

Size structure and seed yield over 4 years in an experimental *Cassia marilandica* (Leguminosae) population

JON K. PIPER

The Land Institute, 2440 East Water Well Road, Salina, KS 67401, U.S.A.

Received October 24, 1991

PIPER, J. K. 1992. Size structure and seed yield over 4 years in an experimental *Cassia marilandica* (Leguminosae) population. *Can. J. Bot.* **70**: 1324–1330.

An experimental population of a perennial species, *Cassia marilandica*, was monitored for 4 years to examine changes in size structure and seed production over time. Plants flowered and set seed the 1st year and annually thereafter. Plant size, seed mass per plant, and reproductive effort were highest in the 2nd year but declined thereafter. Over the first 3 years, density remained constant, but plant size and yield varied. By the 4th year, density, size, and seed yield all declined, owing probably to combinations of drought and insect herbivory. Mean distance to nearest neighbors was consistently positively correlated with plant size but with seed mass in the 2nd and 3rd years only. Plant size was positively correlated with seed mass in each year, with reproductive effort in the first 3 years, but with relative growth rate in the last 2 years only. Population size structure and lifetime reproductive output were generally positively skewed. Except for a slight effect from the 1st to the 2nd year, no cost of reproduction, measured as reduced growth, reproduction, or likelihood of survival was seen.

Key words: *Cassia marilandica*, cost of reproduction, density, Leguminosae, nearest neighbor, perennial, population structure, prairie plants, seed mass.

PIPER, J. K. 1992. Size structure and seed yield over 4 years in an experimental *Cassia marilandica* (Leguminosae) population. *Can. J. Bot.* **70** : 1324–1330.

Afin d'examiner les changements dans la production et les classes de dimension au cours du temps, l'auteur a suivi une population expérimentale de l'espèce pérenne, *Cassia marilandica*, pendant 4 ans. Les plantes ont fleuri et produit des graines dès la première année et chaque année par la suite. La dimension des plants, la masse de graines par plant et l'effort de reproduction sont les plus élevés au cours de la deuxième année et déclinent par la suite. Au cours des trois premières années, la densité demeure constante, mais la dimension des plants et le rendement varient. Vers la quatrième année, la densité, la dimension et le rendement en graines connaissent tous un déclin lié à la sécheresse et au broutage par les insectes. La distance moyenne entre les voisins les plus rapprochés montre une corrélation positive constante avec la dimension des plants, mais seulement à la deuxième et troisième années en ce qui concerne la masse de graines. La dimension des plants montre une corrélation positive avec la masse des graines à chaque année, avec l'effort de reproduction au cours des premières années, mais seulement au cours des deux dernières années avec le taux de croissance. La structure de dimension des populations et la reproduction totale au cours de la vie montrent généralement une courbe positive. Sauf pour un effet peu marqué entre la première et la seconde année, l'auteur n'a observé aucun coût pour la reproduction, tel que mesuré en termes de réduction de croissance, de reproduction ou de chance de survie.

Mots clés : *Cassia marilandica*, coût de reproduction, densité, légumineuses, proche voisin, pérenne, structure de population, plantes de prairies, masse de graines.

[Traduit par la rédaction]

Introduction

Herbaceous perennial seed crops show great potential to alleviate some of the environmental problems that can arise from agricultural practices involving annual crops grown on erodible soils (Wagoner 1990; Soule and Piper 1992). At present, the theoretical arena for the development of successful crops from wild perennials involves considerations of resource allocation, effects of reproduction on subsequent growth and survivorship, and changes in the relationships among density, population size structure, and seed yield over time. Because of the perennial habit, long-term investigations are necessary to predict growth and yield behavior of such crops. Some of the important practical considerations involve predicting yields of representative herbaceous perennial seed crops, how long-term patterns of seed yield change over time in such perennials, how changes in population size structure influence seed yield, and to what extent growth and seed production are density dependent.

One of the challenging arguments presented against the development of perennial seed crops concerns the assumed trade off between seed production and subsequent plant growth and survival. Such a trade off between resources devoted to reproduction versus vegetative growth would lead

to predictions that plants must attain a certain size before reproducing (e.g., Gross 1981; Gross and Werner 1983; Wolfe 1983; Pitelka et al. 1985; Piper 1989), plants are more likely to die after reproducing (e.g., Law 1979), and a large reproductive output in 1 year should be negatively correlated with growth that year or in the following year (e.g., Sohn and Policansky 1977). Whether reproduction results in a demographic cost can be tested in plant populations by examining the correlations between reproduction in 1 year and growth, survival, and reproduction in the following year. Costs of reproduction can then be quantified demographically by comparing growth and survivorship among individuals that differ in reproductive effort.

