

Why biennials delay flowering: an optimization model and field data on *Cirsium vulgare* and *Cynoglossum officinale*

T. J. DE JONG, P. G. L. KLINKHAMER, S. A. H. GERITZ and
E. VAN DER MEIJDEN

Department of Population Biology, Research Group Ecology of Plants and Herbivores, University of Leiden, P. O. Box 9516, 2300 RA Leiden, The Netherlands

SUMMARY

A model is developed to calculate the population growth rate of different lineages within a biennial species, in a density-independent situation. The types differ in the minimum size they require for flowering. The environment is stochastic in the sense that each year a value for combined seed and early seedling survival was drawn from a probability distribution. Other probabilities of survival and growth were entered into the model as fixed rates, which are only dependent on the size of the plant. From demographic data on the delayed biennials *Cirsium vulgare* and *Cynoglossum officinale*, the model predicts that for both species (1) there exists a unique, optimal value of minimum size or weight w^* for flowering, i.e. delayed flowering is profitable, (2) there is weak selection against flowering at sizes larger than optimal w^* but strong selection against flowering at sizes smaller than optimal w^* , and (3) that optimal w^* is 2 g or more. In the field the size requirement was between 1 and 2 g for both species. The optimal value of w^* is mostly determined by the fact that delayed flowering results in an increase in the expected number of seeds and less by delayed flowering resulting in averaging of variable recruitment over the years.

Key-words: monocarp, biennial, minimum-size for flowering, optimization model, demography.

INTRODUCTION

From an evolutionary viewpoint there are two interesting questions with regard to the timing of reproduction in monocarpic plants. First, why do plants flower in a particular season? Second, given the fact that flowering is restricted to a certain period of the year, why do plants sometimes delay their flowering to a later year? This second question will be dealt with in this paper.

It is well-known that under natural conditions a large fraction of the rosettes of so-called 'biennial' species do not flower in the second year (Werner 1975; Van der Meijden & van der Waals-Kooi 1979; Gross 1981). Genetic variation in the timing of reproduction in biennials was found between geographically separated populations for *Daucus carota* (Lacey 1986, 1988), *Verbascum thapsus* (Reinartz 1984) and *Cynoglossum officinale* (M. J. van Dijk *et al.* personal communication). Previous models of the delay in

flowering in biennials were aimed at illustrating the adaptive value of delayed flowering without indicating which individual characters are important, how these characters may be subject to natural selection, and when to measure them. In general, biennial plants require winter cold to reach a condition in which flowering can occur (vernalization). After vernalization the actual flowering or bolting is triggered by daylength (usually long days are required). The majority of biennials respond to cold, long days or both, only if they are of sufficient size (Lang 1965). Although other factors, e.g. recent growth, light quality, and light quantity, may play an additional role, the best predictor for flowering is plant size or a closely related factor (Greulich 1973; Lacey 1986; Klinkhamer *et al.* 1987a,b). Whether a plant will flower may be determined during the cold period (e.g. *Cynoglossum officinale*) or just before bolting (e.g. *Cirsium vulgare*). In the monocarp *Frasera speciosa*, flowers are preformed at least 3 years before the actual flowering occurs (Taylor & Inouye 1985). For life-history studies it is thus essential to know at what time of the year it is fixed that flowering will occur.

As Lacey (1988) argued, for evolutionary studies the pertinent question at the time that the flowering stimulus operates is: 'What is a plant's probability of surviving and seed set next year if it does not flower (i.e. does not respond to the inductive stimulus) this year?' This statement sets the scene for the model presented in this paper. First, we will examine whether within the parameter range that may occur in the field, the fitness of a lineage is maximized by having an individual size requirement for flowering. Then we will examine which value of the minimum required size for flowering ($=w^*$) results in the highest fitness, given the average and variance of the field data we collected over a 4-year period at the sand-dunes of Meijendel (near the Hague, The Netherlands) and compare this value to the sizes at which the plants actually flower in the field. An increase in w^* has two major consequences. First, the generation time will lengthen and therefore the death risk before reproduction increases but also the number of seeds produced, when the individual survives until the flowering stage, increases. Second, if the environment is variable a size requirement for flowering implies that although they may germinate simultaneously, some plants of a cohort may, and others may not, have reached the minimum size for flowering at the time of year that the flowering is fixed. As a result, the number of separate years in which the offspring of a single individual reproduce will increase with w^* , which, in a stochastic environment, will lead to bet-hedging, i.e. to the averaging out of effects from variable recruitment on population growth of the lineage (Klinkhamer & De Jong 1983; Roerdink 1988). This prediction of large 'rosette-banks' in unpredictable environments is analogous to Cohen's (1966) prediction of large seed banks in such environments. To understand the relative importance of the two adaptive explanations given above, we will look at what each mechanism does on its own.

METHODS

Long-term, geometric growth averages (λ) of types (lineages) that differ from each other only in the minimum (or critical) size x^* ($x = \log(w)$) were compared. Natural logarithms are used throughout this paper. λ is defined as:

$$\lambda = \lim(M_t/M_0) \text{ for } t \rightarrow \infty, \quad (1)$$

M denotes the population size. Under density-independent conditions λ is the appropriate fitness-criterion (Kuno 1981; Metz *et al.* 1983; Bulmer 1985; De Kroon *et al.* 1986; Klinkhamer *et al.* 1987c). One expects that the lineage with the highest value of λ will

