Acta Bot. Neerl. 38(2), June 1989, p. 203–218

Quantitative and qualitative aspects of fecundity in *Lychnis flos-cuculi*

A. BIERE, R. CAPPERS and J. VAN ANDEL

Department of Plant Biology, Laboratory for Plant Ecology, University of Groningen, P.O. Box 14, 9750 AA Haren (Gn), The Netherlands

SUMMARY

The determination of the reproductive success of individual plants requires insight into both quantitative and qualitative aspects of fecundity. In this study, variation in flowering phenology, seed yield components and potential seed yield were analysed within and among female half sib families in experimental populations of *Lychnis flos-cuculi* (L.), grown at different levels of nutrient supply. In addition, differences in the quality of seeds from different origins (maternal parent, capsule position) and of different sizes were measured as the rate of germination and the dry matter production of seedlings.

The timing of peak ovule production mainly depended on the start of flowering which varied significantly among half sib families. Within individuals, a twofold variation in ovule number per capsule was present, dependent on the position of capsules within an inflorescence. Due to the very regular developmental pattern of inflorescences, this within-plant variation did not contribute to variation in potential seed yield among individuals of similar stature. Between flowering plants, ovule production varied 35-fold, mainly due to the variation in environmental conditions and maternal parent. At low nutrient levels, the total potential seed yield was tightly buffered by negative correlations among yield components, but in nutrient-rich conditions correlations were positive or non-significant.

Significant differences in the quality of seeds from different origins were observed, but from a population dynamics point of view we can conclude that they are of minor importance for variation in fecundity compared to quantitative differences in seed yield.

Key-words: fecundity, flowering phenology, *Lychnis flos-cuculi*, seed source variability, yield components.

INTRODUCTION

Phenotypic variability in yield components has been shown to play an important role in the population dynamics of plants (e.g. Harper 1967; Kawano 1981; Blom 1983; Werner 1985; Ernst 1987). Identification of the causes of phenotypic variability in yield components and the consequences with regard to life-history traits, such as survival, growth, and fecundity, contribute to the understanding of the relationship between population dynamics and life-history evolution (cf. Sarukhán *et al.* 1984; Ennos 1985; Snaydon 1985; Van Andel & Ernst 1985; Van Groenendael 1985; Kik 1987).

In many plant species, seed production and the phenology of seed formation are important components of fitness. Various environmental factors may cause variation in seed yield components in natural populations, e.g. the availability of resources or pollen (Willson & Price 1979; Lee & Bazzaz 1982; Marshall *et al.* 1985a, 1986), or predation of fruits or seeds (Marshall *et al.* 1985b). Fundamental to the study of life-history evolution is the question how plants regulate the number and quality of their offspring under different environmental conditions. Studies of the response of successive yield components to resource availability (Stephenson 1984; Marshall *et al.* 1985a, 1986) have provided insight into the relative importance of particular reproductive stages in the regulation of seed yield. Lloyd (1980) hypothesized that maternal investment may be adjusted to prevailing conditions in a temporal series of strategy 'decisions', which maximize maternal plant fitness. Species might differ in the timing of limitations on their investment (Lloyd *et al.* 1980), which results in predominantly negative correlations among seed yield components. Between species or populations, such trade-offs among yield components, buffering total yield, are frequently observed (e.g. Primack 1978; Kawano 1981; Primack & Antonovics 1981; Marshall *et al.* 1985a; Winn & Werner 1987). However, within populations, positive or neutral correlations are more commonly observed (Primack 1978; Primack & Antonovics 1981; Marshall *et al.* 1985a), i.e. some plants have larger values for all components of seed yield, probably resulting from microsite heterogeneity, size differences among individuals associated with age or genotype, or higher nutrient efficiency. The first aim of this paper is to analyse the relative importance of different seed yield components in the regulation of seed yield in *Lychnis flos-cuculi* (L.). For this purpose, we will consider the response of genetically distinct individuals from one source population to a range of different nutrient conditions in the prezygotic stages of reproduction. As the rate of ovule abortion is not considered in this study, it quantifies the response of 'potential' seed production. As variation in the phenology of flower or ovule production may result in differential seed-set and contribute to variation in seed yield (e.g. Gross & Werner 1982; Schmitt 1983), genetic and environmental sources of variation in the phenology of ovule production among individuals are also considered.

