

AMERICAN JOURNAL OF Botany

Reproductive Capacity and Seed Size in *Lupinus texensis*

Author(s): Barbara A. Schaal

Source: *American Journal of Botany*, Vol. 67, No. 5 (May - Jun., 1980), pp. 703-709

Published by: Botanical Society of America

Stable URL: <http://www.jstor.org/stable/2442663>

Accessed: 30/03/2010 11:43

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=botsam>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Botanical Society of America is collaborating with JSTOR to digitize, preserve and extend access to *American Journal of Botany*.

<http://www.jstor.org>

REPRODUCTIVE CAPACITY AND SEED SIZE IN LUPINUS TEXENSIS¹

BARBARA A. SCHAAL

Department of Botany, The Ohio State University, Columbus, Ohio 43210

ABSTRACT

The average number of ovules produced per individual of *Lupinus texensis* is much greater than the average number of seeds per plant. Each plant produces approximately 2,000 ovules but only 2.5% develop into seeds. One fourth of the seeds is lost due to abortion and 0.3% is lost due to predation on the plant. Mature seeds from this population exhibit a five-fold range in weight, from 10 to 56 mg. The distribution of seed weights in the field population is skewed and leptokurtic. Seed wt is positively correlated with both seed germination and seedling survivorship. Heritability of seed wt is 0.09. There is no correlation between average seed wt per plant and total number of seeds per plant, seeds per pod, or legumes per plant.

MANY ASPECTS OF PLANT REPRODUCTION, such as seed size, seed number, and reproductive potential have long been of concern. Currently, there is a great deal of interest in the determination of reproductive effort, the proportion of total energy allocated to the reproductive function of a plant species (Abrahamson and Gadgil, 1973; Gaines et al., 1974; Hickman, 1975; Holler and Abrahamson, 1977; Roos and Quinn, 1977), and the apportionment of this reproductive energy between seed size and number. Studies of many animal species, particularly birds (Lack, 1947, 1948) indicate that there is a trade off between size and number of offspring. This inverse relationship between size and number has been demonstrated in the plant genus *Solidago* (Werner and Platt, 1976), although the relationship does not seem to hold for the Compositae as a whole (Levin and Turner, 1977). These results suggest that reproduction for plants, at least for some species, may be a set of balancing alternatives; a gain in seed number is countered by a reduction in seed size (Harper, 1977).

The reproductive capacity or potential of plants is another critical aspect of plant reproduction. Salisbury (1942) noted that reproductive capacity of many plants is extremely great and that there are large differences between species. These differences may be the result of different selective pressures and are related to the ability of a species to persist in time and in space (Harper, Lovell and Moore, 1970;

Harper and White, 1974). Levin and Turner (1977) have shown that the reproductive potential or clutch size in the Compositae varies with latitude and with the growth habit of a species.

In this study several aspects of the reproductive biology of *Lupinus texensis* are considered, specifically those concerned with reproductive capacity and seed size. The following questions are addressed. What is the potential reproductive capacity of the species? Of this potential, what proportion of ovules becomes seeds? At which stage of development and by what processes is actual seed production reduced from its potential? Further, how is energy allocated among the seeds that are produced? Specifically, what is the seed weight distribution; what factors limit the size of seeds; and is there any relationship between seed size and number?

Lupinus texensis Hook. (Leguminosae) is a widespread winter annual endemic to central Texas in the United States. It occurs in vast numbers along roadsides and in fields, and has recently become even more common because of the practice of sowing seed along roadsides. The showy blue flowers of *L. texensis* are borne on terminal racemes and are bee pollinated. Each inflorescence bears from seven to over fifty flowers and each legume bears from one to seven seeds. Growth and flowering are indeterminate, and plants can continue to reproduce for many weeks as long as conditions are favorable. The species is predominantly self-incompatible and does not hybridize with its sympatric congener *L. subcarnosus* (Erbe, 1952).

STUDY SITE AND METHODS—The study site is a natural population of *Lupinus texensis* located near the intersection of US-183 and TX-

¹ Received for publication 26 July 1979; revision accepted 19 February 1980.