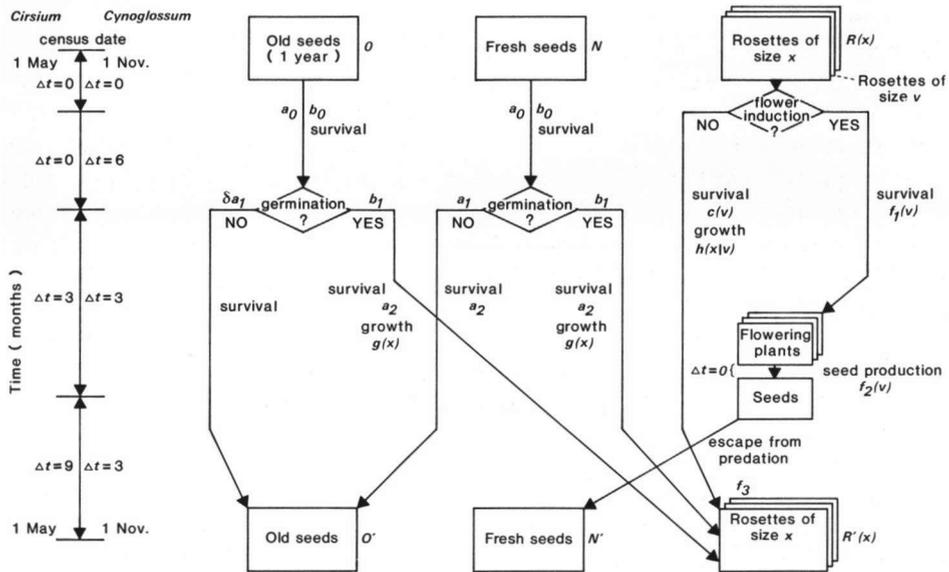


Fig. 1. Flow diagram illustrating the one-step transformations in the model.

eventually dominate the population. If intraspecific competition does take place λ is always close to unity over a long period of time and the above concept is no longer meaningful (see discussion in Klinkhamer & De Jong 1989). The analysis was restricted to the density-independent situation but the expected effects of density-dependence on the outcome of the model will be discussed. The different (hypothetical) types are not allowed to interbreed and all offspring have the same minimum size for flowering (w^*) as their parent. All steps in the calculations are outlined in Fig. 1 and the symbols are explained in Table 1. In the equation:

$$O' = aN + \delta aO, \tag{2}$$

$$N' = \int_{x^*}^{\infty} f(x)R(x)dx, \tag{3}$$

$$R'(x) = (O + N)bg(x) + \int_{-\infty}^{x^*} c(v)h(x|v)R(v)dv, \tag{4}$$

the prime denotes the situation in the next year and all state variables are written in capitals. The population is always censused at the date that flowering is fixed. This date is arbitrarily pinned down on 1 May for *Cirsium* (Klinkhamer *et al.* 1987a; Klinkhamer & De Jong 1988b) and on 1 November for *Cynoglossum* (De Jong *et al.* 1986, De Jong & Klinkhamer 1988c). We simplified phenology by assuming that germination takes place immediately after 1 May for both species and by allowing 3 months for the processes of flowering and producing seeds.

In equation (2) a fraction of the number of seeds in the soil at the census date (N) does not germinate in the next spring but remains dormant for 1 year, after which they are classified as 'old seeds' (O). The viability of seeds may be indefinite ($\delta = 1$) or limited to 2 years ($\delta = 0$). Equation (3) links the number of newly produced seeds in the next year (N') to the number of flowering plants of size x ($R(x)$), i.e. rosettes that had attained a size

Table 1. Definition of parameters

w	Plant dry weight (g)
w^*	Minimum (or critical) required size for flowering
x	Natural logarithm of w
x^*	Natural logarithm of w^*
N	Number of fresh seeds in the soil
O	Number of old seeds in the soil (> 1 year)
$R(x)dx$	Number of rosettes with size between x and $x + dx$
δ	Parameter that may limit the maximum life span of seeds to 2 years
a_0, b_0	Seed survival between census date and germination ($a_0 = b_0$)
a_1	Probability of not germinating
a_2	Probability of surviving 1 year in the soil seed bank
a	$= a_0 a_1 a_2$
b_1	Probability of germination ($a_1 + b_1 = 1$)
b_2	Probability of surviving from the seedling stage to the next census date
b	$= b_0 b_1 b_2$
$c(x)$	Annual survival probability of rosettes, depending on their size x
$f_1(x)$	Probability of survival from induction to the seed plant stage
$f_2(x)$	Seeds produced as a function of size x at the census date
f_3	Seed survival between formation and the census date
$f(x)$	$= f_1(x) f_2(x) f_3$
$g(x)dx$	Probability that a seedling that survives reaches size between x and $x + dx$ at the census date
$h(x v)dx$	Probability that a rosette of fixed size v attains a size between x and $x + dx$ in the following year, provided that it does not die

larger than the minimum size x^* . The function $f(x)$ describes how rosettes survive until the flowering stage, how many seeds are produced per unit of dry weight and how many of these seeds then survive until the census date. Equation (4) shows how the number of rosettes of size x in the next year ($R'(x)$) depends on the recruits from seed (left-hand term) and survival and growth of small rosettes from the previous year that did not flower, i.e. had a size between $-\infty$ and x^* (right-hand term). b is the probability that seeds germinate and survive until the census date, $g(x)$ is the probability that they have by then reached size x . The notation $h(x|v)$ denotes that when we know the exact size v of a plant, the probability distribution of plant sizes in the next year is fixed. The functions $b, f(x), g(x)$ and $h(x)$ are further filled in in the next sections. During simulations, all parameters and functions that occur in equations (2), (3) and (4), and which are summarized in Table 1, were fixed, except for b , which was drawn from a specific probability distribution.

The integrals in equations (3) and (4) were approximated using the composite trapezium-rule (e.g. Stoer & Bulirsch 1979) and the right-hand side in (1) by averaging the annual population growth over a large, but finite, number of years (1000 for *Cirsium*, 500 for *Cynoglossum*). This procedure allowed an estimate of the population growth (λ) with a relative error of less than 3%.

The size at which plants actually flower in the field was determined by marking 180 rosettes of *Cirsium vulgare* (on 15 May 1985) and 151 rosettes of *Cynoglossum officinale* (on 1 November 1983) and recording their fate. Because the sample size proved to be low for *Cynoglossum*, 510 randomly collected additional plants were measured in June 1984. The root-crown diameter (*RCD*) of these plants on 1 November 1983 could be estimated from *RCD* in June because there appeared to be a close correlation between the two in a sample of 97 plants that were repeatedly measured in the intervening period: $r = 0.68$, $RCD_{\text{Autumn}} = 1.74 RCD_{\text{Spring}} - 0.26$. The initial dry weight of *Cirsium* rosettes (*DW*, in g)

Table 2. Probability of germination and survival until the first census date (1 May for *Cirsium vulgare* and 1 November for *Cynoglossum officinale*), b . In order to calculate b we started with the number of seeds actually formed on the plant and assumed 30% and 97% seed survival until the census date in *Cirsium* and *Cynoglossum*, respectively

Year in which seeds are formed	b	
	<i>Cirsium</i>	<i>Cynoglossum</i>
1981	0.00067	0.0284
1982	0.00333	0.0179
1983	*	0.0200
1984	0.00833	0.0610
E(log(b))	-5.93	-3.59
Var(log(b))	1.63	0.31

* = No data available.