Another important consideration involves density effects in perennial populations, as interactions between neighboring plants may explain much of the variation in plant growth, size, and reproductive output primarily by influencing the availability of light and soil resources (e.g., Mack and Harper 1977; Weiner 1984, 1985; Silander and Pacala 1985; Tilman 1989). In some herbaceous perennials, reproductive allocation decreases with increasing density (Thompson and Beattie 1981; Hawthorn and Cavers 1982; Waite and Hutchings 1982; Schmid and Harper 1985). Samson and Werk (1986), however, have

suggested that much of this observed variation in reproductive effort is due to intrinsic size-dependent effects rather than such extrinsic factors as density or competition. They predicted that if the absolute reproductive output (the weight of reproductive parts) is an increasing function of plant size in a population, then (i) plant populations should be characterized by significant linear relationships between vegetative biomass and reproductive biomass and (ii) populations should show size-dependent variation in reproductive effort (percentage allocation to reproduction) if there is a minimum size for reproduction. Indeed, strong linear relationships between absolute allocation to reproductive biomass and vegetative plant size are found in many annual species and in some perennial species, where significant regression coefficients indicate that most of the variation in reproductive mass is explained by variation in vegetative plant size (see also Weiner 1988a). Considerable variation also occurs among species in relationships between percentage allocation to reproduction and plant size. Most annuals show increasing reproductive effort (RE) with size (Samson and Werk 1986). Some perennials show increasing RE with size (Waite and Hutchings 1982; Soule and Werner 1981; Weaver and Cavers 1980; Hartnett 1990), whereas others show decreasing RE with size (Solbrig 1981; Aker 1982; Douglas 1981). Of course, in perennials growth and reproduction in a given year may be determined by RE or growing conditions the previous year.

Another set of questions involves the relationship between population size distribution and seed yield. As populations age following establishment, their size distributions can change. The general tendency is for size distributions of even-aged populations to begin approximately normal, then become increasingly positively skewed or variable with time (Ford 1975; Mohler et al. 1978; Turner and Rabinowitz 1983; Weiner 1985). This change in size frequency may result from three interrelated mechanisms: variable growth rate, competition, and nonuniform mortality. For example, differences in resource exploitation can result in differential growth rates among members of a population (Turner and Rabinowitz 1983). Competition may then serve to exaggerate size differences that may be determined initially by environmental chance or variation in seed size. The few individuals that grow large may suppress the growth of smaller individuals, which leads to nonuniform mortality (Ford 1975; Mohler et al. 1978) an unequal population composed of few large and many small individuals. Moreover, intensity of competitive interactions can increase variability in many aspects of performance, including size and reproductive output (Weiner 1985; Weiner and Thomas 1986). Alternatively, it has been demonstrated that increased density-dependent mortality can reduce size variation (Weiner 1988a).

Seed yield in perennial plants is complex in that a plant's reproductive behavior may depend on size as well as previous year's reproduction and resources available. Conceivably, seed yield may increase over time if it is correlated with increasing plant size, or decrease if the population senesces or exhausts one or more critical soil nutrients. Populations of herbaceous perennials may display an initial flush in seed production, then decline precipitously, maintain yields that are relatively stable or decline slowly, or produce yields that oscillate (examples in Piper and Towne 1988). Unfortunately, few relevant models exist to predict accurately how populations of typical perennial species yield over time.

Because of its relatively high seed production, *Cassia*

marilandica was chosen as a model species in which to examine patterns of population size structure and seed production over time. To examine whether costs of reproduction occur, it is important to measure whether individuals differing in amount of reproduction but similar with respect to age and environment differ in future survival, growth, or reproduction (Horvitz and Schemske 1988). Thus, the experimental population consisted of even-aged individuals; size variability was introduced by varying initial spacing. This study addressed three questions: (i) How do such plant traits as size, seed yield, and reproductive effort, and growth rate change over time? (ii) What are the underlying demographic patterns that are correlated with seed yield? (iii) How do such factors as density, population size structure, and effects of previous reproduction change over time?

Materials and methods

Cassia marilandica L. (Leguminosae, Caesalpinioideae), wild or Maryland senna, is a herbaceous perennial native to the Great Plains from southeastern Nebraska south through the eastern third of Kansas, Oklahoma, and Texas and east to Pennsylvania and Florida. It is infrequent to common in such mesic sites as prairie ravines, creek banks, alluvial thickets, and open woodlands (Great Plains Flora Association 1986). Plants produce annually one to few erect stems from a woody caudex and may grow as tall as 2 m. Flowering in central Kansas takes place from late August to early September, producing racemes of insect (bee) pollinated yellow flowers. The flowers give rise to black legumes that begin ripening in September. Nodulation of roots in response to nitrogen-fixing *Rhizobium* bacteria has not been documented for this species, nor has nodulation in field- or pot-grown individuals inoculated with *Rhizobium* (cowpea type) been observed.

An experimental *Cassia marilandica* population was established from scarified seed in May 1985 on a Tobin silt loam (fine-silty, mixed, mesic Cumulic Haplustolls) formerly in wheat. The seed source was a mixture of collections from 16 natural populations in Kansas and Missouri. The plot was weeded but was not fertilized during the course of the study. Plants were established randomly at various within-row spacings ranging from approximately 5 to 40 cm, with rows 75 cm apart, to produce a range of initial planting densities from 3.3 to 26.7 plants \cdot m⁻². Overall plot dimensions were 24 \times 18 m. In September 1985, 90 individual plants were selected along three transects across rows by line intercept and marked at the base with numbered metal tags. Outside plants were excluded to avoid edge effects. For each plant I measured total basal stem diameter (mm), mean distance to the two nearest neighbors within the row (cm), seed mass (g), and number of shoots. I converted basal stem diameter to basal stem area (mm²) for each shoot and summed the values for each plant. Total basal stem area is a good, nondestructive index of shoot dry mass (mass (g) = 0.51 (BSA) + 43.04, r^2 = 0.59, p = 0.0001, n = 25 plants). These measurements were repeated in 1986, 1987, and 1988. From the measurements, I calculated a value for RE as total seed mass per total BSA and for relative growth rate (RGR) as relative change in BSA from the previous year. To examine relationships between density and plant variables, I correlated mean distance to the two nearest neighbors with aspects of growth and reproduction. To examine effects of plant size, controlling for density, I examined correlations between BSA and growth and reproductive variables by partial Pearson correlation. Lastly, to examine whether reproduction in this species suggests demographic costs I analyzed for possible inverse relationships between seed mass or RE and RGR, RE, and BSA in the following year.

