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THRESHOLD SIZE FOR FLOWERING IN DIFFERENT HABITATS: EFFECTS OF SIZE-DEPENDENT GROWTH AND SURVIVAL

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Abstract. For organisms with indeterminate growth, life history theory predicts that in environments where organisms experience high survival rates or gain fecundity with age or size, natural selection favors delayed maturity. In semelparous perennial plants the onset of reproduction is regulated by a threshold size for flowering. We tested this prediction by comparing sand dune populations of the facultative biennial herb *Cynoglossum officinale*. We collected data on flowering probability, survival, and growth rate in relation to plant size in two habitat types, open areas and poplar thickets, in Meijendel, The Netherlands, and in Holkham, England. Survival of established rosettes was highest in Holkham and lowest in open areas in Meijendel. Relative growth rates in Holkham were about three times as high as those in Meijendel. These findings agreed with the differences in threshold sizes found among the sites: the Holkham field population harbored higher threshold sizes than the Meijendel sites. We used the field data to compare optimal threshold sizes for flowering predicted by three existing models. All three models gave the same rank order for threshold sizes as found in the field: Meijendel open < Meijendel poplar thicket < Holkham. One model, which maximized population growth rate λ , predicted optimal threshold sizes that agreed very well with threshold sizes found in the field. The predictions of the two other models, both maximizing R_0 , were consistently lower than the threshold sizes observed in Meijendel, while their predictions for Holkham were too high.

Key words: *Cynoglossum officinale* life history; facultative biennial; genetic variation; growth rate; hound's-tongue; optimization models; plant size and fitness; semelparous; survival; threshold size for flowering.

INTRODUCTION

The onset of reproduction is a key parameter in the life history of most organisms, and age and size at maturity are life history traits with a high impact on fitness (Stearns 1992). The question of when an organism should start reproducing in order to maximize its fitness returns has been tackled with several optimality models (e.g., Roff 1981, 1986, Stearns and Koella 1986, Kozłowski and Wiegert 1987, Berrigan and Koella 1994). The optimal onset of maturity lies close to the point where the product of $l(x)$ and $m(x)$, survival and fecundity dependent on age or size, reaches its maximum (Roff 1992, Charlesworth 1994). Survival from birth to age x , $l(x)$, is a monotonically declining function of x . A high age-dependent survival rate usually selects for late maturity (Schaffer and Gadgil 1975, Reznick et al. 1990). Fecundity $m(x)$ generally increases with size in plants and ectothermic animals (references in Roff 1992:126), and growth rate is of major importance to life history evolution in these

organisms, most of which grow throughout their lives (Hutchings 1993). In iteroparous species the optimal age or size at maturity is determined by the balance between the benefits of starting to reproduce early and the costs this may have for future survival and reproduction. Semelparous species do not face these trade-offs, and this makes the analysis of the effects of survival and growth on age or size at maturity more straightforward. Their onset of reproduction should be at the moment when the expected returns are maximal: the number of offspring that can be produced at that age or size discounted by the probability of not surviving to that age or size (Kozłowski 1992).

In this paper we focus on the reproductive timing in a plant species with a facultative biennial life history. Facultative biennials are semelparous plants which live one or more years as a vegetative rosette before flowering. In these plants, size rather than age triggers the onset of reproduction (Lacey 1986a); within populations the flowering probability increases with plant size (Werner 1975, Baskin and Baskin 1979, Gross 1981, Lee and Hamrick 1983, Augspurger 1985). Relative growth rate just before flower induction has also been shown to influence the probability of flowering: slow-growing plants are more likely to flower (Young 1985,

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Lacey 1986b). In temperate—seasonal—environments many facultative biennial species need a period of low temperatures—vernalization—and a long-day photoperiod before they are able to flower. The reaction to these stimuli depends on the size of the plant; as long as a certain minimum size has not been surpassed the plant will remain vegetative. For a few facultative biennial species we know at what moment the plant's status for the next year is set (Hiller and Kelly 1979, de Jong et al. 1986, Klinkhamer et al. 1987, Prins et al. 1990, Klinkhamer et al. 1991). This knowledge is important, because it is the size of the plant at this moment that determines whether or not a plant will flower. A size threshold that cues the onset of reproduction has also been found in long-lived semelparous plants (Young 1984), and in other organisms, including mammals (e.g., Skogland 1989), fish (Roff 1991), insects (Woodring 1983), and *Daphnia* (Ebert 1994).

In the past some authors referred to *the* minimum size for flowering, suggesting that this size was the same for all the plants in a population. However, most studies showed a large overlap in plant size of flowering and vegetative individuals. Apparently, different plants have different minimum sizes. Here we use the term “threshold size” for the size an individual plant has to surpass to be able to flower (Wesselingh et al. 1993). This threshold size is equal to or above the physiological minimum size, the minimum mass needed to produce one seed. Threshold size is a complicated character, as it cannot be measured on a single plant. Measuring plant size at the moment that next year's status is set will yield either a minimum value, if the plant remains vegetative, or a maximum value, if the plant flowers. Only with clonal propagation can the threshold size of a genotype be determined (Wesselingh and Klinkhamer 1996). Threshold size for flowering should not be confused with “size at reproduction” or “flowering size.” These refer to the actual size of a plant, not to an internal setting.

Studies on reproductive timing in facultative biennials have shown that extensive variation exists in the age and size at the onset of flowering, both within and among populations (Inouye and Taylor 1980, Reinartz 1984, Lacey 1986b, 1988, Wesselingh et al. 1993). Three models have been developed that address specifically the optimization of threshold size for flowering (Kachi and Hirose 1985, de Jong et al. 1987, 1989). These models showed that in general the optimum threshold size is the result of a balance between size-dependent growth, which determines the increase in seed production, and size-dependent survival.

In this paper we will use field and laboratory measurements on threshold size for flowering, survival, and growth rate collected for the facultative biennial herb *Cynoglossum officinale* in different habitats to (1) test the predictions from general life history theory that size at maturity should increase with increasing survival rate and/or size-dependent growth rate, and (2)

compare the quantitative predictions from the three existing models by using the field data collected in different habitats.

Study species

Cynoglossum officinale L. (Boraginaceae), hound's-tongue, is a facultative biennial herb of open, disturbed sites such as sand dunes and rangelands (de Jong et al. 1990). It is a species of open vegetation on calcareous soils. Germination can only take place after a period of moist conditions with low temperatures to break seed dormancy, and soil disturbance enhances germination (Klinkhamer and de Jong 1988). The vegetative plants form a rosette; the leaves die back at the onset of winter, and the tap root with the meristem overwinters. After winter, the plant either forms a flowering stem, or starts to make new rosette leaves. It is self-compatible, and pollinated by bumble bees and honey bees.

We have studied this species for >10 yr in Meijendel, a sand dune area near The Hague, the Netherlands. Plants show a straightforward reaction to flowering stimuli: if the threshold size has been exceeded at the onset of winter (November) flower primordia are clearly visible during the winter period, when they develop into a bolting stem (de Jong et al. 1986). Plant age, plant nitrogen concentration, and light intensity before the cold period do not affect the probability of flowering at a given plant size. In Meijendel, the plants start bolting in April, and the first flowers open in May. No effects of conditions after winter on flowering probability have been detected (de Jong et al. 1986). This renders this species a good subject for a study on the threshold size for flowering, because the moment at which the flowering “decision” is made, based upon the present size, is known rather precisely.

We studied two populations of *Cynoglossum officinale*, at Meijendel in the Netherlands and Holkham in England. In a previously conducted experiment, plants from Holkham had much higher threshold sizes than Meijendel plants (Wesselingh et al. 1993). Within the Meijendel population we made a further distinction between two habitat types, open areas and poplar thickets, in which *Cynoglossum officinale* has different population dynamics (de Jong and Klinkhamer 1988a).