In addition to quantitative variation in seed yield, reproductive success is also determined by qualitative aspects of fecundity. The contribution of seed mass to quantitative variation in total seed yield is often small compared to yield components that determine the number of seeds (cf. Harper 1977), although recent studies have shown numerous exceptions (e.g. Pitelka *et al.* 1983; Stanton 1984; Marshall *et al.* 1985a, 1986). In contrast, the effect of seed mass on seedling establishment can be very large and, as Winn & Werner (1987) argued, should be considered in order to evaluate the relative importance of quantitative and qualitative aspects of fecundity for reproductive success. This evaluation is the second aim of our study. Qualitative differences in fecundity among individuals may arise from two sources. First, the average seed size may vary between individuals. The effects of individual seed size on seedling performance are well documented (e.g. Schaal 1980; Ernst 1981; Dolan 1984; Hendrix 1984; Mazer *et al.* 1986; Wulff 1986; Mazer 1987). Secondly, seed size may vary considerably within individuals (e.g. Thompson 1984). As pointed out by Werner (1985), different numbers of successful seedlings may be produced by individuals with different seed size distributions, even if they produce equal numbers of seeds of equal average size. The extent of the resultant fecundity variation among individuals determines whether or not this may prove to be a necessary refinement for estimating reproductive success. For this purpose we determined the quality of seeds from different origins (parent plants, capsule positions within individuals) and of different sizes in a

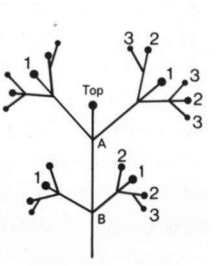

Fig. 1. Schematic representation of the upper part of the inflorescence of *Lychnis flos-cuculi*. Flowering always starts at the top position, and proceeds downwards (nodes A, B, etc.). Within a nodal branch, flowering occurs in the order 1, 2, 3, (primary, secondary, tertiary flowers) etc.

number of individual plants in a population of *Lychnis flos-cuculi* (L.), in addition to estimations of potential seed production. Seed quality was measured as the probability and rate of germination and as roots and shoot production of the resulting seedlings (cf. Van Andel *et al.* 1988).

MATERIALS AND METHODS

Lychnis flos-cuculi (L.) is a rosette-forming perennial plant species, characteristics of wet haymeadows of the plant alliance *Calthion palustris* (Westhof & Den Held 1975). Seeds are able to germinate immediately after dissemination. After having formed a rosette, a flower stalk may sprout from the centre of the rosette. The main rosette produces secondary rosettes, from which secondary flowering stalks may develop. The flowers are hermaphrodite and arranged in a bracteate dichasium, as is the case in many other Caryophyllaceae. Flower initiation occurs at each branch of the flowering stalk in a regular way (Fig. 1). Cross-fertilization is mediated by insect pollination. Seeds were collected from individual field plants and the origin of each seed (parent plant, capsule position) was recorded. Seeds used in the experiments had been air-dried for 1 week and stored thereafter at 4°C and 70% relative humidity.

In order to determine the potential seed production of plants in the course of the generative phase, 405 seedlings were grown from seeds of 'top' capsules of nine field plants, thus providing nine maternal half sib families, under glasshouse conditions. Pots of different volumes were filled with 60, 80, 125, 190 or 300 g of a 1:1 (volume ratio) mixture of potting soil (Bio Mix Super, Nevema) and river sand, which provided five different levels of nutrient supply. For 205 out of 252 plants that came into flower, the phenology of flowering was described by dating each flower in the dichasium. Four components of potential seed yield were measured for each plant: (1) the number of flower stalks, (2) the number of nodes per stalk bearing flowers, (3) the number of flowers per node, and (4) the number of ovules per flower. The latter components was counted in each capsule of a subset of 20 plants. These results have been combined with the data on flowering phenology to estimate the overall potential seed production as well as the contribution of each of the capsules to it, in the course of the generative period.