I thank W. J. Leverich, R. D. Mitchell, D. A. Levin, D. W. Schemeske and D. W. Inouye for comments. This work was supported by NSF grants DEB76-09709 and 79-05198 and by an Ohio State University Graduate School Small Research Grant.

TABLE 1. Flower and seed production in *Lupinus texensis*

| Character | Mean \pm S.E. | Range | N |
|--|------------------|----------|-----|
| inflorescences per plant | 14.24 \pm 1.12 | 0-300 | 90 |
| flowers per inflorescence | 27.21 \pm 1.30 | 4-60 | 300 |
| legumes per plant | 9.37 \pm 1.05 | 0-30 | 58 |
| total seeds per plant | 47.07 \pm 5.77 | 0-183 | 58 |
| average total seeds/legume | 5.02 \pm .09 | 2.5-6.13 | 51 |
| viable seeds per plant | 30.79 \pm 4.23 | 0-154 | 58 |
| average viable seeds/legume | 3.56 \pm 0.11 | 2-5.13 | 51 |
| aborted seeds per plant | 15.1 \pm 1.84 | 0-56 | 58 |
| average aborted seeds/legume | 1.32 \pm 0.10 | 0-3.5 | 51 |
| destroyed seeds per plant ^a | 1.18 \pm 0.27 | 0-11 | 58 |
| average destroyed seeds/legume | 0.14 \pm .03 | 0-.68 | 51 |

^a because of insect or fungal attack.

21 in Travis County, Texas. The population is in a grassy field, and contained an estimated 5,000 plants at the time of sampling in June, 1975. As seeds became mature, but prior to fruit dehiscence, 90 plants were collected from four 1 m² areas of the population. Within each area all plants were removed. In addition to the 90 plants, several thousand seeds were collected by walking a line transect through the population and taking a single legume from each flowering plant.

Plants were taken to the laboratory and the following reproductive characters determined: the number of inflorescences per plant, flowers per inflorescence, legumes per plant, viable seeds per plant and per legume, aborted seeds per plant and per legume, seeds destroyed by predators per plant and per legume, and total seeds (viable + aborted + destroyed) per plant and per legume. Flowers per inflorescence were scored by counting the number of peduncle scars per inflorescence. The number of aborted seeds was determined by counting both empty locules and locules which contained aborted seeds. Seed wt was measured to the nearest mg for every full, mature seed produced. All 90 plants were scored for inflorescences per plant; a sample of 300 inflorescences was used to determine number of flowers per inflorescence and 58 plants were scored for the remaining characters.

The 659 seeds from the mass seed collection in the field were sorted into eight wt classes (see Table 4 for wt classes), and sown in the greenhouse. All seeds were scarified. The percentage germination and survivorship to the two-leaf stage were recorded. Five weeks after planting, all seedlings were harvested, air dried to constant wt, and relative biomass determined. One hundred seeds from the mass field collection were sliced open to check for predators not evident from the outside of the seed.

A sample of 225 of the weighed field collected seeds was sown in the greenhouse, from

which 211 plants were grown to maturity. Bumblebees and honey bees were allowed into the greenhouse to pollinate the flowers, and 476 of the resulting seeds were collected and weighed. A sample of 95 legumes containing five seeds was also collected; each seed was weighed and the position of the seed in the legume recorded. Ovule number was determined for five flowers from each of 24 plants.

Heritability of seed wt was estimated by selecting five seeds from greenhouse grown plants of each 1 mg wt class ranging from seed wts of 20-56 mg. Plants from these seeds were grown to maturity in the greenhouse and flowers were pollinated by bees. Three hundred eighty-four of the resulting seeds were weighed and the heritability estimated by the parent-offspring regression method where heritability, h^2 , is determined from the equation $b = \frac{1}{2} h^2$; b is the regression coefficient (Falconer, 1960).