METHODS

Meijendel field sites

Description.—Meijendel is a sand dune area in the Netherlands along the North Sea coast (52°05' N, 4°06' E). The area measures 1800 ha, and is ≈3.5 km wide. The sand is highly calcareous, and *C. officinale* is abundant. In August 1990, six sites were chosen, three in poplar thickets and three in open, exposed terrain. The smallest distance between two observation sites was 400 m. A description of geomorphology, soil, and vegetation in Meijendel is given by van der Meulen and van der Maarel (1993).

The open sites are characterized by a high percentage of bare sand, sometimes covered by lichens and mosses. Plants in open terrain are likely to suffer from periods of drought. *C. officinale* plants here usually have small, short-stalked leaves. The density of *C. officinale* is generally low, on average <1 rosette/m².

The poplar thickets consist mainly of *Populus nigra*, with some additional trees and scrubs. The forest floor is sparsely vegetated, the main species being *Urtica dioica*, and is covered with leaf litter. The plants in the poplar thickets have large leaves with long petioles. *C. officinale* densities are locally high, up to 20 plants/m² (average \approx 5 plants/m²). The data from the three sites in each habitat type were pooled to form one data set for each habitat, referred to as "open" and "poplar thicket."

Measurements.—The Meijendel field data for this paper (1992–1993) were collected in a field study that began in November 1990. Each year the sites were visited in spring (April–May) and autumn (November–December). We established 5 × 5 m plots at each of the six sites, the number of plots depending on the local density of the *C. officinale* plants. The plants were marked individually with plastic labels. The labels were partly dug in and attached to the plant underground with a thin wire loop tied loosely around the upper part of the root. In this way the death of a plant could be assessed with certainty. From spring 1991 onwards we recorded the status of each plant (vegetative, flowering, dead) and measured its root crown diameter to the nearest 0.1 mm with calipers. Extra plants, chosen at random, were marked to compensate for losses due to mortality and flowering. In autumn 1992 there were 160 rosettes in the open sites and 224 rosettes in the poplar thickets. In April 1993, all seedlings found in the plots were marked, 141 seedlings in the open areas and 219 in the poplar thickets. We recorded seedling survival in November 1993.

Plants directly outside the plots were harvested in autumn and spring to obtain regressions of plant dry mass (after removal of dead aboveground parts) on root crown diameter. The regression equations were used to estimate dry mass for the autumn and spring visits, respectively.

Holkham field site

Description.—Holkham National Nature Reserve is situated on the North Sea coast of Norfolk (52°58' N, 0°48' E). The ecology of *Cynoglossum officinale* in Holkham was studied in 1973–1976 by Boorman and Fuller (1984). The strip of sand dune area within the reserve measures 50 ha, and its maximum width is 500 m. The terrain is very open; most of the area is either bare sand or covered with mosses, lichens, and small herbs. The vegetation resembles that in the open areas in Meijendel. Rabbits are abundant, and their grazing keeps the vegetation short and open. The temperature and precipitation in Holkham are comparable to those

in Meijendel. Mean monthly temperatures are similar for both sites in May–October, but almost 1°C higher in Holkham in November–April (7.3°, 5.1°, 3.7°, 4.0°, 5.9°, and 8.4°C in Holkham vs. 6.7°, 4.0°, 2.7°, 2.8°, 5.0°, and 7.7°C in Meijendel; 30-yr monthly averages of hourly temperature measurements, KNMI 1992). This difference is caused by the buffering effect of the North Sea against cold northerly and easterly winds.

Measurements.—In May 1992, the root crown diameters of 250 plants were measured and the plant's status (vegetative or flowering) noted. In November 1992 we marked 350 plants in the Holkham population. The measurements were done at five sites, all within 700 m of each other. In April 1993 we recorded root crown diameter and status of the marked plants, and marked new plants at random to replace the dead and flowering ones. A sixth site was then added. We marked 211 seedlings and recorded their survival in November 1993. In November 1993 all plants were measured again. Plants were harvested in autumn and spring to obtain regressions of plant dry mass on root crown diameter.

Laboratory experiments: relationship between plant size and flowering probability

Meijendel vs. Holkham.—A laboratory comparison between Meijendel and Holkham has already been published (Wesselingh et al. 1993). Since we did not observe 100% flowering in the Holkham sample in this first experiment, we did a second growth room comparison in 1993, in which we grew the plants to larger sizes. Seeds were collected from both populations in 1992, on four plants in Holkham and eight plants in Meijendel, four in open sites and four in poplar thickets. The seeds were germinated in Petri dishes on moist filter paper at 20°C/10°C with 16 h light from a fluorescent tube. The seedlings were planted in containers (diameter 12 cm, volume 1.5 L) in dune sand. Nutrients were provided by the addition of 4.5 g Osmocote Plus (slow release of nutrients lasting 3–4 mo, composition 15N + 11P + 13K + 2MgO; Sierra Chemical Company, Milpitas, California). The containers were placed in a growth room with 18 h light, provided by Philips HPI-T 400 W high-pressure mercury lamps, at 20°C (night: 16°C) and 70% relative humidity. We obtained plants of different sizes by varying the length of the growing period before they were transferred to a cold room for an artificial winter period. Plant age at the onset of "winter" thus ranged from 66 to 105 d. On each plant we measured the root crown diameter to the nearest 0.1 mm and the length of the longest leaf in millimeters and counted the number of leaves (both living and dead). We fitted a multiple regression of plant dry mass on nondestructive measurements ($R = 0.942$), with data from an extra 15 plants that were harvested and dried to determine dry mass.

The artificial winter consisted of 10 wk in a 5°C room, with 8 h light. After this period the plants were

brought back to warmer conditions, first to 18°C/12°C with 14 h light for a week, and then back to the initial regime of 20°C/16°C at 18 h light. The final sample sizes were 34 for Meijendel and 40 for Holkham. We recorded whether or not plants flowered during a 3-mo period after the return to the growth room.

Meijendel open vs. poplar thicket.—In an artificial selection experiment on threshold size (Wesselingh and de Jong 1995) we used seeds from both habitat types in Meijendel. We did not distinguish between the two habitat types then, because it was not relevant for the question being asked in that particular paper. We will show the results of the comparison between the two habitat types here. The method used (Wesselingh and de Jong 1995) closely resembles that in the Holkham-Meijendel comparison described above; only the light conditions were slightly different (fluorescent tubes instead of high-pressure lamps). One hundred plants were used for each habitat.

Data analysis

Relationship between plant size and flowering probability.—To describe the relationship between plant size and flowering probability and to test for differences between groups we used a logistic equation (Klinkhamer et al. 1987, 1991)

$$p = \frac{1}{1 + e^{\mu + \alpha x}} \quad (1)$$

where x is plant size just before the cold treatment (estimated dry mass in grams), and p is the flowering probability. The parameters μ and α are estimated by maximization of the likelihood function $L(\mu, \alpha)$, yielding an L_{\max} (Klinkhamer et al. 1987). Differences among fitted curves for k groups can be tested by calculating the $\ln(L_{\max})$ for both the pooled data and the groups separately, with the test statistic Λ , which compares the goodness-of-fit for the pooled data with that of the separate groups. Λ follows approximately a χ^2 distribution with $2k - 2$ degrees of freedom. When multiple comparisons between curves were made, the resulting P values were corrected with a sequential Bonferroni test (Rice 1989). The method is described in detail by Klinkhamer et al. (1987, 1991) and Wesselingh et al. (1993).

Relationship between plant size and survival.—In this study we only measured survival after the seedling stage, from the first autumn onwards ("adult" survival). Survival increases with size, and this relationship is often hyperbolic (Kachi and Hirose 1985, de Jong et al. 1989). A hyperbolic function, asymptotic to a/b , was fitted to each data set on plant size x and subsequent survival c

$$c(x) = \frac{ax}{1 + bx} \quad (a, b > 0; b > a). \quad (2)$$

We distinguished annual survival (autumn 1992–autumn 1993), winter survival (autumn 1992–spring

1993), and summer survival (spring 1993–autumn 1993). Data sets consisted of vegetative plants only, except for winter survival. Here plants that flowered the next spring were included. The parameter values for each function were estimated by maximum-likelihood techniques, and we tested whether the use of the hyperbola yielded a better fit than a constant, size-independent survival, determined by the fraction of plants surviving in each data set.