Results

All measured characteristics of the population changed over the 4 years (Table 1). The percentage of plants that reproduced

TABLE 1. Characteristics of *Cassia marilandica* plants over 4 years

Year	n	BSA (mm ²)	CV	Seed mass (g)	CV	No. of shoots	CV	Reproductive effort	CV	Relative growth rate	CV
1985	90	84.3±6.7b	75	10.5±1.5b	132	1.00±0.00b	0.0	0.094±0.011b	111	2.28±0.38a	159
1986	89	179.5±13.0a	68	28.5±3.5a	116	2.60±0.16a	59.2	0.137±0.013a	90	-0.36±0.06b	153
1987	82	93.4±9.1b	88	5.9±1.0bc	155	2.77±0.21a	69.3	0.041±0.006c	130	-0.64±0.09b	93
1988	46	17.7±3.6c	137	0.2±0.1c	439	2.33±0.22a	65.2	0.008±0.005d	447		

NOTE: Values are means ± SE. Values for reproductive effort and relative growth rate are defined in the text. Means within a column followed by the same letter do not differ at *p* < 0.05 (ANOVA; Duncan's multiple range test).

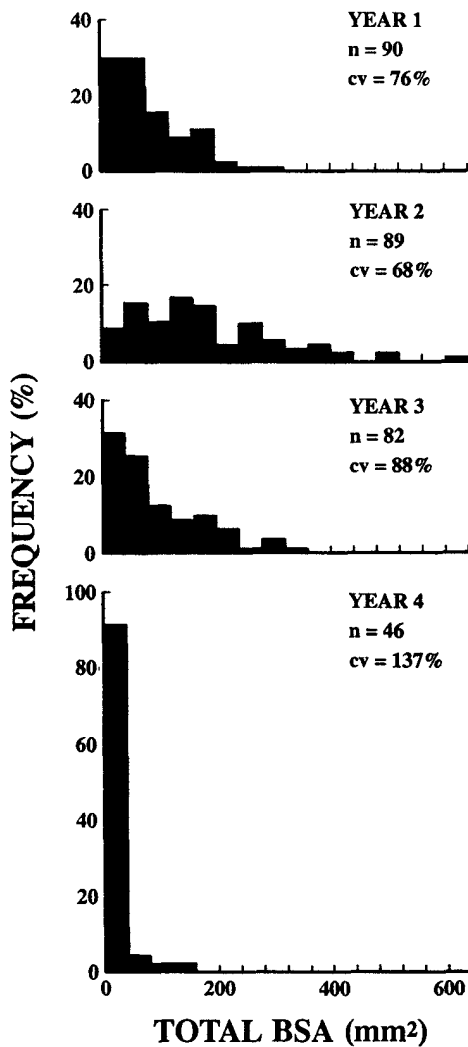


FIG. 1. Changing pattern of *C. marilandica* individual plant size shown as the frequency of plants in 16 size classes.

was 68% in 1985, 95% in 1986, 63% in 1987, but only 6.5% in 1988. Plants were small in the establishment year, then size peaked in the 2nd year, and plants were progressively smaller after that. Seed mass per plant was correspondingly highest in the 2nd year but negligible by the 4th year. Average density remained fairly constant for the first 3 years, then dropped in 1988 as mortality created gaps within rows. Plants consisted of just one shoot in the 1st year, then averaged between 2 and 3 shoots, with one plant producing 13 shoots, in later years. However, average shoot size decreased progressively from the

TABLE 2. Mean BSA/shoot (mm²) over 4 years in an experimental *Cassia marilandica* population

Year	n	BSA/shoot
1985	90	84.3a
1986	231	69.6b
1987	227	34.4c
1988	106	7.8d

NOTE: Means followed by the same letter do not differ at *p* < 0.05 (ANOVA, Duncan's multiple range test).

TABLE 3. Pearson correlations between mean distance to two nearest neighbors, and BSA, seed yield, and reproductive effort (RE) for *C. marilandica* plants within an experimental population over 4 years

Year	n	BSA	Distance vs. yield	RE
1985	90	0.43***	0.03	-0.15
1986	89	0.48***	0.56***	0.36***
1987	82	0.53***	0.36***	0.21
1988	46	0.43**	0.16	-0.03

**p* < 0.05.
 ***p* < 0.01.
 ****p* < 0.001.

1st to the 4th year (Table 2). Mortality in the plot reduced the sample size only slightly from 1985 to 1987, then drastically from 1987 to 1988.