Seed and seedling performance were analysed to determine the quality of field-collected seeds from different origins (parent plant, capsule position) and of different sizes (small $<0{\cdot}60$ mm: 13·59 mg per 100 seeds, medium 0·60–0·63 mm: 14·97 mg, large $>0{\cdot}63$ mm: 16·23 mg). Seeds were germinated in Petri dishes on moist filter paper in a growth cabinet

with a diurnal regime of 25°C at light (12 or 16 h) and 15°C at dark. Seedlings were transplanted immediately after germination into pots filled with 190 g of a standard soil mixture. They were allowed to grow for exactly 42 days (from the day of germination onwards) in a growth cabinet (23°C light (12 h) and dark, 70–90% relative humidity). For each plant, dry weights of shoots and roots were measured separately. Data analysis was performed using the statistical package SPSS (Nie *et al.* 1975). The variability of seed yield components is given as the coefficients of variation (CV), i.e. standard deviations expressed as a percentage of the mean.

RESULTS

Quantitative variation in fecundity

More than 60% of the plants, grown from seeds of nine different maternal parents, produced one or more flower stalks in their first year. Overall, 153 plants remained in the rosette form with up to 10 secondary rosettes. The percentage of flowering plants varied significantly among nutrient levels ($\chi^2[4] = 19{\cdot}91$, $P < 0{\cdot}001$, Table 1a) and ranged from 44 to 92% among progeny groups from different maternal parents ($\chi^2[8] = 25{\cdot}97$, $P < 0{\cdot}01$). No interaction between nutrient level, progeny group and flowering percentage was observed ($G = 37{\cdot}2$, $d.f. = 32$, $P = 0{\cdot}24$, see Sokal & Rohlf 1981, p. 747), indicating that the difference in flowering percentage among progeny groups was independent of nutrient conditions. In the population of flowering plants, phenology and quantitative variation in potential seed production was studied.

Flowering phenology. The start of flowering was completed within a period of 3 weeks. A maximum difference of 11 days in mean day of anthesis was observed among progeny groups from different maternal parents. These differences were highly significant and showed interaction with environmental (nutrient) conditions (Table 2).

Independent of the parent or nutrient supply involved, the sequence of flowering within an inflorescence proceeds according to a regular pattern. From Fig. 2 it is apparent that flowers of corresponding order on subsequent nodal branches (e.g. A-1, B-1, C-1, etc.) develop shortly after one another, while flowers of subsequent orders within nodal branches (e.g. A-1, A-2, A-3, etc.) are produced at larger time intervals. As a consequence, the number of nodes on which flowers will be produced can be detected shortly after the start of flowering (Fig. 3a, shaded bars) and most of the primary and secondary order flowers on a flower stalk are produced within a few days after flowering is initiated (Fig. 3b, shaded bars).

The maximum number of flowers that can be produced at a particular node position decreases from the top downwards (Fig. 3a) due to a reduction in the number of branches per node. For plants producing flowers at A nodes, the number of branches on these nodes is, without exception, two. For B–E nodes, however, the mean numbers of 1·91, 1·03, 1·01 and 1·00 are recorded in that order. An increase in the level of nutrient supply results in a larger number of nodes that bear flowering branches (Table 2b) and a 'saturation' of the number of flowers at subsequent nodal branches (Fig. 3a). In addition, an increased number of auxiliary branches is formed (Table 2a) which start flowering a few days after the primary stalk.

Plants at lower levels of nutrient supply complete flowering within 3 weeks after the start at top position. If we consider the differences in the start of flowering among progeny groups, up to 11 days, we can conclude that at low nutrient levels the variation in the first

Table 1. Components of potential seed production at five different levels of nutrient supply (soil volume of rooting medium). (A) Four major components. (B) Detailed information on the mean number of flowers per stem. Coefficient of variation in parentheses

A

Soil (g)	Flowering plants		Number of stems per flowering plant		Mean number of flowers per stem		Mean number of ovules per flower	
	n	%*						
60	32	35·6	1·21	(57)	11·5	(43)	161	(15)
80	56	62·2	1·59	(67)	17·7	(45)	146	(19)
125	58	64·4	2·30	(57)	20·2	(50)	146	(5)
190	69	76·7	2·79	(69)	19·6	(57)	154	(20)
300	37	82·2	4·68	(38)	19·2	(40)	158	(7)