Relationship between plant size and growth.—We calculated growth rates for the whole year (autumn 1992–autumn 1993) and for the winter period (autumn 1992–spring 1993). We plotted \ln -transformed dry mass (x) at the end of an interval against $\ln(x)$ at the start of the interval, and calculated a linear regression: $\ln(x_{t+1}) = f + g \ln(x_t)$. This choice is based on the assumption that plants have sigmoid growth through time (Kachi and Hirose 1985, de Jong et al. 1989). In this case the relative growth rate for an interval, defined as $\ln(x_{t+1}) - \ln(x_t)$, decreases linearly with \ln -transformed plant size, with slope $g - 1$. Relative growth rate as a function of initial dry mass thus becomes $f + (g - 1)\ln(x)$, and the size of a plant after a period of growth is given by $x_{t+1} = e^{f+g\ln(x)}$. For the winter growth interval we calculated the regression for vegetative and flowering plants separately. Differences in annual growth rates among sites were tested by analysis of covariance (STSC 1991, Sokal and Rohlf 1995). We used the variance D of the residuals of each linear regression as a relative measure of the variability in growth rate (cf. Kachi and Hirose 1985, de Jong et al. 1989).

Optimization models

All three models use most of the basic relations between plant size and survival and plant size and growth rate illustrated in Fig. 1. The parameter values for these functions (Table 3) were derived from the field data collected in 1992–1993 at all three sites. For the Meijendel sites we performed calculations for two additional intervals: 1991–1992 and 1993–1994 (parameter values not shown).

Model A or R_0 -model (Kachi and Hirose 1985).—This model was originally developed for *Oenothera glazioviana*, also a sand dune biennial. The model was adapted to fit the life history of *Cynoglossum officinale*. A run of the model begins with 10 000 established seedlings in November, with sizes drawn randomly from a normal distribution of \ln -transformed dry mass. The size of each rosette is compared with the threshold size chosen for this particular run, and plants with sizes beyond the threshold size will flower in the next spring. The probability of survival until next spring is calculated from plant size in November, and compared with a random number between 0 and 1; plants survive if the survival probability is higher than the random number. Survivors grow according to the winter growth function, and because they surpassed the threshold size,

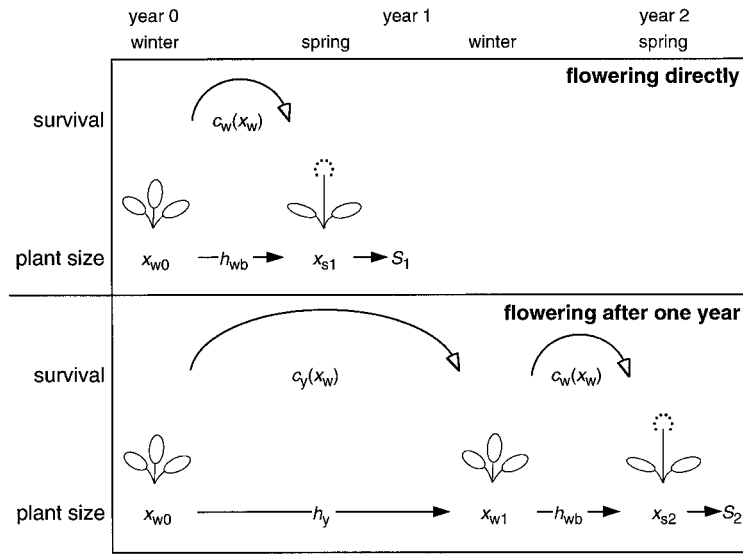


FIG. 1. Schematic representation of the steps in life history of the facultative biennial *Cynoglossum officinale*. Top diagram shows a plant that flowers in the next spring; bottom diagram shows one that delays flowering by 1 yr. For each step the corresponding plant size x , survival function c , and growth function h are indicated. The comparison between the two strategies (immediate flowering or 1-yr delay) is central in model B, but the functions depicted are also used in the other two optimization models.

they produce a number of seeds depending on their size in spring, and die after reproduction. Seeds produced do not enter the population. Nonflowering plants have to survive until the next November, and will gain or lose mass determined by the annual growth function. The procedure is repeated until the last plant has died. The total number of seeds produced can then be multiplied by the probability of germination and establishment, to determine the expected lifetime offspring production R_0 . In our analysis this step is not necessary, since we are only interested in the relative offspring productions of the threshold sizes simulated. The model is run for a range of threshold sizes, and the fitness curve can be drawn. The results of individual runs of this model were quite variable. To reduce this stochastic effect on the fitness curve, we did repeated runs to ensure that for each threshold size at least 1000 plants survived to produce seeds, and calculated the average seed production per plant over all runs for each threshold size. We standardized the results by expressing all values as a percentage of the highest seed production value in a data set, which was set to 100%.

Model B or safe-site model (de Jong et al. 1987).—The second model (de Jong et al. 1987) is a deterministic safe-site model. It also uses R_0 as the fitness criterion. It investigates whether at a given size delay of flowering with one year yields more offspring than immediate reproduction. In this model it is favorable to delay flowering for another year as long as the increase in seed production by growth compensates for the risk of death during that year, or, in mathematical terms:

$$\frac{B_{t+1}}{B_t} > \frac{1}{C_t} \tag{3}$$

where B is seed production and C the probability of survival to the next year, both as a function of plant size. The gain in seed production, the ratio B_{t+1}/B_t , decreases with size, as the relative growth rate of the plant slows down toward larger sizes. Survival usually increases with size, until a maximum is reached. The optimum threshold size under the given conditions lies where the two functions that describe the fecundity ratio and the inverse survival probability intersect (de Jong et al. 1987).

We elaborated Inequality 3 further to fit the life history of *Cynoglossum officinale* by including the size-dependent functions for survival and growth from the moment the state is fixed (early winter) to the moment of flowering (spring). Inequality 3 thus becomes

$$\frac{c_w(x_{w1}) \cdot S(x_{s2})}{c_w(x_{w0}) \cdot S(x_{s1})} > \frac{1}{c_y(x_{w0})} \tag{4}$$

x is plant size (dry mass in grams), with subscripts for the time of year: x_w is plant size in winter, x_s plant size in spring. The number in the subscript refers to the calendar year following the initial winter w_0 . c_w and c_y describe plant survival as a function of x , over winter and for a whole year from one winter to the next, respectively. $S(x_s)$ gives seed production as a function of spring size. We rearranged the inequality so that all survival functions appear on the right-hand side of the sign

$$\frac{S(h_{wb}(h_y(x_{w0})))}{S(h_{wb}(x_{w0}))} > \frac{c_w(x_{w0})}{c_y(x_{w0}) \cdot c_w(h_y(x_{w0}))} \tag{5}$$

On the left-hand side, plant size in spring is calculated from the size in the previous winter x_w with the growth