The index of RE, grams of seed produced per unit stem area, was highest in the 2nd year, then fell in years 3 and 4 (Table 1). RGR, measured as relative annual change in total BSA (mm² · mm⁻² · year⁻¹), was positive from the first to the second growing seasons, then negative in the following years as plants became smaller.

For BSA, seed mass, and RE, variability among individuals measured as coefficients of variation generally increased over time. Variability of seed mass was consistently greater than that of BSA and increased faster over time.

The frequency distribution of plant sizes changed shape over the 4 years (Fig. 1), but the smallest size category contained the largest percentage of individuals in 3 of 4 years. In 1986 the size structure of the population approached a normal distribution, but the distribution was positively skewed in the other years. By the 4th year, more than 90% of plants were in the smallest size class, the "reverse J" distribution.

Change in mean plant size was reflected in seed production, as seed yield was a linear function of plant size in the first

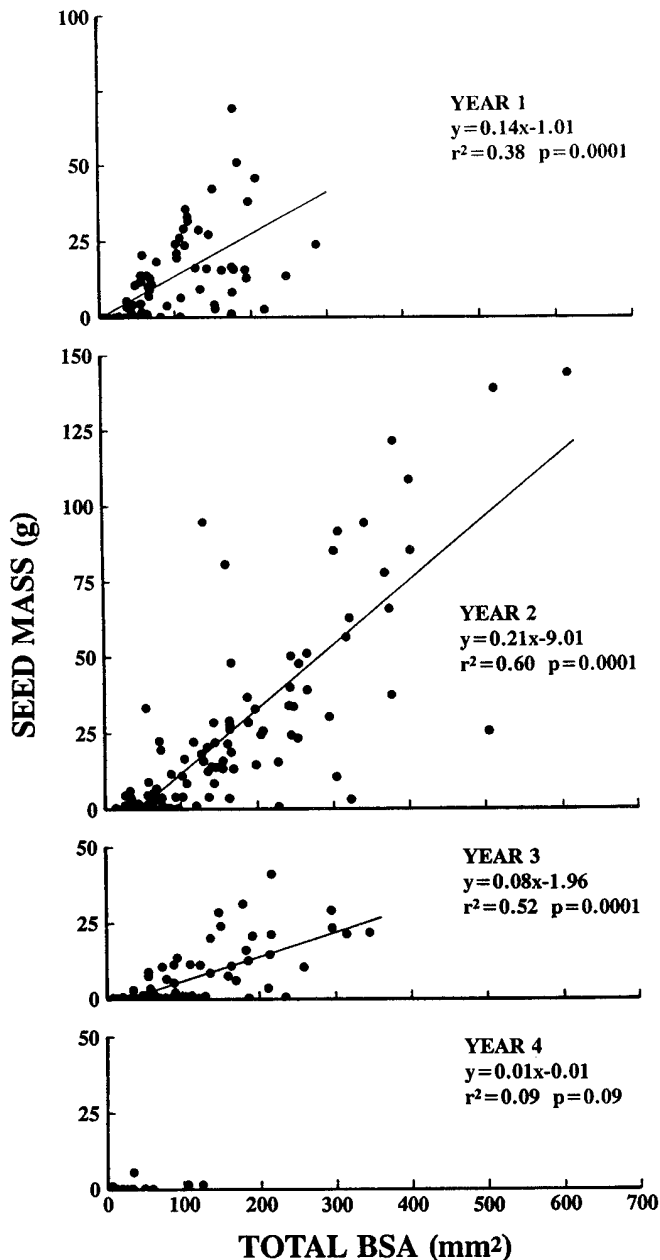


FIG. 2. Regressions of seed production per plant on plant size for 4 years in an experimental population of *C. marilandica*. Regression equations include points where BSA ≥ 5.85 mm².

3 years (Fig. 2). Plant size explained 38 to 60% of the variation in seed yield during the first 3 years but only 9% by the 4th year. The relationship between plant size and seed production changed over time, with the slope of the regression line highest in the 2nd year, and decreasing thereafter. Negative y-intercepts of the regression equations indicated that there is a minimum threshold for reproduction in this species. Although the range of plant sizes with no seed production was broad, no plants with a total BSA less than 5.85 mm² produced seed in any year.

Density affected some plant variables (Table 3). Plant size increased with distance to nearest neighbors in all years, but the relationship between density per se and reproduction was variable, as distance was correlated with yield in years 2 and