B

Soil (g)	Mean number of flowers per stem				Mean number of nodes per stem (primary stem)		Mean number of flowers per node (primary stem)	
	Primary stem		Secondary stem					
60	13·4	(40)	2·4	(42)	2·18	(25)	6·2	(32)
80	25·5	(40)	4·5	(40)	2·86	(26)	9·2	(35)
125	34·3	(38)	9·4	(44)	3·28	(23)	10·8	(35)
190	36·5	(37)	10·1	(43)	3·90	(26)	9·7	(40)
300	52·0	(47)	10·3	(50)	5·24	(16)	9·8	(41)

*Total number of plants per nutrient level = 90, except for soil volume = 300 ($n = 45$).

day of anthesis between half sib families constitutes a substantial part of the temporal variation in fecundity. At higher nutrient levels, the increased production of tertiary and higher order flowers and of flowers on auxiliary branches increases the flowering period to *c.* 6 weeks.

Potential seed production. Up to 35-fold differences in potential seed production were observed between flowering individuals. Among nutrient levels this variation was 3·6-fold. Due to the specific developmental pattern of the inflorescence, i.e. the almost simultaneous production of primary and secondary ovaries at different branches, differences among nutrient levels become apparent early in the generative phase (Fig. 4).

Table 1 lists four major components of potential seed production. The number of flower stalks per plant seems to be a more variable character (CV = 73%) than the mean number of flowers per stem (CV = 57%) and the mean number of ovules per flower (CV = 14%), both between individuals within nutrient treatments and among nutrient levels. The relative constancy of the mean number of flowers per stem at higher levels of nutrient supply results from the production of a large number of secondary stems with only a small number of flowers at high levels of nutrient supply (Table 1b). Variation in the number of flowers on primary stems among nutrient levels is due to variation in the number of nodes per stem rather than to variation in the number of flowers per node (Table 1b).

A significant part of the variation in each of these components can be ascribed to the maternal parent of the individuals (Table 3). Family means of maternal half sibs ranged

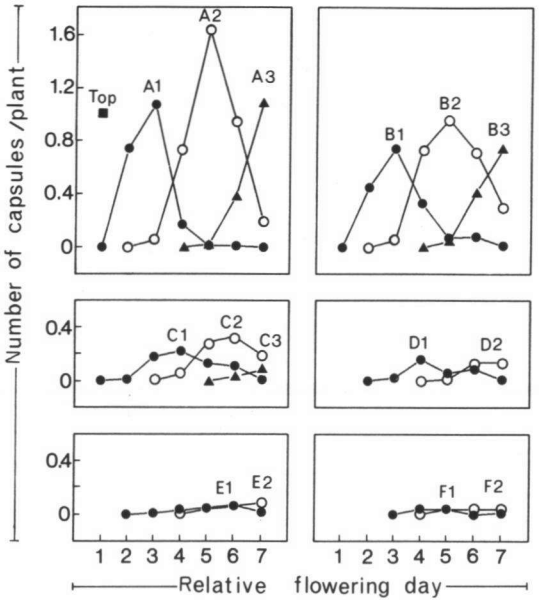

Fig. 2. Mean number of capsules per plant initiated at each flower position, relative to the first flowering day (top position). Data for primary stalk. A–F refer to subsequent node positions towards the stem base. Only primary (●), secondary (○) and tertiary capsules (▲) are indicated.