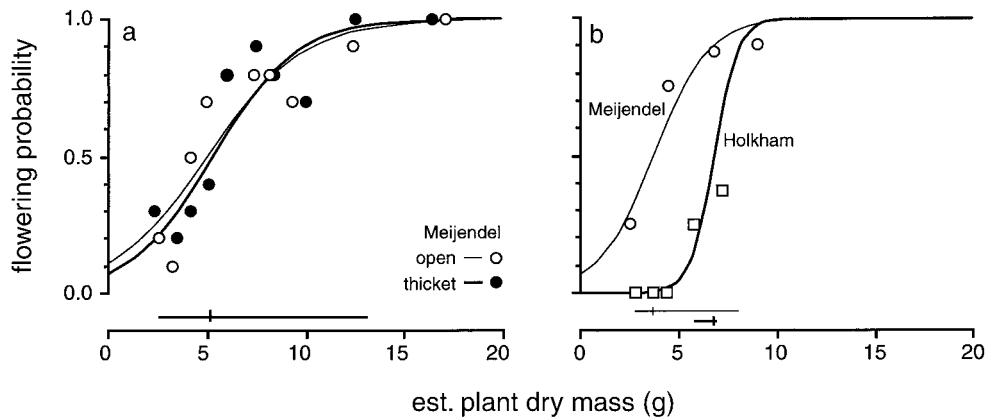


FIG. 2. Comparisons of threshold sizes for flowering in *Cynoglossum officinale* under laboratory conditions for (a) plants grown from seeds from open sites and poplar thickets within Meijendel, and (b) plants grown from seeds from Meijendel (open and poplar thicket mixed) and Holkham. The lines are the fitted logistic curves. In order to visualize the data set on which a curve is based, we calculated mean estimated dry mass and fraction flowering in subsamples of (a) 10 or (b) 8 plants, which individually score either 1 (flowering) or 0 (vegetative). Each symbol (\circ or \bullet Meijendel, \square Holkham) represents such a subsample. Total sample sizes are (a) 100 for both open and poplar thicket, (b) 34 for Meijendel and 40 for Holkham. The lines at the bottom of the graph depict the range of threshold sizes found at each site, by connecting the estimated size of the smallest flowering plant with the size of the largest nonflowering plant. The crossbar on each line is the median threshold size, the estimated dry mass at which 50% of the plants flower. Corresponding curves and lines share the same line thickness.

function h_{wb} for plants that will bolt and flower in the next spring. The annual growth function h_y calculates x_{w1} from x_{w0} . We plotted both ratios in Inequality 5 against x_{w0} . The size at which the two curves intersect is the size at which the strategy should switch from “delay” to “no delay”: below this size a plant should delay flowering, above it it should flower in the following spring.

To obtain confidence intervals around both curves, we introduced the variability in the growth functions h that is determined by D , the variance of the residuals of the regression line (see *Data analysis: Relationship between plant size and growth*). We calculated an upper limit to each ratio curve by combining the different growth functions with modified intercepts f ($f + D$ or $f - D$) in such a way that the ratio became maximal, and in the same way we obtained a lower limit. We could then calculate the sizes at which the lower boundary of one curve intersected the upper boundary of the second, and vice versa. This yielded an interval around the switch point, which can be considered as a “confidence region.”

Model C or r-model (de Jong et al. 1989).—This model simulates the dynamics of a population divided into size classes. The number of plants in each size class is calculated from the probabilities of transition from the other size classes, by vegetative growth, multiplied by the survival probability and the number of plants in each previous size class. Plant numbers in size classes beyond the threshold size are converted to seed numbers that fill the (transient) seed bank. From this seed bank new seedlings are recruited into the size classes through a lognormal distribution of established

seedling sizes. The original model also incorporated stochastic variation in seedling recruitment, but since the results with and without this stochastic component were not fundamentally different, we left it out in the version of the model used here. Another difference with the original model is that we truncated growth rates at two standard deviations from the mean, to exclude unrealistically high and low growth rates. This is in accord with the procedure for calculating growth rates in model A. The model starts off with 100 000 seeds, that grow to become established seedlings in the first simulation year. In the second year, the first plants reproduce. Plant and seed numbers are normalized after each simulation round by expressing them as a fraction of the total number. This ensures that plant numbers do not grow infinitesimally small or large. It takes about 50 yr before the population reaches a stable size distribution, and then the annual population growth rate λ , calculated as the ratio of the current population size divided by the size in the previous year, becomes constant. For each threshold size the simulation is run for 150 yr, and then λ ($=e^r$, with r the intrinsic rate of increase) is calculated. The λ 's within a data set are then re-scaled with the highest value set to 100%.

RESULTS

Plant size and flowering probability

Meijendel open and poplar thicket.—For plants grown in the laboratory, the relationships between plant size and flowering probability for the two habitat types within Meijendel were not statistically different ($\Lambda = 0.2443$, $P = 0.8850$; Fig. 2a). In the natural habitat,

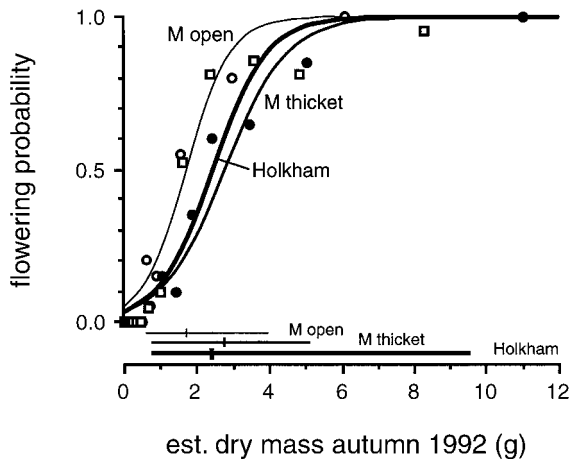


FIG. 3. The relationship between plant size and flowering probability in spring from size measurements in autumn for the three sites. The lines are the logistic curves for Meijndel open (\circ), Meijndel poplar thicket (\bullet), and Holkham (\square) in increasing thickness. The circles and squares each indicate the mean estimated dry mass and the fraction flowering in a subsample of plants (sample size between 20 and 30) in each data set sorted by increasing size. The lines at the bottom of the graph, with the same thickness as the corresponding curve, depict the range of threshold sizes found at each site, by connecting the size of the smallest flowering plant with the size of the largest nonflowering plant. The crossbar on each line is the median threshold size, the dry mass at which 50% of the plants flower. Sample sizes are: Meijndel open, $n = 115$; Meijndel poplar thicket, $n = 189$; Holkham, $n = 315$. Meijndel open differs significantly from Meijndel poplar thicket and Holkham. The largest (flowering) plant measured in each population in autumn 1992 had an estimated dry mass of 8.94 g (Meijndel open), 20.46 g (Meijndel poplar thicket), and 65.45 g (Holkham).

however, the curves differed significantly between the open sites and the poplar thickets ($\Lambda = 13.386$, $P = 0.0036$; Fig. 3). The range of threshold sizes in the wild was shifted toward lower dry mass for the open sites. The fraction flowering in the poplar thicket populations increased more gradually with plant size, and large, nonflowering plants were found, up to 5.10 g estimated dry mass. At both sites the smallest flowering plant had a dry mass < 1 g (0.62 g in the open sites, 0.80 g in the poplar thickets), while the smallest flowering plants in the growth room experiments weighed > 2.5 g (Fig. 2a; 2.6 g; Fig. 2b; 2.8 g).

Meijndel and Holkham.—The laboratory comparison between Holkham and Meijndel showed a highly significant difference in threshold sizes ($\Lambda = 25.0392$, $P < 0.0001$; Fig. 2b), with much higher threshold sizes in Holkham. This result is in concordance with the previous comparison of threshold sizes presented by Wesselingh et al. (1993). In the comparison of relationships between plant size in autumn 1992 and flowering probability in spring 1993 in the field, only the open site populations differed significantly from the plants in Holkham ($\Lambda = 8.153$, $P = 0.0340$; Holkham-Meijndel poplar thicket: $\Lambda = 1.426$, $P = 0.4902$; Fig.

3). Nevertheless, the largest nonflowering plants were found at the Holkham site, which had the widest threshold size range both in spring and autumn. The largest nonflowering plant in the autumn measurements in Holkham was 9.54 g, which was almost twice as heavy as the largest nonflowering plant in the poplar thickets in Meijndel. The size of the smallest flowering plant in Holkham was similar to that in Meijndel: 0.86 g.