RESULTS—Reproductive characteristics of the *Lupinus texensis* population are given in Table 1. The number of inflorescences per plant ranged from 0 to 30 with a mean of 14.24 ± 1.12 inflorescences per plant. The average number of flowers per inflorescence was 27.21 ± 1.30 (range 4-60). The number of ovules per ovary ranged from 3-7 with a mean of $5.01 \pm .06$. Five ovules per ovary was the mode (59.2%), four and six ovule ovaries were also frequent (20.8% and 16.7%, respectively), and three (0.8%) and seven (2.5%) ovules per ovary were rare. Ovule number varied within a given plant. The mean expected number of flowers per plant (average number of flowers per inflorescence \times average number of inflorescences) is 387. If each ovary contains the average of 5.01 ovules, then the average plant would be capable of producing 1,939 seeds. The measured average total seed production (aborted seeds + viable + destroyed) in this field population was far less, 47.07 seeds per plant. The average number of full, mature seed

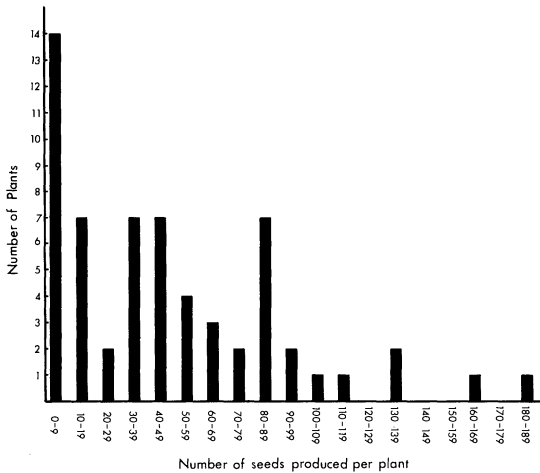


Fig. 1. Distribution of seed production per plant in *Lupinus texensis*.

was even less, 30.79. The mean number of legumes per plant was 9.37 ± 1.05 and the mean number of total seeds per legume was 5.02 ± 0.09 , a value equivalent to the number of ovules, but only 3.56 ± 0.11 were viable.

Seeds were not viable due either to ovule abortion (detected by a locule that contained an aborted seed) or to predation. Before dispersal some seeds were attacked either by insects or fungi. All seed predation was visible externally; the 100 seeds which were sliced open revealed no concealed predators. On a per plant basis, mean number of aborted seeds was 15.1 ± 1.84 and mean number of destroyed seeds was 1.18 ± 0.19 . The average legume had 5.02 ± 0.09 ovules which were fertilized; 1.32 ± 0.10 ovules were aborted; 0.14 ± 0.03 ovules produced seed which subsequently was attacked and destroyed by predators and the remaining 3.56 ± 0.11 ovules matured and produced viable seeds which were then dispersed from the parent plant. Average seed wt for these mature seeds was 32.247 ± 0.344 mg.

The distribution of seed production per plant is shown in Figure 1. The seed production distribution is leptokurtic; many more plants produced relatively few seeds than produced many seeds. In this population the modal class is 0-9 seeds. Most of the plants (8) within this class produced no seeds at all. Most of the seed production in the population was from the first five classes (plants which produced from 0-49 seeds) although single plants can contribute substantially to the seed pool. One individual plant which produced 187 seeds was responsible for 6.7% of the total seed production of the population sample.

Seed wt of *L. texensis* varies greatly, from 10 to 56 mg (Fig. 2). Seed wt distribution is