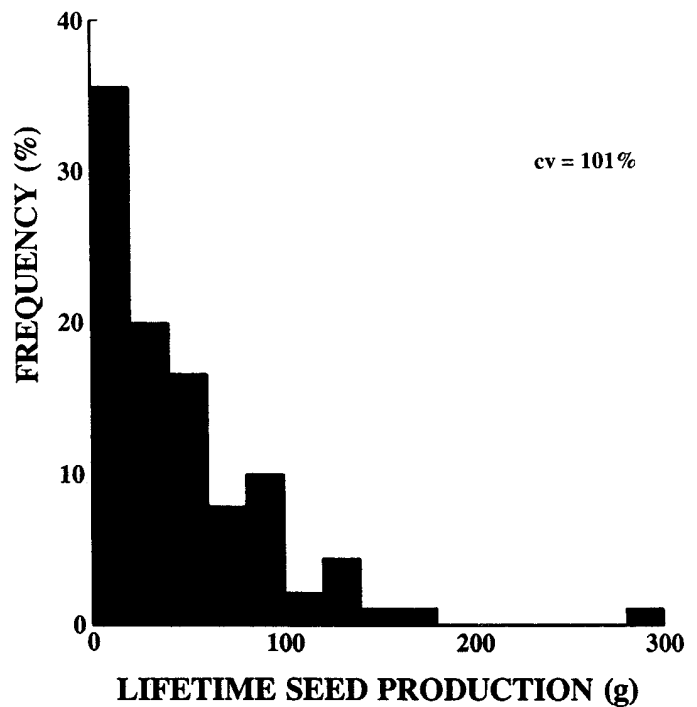


FIG. 3. Frequency distribution of lifetime seed production for 90 individual plants within an experimental *C. marilandica* population.

TABLE 4. Pearson correlations between total BSA (mm²) and seed yield (g), RE, and RGR for *C. marilandica* plants within an experimental population over 4 years

Year	<i>n</i>	Yield	BSA vs. RE	RGR
1985	90	0.63***	0.39***	—
1986	89	0.78***	0.26***	0.07
1987	82	0.73***	0.47***	0.48***
1988	46	0.33*	0.06	0.57***

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

3, and with RE in year 2 only. Although I expected that greater spacing between plants would also promote the production of more shoots per plant, distance was correlated with number of shoots per plant in 1986 only ($r = 0.36$).

Weiner (1988b) has suggested that when reproductive output is the measure of performance, as in a seed crop, it may be useful to look at inequality among individuals in cumulative lifetime fecundity. In the present study, distribution of lifetime reproductive output (Fig. 3) mirrored the general size distributions shown in Fig. 1, with approximately 36% of plants within the smallest category for seed production.

“Cost” of reproduction may be measured in terms of increased likelihood of mortality, decreased growth, or reduced reproductive output. Likelihood of mortality from 1987 to 1988 was not related to BSA, density, yield, or RE ($p > 0.05$, *t*-test), and, whereas RGR was positively correlated with current year’s BSA in 1987 and 1988 (Table 4), it was consistently inversely related to previous years’ BSA (1986, $r = -0.43$, 1987, $r = -0.32$; 1988, $r = -0.35$; all $p < 0.05$). Moreover, RGR was not correlated with previous

TABLE 5. Annual and growing season (May–September) precipitation (cm) at Salina, Kans., over 4 years

Year	Annual	Growing season
1985	100.1	51.2
1986	80.2	49.0
1987	83.5	44.2
1988	46.1	32.8
30-year average	73.5	46.2

NOTE: Data are from National Oceanic and Atmospheric Administration (1985–1988).

years' yield or RE except in 1986 (RGR vs. previous yield: $r = -0.26$; RGR vs. previous RE: $r = -0.26$; $p < 0.05$). This means that in most years larger plants showed the lowest relative increases in growth, or the greatest declines in size, but there was little differential cost to future growth owing to current resource devotion to reproduction.

Discussion

Because *Cassia marilandica* is adapted to relatively mesic habitats, its decline in growth and survival in the final year of this study was probably attributable to lower precipitation received in the 4th year (Table 5). Annual precipitation was well above normal from 1985 to 1987 but below normal in 1988. Similarly, growing season (May–September) precipitation was near normal during the first 3 years but 30% below normal in 1988. However, since *C. marilandica* does not appear to fix atmospheric nitrogen via bacterial symbiosis, there may have been a significant decline in soil nitrogen fertility, or another nutrient such as phosphate, over time in this population that would also have contributed to a general decline in plant vigor. Another factor that could have contributed to the relatively small yield in 1988 was a fairly high level of seed predation by a larva, probably *Sennius abbreviatus* (Say) (Bruchidae) (Baskin and Baskin 1977).

Approximately 40–60% of the variation in *C. marilandica* seed yield was attributable to plant size in the first 3 years, indicating that in this species seed yield is a linear function of plant size. My results were similar to those obtained by Hartnett (1990) for four species of perennial composites. In his populations, each species showed positive linear relationships between reproductive (inflorescence) mass and plant size, with regression lines having negative y-intercepts. Other studies showing a simple linear relationship between plant size and reproductive output have been reported by Gross and Werner (1983), Samson and Werk (1986), Ohlson (1988), Rees and Crawley (1989), and Thompson et al. (1991).

The various theories proposed to explain resource allocation patterns assume that vegetative and reproductive processes compete for a common pool of resources and that an increase in one activity necessarily results in a proportional decrease in the other activity. Indeed, a few studies seem to have demonstrated such trade offs between current reproductive effort and subsequent growth, survival, or competitive ability (Hamblin and Rowell 1975; Sohn and Policansky 1977; Meagher and Antonovics 1982; Cook 1983; Montalvo and Ackerman 1987).