Field population characteristics

Rosette survival.—Of nine hyperbolas fitted, only two gave a significantly better fit than a size-independent survival rate, estimated as the fraction of plants surviving in each data set, regardless of size (Table 1). Summer survival was significantly size dependent in both open habitats, Meijndel open and Holkham. In all three measurement intervals Holkham had the highest survival rate, with survival fractions ranging from 0.93 to 0.96. Of all plants marked in Holkham that remained vegetative in 1993, only 6.7% died before autumn 1993. The open sites in Meijndel had the lowest annual survival rate (46.1%), and the poplar thicket populations were intermediate (71.5%). These differences were mainly caused by differences in (size-independent) winter survival, which showed the same ranking of sites. Summer survival was generally high, with asymptote values > 0.90 for all three sites.

Rosette growth.—All nine regressions of dry mass (ln-transformed) at the end of an interval on initial dry mass had slopes below unity, and thus a negative slope for the relationship between relative growth rate and initial dry mass (Fig. 4). This means that growth slowed down as plants became larger. Six of these slopes were significantly different from unity. The annual rosette growth rate in Holkham was considerably higher than the growth rates at both Meijndel sites. An analysis of covariance on dry mass in autumn 1993 with dry mass in autumn 1992 as the covariate demonstrated that this difference was highly significant (covariate: $F_{1,346} = 321.73$, $P < 0.0001$, main effect of site: $F_{2,346} = 31.655$, $P < 0.0001$). Multiple range tests revealed no significant difference between the two habitat types in Meijndel, but rosettes in Holkham grew about three times as much annually as the plants in Meijndel. This large difference already started to develop between November and April. The smaller rosettes in Holkham, particularly, managed to gain considerable mass in early spring. Furthermore, at the end of their first growing season seedlings in Holkham attained a dry mass three times as high, on average, as in Meijndel (Wesselingh 1995). The winter growth rates for Meijndel plants were almost constant over the size range, and not very high. Winter growth in the poplar thickets in Meijndel was significantly lower for plants that remained vegetative than for plants that flowered in the next spring (analysis of covariance on dry mass in spring with dry mass in autumn as covariate; main effect of status for Meijndel poplar thicket: $P = 0.0001$, Meijndel open:

TABLE 1. Survival of *Cynoglossum officinale* at the three field sites over three intervals: a whole year (autumn–autumn), winter, and summer. The fraction of plants surviving the interval, the parameters *a* and *b* of the fitted hyperbola, and the resulting asymptotic survival are given.

	Site		
	Meijendel open	Meijendel poplar thicket	Holkham
Annual survival 1992–1993			
Fraction surviving (<i>n</i>)	0.462 (104)	0.714 (154)	0.933 (208)
<i>a</i>	5.009	53.01	304.6
<i>b</i>	9.182	72.67	322.3
Asymptote	0.545	0.729	0.945
<i>P</i> value	0.2008	0.6523	0.4760
Winter survival 1992–1993			
Fraction surviving (<i>n</i>)	0.765 (149)	0.852 (216)	0.958 (330)
<i>a</i>	97651	23.31	149.8
<i>b</i>	127630	26.19	153.4
Asymptote	0.765	0.890	0.977
<i>P</i> value	0.9859	0.1221	0.0771
Summer survival 1993			
Fraction surviving (<i>n</i>)	0.780 (109)	0.913 (207)	0.952 (333)
<i>a</i>	8.646	63.19	44.80
<i>b</i>	8.967	67.57	45.37
Asymptote	0.964	0.935	0.987
<i>P</i> value	0.0094 †	0.2697	0.0021 †

† Boldface *P* values (χ^2 test) indicate that the hyperbola improved the fit significantly when compared with the use of a single, size-independent survival value, the fraction surviving in a data set. (The fit of the hyperbola was always better.)

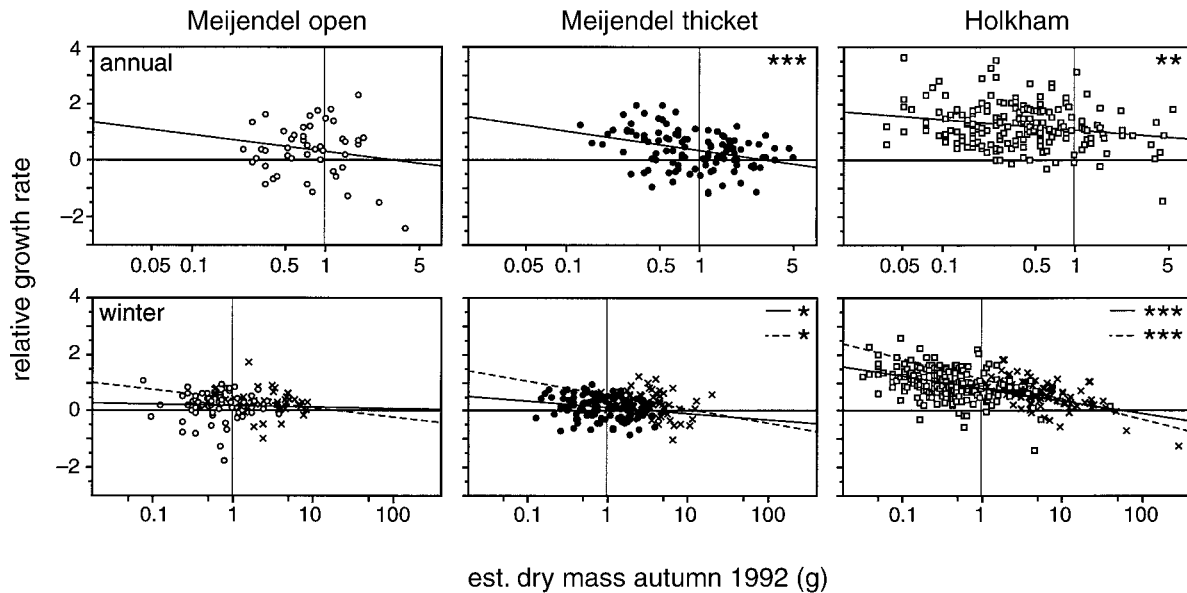


FIG. 4. The relationship between ln-transformed estimated dry mass, annual relative growth rate (autumn–autumn, top row), and winter relative growth rate (autumn–spring, bottom row) at the three field sites of *Cynoglossum officinale*, defined as $\ln(\text{dry mass}_{t+1}) - \ln(\text{dry mass}_t)$. Annual growth rates were calculated for rosettes that remained vegetative in 1993 and survived until the autumn census in that year. Winter growth is subdivided into vegetative rosettes (○ ● □, solid lines) and plants that flowered after winter (×, dashed lines). The significance of the regression lines (slope $\neq 0$) is indicated (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

TABLE 2. Functions and parameters used in the comparison of three optimization models for threshold size for flowering, based on field data collected for *Cynoglossum officinale* at three sites (Meijndel open, Meijndel poplar thicket, and Holkham) in 1992–1993, except for the survival from seed to establishment, which was taken from de Jong et al. (1989). Seed production, $S = 20.845 \times (DM_{spring})^{0.98}$.

Function	Model†	Parameter	Site		
			Meijndel open	Meijndel thicket	Holkham
In seedling dry mass (mean ± 1 SD, g)	AC		-3.19 ± 1.52	-2.46 ± 0.67	-1.90 ± 1.36
Survival seed → established rosette	C		0.0276	0.0276	0.0276
Survival‡					
Autumn → autumn c_y	ABC	a	5.01	53.1	304.6
		b	9.18	72.7	322.3
Autumn → spring c_{wb}	ABC	a	97651	23.3	149.8
		b	127630	26.2	153.4
Growth§					
Year h_y	ABC	f	0.304	0.342	1.075
		g	0.740	0.703	0.837
		D	0.885	0.392	0.529
Winter, bolting h_{wb}	ABC	f	0.419	0.538	1.101
		g	0.862	0.781	0.688
		$D $	0.171	0.180	0.140

Note: See *Methods: Data analysis* and *Optimization models* for definitions of the parameters.
 † Letters (A, B, C) indicate the model in which the function was used.
 ‡ Survival of established rosettes: $c(x) = ax/(1 + bx)$ (see *Methods: Relationship between plant size and survival*).
 § The growth equation is $\ln DM_{t+1} = f(\pm D) + g \ln DM_t$, where DM = dry mass at times $t + 1$ and t , respectively, and D is a relative measure of the variability in growth rate (see *Methods: Relationship between plant size and growth*).
 || Not in model C, where a fixed winter growth rate was used.