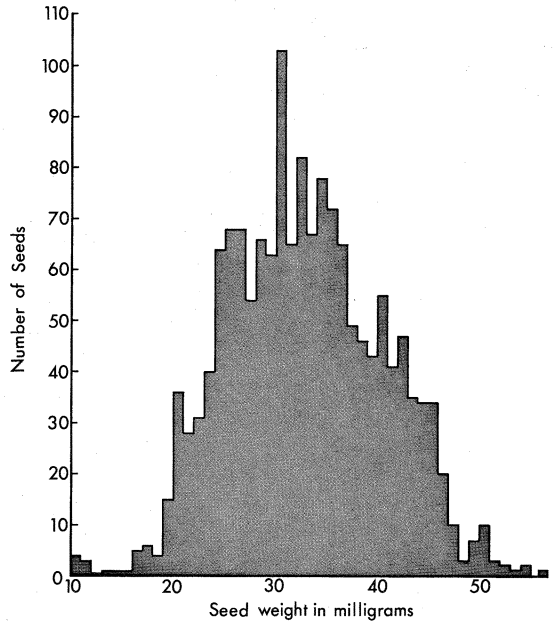


Fig. 2. Distribution of seed weights in a population of *Lupinus texensis*.

both significantly leptokurtic, $g_2 = 2.84 \pm 0.123$ ($t = 22.5$, $p < .05$), and skewed to the right, $g_1 = 0.149 \pm 0.062$ ($t = 2.4$, $p < .05$). Mean seed wt for the field population was 32.247 ± 0.344 mg; the modal class is 30 mg and the median is 31.51 mg. The seed weight distribution of the greenhouse grown plants also is leptokurtic, $g_2 = 3.26 \pm 0.22$ ($t = 14.55$, $p < .05$), but shows no significant skewing $g_1 = 0.068 \pm 0.046$ ($t = 1.47$, $p > .05$). Mean seed wt of the greenhouse population was 30.53 ± 0.39 mg. The modal class is 30 mg and the median is 30.4 mg. The two samples differ significantly in their mean seed wts ($t = 3.91$, $p < .05$) and in skewness ($t = 2.003$, $p < .05$). Kurtosis of the natural and greenhouse samples does not differ significantly ($t = 1.21$, $p > .05$).

Seed wt varies with the position of the seed in the legume (Table 2). Mean seed wt of position 1, farthest from the style, was 27.82 mg and is significantly less ($p < .05$) than the mean seed wt of the other four seed positions in the legume, 30.84 mg for position 2 ($t = 4.2$), 31.25 mg for position 3 ($t = 4.8$), 30.97 mg for position 4 ($t = 4.5$), 30.2 mg for position 5 ($t = 4.2$), and for the sample as a whole ($t = 2.03$). Mean seed wts of the other four positions did not differ significantly from each other or from the mean of the population. There is no systematic trend in the change of seed wt for these other four positions in the legume. The linear regression equation of parent-offspring seed

TABLE 2. Average seed weight by position in legume

| Position ^a | Mean seed weight (mg) ± S.E. | N |
|-----------------------|------------------------------|-----|
| 1 | 27.82 ± 1.15 | 95 |
| 2 | 30.84 ± .87 | 95 |
| 3 | 31.25 ± .84 | 95 |
| 4 | 30.97 ± .85 | 95 |
| 5 | 30.20 ± .76 | 95 |
| Total | 30.53 ± .39 | 475 |

^a Position 1 is closest to the peduncle.

wts is $y = 0.49X \pm 37.31$. Seed wt heritability is equal to $0.098 \pm .004$.

Linear regressions of seed wt and several aspects of seed production also were calculated (Table 3). Mean seed wt per plant is not significantly correlated with number of legumes ($r = .014$), total number of seeds ($r = .051$), average number of seeds per legume ($r = .227$), total number of viable seeds ($r = -.014$), number of seeds destroyed by predators ($r = -.086$), or number of aborted seeds ($r = -.165$). There is no significant relationship between seed size and seed number. A regression of total seeds per plant and mean seeds per legume shows a significant relationship ($r = .431$, $P < .05$) indicating that as number of seeds increases the average number of seeds per legume also increases.