E = the expectation or arithmetic mean.

was estimated from a regression through the origin with the length of the longest leaf (LL , in cm). The equation used throughout this paper is: $DW = 0.069LL^2$ ($r = 0.91$, $n = 50$). As the *Cynoglossum* leaves die off after frost, rosette size cannot be measured and root weight in late autumn appears to be the relevant variable for predicting the further fate of the plant. Root dry weight (DW , in g) was estimated from RCD (in cm) in the regression: $DW = 1.09RCD^2$ ($r = 0.96$, $n = 38$).

Parametrization

Demography of the two species at the coastal sand-dunes of Meijndel is described in De Jong & Klinkhamer (1988a,b), Klinkhamer & De Jong (1988a) and Klinkhamer *et al.* (1988) and the growth curves in De Jong *et al.* (1987b).

(a) *Cirsium vulgare*. After bolting in May, the first flowers open in June and ripe seeds are dispersed in July and August. Seeds have no innate dormancy, they germinate mostly in spring after several warm days if the conditions are humid. Vernalization is required for flowering, but there does not seem to be a minimum rosette size for vernalization: even plants that are quite small before winter, flower if the nutrient supply in spring is abundant. There is, however, a minimum size required for plants to commence bolting in response to a long-day stimulus in spring. Additional factors that may have an effect on flowering are age and light (Klinkhamer *et al.* 1987a; Klinkhamer & De Jong 1988b).

The major cause of seed mortality is seed predation immediately after dispersal in July and August ($f_3 = 0.3$). Once the seeds are buried mortality is probably low. The few *Cirsium* seeds that remain dormant remain viable over a number of years (Van Breemen & van Leeuwen 1982).

The survival during the first, vulnerable life-stages is generally extremely variable and dependent on such factors as predation and rainfall. We assume that the probability of surviving until the first census date, b , is log-normally distributed with mean and variance as given in Table 2 and truncated at $\log(b_1)$. The rationale behind this assumption is that when, in biological systems, a number of variables exert their effect successively on a

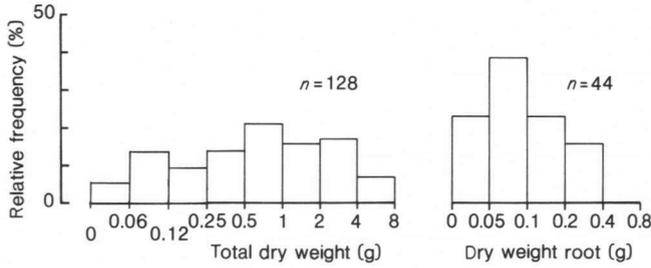


Fig. 2. Frequency distribution of the dry weight of established seedlings at the census date (1 May 1985 for *Cirsium vulgare*, see left graph; 1 November 1983 for *Cynoglossum officinale*, see right graph). (The seeds from which the seedlings descend were formed in the summer of 1983 and 1982 for *Cirsium* and *Cynoglossum*, respectively.) n = number of seedlings.

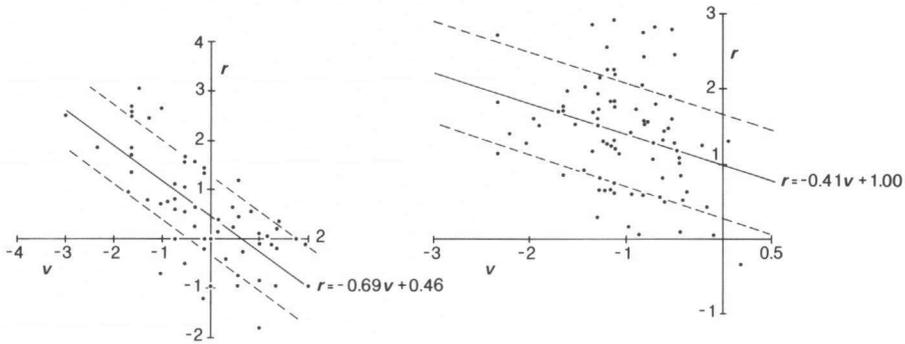


Fig. 3. The relation between the logarithm of the annual rate at which rosettes multiply their weight (r) and the logarithm of initial dry weight (v) for *Cirsium vulgare* (a) and *Cynoglossum officinale* (b). Weight measurements started on 1 May 1984 for *Cirsium* and 1 November 1985 for *Cynoglossum*. The correlation coefficient is -0.71 ($P < 0.001$; $n = 64$) for *Cirsium* and -0.29 ($P < 0.01$; $n = 83$) for *Cynoglossum*. The standard deviation (σ) of the regression line is indicated in the figure.

variable, their effect is multiplicative and when the number of variables is large, the expected outcome of this process is a log-normal distribution (see Slob 1987).

On the first opportunity for flower induction (1 May for *Cirsium*) seedling weight approximately follows a log-normal distribution (Fig. 2).