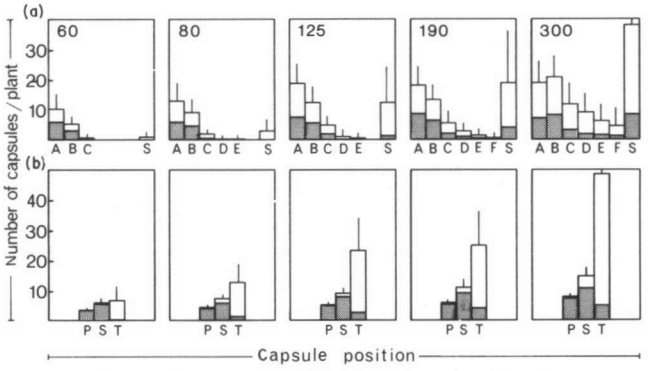

Fig. 3. Mean number of capsules per plant at the end of the flowering period for plants grown at different nutrient levels (60–300 g soil volume). Above (a): capsules on branches from subsequent nodes of the primary flower stalk (A, B, C, etc.) and on secondary stalks (S). Below (b): capsules on different positions within branches (P: primary, S: secondary, T: tertiary and higher order positions). Vertically shaded bars indicate the number of capsules initiated 1 week after the start of flowering. Vertical lines indicate standard errors of the mean.

from 30·8 to 69·4 for the number of flowers per plant, mainly due to variation in the number of stems per plant (1·40–3·78). Interactions between offspring family and nutrient level were small or insignificant (Table 3) for each of the seed yield components, suggesting that neither the direction, nor the extent of the response to environmental conditions varies among half sib families.

The number of ovules per ovary, determined in each of the ovaries in a subset of 20 plants, varied among flower positions within the inflorescence. Its value is directly related

Table 2. Analysis of variance for first flowering day

Source of variation	*d.f.*	Mean squares	*F*
Parent plant	8	297·22	23·58***
Nutrient level	4	203·43	16·14***
$P \times N$	32	38·67	3·07***
Error	184	12·60	
Total	228	29·60	

***$P < 0{\cdot}001$.

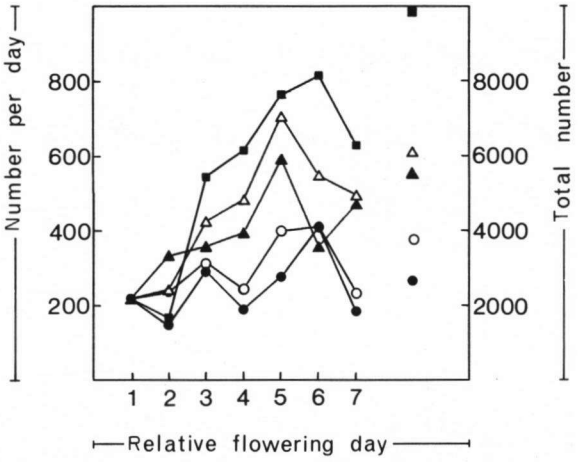

Fig. 4. Mean number of ovules per plants produced per day (graphs) on the primary flowering stalk, during the first week following the start of flowering at top position, at different levels of nutrient supply: (●) 60, (○) 80, (▲) 125, (△) 190, (■) 300 g soil volume. Single dots represent the total number of ovules produced per plant over the entire flowering period.

to the number of carpels per ovary, which ranges from 4 to 7, with 5 as a normative mean. Both the number of carpels per ovary and the number of ovules per carpel decrease from the top position downwards and within branches from the primary position (A-1, B-1, etc.) to the secondary position (A-2, B-2, etc.), as illustrated in Table 4. As a result, the contribution of later developed flowers to overall potential seed production is considerably reduced.

As a consequence, the average number of ovules per ovary for plants as a whole should be reduced at high nutrient levels, because the proportion of tertiary and higher order capsules with low numbers of ovules is higher in these nutrient-rich conditions (Fig. 3b). However, this reduction is counteracted by an increase in the number of ovules per ovary for each capsule position (Top, Primary, Secondary, Tertiary) with increased levels of nutrient supply (ANOVA $F(4,19) = 4{\cdot}344$, $P < 0{\cdot}001$). As a result, the average numbers of ovules per ovary for plants as a whole is independent of nutrient supply (Table 1a, ANOVA $F(4,19) = 0{\cdot}319$, $P = 0{\cdot}86$).