The relationships between seed wt and seed germination, seedling biomass, and seedling survivorship were determined (Table 4). The percentage germination of seeds less than 17 mg was 41.9%. Germination increased to 90.1% for the 18–22 mg seed class and continued increasing with increasing seed wt up to 100% for the very heaviest seed. An arcsine transformation was applied to the germination and survivorship percentages and product-moment correlation coefficients calculated. The percentage germination is significantly correlated to seed wt, $r = .801$, $p < .05$. Seedling survivorship is also correlated to seed wt, $r = .774$, $p < .05$. Survivorship to the two leaf

stage is 84.6% for the lightest seed wt class; for the other seed classes survivorship is between 94 and 100%. Seedling biomass after five weeks shows a fourfold increase from the lightest seed class to the heaviest class. Mean seedling biomass is 8.01 ± 1.06 mg for the 17 mg seeds and increases linearly with seed wt up to 35.84 ± 0.54 mg for the heaviest seeds. There is a strong correlation ($r = .994$, $p < .05$) between seed and seedling biomass.

DISCUSSION—Reproductive potential—The reproductive potential of *L. texensis* is much greater than its actual seed production. On the average a plant produces about 2,000 ovules. In this population only about 2.5% of the ovules developed into seeds. Seed production was reduced 28% further by abortion. Only a very small proportion, 0.29%, of the total seed was lost because of seed predation on the plant, although seed predation after dispersal also occurs. The marked difference between potential and realized seed production appeared to be due in part to lack of successful pollination since when a receptive stigma is pollinated all ovules are usually fertilized. The number of seeds per legume was 5.02 while the average number of ovules per flower was 5.01.

Seed set for this population of *L. texensis* was typical of populations in central Texas during 1975 and is typical of this site for subsequent years. A great deal of the reproductive effort of *L. texensis* is put into flowers and ovules that do not become seeds. There are several possible explanations for the large number of flowers that do not set seed. Large numbers of flowers may be necessary to attract pollinators to a population. Several studies have suggested that plant species compete for pollinators when pollinators are limiting (Levin and Anderson, 1970). Wilson and Price (1977), in an analysis of inflorescence size in *Asclepias*, suggest that inflorescence size is related to pollinator attraction and also adequate pollen production. The production of pollen may

TABLE 3. Linear regressions of seed production and seed weight^a

| Characters | Equation | r |
|---|-----------------------|-------------------|
| legumes per plant vs. mean seed weight | $Y = .00001X + .032$ | .014 |
| total seeds per plant vs. mean seed weight | $Y = .000007X + .032$ | .051 |
| mean seeds/legume vs. mean seed weight | $Y = .002X + .021$ | .227 |
| viable seeds vs. mean seed weight | $Y = 0.00003X + .032$ | -.014 |
| viable + destroyed seeds vs. mean seed weight | $Y = -.012X + 33.1$ | -.020 |
| destroyed seed vs. mean seed weight | $Y = -.00007X + .026$ | -.086 |
| aborted seed vs. mean seed weight | $Y = -.056X + .27$ | -.165 |
| seeds per plant vs. mean seeds per legume | $Y = .006X + 4.73$ | .431 ^b |

^a seed weight is in mgs.

^b $p < .05$.

TABLE 4. Seedling survivorship and biomass as a function of seed weight

| Seed class | No. seeds planted | No. seeds germinated | Percent germination | No. seedlings surviving | Percent ^a surviving | Mean seedling biomass |
|------------|-------------------|----------------------|---------------------|-------------------------|--------------------------------|-----------------------|
| <17 mg | 31 | 13 | 41.9 | 11 | 84.6 | 8.09 ± 1.06 mg |
| 18-22 | 81 | 73 | 90.1 | 69 | 94.5 | 12.94 ± .33 |
| 23-27 | 120 | 113 | 94.2 | 112 | 99.1 | 16.52 ± .28 |
| 28-32 | 120 | 115 | 95.8 | 113 | 98.3 | 19.40 ± .32 |
| 33-37 | 107 | 102 | 95.3 | 102 | 100 | 21.22 ± .36 |
| 38-42 | 98 | 95 | 96.9 | 91 | 95.8 | 26.22 ± .42 |
| 43-47 | 50 | 49 | 98.0 | 49 | 100 | 31.37 ± .54 |
| >48 | 52 | 52 | 100 | 52 | 100 | 35.48 ± .54 |
| Total | 659 | 610 | 92.6 | 599 | 98.2 | 21.57 ± .31 |