Rosettes were measured at the census date and on the same date 1 year later. In both species the majority of rosettes gain weight during this period (Fig. 3). If plants grow exponentially with, on average, a constant relative growth rate (r), then the dry weight in year n is proportional to the dry weight in the next year:

$$w_{n+1} = e^r w_n,$$

or, returning to our previous notation and substituting $x = \log(w_{n+1})$ and $v = \log(w_n)$, we obtain

$$x = v + r.$$

The slope of the regression line of x versus v was 0.31 , which is significantly less than one ($F = 61.49$, $P \ll 0.001$). This means that small rosettes multiply their weight with a larger

Table 3. Summary of used parameters and functions. The notation $N(x|\mu, \sigma^2)$ is the density of the normal distribution with mean μ and variance σ^2

Parameter function	<i>Cirsium vulgare</i>	<i>Cynoglossum officinale</i>
δ	1	0
a_0, b_0	1.00	0.95
a_1	0.02	0.25
a_2	0.80	0.90
a	0.016	0.225
b_1	0.98	0.75
b_2	see Table 2	see Table 2
$\log(b)$	For each year values were drawn from a normal distribution with mean -5.93 and variance 1.63	For each year values were drawn from a normal distribution with mean -3.59 and variance 0.31
$c(x)$	$5.44e^x/(1 + 6.06e^x)$	$12.60e^x/(1 + 15.24e^x)$
$f_1(x)$	$c(x)^{1/4}$	$c(x)^{3/4}$
$f_2(x)$	$150e^x$	$60e^x$
f_3	0.3	0.97
$f(x)$	$45c(x)^{1/4}e^x$	$58c(x)^{3/4}e^x$
$g(x)$	$N(x -0.43, 2.03)$	$N(x -2.45, 0.57)$
$h(x \nu)$	$N(x 0.46 + 0.31\nu, 0.63)$	$N(x 1.00 + 0.59\nu, 0.51)$

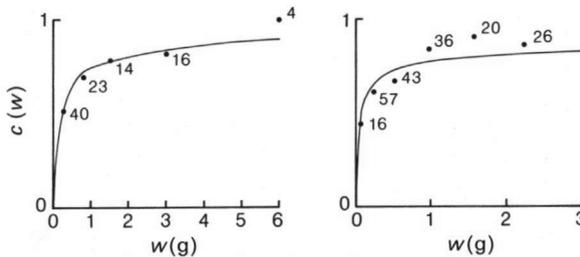


Fig. 4. Annual survival ($c(w)$) of rosettes of *Cirsium vulgare* (a) and *Cynoglossum officinale* (b), starting on 1 May 1984 and 1 November 1985, respectively. The fitted hyperboles are given in Table 3. The initial number of plants is denoted in the figure.

factor rather than large rosettes. If the initial weight of a rosette is fixed at ν , the probability distribution of its weight in the next year, x , depends only on the distribution of r , which was chosen to be normal with conditional mean $\alpha + \beta\nu$ and fixed variance σ^2 . The parameters α and β were estimated from the regression of r versus ν (Fig. 3; cf. Kachi & Hirose 1985). The consequence of this choice of parameters (Table 3) is that very large rosettes are expected to reach a plateau in their site at $\nu = 0.66$, i.e. when they weigh $e^{0.66} = 1.94$ g. Of course this only refers to the expectation of annual growth: some plants still grow and others will decline, according to the probability distribution $h(x|\nu)$.

Survival increases with size. This relationship is generally hyperbolic (cf. Gross 1981) and was approximated as such (Fig. 4).

The total number of seeds that a plant can produce depends on plant weight at the time of induction, on how much it will grow between flower induction and seed production

and then on what fraction of its weight can be converted into seeds. Allocation to seeds is a very constant fraction of size: in a sample of 14 flowering plants we obtained a rank correlation coefficient of 0.002 ($P=0.50$) between the total dry weight and the fraction of total dry weight allocated to seeds. Because under favourable conditions dry weight increases roughly threefold in the period May–July and the seeds comprise nearly 10% of the final dry weight, it follows that per gram of dry weight (at the census date) maximally 150 seeds can be produced (weight per seed is 0.002 g). After formation, 30% of the seeds survive until the next census date.

(b) *Cynoglossum officinale*. Bolting occurs in the first half of May, after which the first flowers open in June. Seeds are ripe in July/August and dispersed during the following months. Seeds only germinate in early spring (February to April). Cold is required for flowering and primordial flowers are visible in winter. There clearly exists a size requirement for flowering. Bolting is probably controlled by long days in spring. The only additional factor that may perhaps influence flowering is winter cold (flowering is more frequent after mild winters, De Jong *et al.* 1986; De Jong & Klinkhamer 1988c).

Not all the seeds are immediately dispersed after ripening, some remain attached to the parent plant and they need at least 6 weeks of winter cold (under wet conditions) before they germinate. We estimate that 75% of the seeds germinate in the first spring ($b_1 = (1 - a_1) = 0.75$, cf. Van Breemen 1984). The maximum life span of seeds in the field is restricted to 2 years because of attack by microorganisms (Lhotská 1982).

In *Cynoglossum* the slope of the regression line of x versus v was 0.59, which is also significantly less than one ($F=7.69$, $P<0.01$). Rosettes are expected to have zero growth at $v=2.43$, i.e. when they weigh $e^{2.43} = 11.35$ g (Fig 3).

In *Cynoglossum* dry weight increases roughly sixfold between induction (1 November) and flowering in May and seeds comprise approximately 30% of the final dry weight (Klinkhamer & De Jong 1987). Therefore, 60 seeds can be produced per gram of dry weight on 1 November (weight per seed is 0.03 g). After formation 97% of the seeds survive until the census date.

RESULTS

The consequence of having a larger minimum size for flowering, w^* , is that the annual fraction of plants that flowers is smaller and, on average, plants have a longer generation time and will produce more seeds (Table 4). Note that the percentage of flowering increases very steeply as $w^* \rightarrow 0$, even at $w^* = 0.1$ there is a considerable delay in flowering: 7% and 39% of the rosettes do not flower in *Cirsium* and *Cynoglossum*, respectively. In both species λ is small for types with low values for w^* (Fig. 5). This means that there is strong selection against flowering at a very small size. Values larger than optimal w^* give only a slight reduction in fitness. There is a unique, optimum value for w^* in *Cirsium*, even in growing populations ($\lambda > 1$) (Fig. 5). In *Cynoglossum* there are only small differences in fitness between types as long as $w^* > 2$ g.