Other studies, however, have failed to demonstrate such a cost of reproduction. For example, Pitelka et al. (1985) found that clonal growth was not reduced by flowering in *Clintonia borealis*, although flowering in that species is ramet size

dependent. Similarly, in a study of *Agropyron repens* by Reekie and Bazzaz (1987), not only did reproduction not reduce overall growth, but reproduction enhanced overall growth in some cases where resources were most favorable. Horvitz and Schemske (1988), studying the perennial tropical herb *Calathea ovandensis*, found that plants with high reproductive effort did not produce significantly fewer inflorescences, less leaf area, or fewer fruits than did plants with low reproductive effort. Moreover, there were no differences in growth and survival between plants with low and high reproductive effort. Jackson (1990) detected no differences in growth between high and low seed-yielding forms of *Tripsacum dactyloides*. These results suggest that, in populations of some plant species at least, increased reproductive success may not always be associated with a significant decline in future growth or reproductive success.

The lack of significant negative correlations between reproductive measures (i.e., seed yield, RE) and previous years' yield or RE suggests that costs, even if present, are not great. Unfortunately, allocation to rootstock was not examined in this study. Allocation to roots might have explained some of the lack of relationship between RGR and yield.

There are several reasons why one should not automatically assume a trade off between growth and reproduction. For example, extra resources may be input prior to or during reproduction for the sole purpose of reproduction, green flowers and fruits can contribute photosynthate to their own development, or reproduction and vegetative growth may be limited by different resources altogether (Tuomi et al. 1983; Willson 1983; Watson 1984). One or more of these mechanisms may help explain why there appeared to be few negative correlations between reproduction and growth measurements in *C. marilandica*.

Several studies within natural and agricultural populations have shown that the size and proximity of neighbors can affect growth (e.g., Waller 1981; Liddle et al. 1982; Cannell et al. 1984), reproductive allocation (Donald and Hamblin 1976), and survivorship (Watkinson et al. 1983) of plants. In the present study, density remained constant for the first 3 years, then, as a result of mortality, density by the 4th year declined to half of the original planting density. Few variables were consistently correlated with density, however. Reproductive effort was inversely related to density in 1 year, but there was no relationship in the other years. Also, density affected size consistently, and size in turn was generally correlated with both seed mass and RE. Thus size, but not likelihood of survival, was density dependent. No apparent association between survivorship and size points to a density-independent mortality factor such as drought stress.

Because much information on size structure of populations is masked by looking at population means only (Mack and Harper 1977; Mithen et al. 1984), additional information on changing population dynamics can be obtained from monitoring changes in the frequency distribution of individual plant size over time. Since size is correlated with fecundity, size inequality, which reflects the degree to which biomass or seed yield is concentrated within a small fraction of the population, is of interest to both evolutionary and applied ecological studies. Except for the 2nd year, the study population assumed a skewed, unequal distribution, with most individuals in the smaller size classes. The population displayed its greatest variability in the 4th year. Among the possible mechanisms leading to this distribution, differential growth rate seemed

more important than nonuniform mortality, as density-dependent mortality should be concentrated among the smallest plants and should thereby reduce skewness.

Study of variation in plant traits is necessary for predicting and interpreting population changes over time. A change in the distribution of population attributes could indicate, for example, whether individuals respond more or less similarly when under stress or optimal conditions, or with time. Competition may increase variability in many aspects of plant performance, including individual size, reproductive output, and phenology (Weiner 1985; Weiner and Thomas 1986). In experimental populations of *Trifolium incarnatum* and *Lolium multiflorum*, variability in size increased with density, and variability in reproductive output was always greater than variability in size (Weiner 1985). In the experimental *Cassia marilandica* population studied here, coefficients of variation for both plant size and seed yield increased over time but were two to four times greater, and increased faster, for seed mass than for plant size even though density remained constant or fell.

The decrease in variability from the 1st to the 2nd year, followed by the increase in inequality from years 2 to 4, may have reflected differences in the nature of plant interactions in this population over time. Initially, competition may have been for light and larger plants differentially suppressed the growth of smaller plants. In later years, as soil resources, especially moisture, became limiting, competition may have become more two sided (see review in Weiner and Thomas 1986).

The results point to an apparent paradox between population versus individual responses to reproduction after the 2nd year. As a whole, the population declined after the 2nd year, owing probably to reduction of soil resources, but this decline was not experienced differentially among plants of different sizes. Largest plants declined the fastest, but this effect appeared to have little relationship to previous reproduction per se. The only negative effect of reproduction on subsequent growth occurred during the period from the establishment year to the 2nd year when higher-yielding plants did not grow as fast as lower-yielding plants. However, this effect disappeared from the 2nd to the later years. Also, positive correlations between reproductive output and future growth can result from variation in the total resources available. In other words, some individuals may outperform others in both reproductive output and growth.

An argument presented against the development of perennials as seed crops concerns their low seed yield relative to annual crops. Therefore, it is worth noting that extrapolated mean yields of this population in the 2nd year were approximately 2000 kg · ha⁻¹, a value comparable with the benchmark yield for winter wheat in Kansas. The importance of *C. marilandica* in addressing the issue of high seed yield in herbaceous perennials is clear in demonstrating the possibility for such plants, grown with few inputs, to yield similarly to highly bred annual grain crops. It remains to be discovered whether high yield in this plot could be sustained through a combination of artificial selection and careful management of the population.