Table 3. Analyses of variance for components of potential seed yield. Data were ln-transformed prior to analysis except for the number of flowers per stem and per node. *F*-values and the percentage of the total variance are indicated

Source of variation	*d.f.*	Number of flowers per plant		Number of stems per plant		Mean number of flowers per stem		Mean number of nodes per stem		Mean number of flowers per node	
		F	% *V*	*F*	% *V*	*F*	% *V*	*F*	% *V*	*F*	% *V*
Nutrients	4	79·20***	57·5	30·68***	32·9	9·24***	14·5	69·07***	54·1	9·28***	14·4
Parent	8	5·54***	5·4	5·58***	10·7	3·98***	9·1	7·18***	7·9	3·94***	8·7
$N \times P$	32	1·72*	5·0	1·02	1·1	1·16	2·6	1·74**	5·4	1·23	3·7
Error	160		32·0		55·4		73·7		32·7		73·2

*$P<0·05$, **$P<0·01$, ***$P<0·001$.

Table 4. Mean number of ovules per capsule and its constituent components ± the standard error of the mean, for different capsule positions. Number of observations in parentheses

Capsule position	Number of ovules per carpel	Number of carpels per capsule	Number of ovules per capsule
Top	40·5 ± 6·2 (17)	5·35 ± 0·60 (166)	216·7
A1	36·2 ± 6·1 (40)	5·03 ± 0·27 (318)	182·1
A2	31·8 ± 4·5 (68)	5·00 ± 0·20 (477)	159·0
A3	28·1 ± 4·8 (37)	4·99 ± 0·22 (163)	140·2
A4	25·5 ± 3·6 (11)	4·89 ± 0·42 (54)	124·7
B1	36·7 ± 5·6 (26)	5·02 ± 0·22 (259)	184·2
B2	31·2 ± 5·1 (43)	4·99 ± 0·16 (338)	155·7
B3	27·4 ± 4·8 (30)	4·98 ± 0·14 (107)	136·5
B4	24·5 ± 1·6 (4)	4·76 ± 0·66 (35)	116·6
C1	31·5 ± 4·9 (10)	5·02 ± 0·21 (95)	158·1
C2	29·2 ± 7·2 (10)	5·00 ± 0·17 (99)	146·0
D1	32·7 ± 3·0 (2)	5·00 ± 0·00 (35)	163·5

We conclude that the variation in the number of ovules per capsule can be considered as an important temporal aspect of ovule production, but that it is of minor importance for the extent of variation in potential seed production between individuals and levels of nutrient supply.

Correlations among seed yield components. Each of the seed yield components was positively correlated with the total potential seed yield (Table 5b). Early generative characters showed a closer relationship with the potential seed yield at the lowest level of nutrient supply whereas the number of flowers per node and ovules per flower were more important correlates at the highest nutrient levels. But, in general, only minor differences in the pattern of correlations with potential seed yield were observed in different environments.

Phenotypic correlations between components of potential seed yield were predominantly negative or non-significant within the four environments of the lower nutrient supply (Table 5a). This pattern was consistent among individuals of different female half sib families as well. In contrast to these moderate levels of nutrient supply, no such trade-offs were observed at the highest nutrient level (Table 5a). Apparently, the pattern of correlations among yield components changes in response to the environment. The low values for total phenotypic correlations between the number of stalks or nodes and the number of flowers produced on them, appear to result from the contrasting effects of negative correlations within nutrient levels and the positive environmental components of these correlations (Table 5a).

Seed source variation

Germination. Seeds from different sources in a field population (parent plants, capsule positions) and of different seed size classes (small, medium, large) were germinated, and the seedlings were grown under standard conditions, to detect quality differences. The experimental groups are described in the legend to Table 6.

Table 5. Phenotypic correlations. (A) Among seed yield components, and (B) between each seed yield component and ovule yield (Y), at five different levels of nutrient supply

	A				B			
	SP×FS	N×F	N×O	F×O	SP×Y	N×Y	F×Y	O×Y
Soil (g)								
60	−28	−11	−93*	+09	+71***	+70***	+43*	−47
80	−43**	−31*	+00	+19	+86***	+44**	+72***	+73
125	−52***	−36**	+56	−87	+85***	+65***	+49***	+12
190	−58***	−34**	+54	−61	+71***	+04	+22	+78*
300	+08	+32*	+80	−07	+59***	+10	+76***	+99***
Within	−41***	−21**	+19	−24	+69***	+33***	+69***	+53*
Between	+44	+59	−47	−03	+99***	+97***	+87***	−23
Total	−20**	+04	+03	−17	+82***	+72***	+77***	+32
HS fam.	−62*	−31	ND	ND	+78**	+35	+76**	ND

ND = Not determined. $*P<0{\cdot}05$, $**P<0{\cdot}01$, $***P<0{\cdot}001$.