Because the distribution of seedling recruitment, $\log(b)$, was estimated from only 3 (or 4) data points it is essential to investigate how much the curves change if we choose different values for the variance in $\log(b)$. Optimal w^* decreases with the variance in $\log(b)$ (Fig. 5). This result is unexpected because previous analysis suggested that as the variance in b increases it becomes increasingly favourable for a lineage to 'average between years', i.e. to have a low percentage of flowering in each year (Klinkhamer & De Jong 1983). The

Table 4. An illustration of changes in the population behaviour due to changes in w^* . Parameter values given in Table 3. Results are geometrical averages over a number of years

w^* (g)	<i>Cirsium vulgare</i>			<i>Cynoglossum officinale</i>		
	λ	Flowering (%)	Per capita seed production	λ	Flowering (%)	Per capita seed production
0.1	0.55	93	256	0.86	61	27
0.5	0.65	69	344	1.18	30	88
1.0	0.76	52	451	1.30	21	147
3.0	0.90	21	862	1.43	10	359
5.0	0.92	10	1249	1.45	7	549
9.0	0.89	3	1992	1.44	4	904

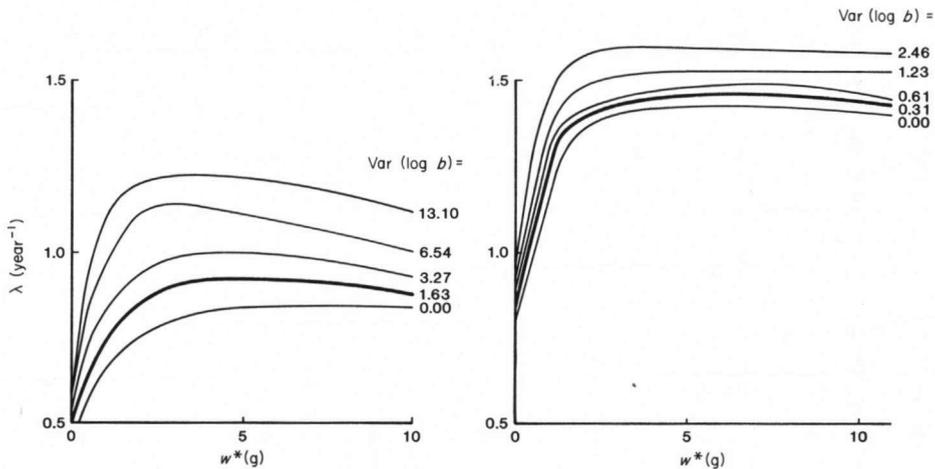


Fig. 5. λ as a function of the minimum size for flowering, w^* , in *Cirsium vulgare* (a) and *Cynoglossum officinale* (b). For *Cirsium* $E(\log(b)) = -5.93$, for *Cynoglossum* $E(\log(b)) = -3.59$. $\text{Var}(\log(b))$ was varied. The bold line gives the variance measured in the field.

explanation is that, if $E(\log(b))$ is constant, $E(b)$ increases as we choose higher values for $\text{Var}(\log(b))$. As the variance in recruitment increases there will be more years with a very low recruitment but also more years with a very high recruitment and λ may in fact be higher! It can be seen in Fig. 5 that increasing $\text{Var}(\log(b))$ leads to a higher population growth and smaller optimum values of w^* . Simulation results, which are not included here, show that increasing $\text{Var}(b)$, without changing $E(b)$, does lead to larger values for an optimum w^* .

If we take out the variance in recruitment ($\text{Var}(\log(b)) = 0$), then it is still favourable to have $w^* > 0$. These simulations in an environment with constant recruitment confirm for both species that in growing populations there will be selection for earlier reproduction (Fig. 6).

If delayed reproduction does not lead to an increase in seed production ($f_2 = \text{constant}$), and therefore only has a beneficial effect through the averaging of variations in b , the

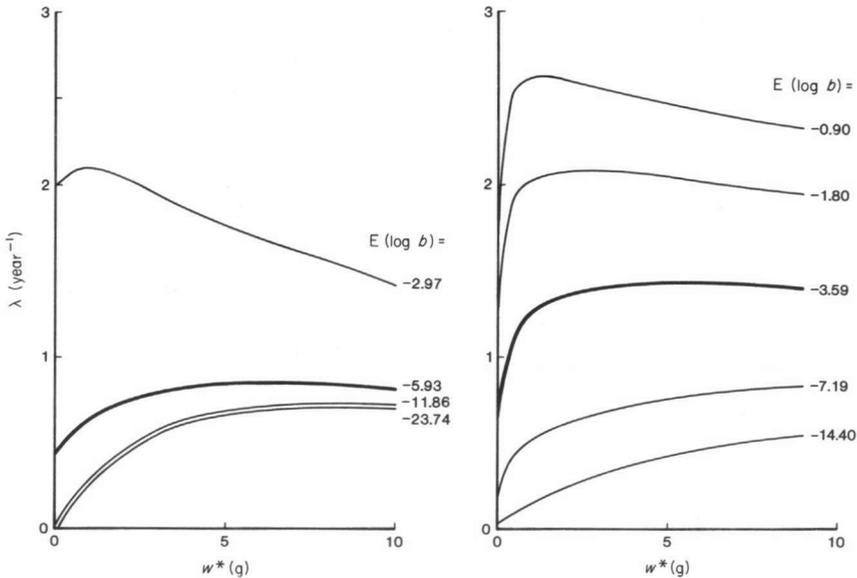


Fig. 6. λ as a function of the minimum size for flowering, w^* , in *Cirsium vulgare* (a) and *Cynoglossum officinale* (b) with constant survival in the seedling stage, $\text{Var}(\log(b))=0$. $E(\log(b))$ was varied. The bold line gives the average seedling survival measured in the field.