$P = 0.0965$, Holkham: $P = 0.1048$). The main difference between the two Meijndel habitat types was the smaller variance in growth rate in the poplar thickets, which was in general lower than in the open sites in Meijndel and Holkham.

The higher Y intercept for the Holkham annual growth rate (Fig. 4) together with its gradual slope gave a very high value for the X intercept. The X intercept indicates the mass at which the average expected growth is zero. For both Meijndel sites this was at about $e^{1.15} = 3.2$ g dry mass, while in Holkham annual growth was estimated, by extrapolation, to be positive up to a dry mass of $e^{6.59} = 725$ g.

Model predictions

Model A, in which lifetime offspring production R_0 was used as the fitness criterion, yielded maximum values of R_0 for Meijndel open between 2.6 and 11.4 seeds. For poplar thicket the maximum seed production ranged from 14.0 to 47.9 seeds, while in Holkham a maximum seed production of 3188 seeds per mother plant was attained. Survival from seed to established plant in first autumn is on average 0.0276 (Table 2), and varies between 0.018 and 0.061 in Meijndel (de Jong et al. 1989). This means that for a zero population growth rate 36.2 seeds per plant should be produced (16.4–55.9 seeds). According to this model, the pop-

TABLE 3. Median and range of threshold sizes (dry mass in grams) for *Cynoglossum officinale* in three consecutive years in two habitat types in Meijndel and in 1992–1993 in Holkham, and optimal flowering size predictions from model B. For the model the intersection between the seed production ratio B and the survival ratio C [predicted value] is given, together with the confidence range formed by the intersects of the confidence limits of both ratios (see *Results: Model predictions*). The field threshold size data are based on size measurements in November and status observations in the following spring.

Year	Meijndel open		Meijndel thicket		Holkham	
	Median [predicted value]	Range	Median [predicted value]	Range	Median [predicted value]	Range
1991–1992 field	2.44	0.49–5.10	5.13	0.76–7.06
Model B	[0.75]	0.22–2.63	[1.91]	0.77–4.74		
1992–1993 field	1.69	0.62–3.95	2.76	0.80–5.10	2.44	0.86–9.54
Model B	[0]	0–5.60	[0.78]	0.25–2.82	[433]	17–11 074
1993–1994 field	1.92	0.76–3.76	4.81	2.00–7.06
Model B	[0.30]	0.00–1.64	[0.99]	0.40–3.73		

ulations in open sites in Meijndel would be declining in all three years. In the poplar thickets the population growth rate is sometimes positive, sometimes negative, while in Holkham the population would be increasing very strongly, provided that the seed and seedling survival fractions in Holkham are comparable to those in Meijndel. Seedling survival from April to November 1993 was 40.9% in Holkham, 40.5% in Meijndel open, and 51.1% in Meijndel poplar thicket.

Predicted optimal threshold sizes are lowest in Meijndel open; in 1992–1993 the highest fitness was predicted for plants with threshold sizes below the average seedling size of 0.04 g (Fig. 5). Optimal threshold sizes for the other years are below 1 g dry mass, and at the lower end of the range of observed threshold sizes in the field. The model produces more flat fitness profiles for Meijndel thicket, and higher optimum values. Two of the three optima are again in the lower part of the threshold size range, only for 1991–1992 the profile peaks in the middle of this range. The optimum threshold size predicted for Holkham is ≈ 1700 g dry mass, much higher than the threshold size range observed, which has its upper limit at 10 g.

The results of Model B, the safe-site R_0 model, are given in Table 3. The optimum threshold size should be just below the dry mass at which seed production ratio B and survival ratio C intersect. The range around this optimum value is determined by the range of autumn sizes in which the two ratio curves with their upper and lower bounds (confidence regions) overlap. For both Meijndel sites the predicted threshold sizes are consistently lower than the threshold sizes observed in the field. Predicted and observed ranges differ in the upper limit, which in the model predictions is usually only half of the observed upper bound, with the exception of Meijndel open in 1992–1993. For this data set, model B gave a threshold size of 0 g, just like model A. Again, the predictions for Holkham were far above the threshold sizes observed; model B predicted an optimum threshold size >400 g, in a range from 17 g to over $>11\,000$ g.

Model C yielded fitness profiles similar to Model A: either a sharp-peaked profile or a very flat one with a hardly distinguishable optimum, both with fitness steeply dropping off towards lower threshold sizes and a more gradual decline towards higher threshold sizes (Fig. 6). Model C's predictions in general fall into the lower end of the observed range of threshold sizes, with the exception of Meijndel open in 1992–1993 and Holkham. For the latter, Model C is the only optimization model with realistic optimum threshold size values. The high optimum threshold size for Meijndel open is likely to be an effect of a very high value of D , the variance around the annual growth rate, in 1992–1993 (Table 2). A simulation (not shown) with parameter values of 1992–1993, but with equal D for all three sites, resulted in a more strongly declining fitness profile for Meijndel open, intermediate between Meijndel

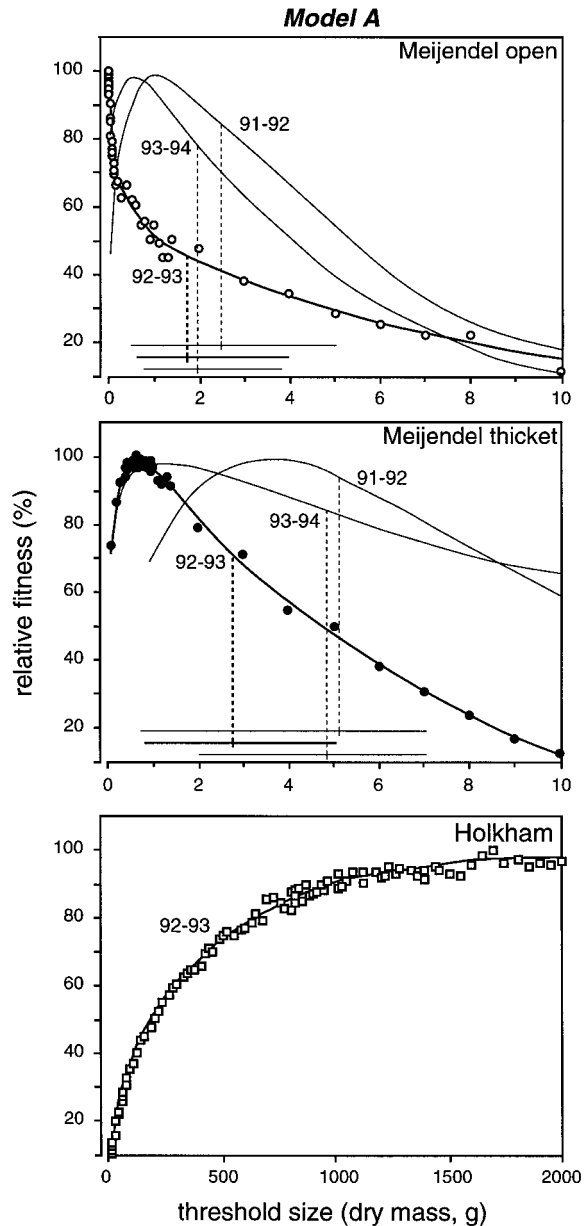


FIG. 5. The relationship between threshold size (dry mass in grams) and relative fitness for the three field sites of *Cynoglossum officinale* in 1992–1993 according to Model A (Kachi and Hirose 1985). Parameters used are given in Table 2. Symbols indicate the relative seed production, averaged over all plants simulated (with at least 1000 plants with seed production > 0). For both Meijndel sites two fitness curves based on field data in two other seasons, 1991–1992 and 1993–1994, are also shown. At the bottom of each Meijndel graph are schematic representations of the range (horizontal line) and median threshold size (intersection with dashed line) in the field for that particular site and year (cf. Fig. 3), with dashed lines extending upwards from the median threshold size to the corresponding fitness profile.