Cassia marilandica is a short-lived perennial whose size, seed yield, and reproductive effort peaked in the 2nd year, then declined after that, although the 4th year may have been spurious. Although 4 years may be insufficient time to characterize long-term yield patterns in this species, the trends in this population were that the 1st year represented the growth and

establishment phase, year 2 was the year of maximum size and reproduction, with the population declining after that. Density remained relatively constant until it fell in year 4. It is difficult to predict how the population would have fared had precipitation been more similar among years.

The potential agricultural value of perennial seed crops is clear. Mixtures of such species could reduce energy expenditures on tillage, reduce soil erosion, provide much of their own nitrogen fertility, encourage and harbor biological control agents, and minimize weed growth. A logical next step in perennial crop research is to examine ways of maintaining sufficient yields through combinations of selection, intercropping, and management. A large part of future research involves combining what is known about demographic patterns within perennial monocultures with patterns of inter- and intra-specific interaction in mixtures.

Acknowledgements

I thank Michel Cavigelli and Melissa Sarlat for assistance in the field. Laura Jackson, Tom Lee, Susan Weaver, and two anonymous reviewers provided helpful comments on an earlier draft of the manuscript.

- Aker, C. L. 1982. Regulation of flower, fruit and seed production by a monocarpic perennial, *Yucca whipplei*. *J. Ecol.* **70**: 357–372.
- Baskin, J. M., and Baskin, C. C. 1977. Predation of *Cassia marilandica* seeds by *Sennius abbreviatus* (Coleoptera: Bruchidae). *Bull. Torrey Bot. Club*, **104**: 61–64.
- Cannell, M. G. R., Rothery, P., and Ford, E. D. 1984. Competition within stands of *Picea sitchensis* and *Pinus contorta*. *Ann. Bot.* (London), **53**: 349–362.
- Cook, R. E. 1983. Clonal plant populations. *Am. Sci.* **71**: 244–253.
- Donald, C. M., and Hamblin, J. 1976. The biological yield and harvest index of cereals as agronomic and plant breeding criteria. *Adv. Agron.* **28**: 361–405.
- Douglas, D. A. 1981. The balance between vegetative and sexual reproduction of *Mimulus primuloides* (Scrophulariaceae) at different altitudes in California. *J. Ecol.* **69**: 295–310.
- Ford, E. D. 1975. Competition and stand structure in some even-aged plant monocultures. *J. Ecol.* **63**: 311–333.
- Great Plains Flora Association. 1986. *Flora of the Great Plains*. University Press of Kansas, Lawrence, Kans.
- Gross, K. L. 1981. Predictions of fate from rosette size in four "biennial" species: *Verbascum thapsus*, *Oenothera biennis*, *Daucus carota*, and *Tragopogon dubius*. *Oecologia* (Berlin), **48**: 209–213.
- Gross, R. S., and Werner, P. A. 1983. Probabilities of survival and reproduction relative to rosette size in the common burdock (*Arctium minus*: Compositae). *Am. Midl. Nat.* **104**: 184–193.
- Hamblin, J., and Rowell, J. G. 1975. Breeding implications of the relationship between competitive ability and pure culture yield in self-pollinated grain crops. *Euphytica*, **24**: 221–228.
- Hartnett, D. C. 1990. Size-dependent allocation to sexual and vegetative reproduction in four clonal composites. *Oecologia* (Berlin), **84**: 254–259.
- Hawthorn, W. R., and Cavers, P. B. 1982. Dry weight and resource allocation patterns among individuals in populations of *Plantago major* and *P. rugellii*. *Can. J. Bot.* **60**: 2424–2439.
- Horvitz, C. C., and Schemske, D. W. 1988. Demographic cost of reproduction in a neotropical herb: an experimental field study. *Ecology*, **69**: 1741–1745.
- Jackson, L. L. 1990. Life history consequences of greater seed production in a perennial grass, *Tripsacum dactyloides*: a comparison of high and low seed-yielding genotypes. Ph.D. thesis, Cornell University, Ithaca, N.Y.
- Law, R. 1979. The cost of reproduction in annual meadow grass. *Am. Nat.* **113**: 3–16.