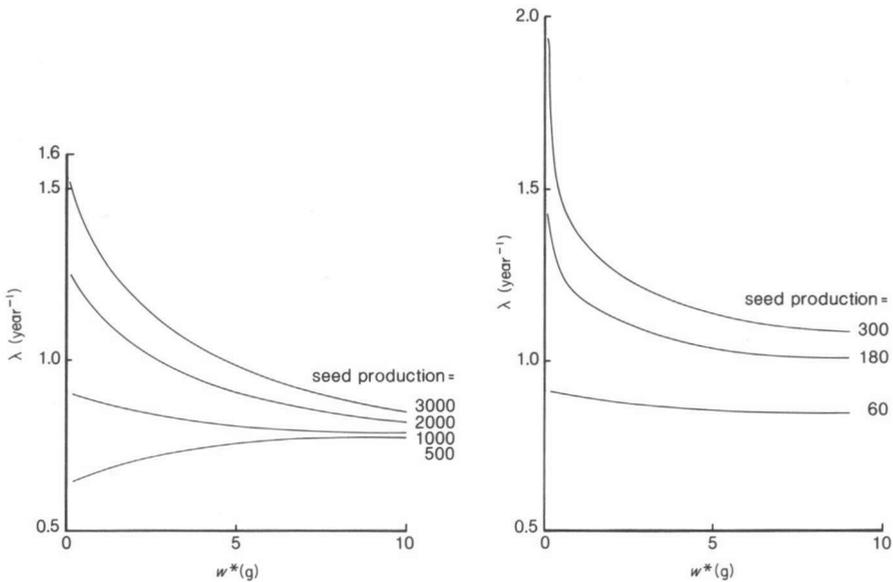


Figure 7. λ as a function of the minimum size for flowering, w^* , in *Cirsium vulgare* (a) and *Cynoglossum officinale* (b) with $E(\log(b)) = -5.93$ and $\text{Var}(\log(b)) = 1.63$ for *Cirsium* and $E(\log(b)) = -3.59$ and $\text{Var}(\log(b)) = 0.31$ for *Cynoglossum*. The per capita seed production is independent of weight, w , and was varied.

picture changes drastically: there will be selection for either flowering at very low or at very high values of w^* . In most cases plants should reproduce as early as possible, regardless of their size (Fig. 7). Additional simulations to Fig. 7 showed that if the seed bank is

Table 5. Flowering behaviour in relation to size at the census date (15 May 1985 for *Cirsium vulgare* and 1 November 1983 for *Cynoglossum officinale*). *n* = number of plants

Weight class (g)	<i>Cirsium vulgare</i>		<i>Cynoglossum officinale</i>			
	Flowering %	<i>n</i>	Flowering %	<i>n</i>	Flowering* %	<i>n</i>
0.0–0.5	6.8	44	2.2	135	5.5	280
0.5–1.0	21.9	41	40.0	10	32.0	106
1.0–2.0	57.5	33	75.0	4	63.6	77
2.0–3.0	62.5	24	†	†	77.1	35
3.0–4.0	70.0	20	100.0	2	77.8	9
4.0–8.0	83.3	18	†	†	100.0	3
> 8.0	100.0	‡	100.0	‡	100.0	‡

*Indirect measurements (see methods section).

†No data available.

‡Plants of this size were not found at the dunes but 100% flowering is inferred from experience with the cultivation of these species under nutrient-rich conditions.

eliminated from the model there exists a clear optimum for w^* between 0.03 and 0.15 g. Figures 6 and 7 suggest that in the field situation the benefits from delayed flowering come rather from an increased seed production than from the averaging of temporal variation in recruitment.

A comparison of model predictions and field data

Figure 5 shows that in the simulation run representing the average of the field data, plants of both species should not flower below a weight of 2–3 g at the time of year that flower induction may take place. For both species it is difficult to pinpoint w^* in the field. There exists a gradual increase in the probability of flowering with plant size, which indicates the influence of other factors, the existence of genetic variation in flowering behaviour and/or measurement error. We do not know the relative importance of these three factors. The size at which 50% of the plants flower is (for both species) between 1 and 2 g (Table 5). Additional information for *Cynoglossum* comes from two greenhouse experiments. In one experiment we found a clear dividing line between flowering and vegetative plants at 0.96 g dry weight (De Jong *et al.* 1986). In another experiment the minimum size for flowering was approximately 2 g (M. J. van Dijk *et al.* personal communication). Therefore, it seems that model predictions of an optimum value for w^* , of 2 g or more, are somewhat above the values observed in the field.

DISCUSSION

The adaptive value of a delay in flowering

The model demonstrates that lineages in which each individual has a size-requirement for flowering obtain the highest fitness in a large part of the parameter space that we investigated. The advantages of delayed flowering (higher seed production, more averaging of variation, less energy spent on the development of reproductive structures)

seem to compensate for the disadvantages (higher death risk during life, lower relative growth rate when large). A similar result was obtained from a simulation model of the population dynamics of *Oenothera glazioviana* on sand dunes in Japan (Kachi & Hirose 1985). In retrospect it can be said that the theoretical predictions of short generation times in early successional habitats, that originate from animal ecology (e.g. MacArthur & Wilson 1967), may be less valid for plants, because plants are more plastic in size and are not so constrained by maximum adult sizes as some groups of animals are. Therefore, as long as the relative growth rates of rosettes are independent of their size, there is no benefit in reproduction, in the splitting up into different particles, as long as these particles encounter the same constraints.

We found that when a delay in flowering does not lead to a higher seed production, a type with a very low value for w^* attains the highest fitness (Fig. 7). This result is consistent with earlier model results (Klinkhamer & De Jong 1983, Roerdink 1988) which showed that some delay in flowering (5–10%) is profitable. According to Table 4 these high flowering fractions would correspond with values for w^* which are below 0.1 g. Our assertion is that the optimal delay in flowering, due to averaging the variation in recruitment, is small compared to the optimal delay of flowering due to an increased seed production.

Error analysis

As our demographic study lasted only 4 years, and these data were used to estimate model parameters in simulations which ran over a larger number of years, it will be clear that considerable sampling error may have occurred. In addition, because the probability distribution of b is likely to be approximately log-normal, or at least shifted strongly to the left, this automatically means that the high values of b , which strongly determine its arithmetic mean, are likely to be missed in a small sample. In the first 3 years of our study the recruitment was poor (cohort 1981, 1982 and 1983 in Table 2) whereas the last year (cohort 1984) was more favourable for seedling establishment. There was a considerable drop in population density over the whole period. The data on rosette growth were only obtained from 1 May 1984 to 1 May 1985 for *Cirsium* and from 1 November 1985 to 1 November 1986 for *Cynoglossum*. Our impression from the vegetation development in the field and the rainfall data, is that these years were very favourable for vegetative growth. Consequently, we may have underestimated the average seedling survival and may have overestimated the average rosette growth. The expected result of adjusting for this bias is selection for earlier reproduction, i.e. for smaller values of w^* .