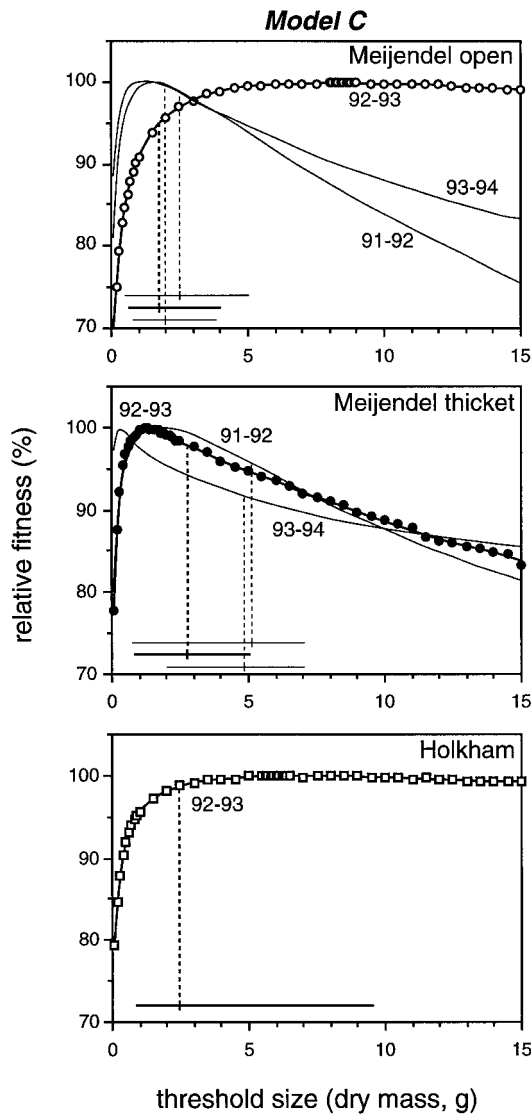


FIG. 6. The relationship between threshold size (dry mass in grams) and relative fitness for the three field sites of *Cynoglossum officinale* in 1992–1993 according to Model C (de Jong et al. 1989), which maximizes r . Parameters used are given in Table 2. For both Meijndel sites the fitness curves based on field data in two other seasons, 1991–1992 and 1993–1994, are also shown. At the bottom of each graph are schematic representations of the range (horizontal line) and median threshold size (intersection with dashed line) in the field for that particular site and year, with dashed lines extending upwards from the median threshold size to the corresponding fitness profile.

del poplar thicket and Holkham. The optimum threshold sizes in this simulation were 2.0 g for Meijndel open, 1.25 g for Meijndel poplar thicket, and 3.0 g for Holkham. All Meijndel simulations yielded a maximum λ below 1 (Meijndel open 0.55–0.73, Meijndel poplar thicket 0.59–0.70), indicating a declining population size (maximum $r = \ln \lambda = -0.46$). For Holk-

ham the maximum λ is 1.21, which means the population is growing ($r = 0.20$).

DISCUSSION

Threshold size, survival, and growth rate

Life history theory predicts that a large size at maturity is favored by a high growth rate, a large rate of increase in fecundity with increases in body size, a high life expectancy, or a mortality rate that declines with body size (Roff 1992:241). The pattern of differences in both survival rates and growth rates found confirms these general predictions qualitatively, as do the rank orders of predictions from the three optimization models. In Holkham the highest values for threshold size, survival rate, and growth rate were found. In Meijndel, survival rates for *Cynoglossum* in the open are lower than in the poplar thickets, and this coincides with lower threshold sizes found in the open sites.

In studies like these one should always be aware of the fact that character values found at one moment in time are the result of a much longer selection process. Are the survival and growth data for 1992–1993 representative for the sites in general? For Meijndel, we can compare the 1992–1993 data with other years at the same sites. The summer survival for 1993 was among the highest in the total data set. Winter survival from 1992 to 1993, on the contrary, was the lowest value measured at both sites in four winter seasons. In only 4 out of 16 cases a hyperbola increasing with plant size fitted the relation between survival rate and plant size significantly better than a constant survival rate. The survival values measured in Holkham were also high in comparison with other years in Meijndel. Boorman and Fuller (1984) provided estimates of annual rosette survival in Holkham from 1973 to 1976. It ranged from 20 to 92%, and in 1973–1975 the *Cynoglossum* population declined in size. The survival measured in 1992–1993 is probably at the high end of the range of survival rates found in Holkham.

Relative growth rates measured in Meijndel in 1992–1993 were at the lower end of the range for four observation years. The rank order of years was remarkably similar over the two habitat types. As to the degree of size dependency, 18 out of 22 regressions of growth rate on plant size were significantly negative. Again, growth rates measured in Holkham in 1992–1993 were higher than in any of the years in Meijndel. We have no data on growth rates in other years in Holkham, but the large difference between Meijndel and Holkham leads us to believe that growth rates attainable in Holkham are generally higher than in either site in Meijndel.

We conclude that an interplay between (size-independent) survival and (size-dependent) growth rates shapes the life history of *Cynoglossum officinale* by selection for lower threshold sizes in environments with high mortality and low growth rates. Lacey (1988)

found latitudinal differences in age at maturity of the facultative biennial *Daucus carota* which could be explained by differences in survival: second-year survival was low in a population in southern North America, and plants from this population matured early. Growth rates were highest at the most northern site, in Ottawa. Flowering in *Verbascum thapsus* was induced at smaller rosette sizes in the south of its North American range (Reinartz 1984). *Verbascum thapsus* grows only in unshaded sites, and the colonization of plots by other plants can prevent completion of the life cycle. This colonization process occurred faster in the south, and a low threshold size may ensure that the flowering stage is reached in time. This is an example of selection on threshold size for flowering through age-specific survival in ephemeral stands, in contrast to more persistent populations like the ones we studied.

Cynoglossum officinale thrives in places where rabbit grazing is heavy (Boorman and Fuller 1984). Rabbits do not eat *C. officinale*, although they can damage plants by digging, but their grazing keeps more competitive species at bay. The Holkham site is very open. It lies near to the sea, which provides a high influx of wind-borne nutrients. This also precludes the establishment of species that are sensitive to salt spray, and the rabbit population is quite large. The Meijndel sites are farther away from the sea, and the sites are in a later successional stage. Rabbits are present in much lower densities, and the open areas in Meijndel show an increase in grass cover.

Direct causes of mortality are difficult to identify. The increase in summer survival with plant size in the open sites suggests that water availability is an important factor affecting survival in this season (de Jong and Klinkhamer 1988b). A visible cause of mortality in Meijndel was infestation by the root-boring weevil *Mogulones cruciger* Herbst (formerly *Ceutorhynchus cruciger* Herbst; Colonelli 1986). Prins et al. (1992) found that the level of infestation ranged from 31 to 61% in flowering plants, and infestation caused a 30% reduction in seed production. The weevils that mature in summer lay their eggs on rosettes in early autumn, and the larvae develop in the roots of overwintering rosettes. The presence of *Mogulones* larvae is likely to be an important cause of mortality in winter. An important finding is that *Mogulones* is predominantly found on large plants, and the probability of infestation increases with plant size (Prins et al. 1992). As far as we know *Mogulones cruciger* does not occur in Holkham (L. A. Boorman, *personal observations*). This difference between Meijndel and Holkham may well be an important factor in the selection process that has led to lower threshold sizes in Meijndel. The probability of being attacked by a herbivore increases with plant size in other plant species (Young 1985, Soldaat 1991, Vrieling 1991), and we expect that in plants that are subject to herbivory with a highly detrimental impact,

this relationship is important in selection on size at maturity.