^a Of germinated seed.

be a significant aspect of the reproduction of *L. texensis*. Bees forage only for pollen; no nectar is produced. In natural populations virtually all the pollen is removed from open flowers by bees (B. A. Schaal and W. J. Leverich, unpubl.). Although only few flowers become female parents, all flowers can contribute to the male gamete pool. Finally, the large difference between actual and potential seed production may also be a by-product of the extended flowering period of *L. texensis*. A single inflorescence may bear flowers for over 4 wks although each individual flower is fertile only a few days at most. Many flowers must be produced to maintain this extended flowering period. If pollinators are scarce, increasing the length of flowering time increases the probability of successful pollination and thus seed production.

The average number of seeds produced per plant varies widely among plant species. Salisbury (1942) found a relationship between seed production and habitat. Plants of intermittently available habitats had the highest average number of seeds; for 41 species the mean seed number was 28,284 per plant. The lowest mean average seed number per plant was for species of shaded habitats, 280 seeds per plant. Salisbury's data do not include plants which produce no seeds. When plants with no seeds are removed from the *L. texensis* data, mean number of seeds per plant is still very low, 53.54. *Phlox drummondii*, an annual which grows in the same Texas habitats as *L. texensis*, also has a very low average number of seeds, 22.72 (Leverich and Levin, 1979). *Phlox* and *Lupinus* occur in what Salisbury might consider a semi-open habitat. In Salisbury's study the average seed production for this habitat was 2,379 seeds per individual, far greater than either *Phlox* or *Lupinus*. Mean seed number for two colonizing annuals, *Sedum smallii* and *Minuartia uniflora*, also was relatively low, 114.4 and 305.2 seeds, respectively (Sharitz

and McCormick, 1973). These studies indicate that not all annuals, even of open habitats, have the extremely high reproductive capacities found by Salisbury.

The skewed frequency distribution of seeds per plant in the *L. texensis* population is similar to that reported for *Phlox drummondii*. In both species the modal class is the zero class, plants which produce no seeds at all. Increasing number of seeds per plant are produced in decreasing frequency. A similar distribution is observed for several other genera (e.g., *Papaver*, *Silene*; Salisbury, 1942) when the zero class is omitted. Many other species (e.g., *Drosera*, *Gentiana*; Salisbury 1942) have a distribution where the modal class is not zero or one, but rather some other seed number. These distributions still exhibit the long right hand tails of the *Lupinus*-type distribution. Most reproduction in these plant species is due to the many individuals which produce few seeds, although a single large individual can have a disproportionately large contribution to the total seed production of a population. In *P. drummondii*, 10% of the plants produced 50% of the viable seed (Leverich and Levin, 1979).

Seed size—Seed size for many plant species is one of the more stable morphological characteristics (Harper et al., 1970). A number of species show remarkably little variation in size even when grown under several hundredfold differences in density (Puckeridge and Donald, 1967). In contrast seed size in *Lupinus texensis* shows a fivefold range of seed weights within this single population. Wide variation in seed wt has been reported in several other species, such as from a single plant of *Mucuna andreaana* (Janzen, 1977), from a single plant of *Trifolium subterraneum* (Black, 1957), and between populations of *Opuntia echos* (Racine and Downhower, 1974). Harper et al. (1970) suggest that species which vary widely in seed size are generally determinate in flow-

ering while those which show little variation are indeterminate in flowering. However, *Lupinus* is indeterminate.

While seed wts range widely within the *L. texensis* population, the distribution of seed wt within the population is leptokurtic; both large and small seed wts are less frequent than expected for a normal distribution. The positive skewing to the right observed in the natural seed population appears to be environmentally related. Seed wts of plants grown in the greenhouse are not skewed. Janzen (1977) has found a similar skewing of seed wts in natural *Mucuna andreaana* populations in Costa Rica.