The demographic data that we used were obtained by averaging the data on approximately 100 local populations of each of the two species from the dunes of Meijndel. Because these populations were scattered over an area of over 600 ha, they certainly represented both the favourable and unfavourable habitats during the observation period. Although it is unclear on what scale to measure survival probabilities that are relevant to populations (interaction groups), it is also evident that the interaction sphere of these populations is limited to only a fraction of the total Meijndel area. On a 2 m × 2 m scale, 21% of the local populations of *Cynoglossum* and 73% of those of *Cirsium* had, during the study period, at least 1 year in which zero seedlings were established (De Jong & Klinkhamer 1988a). Consequently, the method of averaging data to estimate survival probabilities must have underestimated the amount of variation that a population has to cope with in its restricted habitat. Because optimal w^* was not very sensitive to an increase in $\text{Var}(\log(b))$ (Fig. 5), this argument does not disprove the model's

results. One should bear this in mind, however, with any modelling attempt that uses demographic data that represent averages over a number of different habitats or years.

*The discrepancy between predicted and observed optimal values for w^**

The predicted optimal values of w^* are, for both species, above what was observed in the field. In addition to the effects of the sampling error discussed above, there are at least three important features that are not incorporated in our model. First, density-dependence may take place and alter the direction of selection (Klinkhamer & De Jong 1988). Generally, however, the occurrence of density-dependence will lead to more conservative behaviour because early reproduction does not lead to the 'compounding of interest' in the way that it does in growing populations. To illustrate this point: in a model that took density dependence into account (by assuming that 'safe-sites' were necessary for recruitment and only one plant could establish in such a site), it was shown that the condition required for a delay in flowering to be favourable was that the relative gain in seed production should fully compensate for the increased death risk (De Jong *et al.* 1987a). One can now test this prediction by substituting the functions $h(x|v)$ and $c(v)$. The result of this exercise is that delayed flowering is profitable as long as $w < 1.77$ g in *Cirsium* and $w < 6.96$ g in *Cynoglossum*. In particular, the latter prediction of w^* is far above values observed in the field.

Second, we equated fitness to λ , a measure which combines seed production and generation time. Seed production is only one adaptation for cross-fertilizing plants. The other is to sire seeds on other plants. For several species, including *Cynoglossum* (Klinkhamer *et al.* 1989), it was found that pollinators respond differently to small and large plants (Geber 1985). They frequent the large plants more often and visit more flowers in succession on large plants. This may have the effect that a single flower on a large plant receives more visits than a similar flower on a small plant, in which case large plants may be more successful as pollen donors (Statton *et al.* 1986). On the other hand, self-pollination due to geitonogamy may prevail in large plants, which may be either positive or negative, depending on the degree of self-incompatibility and inbreeding depression. At this stage, without a specific model, it is not clear what the effects of size on the male component of fitness will be.

Third, one might want to add variability in reproductive effort ($f_2(x)$), which is now chosen to be constant. In *Cirsium*, in particular, seed production may sometimes fail due to insect parasites in the stem, which will both lower the mean value of $f_2(x)$ and increase its variance. The expected result of incorporating this into the model will be a depressive effect on λ , thus it will promote selection for larger optimal values for w^* (cf. Fig. 6).

Provided that density-dependence and variability in reproductive effort both lead to larger predicted values of optimum w^* , the departure of model predictions from field observations becomes more interesting. The question is why *Cirsium* and *Cynoglossum* do not lengthen their generation time even more! An interesting approach would be to examine whether genetic variation in w^* exists within populations, and whether the outcome of the model reflects a discrepancy between the genetic structure of the population and the environmental conditions prevailing in a certain period.

Concluding remarks

From the integration of results, several points became apparent that were not obvious to us at the start. A casual comparison of the annual rates of flowering of the two species shows large differences: *Cirsium* 40%, *Cynoglossum* 2–20%. There are several differences between the species which explain this. At the time that flowering is first induced, *Cirsium*

seedlings are approximately eight times heavier than *Cynoglossum* seedlings. The rapid growth of *Cirsium* seedlings is due to the fact that they grow on more nutrient-rich sites and that they have a higher maximal relative growth rate (De Jong & Klinkhamer 1988a; De Jong *et al.* 1987b). Rosettes are expected to have zero growth if they weigh 1.94 g in *Cirsium* whereas *Cynoglossum* rosettes may expect positive growth until they weigh 11.35 g. This is probably not due to the self-shading of leaves, but *Cirsium* rosettes, in particular, become more vulnerable to trampling or other mechanical damage when they become larger. In addition herbivores may prefer larger plants (Van Leeuwen 1983 for *Cirsium vulgare*).

In conclusion, it can be said that the *Cynoglossum* rosettes grow slowly and steadily whereas *Cirsium* rosettes grow faster initially but soon reach a point at which they gain no more weight (Fig. 3). At the time of flower induction, a random sample of *Cirsium* rosettes had, on average, a much higher weight than a similar sample from *Cynoglossum* (Table 5), which also partly explains the much higher rate of flowering in this species. It is remarkable (Table 5) that the two species behave so similarly with respect to the size-dependency of flowering.

ACKNOWLEDGEMENTS

This research was subsidized by the Netherlands Organization for Scientific Research (NWO). Diana Prins kindly supplied data on the rosette survival of *Cynoglossum officinale*. We thank Nikki Kachi for his comments. This is a publication of the 'Meijendel-comité', new series No. 97.