- Liddle, M. J., Budd, C. S. J., and Hutchings, M. J. 1982. Population dynamics and neighbourhood effects in establishing swards of *Festuca rubra*. *Oikos*, **38**: 52–59.
- Mack, R. N., and Harper, J. L. 1977. Interference in dune annuals: spatial pattern and neighbourhood effects. *J. Ecol.* **65**: 345–364.
- Meagher, T. R., and Antonovics, J. 1982. The population biology of *Chamaelirium luteum*, a dioecious member of the lily family. *Ecology*, **63**: 1690–1700.
- Mithen, R., Harper, J. L., and Weiner, J. 1984. Growth and mortality of individual plants as a function of "available area". *Oecologia* (Berlin), **62**: 57–60.
- Mohler, C. L., Marks, P. L., and Sprugel, D. G. 1978. Stand structure and allometry of trees during self-thinning of pure stands. *J. Ecol.* **66**: 599–614.
- Montalvo, A. M., and Ackerman, J. D. 1987. Limitations to fruit production in *Ionopsis utricularioides* (Orchidaceae). *Biotropica*, **19**: 24–31.
- National Oceanic and Atmospheric Administration. 1985–1988. Climatological data: Kansas. Vols. 99–102.
- Ohlson, M. 1988. Size-dependent reproductive effort in three populations of *Saxifraga hirculus* in Sweden. *J. Ecol.* **76**: 1007–1016.
- Piper, J. K. 1989. Light, flowering, and fruiting within patches of *Smilacina racemosa* and *Smilacina stellata* (Liliaceae). *Bull. Torrey Bot. Club*, **166**: 247–257.
- Piper, J. K., and Towne, D. 1988. Multiple year patterns of seed yield in five herbaceous perennials. *Land Inst. Res. Rep.* **5**: 14–18.
- Pitelka, L. F., Hansen, S. B., and Ashmun, J. W. 1985. Population biology of *Clintonia borealis*. I. Ramet and patch dynamics. *J. Ecol.* **73**: 169–183.
- Reekie, E. G., and Bazzaz, F. A. 1987. Reproductive effort in plants. 3. Effect of reproduction on vegetative activity. *Am. Nat.* **129**: 907–919.
- Rees, M., and Crawley, M. J. 1989. Growth, reproduction and population dynamics. *Funct. Ecol.* **3**: 645–653.
- Samson, D. A., and Werk, K. S. 1986. Size-dependent effects in the analysis of reproductive effort in plants. *Am. Nat.* **127**: 667–680.
- Schmid, B., and Harper, J. L. 1985. Clonal growth in grassland perennials. I. Density and pattern-dependent competition between plants with different growth forms. *J. Ecol.* **73**: 793–808.
- Silander, J. A., and Pacala, S. W. 1985. Neighborhood predictors of plant performance. *Oecologia* (Berlin), **66**: 256–263.
- Sohn, J. J., and Policansky, D. 1977. The costs of reproduction in the mayapple *Podophyllum peltatum* (Berberidaceae). *Ecology*, **58**: 1366–1374.
- Solbrig, O. T. 1981. Studies on the population biology of the genus *Viola*. II. The effect of plant size on fitness in *Viola sororia*. *Evolution* (Lawrence, Kans.), **35**: 1080–1093.
- Soule, J. D., and Piper, J. K. 1992. *Farming in nature's image*. Island Press, Washington, DC.
- Soule, J. D., and Werner, P. A. 1981. Patterns of resource allocation in plants, with special reference to *Potentilla recta* L. *Bull. Torrey Bot. Club*, **198**: 311–319.
- Thompson, B. K., Weiner, J., and Warwick, S. 1991. Size-dependent reproductive output in agricultural weeds. *Can. J. Bot.* **69**: 442–446.
- Thompson, D. A., and Beattie, A. J. 1981. Density-mediated seed and stolon production in *Viola* (Violaceae). *Am. J. Bot.* **68**: 383–388.
- Tilman, D. 1989. Competition, nutrient reduction and the competitive neighbourhood of a bunchgrass. *Funct. Ecol.* **3**: 215–219.
- Tuomi, J., Hakala, T., and Haukioja, E. 1983. Alternative concepts of reproductive effort, costs of reproduction and selection in life history evolution. *Am. Zool.* **23**: 25–34.
- Turner, M. D., and Rabinowitz, D. 1983. Factors affecting frequency distributions of plant mass: the absence of domination and suppression in competing monocultures of *Festuca paradoxa*. *Ecology*, **64**: 469–475.
- Wagoner, P. 1990. Perennial grain development: past efforts and potential for the future. *Crit. Rev. Plant Sci.* **9**: 381–409.
- Waite, S., and Hutchings, M. J. 1982. Plastic energy allocation patterns in *Plantago coronopus*. *Oikos*, **38**: 333–342.
- Waller, D. M. 1981. Neighborhood competition in several violet populations. *Oecologia* (Berlin), **51**: 116–122.
- Watkinson, A. R., Lonsdale, W. M., and Firbank, L. G. 1983. A neighbourhood approach to self-thinning. *Oecologia* (Berlin), **56**: 381–384.
- Watson, M. A. 1984. Developmental constraints on population growth and patterns of resource allocation in a clonal plant. *Am. Nat.* **123**: 411–426.
- Weaver, S. E., and Cavers, P. B. 1980. Reproductive effort of two perennial weed species in different habitats. *J. Appl. Ecol.* **17**: 505–513.
- Weiner, J. 1984. Neighbourhood interference amongst *Pinus rigida* individuals. *J. Ecol.* **72**: 183–195.
- Weiner, J. 1985. Size hierarchies in experimental populations of annual plants. *Ecology*, **66**: 743–752.
- Weiner, J. 1988a. The influence of competition on plant reproduction. *In Plant reproductive ecology*. Edited by J. Lovett Doust and L. Lovett Doust. Oxford University Press, New York. pp. 288–245.
- Weiner, J. 1988b. Variation in the performance of individuals in plant populations. *In Plant population ecology*. Edited by A. J. Davy, M. J. Hutchings, and A. R. Watkinson. Blackwell Scientific Publishers, Oxford. pp. 59–81.
- Weiner, J., and Thomas, S. C. 1986. Size variability and competition in plant monocultures. *Oikos*, **47**: 211–222.
- Willson, M. F. 1983. *Plant reproductive ecology*. John Wiley & Sons, Inc., New York.
- Wolfe, L. M. 1983. The effect of plant size on reproductive characteristics in *Erythronium americanum* (Liliaceae). *Can. J. Bot.* **61**: 3489–3493.