Optimization models

All three models correctly predict the qualitative rank order of threshold sizes: Meijndel open < Meijndel thicket < Holkham. When we compare predictions from the three models with threshold sizes found in the field, the results of model C (de Jong et al. 1989) show the closest fit. When threshold sizes that result in >95% relative fitness are used as a range around the optimum, model C produces ranges most comparable to threshold size ranges found in the field. The predictions of model A (Kachi and Hirose 1985) and B (de Jong et al. 1987) are generally below the field threshold size values for Meijndel, and too high in the Holkham case. All models have an occasional outlier, where the fitness profile deviates from the general picture. This stresses the importance of using parameter sets for more than just one year. The growth rate estimates prove to be a problem in predicting optimal threshold sizes in some years. A large variation around the mean growth rate (Meijndel open in 1992–1993) or an X intercept that requires extrapolation far beyond plant sizes found in the field (Holkham) may lead to unrealistic results from the models. This problem is not readily solved: the growth data (Fig. 4) give no justification for choosing another than a log-linear relation between plant size and growth rate.

The difference in model performance coincides with the fitness measure used. Models A and B use lifetime offspring production R_0 , and model C population growth rate λ as the entity to be maximized. This is different from Roff (1992), who compared a range of optimization models for age and size at maturity (including Model A by Kachi and Hirose 1985), and found that despite differences in formulation and choice of fitness measure their qualitative predictions were the same. With respect to semelparous perennials it has been emphasized that R_0 is the proper fitness criterion (Reinartz 1984, Kelly 1985), i.e., that the type with the highest R_0 outcompetes all others given the assumptions about density dependence. Kozłowski (1993) showed that R_0 is the appropriate fitness measure in stationary populations only. The data on *Oenothera glazioviana* Kachi and Hirose (1985) used to test their model, yielded a population growth rate r close to zero, and predicted optimal threshold sizes for this species that corresponded very well with threshold sizes found in the field. In the case of *Cynoglossum officinale* presented here, populations are either declining (Meijndel) or strongly increasing (Holkham), as shown by the results of model A and C, and this may explain why the predictions deviate from observed threshold size values for R_0 -based models. In growing populations (Holkham) a shorter generation time and thus a lower threshold size is favored; R_0 models predict threshold sizes that are too high, as seen for Holkham. In de-

clining populations (Meijndel) a delay of reproduction is adaptive, and here the R_0 -based optima are too low.

From frequent visits to the Meijndel study area in the past 15 yr it has become clear that the population as a whole goes through phases of increase and decline. The measurement period 1991–1994 shows a decline in overall abundance of *Cynoglossum officinale*, as confirmed by the models, while in 1996 the species is again on the rise (P. G. L. Klinkhamer and T. J. de Jong, *personal observations*). The same process accounts for Holkham: while population size decreased strongly in 1973–1975 (Boorman and Fuller 1984), *Cynoglossum* was abundant in 1992–1993. Populations thrive on disturbed sand, but slowly decline when perennial species increase in frequency. This means that the populations will probably never reach a stable equilibrium, and selection pressures will shift almost constantly. The threshold sizes in a population at one moment will reflect the “ghost of selection past.” This may explain why, although the ranges of predicted and observed threshold sizes for model C coincide, the optimum value from the model does not correspond to the modal threshold size in the field. This confirms the need for more years of observation, and for *Cynoglossum* the ideal number of years seems to be 5–10. Only by including these long-term dynamics can the process of selection on threshold size for flowering be captured and understood completely.

Population growth rates r of certain types reflect the selection pressure in the population, and demographic data used in matrix models can be employed to quantify natural selection in the field over an observation period (McGraw and Caswell 1996). If the highest r is zero for a certain type that is also the most prevailing type in the population, we can conclude that the population has an evolutionarily stable strategy. If the highest possible $r > 0$, then over a sufficient time period only one lineage will persist and this lineage will attain a growth rate of zero. Although the type with highest r is increasing in frequency over the time frame we consider, it has been seriously questioned whether r also gives an indication of the final outcome of the selective contest (Levin et al. 1984). The answer to this question depends to a large extent on the assumptions one makes about density dependence. As pointed out above, the use of R_0 is prevalent in the literature on timing of reproduction in biennials. Contrary to this we find that model C, based on r , provides the best predictions. One drawback of the R_0 models (Kachi and Hirose 1985, Kelly 1985, de Jong et al. 1987) is that they are confined to a single patch or population. In the case of *Cynoglossum*, populations are not stable. Seeds may be carried by animals to establish new populations. It is likely that the number of seeds a genotype produces during the period that a patch is available greatly affects its chances of establishing a new population. Early reproduction will enhance dispersal, and in a metapopulation model this will be selected for, even though in a single

patch this type would lose if selection were carried on for a long period (Harrison and Hastings 1996). We think the metapopulation structure is important in promoting early reproduction in *Cynoglossum*, and although selection in metapopulations needs more work from theoretical biologists, we suggest that, concurring with McGraw and Caswell (1996), in such a situation r may be the best approximation for fitness we have.

There are three factors not incorporated in the models that may have a significant impact on the outcomes. The first is male fitness: by using seed production only female fitness is estimated (Primack and Kang 1989). It is known that *Cynoglossum officinale* varies the relative investment in male and female function: small plants increase pollen production by forming relatively more flowers that do not produce any seeds, thereby becoming more “male” (de Jong and Klinkhamer 1989, Klinkhamer and de Jong 1993). A difference in male fitness in favor of small plants would lead to smaller optimal threshold sizes than predicted.

A second factor is the correlation between growth rate and survival. When plants within 1-g size classes (dry mass in November) are split up into plants that flowered in summer or survived until next November, and plants that died before the November census, the first group has significantly higher growth rates in the preceding summer (three years combined, 16 one-tailed comparisons within size classes, Wilcoxon’s matched-pairs signed-rank test: Meijndel open: $T = 24$, $P = 0.0107$; Meijndel poplar thicket: $T = 18$, $P < 0.0046$). This correlation is observed more often (e.g., Werner and Caswell 1977, Young 1985), and can easily be explained by a deteriorated plant condition and increased susceptibility for herbivory or diseases, caused by, for instance, an unfavorable microhabitat. This can lead to both lower growth rates and an increased mortality from disease, infestation by pests, or drought. It is difficult to predict the effect of this phenomenon on model outcomes, and depends on the way it is incorporated. Growth rates in Meijndel are not correlated between successive years: plants that grow fast one year do not have higher growth rates than average in the next year (R. A. Wesselingh, *unpublished data*). The correlation would only be present within years, not over years, and we would expect to see little effect on optimum threshold sizes.

The third factor not incorporated in the models is correlation of flowering probability with growth rate just before the moment of flower induction. Lacey (1986b) found an increase in flowering with a decrease in recent growth rate for *Daucus carota*, confirming the predictions of the Wilbur-Collins model (Wilbur and Collins 1973). We also found a correlation between recent growth rate and flowering probability in the open sites in Meijndel, but it was the other way around: plants that flowered had higher growth rates in the summer just before flower induction than plants that remained vegetative (four years combined, one-tailed

comparisons within size classes, Wilcoxon's matched-pairs signed-rank test: Meijndel open: $n = 15$, $T = 15$, $P = 0.0042$; Meijndel poplar thicket: $n = 23$, $T = 119$, $P > 0.05$). Any relation between flowering probability and growth rate is a form of phenotypic plasticity in threshold size, and this would require a different type of model, aimed at comparing the adaptiveness of different strategies (plastic and nonplastic). The lack of differences in threshold size between Meijndel open and poplar thicket in the laboratory experiment, and the fact that the median and range of threshold sizes are not constant over years (e.g., Fig. 5), are further indications that threshold size for flowering may be phenotypically plastic in *Cynoglossum officinale*. This aspect deserves further attention.

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