Number of stalks per plant (SP), flowers per stalk (FS), and for primary stalks the number of nodes per stalk (N), flowers per node (F) and ovules per flower (O). Bottom: components within and between nutrient levels calculated from analyses of variance and co-variance, and correlations among family means of female half sib families. Values × 100.

Table 6. Mean shoot and root dry weight (±standard error) of plants from different seed sources, grown for 6 weeks in three experiments*

Experiment	Number of plants	Shoot dry wt (mg)	Root dry wt (mg)	Total dry wt (mg)
1	205	840±126	301±70	1141
2	591	681±131	277±77	958
3	150	726±168	340±91	1066

*Exp. 1: Seeds from top and A3 capsules from six parents.
Exp. 2: Seeds from top, A1 and A2 capsules from three parents, differentiated into three seed size classes.
Exp. 3: Seeds from top, A1, A2, A3, B1, B2, B3, C1 capsules from three parents.

In all the experimental groups, 80–100% of the seeds germinated within 2 months. Differences in germination behaviour among progeny groups can, for a large part, be reduced to the initial rate of germination. Smaller seeds tend to germinate at a slower rate; seeds from earlier capsules tend to germinate faster; and variation among progeny groups from different maternal parents can be observed (see Fig. 5 for examples).

As no consistent differences in germination rates were observed between medium sized seeds from earlier and later produced capsules (not shown), differences in the germination rate among capsules may simply reflect mean seed size differences. By contrast, Fig. 6 suggests that parental differences in germination rate cannot be explained on the basis of co-varying mean seed size or seed size distributions alone (cf. parental groups 9 and 10 for

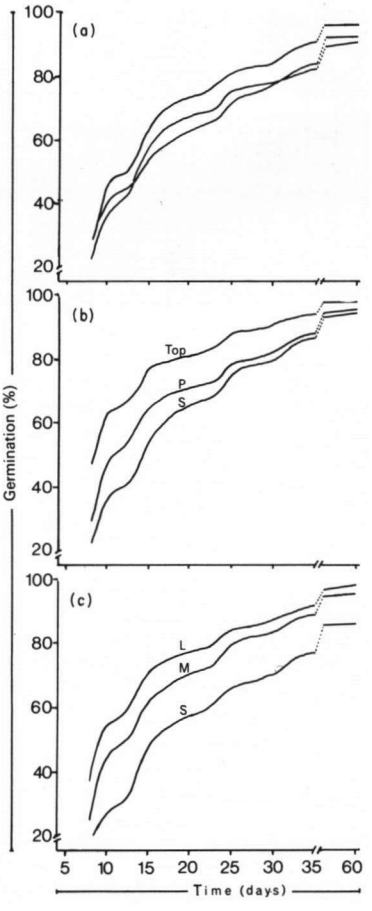

Fig. 5. Germination curves, split up according to the origin of seeds. (a) Parents, (b) capsule positions, (c) seed sizes (Large, Medium, Small).

example) and that interaction between seed size and parental origin is present. Apart from that, an effect of average seed size (decreasing from parent 1–10) is also apparent.

Biomass production. Seedlings from different seed sources (see legend to Table 6) were each grown individually for 42 days in a growth cabinet, from the day of germination onwards. Each plant had produced a well developed root and shoot at harvest time (mean dry weights in Table 6). Despite the equal length of their period of growth, significant variation in production was observed among seedlings that germinated on different days. The pattern of this variation was not consistent. A non-significant, a positive ($P < 0{\cdot}001$) and a negative ($P < 0{\cdot}05$) correlation between shoot biomass and the day of germination were found in experiments 1, 2 and 3, respectively. Therefore, the day of germination was used as a co-variate in the analyses of variance of shoot and root dry weight production (Table 7).