Much of the variation in seed wt of individual *Lupinus texensis* plants is environmentally determined by the position within the fruit. Seeds near the peduncle are significantly lighter than other seeds in the legume. Position effects have also been found in other legume species (e.g., *Pisum sativum* Linck, 1961). These position effects may result from differences in nutrient uptake or competition between ovules or developing seed or any combination of these. The strong environmental component of seed wt variation in *L. texensis* is reflected in the estimate of heritability for seed wt, $h^2 = 0.1$, which is low when compared with other species. For example, seed wt heritability for *Glycine max* is 0.193 (Fehr and Weber, 1968) and 0.6 for *Sorghum vulgare* (Voight, Gardner and Webster, 1966). These high heritabilities for seed wt are found in crop or cultivated species where uniform seed wts may be directly or indirectly selected for. Little is known about seed wt heritability of natural populations. In several natural species, seed size variation is genetically determined and is closely related to environmental factors such as temperature, altitude, or soil moisture (Baker, 1972; McWilliams, Landers and Mahlstedt, 1968; Schimpf, 1977).

Seed size is thought to be under strong stabilizing selection. Small seeds contain less endosperm than large seeds and this leads to decreased seedling survivorship and competitive ability (Harper, 1977). On the other hand, large seeds may also be selected against since they may be less readily dispersed (Baker, 1972), may be preyed upon preferentially (Smith, 1974) or may produce seedlings which undergo greater competition (Black, 1958). Seed size may also be restricted when the energy allocated to reproduction is limited. In such species an inverse relationship between seed size and number is expected. Large seed may not be produced without decreasing seed number which in turn may decrease population size. In *Lupinus texensis* seed wt is directly related to several fitness components. Very

small seeds have a lower germination rate and produce seedlings which are small and have a lower survivorship than seed which are large in size.

The mechanism of selection against large seeds in *L. texensis* is less clear. In several plant species and many animal species there is a compromise between seed size and number. Such a direct relationship has been observed in *Solidago* (Werner and Platt, 1976). In *Scheelea* palm the energy content of seeds is inversely related to the number of seeds per fruit (Bradford and Smith, 1977). On the other hand, data from *L. texensis* indicate independent determination of seed size and number. There is no correlation between seed wt and total number of seeds per plant, seeds per pod, and legumes per plant. The finding that seed size is not related to seed number is not unexpected for a plant of indeterminate growth such as *L. texensis*, in which growth continues and new inflorescences and more seeds are produced under favorable conditions. Similar results have been obtained for *Mucuna* (Janzen, 1977) and suggest the mode of growth, determinate or indeterminate, may be significant in determining reproductive strategies.

LITERATURE CITED

- ABRAHAMSON, W. G., AND M. GADGIL. 1973. Growth form and reproductive effort in goldenrods (*Solidago*, Compositae). *Amer. Natur.* 107: 651-661.
- BAKER, H. G. 1972. Seed weight in relation to environmental conditions in California, *Ecology* 53: 997-1010.
- BLACK, J. N. 1957. The early vegetative growth of three strains of subterranean clover (*Trifolium subterraneum* L.) in relation to size of seed. *Aust. J. Agr. Res.* 8: 1-14.
- . 1958. Competition between plants of different initial seed sizes in swards of subterranean clover (*Trifolium subterraneum* L.) with particular reference to leaf area and the light microclimate. *Aust. J. Agr. Res.* 9: 299-318.
- BRADFORD, D. F., AND C. C. SMITH. 1977. Seed predation and seed number in *Scheelea* palm fruits. *Ecology* 58: 667-673.
- ERBE, L. 1957. Studies on the crossability of *Lupinus texensis* and *L. subcarnosus*. *Madroño* 14: 17-18.
- FALCONER, D. S. 1960. Introduction to quantitative genetics. Ronald Press, New York.
- FEHR, W. R., AND C. R. WEBER. 1968. Mass selection by seed size and specific gravity in soybean populations. *Crop Sci.* 8: 551-554.
- GAINES, M. S., VOGT, K. J., HAMRICK, J. L., AND L. CALDWELL. 1974. Reproductive strategies and growth patterns in sunflowers (*Helianthus*). *Amer. Natur.* 108: 889-894.
- HARPER, J. L. 1977. Population biology of plants. Academic Press, London.
- , LOVELL, P. H., AND K. G. MOORE. 1970. The shapes and sizes of seeds. *Ann. Rev. Ecol. and Syst.* 1: 465-492.