REFERENCES

- Bulmer, M. G. (1985): Selection for iteroparity in a variable environment. *Am. Nat.* **126**: 63–71.
- Cohen, D. (1966): Optimizing reproduction in a randomly varying environment. *J. Theoret. Biol.* **12**: 119–129.
- De Jong, T. J. & Klinkhamer, P. G. L. (1988a): Population ecology of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a coastal sand-dune area. *J. Ecol.* **76**: 366–382.
- & — (1988b): Seedling establishment of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a sand-dune area: the importance of water for differential survival and growth. *J. Ecol.* **76**: 393–402.
- & — (1988c): *Cynoglossum*. In: Halevy, A. H. (ed.): *Handbook of Flowering Plants* 6. CRC Press, Boca Raton.
- , — & Metz, J. A. J. (1987a): Selection for biennial life histories in plants. *Vegetatio* **70**: 149–156.
- , —, Nell, H. W. & Troelstra, S. R. (1987b): Growth and nutrient accumulation of the biennials *Cirsium vulgare* (Savi) Ten. and *Cynoglossum officinale* L. *Oikos* **48**: 62–72.
- , — & Prins, A. H. (1986): Flowering behaviour of the monocarpic perennial *Cynoglossum officinale* L. *New Phytol.* **103**: 219–229.
- De Kroon, H., Plaisier, A., Van Groenendael, J. & Caswell, H. (1986): Elasticity: the relative contribution of demographic parameters to the population growth rate. *Ecology* **67**: 1427–1431.
- Geber, M. A. (1985): The relationship of plant size to self-pollination in *Mertensia ciliata*. *Ecology* **66**: 762–772.
- Greulach, V. A. (1973): *Plant Function and Structure*. MacMillan, New York.
- Gross K. L. (1981): Predictions of fate from rosette size in four 'biennial' plant species: *Verbascum thapsus*, *Oenothera biennis*, *Daucus carota*, and *Tragopogon dubius*. *Oecologia (Berlin)* **48**: 209–213.
- Kachi, N. & Hirose, T. (1985): Population dynamics of *Oenothera glazioviana* in a sand-dune system with special reference to the adaptive significance of size dependent reproduction. *J. Ecol.* **73**: 887–901.
- Klinkhamer, P. G. L. & De Jong, T. J. (1983): Is it profitable for biennials to live longer than two years? *Ecol. Modell.* **20**: 223–232.
- & — (1987): Plant size and seed production in the monocarpic perennial *Cynoglossum officinale* L. *New Phytol.* **106**: 773–783.
- & — (1988a): The importance of small-scale disturbance for seedling establishment in *Cirsium*

- vulgare* and *Cynoglossum officinale*. *J. Ecol.* **76**: 383–392.
- & — (1988b): *Cirsium*. In: Halevy, A. H. (ed.): *Handbook of Flowering Plants* 6. CRC Press, Boca Raton.
- & — (1989): A deterministic model to study the importance of density-dependence for regulation and the outcome of intra-specific competition in populations of sparse plants. *Acta Bot. Neerl.* **38**: 57–65.
- , — & De Bruyn, G. J. (1989): Plant size and pollinator attraction in *Cynoglossum officinale*. *Oikos*, (in press).
- , — & Meelis, E. (1987a): Delay of flowering in the 'biennial' *Cirsium vulgare*: size-effects and devernialization. *Oikos* **49**: 303–308.
- , — & — (1987b): Life-history variation and the control of flowering in short-lived monocarps. *Oikos* **49**: 309–314.
- , —, Metz, J. A. J. & Val, J. (1987c): Life history tactics of annual organisms: the joint effects of dispersal and delayed germination. *Theoret. Pop. Biol.* **32**: 127–156.
- , — & van der Meijden, E. (1988): Production, dispersal and predation of seeds in the biennial *Cirsium vulgare*. *J. Ecol.* **76**: 403–414.
- Kuno, E. (1981): Dispersal and the persistence of populations in unstable habitats: a theoretical note. *Oecologia (Berlin)* **49**: 123–126.
- Lacey, E. P. (1986): The genetic and environmental control of reproductive timing in a short-lived monocarp *Daucus carota*. *J. Ecol.* **74**: 73–86.
- (1988): Latitudinal variation in reproductive timing of a short-lived monocarp, *Daucus carota* (Apiaceae). *Ecology* **69**: 220–232.
- Lang, A. (1965): Physiology of flower initiation. In: Rühländ, W. H. (ed.): *Encyclopedia of Plant Physiology* 15. Springer-Verlag, Berlin.
- Lhotská, M. (1982): Beitrag zur Keimungsökologie und Diasporologie der Tjechoslowakischen Vertreter der Gattung *Cynoglossum*. *Folia Geobot. Phytotaxon, Praha* **17**: 269–293.
- MacArthur, R. H. & Wilson, E. O. (1967): *The Theory of Island Biogeography*. Princeton University Press, Princeton NJ.
- Metz, J. A. J., De Jong, T. J. & Klinkhamer, P. G. L. (1983): What are the advantages of dispersing: a paper by Kuno explained and extended. *Oecologia (Berlin)* **57**: 166–169.
- Reinartz, J. A. (1984): Life history variation of the common mullein (*Verbascum thapsus*). I. Latitudinal differences in population dynamics and timing of reproduction. *J. Ecol.* **72**: 897–912.
- Roerdink, J. B. T. M. (1988): The biennial life strategy in a random environment. *J. Math. Biol.* **26**: 199–215.
- Slob, W. (1987): *Strategies in applying statistics in ecological research*. Ph.D. thesis, Free University of Amsterdam.
- Statton, M. L., Snow, A. A. & Handel, S. N. (1986): Floral evolution: attractiveness to pollinators increases male fitness. *Science* **232**: 1625–1627.
- Stoer, J. & Bulirsch, R. (1979): *Introduction to Numerical Analysis*. Springer-Verlag, Berlin.
- Taylor, O. R. & Inouye, D. W. (1985): Synchrony and periodicity of flowering in *Frasera speciosa* (Gentianaceae). *Ecology* **66**: 521–527.
- Van Breemen, A. M. M. (1984): Comparative germination ecology of three short-lived monocarpic Boraginaceae. *Acta Bot. Neerl.* **33**: 283–305.
- & van Leeuwen, B. H. (1982): The seed bank of three short-lived monocarpic Boraginaceae. *Acta Bot. Neerl.* **32**: 245–246.
- Van Leeuwen, B. H. (1983): The consequences of predation in the population biology of the monocarpic species *Cirsium palustre* and *Cirsium vulgare*. *Oecologia (Berlin)* **58**: 178–187.
- Van der Meijden, E. & van der Waals-Kooi, R. E. (1979): The population ecology of *Senecio jacobaea* in a sand dune system. I. Reproductive strategy and the biennial habit. *J. Ecol.* **67**: 131–153.
- Werner, P. A. (1975): Predictions of fate from rosette size in teasel (*Dipsacus fullonum* L.). *Oecologia (Berlin)* **20**: 197–201.