribution of offspring at various ages, the distribution of actual reproduction among individuals has an important influence on the evolutionary potential of a population. In the Nixon population the bulk of reproduction was carried out by relatively few individuals. About 45% of the individuals which germinated failed to reproduce at all, and more than half of the total progeny of the generation was born on only 10% of the individuals (or about 2% of the original cohort). Age-specific survivorship and reproduction data collected by genotype are required before the impact of this disproportionate contribution may be fully assessed, but it is evident that such a skewed distribution of maternity could have a strong role in determining progeny genotype distributions and the genetic structure of subsequent generations.

A wide range of sizes among individuals was observed early in the vegetative life of the population, and a correlation between stature at an early age and eventual reproductive output was established. In general the plants which produced the majority of the offspring were those that were more vigorous early in the growing season, and there is a strong correlation between number of nodes on December 30 and the total number of capsules a plant matured. It is interesting to consider how differences in vigor at an early age are reflected in the fitnesses of individuals. Fitness has components of viability and fertility, which we have some estimate of through the survivorship and fecundity schedules. Comparing the survivorship curves (fig. 7) for the two size classes described earlier, there is very little difference between the two until near the end of the growing season. But there is a relatively greater disparity in the fecundity curves for the two classes (fig. 7) with the larger plants far exceeding their smaller siblings in eventual reproductive performance. This inequality is accentuated by what difference there is in survivorships to give the wide separation in $l_x b_x$ curves (fig. 8). This means that as a group the small plant class never approaches the large plant class in reproductive values (fig. 9).

When the replacement rates are calculated (from seed output) for the two classes, values of $R_0^{\text{small}} = 1.34$ and $R_0^{\text{large}} = 5.13$ are obtained. These are good indices of the relative successes of the two classes. If the values of R_0 are used as measures of fitness, and if average fitness of the larger plants is taken as unity, then $w^{\text{small}} = R_0^{\text{small}}/R_0^{\text{large}} = 0.261$. The smaller class thus has an average fitness about one-fourth that of the larger class with the difference stemming from disparities in both survivorship (viability) and fecundity (fertility).

While in this case there are few facts to elucidate the causes of the differences in size at an early age, it is quite evident that on the average early vigor is of paramount importance in determining realized fitness. Although there is probably a large

environmental component in early stature, any genetic component involved would be under very strong selection. It is important to realize, therefore, that while survivorship and fecundity schedules adequately describe the numerical dynamics of populations it is the comparison of schedules for various subcomponents which will be the most informative about evolutionary processes. Ideally these comparisons would be between genotypes.

A final inquiry is the position of P. drummondii within an r- and K-selection spectrum (MacArthur and Wilson 1967). From the correlates suggested by Pianka (1970) as characteristic of r- and K-selected species, P. drummondii would lie in a central region of the continuum but tend in the K-direction; its location in figure 11 is illustrative of this. Its habitat is open, but not uncertain; both the habitat and climate are to a large extent predictable. Entire populations do not routinely suffer catastrophic mortality. Survivorship is types I and II. Although population size may fluctuate from year to year, it does not do so markedly; it is buffered by the seed pool, because in bad years only a fraction of seed may germinate. Furthermore, in P. drummondii r_{max} is not large. However, if there were a general dichotomy between annuals as r-selected and perennials as K-selected, the species would tend in the wrong direction.

Pianka (1970) predicts a rather drastic shift from r- to K-selection when generation time is lengthened and the threshold of perenniality is reached. But among flowering plants the general case is that annual taxa are usually derived from perennial ancestors (Stebbins 1950). In plants, therefore, one might anticipate a shift from K- to r-selected characteristics as generation time is shortened. Phlox drummondii probably was derived from a perennial stock similar to the extant P. pilosa (Wherry 1955), which is a perennial, and a component of climax prairies. In the distribution of figure 11 P. pilosa would certainly lie to the right of P. drummondii, although there are no measurements to plot a precise location.

In spite of acquiring the annual habit P. drummondii has not evolved a set of strongly r-correlated characteristics. There are two other annual phlox species which apparently have higher seed set per plant than P. drummondii; they probably fall somewhat higher in the r-direction than P. drummondii, but still have not completely turned the corner toward strong r-adaptation. Thus caution should be exercised in assuming that annual plants in general would be manifestly r-selected.

Among plants is probably found a complete spectrum, from strongly K- to strongly r-selected species, but it does not necessarily coincide with the spectrum of generation lengths. There are clearly annuals with relatively low r_{max} values; evolution of a very high r_{max} most likely accompanies the further specialization as a fugitive species or as a member of disturbed or early successional communities.

SUMMARY

Complete survivorship and fecundity schedules were constructed from observations of a natural population of the winter annual Phlox drummondii. The data were collected through the complete generation of a cohort of individuals, including the dormant seed phase of the life cycle. Survivorship is shown to approach type II during the period of seed dormancy and to approach type I for the population after

germination. Reproduction was found to be unevenly distributed among individuals, the majority of offspring being produced by a small fraction of the cohort. Estimates of the net reproductive rate R_0 and the intrinsic rate of increase r are compared with those of other organisms. The rates are lower than those expected of colonizing or r-selected species. It is suggested that certain annual plants like *P. drummondii* may have acquired a shortened generation length, but lack the further demographic specialization of many annuals as fugitives or weeds.

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