- , AND J. WHITE. 1974. The demography of plants. *Ann. Rev. Ecol. Syst.* 4: 419-463.
- HICKMAN, J. C. 1975. Environmental unpredictability and plastic energy allocation strategies in the annual *Polygonum cascadense* (Polygonaceae). *J. Ecology* 63: 689-701.
- HOLLER, L. C., AND W. G. ABRAHAMSON. 1977. Seed and vegetative reproduction in relation to density in *Fragaria virginiana* (Rosaceae). *Amer. J. Bot.* 64: 1003-1007.
- JANZEN, D. H. 1977. Variation in seed size within a crop of a Costa Rican *Mucuna andreana* (Leguminosae). *Amer. J. Bot.* 64: 347-349.
- LACK, D. 1947. The significance of clutch size, Parts I and II. *Ibis* 89: 302-352.
- . 1948. The significance of clutch size, Part III. *Ibis* 90: 25-43.
- LEVERICH, W. J., AND D. A. LEVIN. 1979. Age-specific survivorship and fecundity in *Phlox drummondii* Hook. *Amer. Nat.*, 113: 881-903.
- LEVIN, D. A., AND W. W. ANDERSON. 1970. Competition for pollinators between simultaneously flowering species. *Amer. Nat.* 104: 455-467.
- LEVIN, D. A., AND B. L. TURNER. 1977. Clutch size in the Compositae. In B. Stonehouse and C. Perrins [eds.]. *Evolutionary Ecology* University Park Press, London.
- LINCK, A. J. 1961. The morphological development of the fruit of *Pisum sativum*, var. Alaska. *Phytomorphology* 2: 79-84.
- MCWILLIAMS, E. L., LANDERS, R. Q., AND J. P. MAHLSTEDE. 1968. Variation in seed weight and germination in populations of *Amaranthus retroflexus* L. *Ecology* 49: 290-296.
- PUCKERIDGE, D. W., AND C. M. DONALD. 1967. Competition among wheat plants sown at a wide range of densities. *Aust. J. Agr. Res.* 18: 193-211.
- RACINE, C. H., AND J. F. DOWNHOWER. 1974. Vegetative and reproductive strategies of *Opuntia* (Cactaceae) in the Galapagos Islands. *Biotropica* 6: 175-186.
- ROOS, F. H., AND J. A. QUINN. 1977. Phenology and reproductive allocation in *Andropogon scoparius* (Gramineae) populations in communities of different successional stages. *Amer. J. Bot.* 64: 535-540.
- SALISBURY, E. J. 1942. The reproductive capacity of plants. Bell, London.
- SCHIMPF, D. J. 1977. Seed weight of *Amaranthus retroflexus* in relation to moisture and length of growing season. *Ecology* 58: 450-453.
- SHARITZ, R. R., AND J. F. MCCORMICK. 1973. Population dynamics of two competing annual plant species. *Ecology* 54: 723-740.
- SMITH, C. C. 1974. The coevolution of plants and seed predators. In L. E. Gilbert and P. H. Raven [eds.]. *Coevolution of Animals and Plants*, University of Texas Press, Austin.
- VOIGT, R. L., GARDNER, C. O., AND O. J. WEBSTER. 1966. Inheritance of seed size in Sorghum, *Sorghum vulgare* Pers. *Crop Sci.*, 6: 582-586.
- WERNER, P. A., AND W. J. PLATT. 1976. Ecological relationships of co-occurring goldenrods (*Solidago*: Compositae). *Amer. Nat.* 110: 959-971.
- WILSON, M. F., AND P. W. PRICE. 1977. The evolution of inflorescence size in *Asclepias* (Asclepiadaceae). *Evolution*. 31: 495-511.