Maternal parent and seed size explained a significant part of the variation in dry weight. Yet, absolute differences in dry weight among individuals from different seed sources were small. Plants from large seeds produced, on average, 5·3% more biomass than individuals

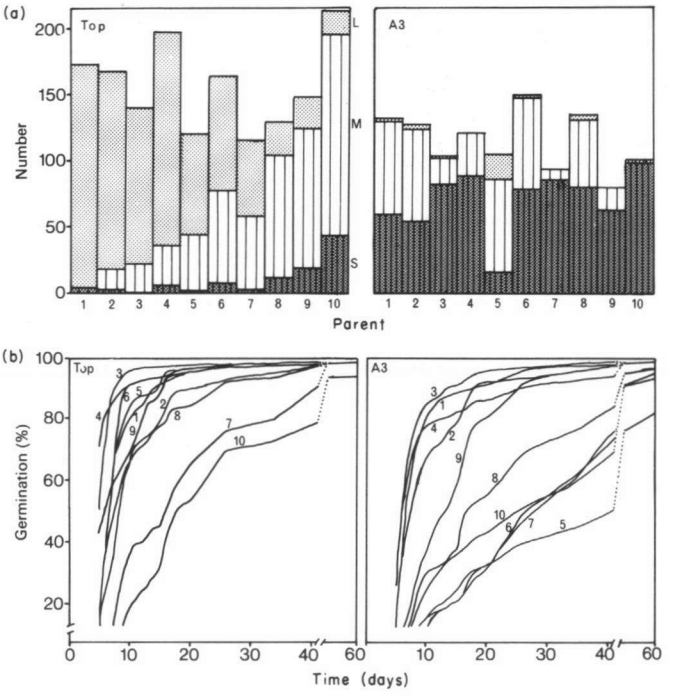

Fig. 6. (a) Seed size distribution (Large, Medium, Small) and (b) germination of seeds from top capsules (left) and A3 capsules (right) of 10 different parents.

from small seeds. Variation among progeny groups from different maternal parents was of the same order of magnitude. In contrast to the germination results, there was no indication of an interaction between seed size and parent. Likewise, the effects of seed size did not interact with the position, i.e. the moment of initation, of the capsule in which the seeds were produced. Effects of capsule position were only significant when a wide spectrum of capsule types was used (Experiment 3). Progeny from later-formed capsules produced less biomass. The extent of this decrease varied among parents, resulting in a significant interaction between parent and capsule position.

DISCUSSION

Phenology of potential seed production

Variation in the phenology of ovule production among individuals is determined by (a) environmental (nutrient) conditions, which can prolong the flowering period, and (b) the start of flowering, which varies considerably among half sib families and determines the timing of peak ovule production. The first observation is in accordance with data of Schmitt (1983), which suggest that the duration of flowering in the annual *Linanthus androsaceus* might be due largely to the environment, i.e. by plant size. The first flowering date in this species was more likely to be determined by a programmed response to an environmental cue. Schmitt (1983) suggested that if natural selection has affected phenological traits in *Linanthus*, it acted on the flowering date. In *Lychnis flos-cuculi*, it appears that considerable variation for the first flowering date is still present among half sib

Table 7. Analyses of variance of root and shoot dry weight in three experiments (see legend to Table 6)

	Shoot			Root		
	Exp. 1	Exp. 2	Exp. 3	Exp. 1	Exp. 2	Exp. 3
Co-variate						
Date of germination						
d.f.	1	1	1	1	1	1
MS	58·2	2323·9	946·6	0·0	374·6	124·7
P	0·036	0·000	0·000	NS	0·000	0·000
Main effects						
Parent (PA)						
d.f.	5	2	2	5	2	2
MS	70·6	125·0	196·4	63·5	30·7	19·0
P	0·001	0·000	0·000	0·001	0·002	0·049
Capsule position (CA)						
d.f.	1	2	7	1	2	7
MS	3·5	23·8	45·8	14·4	1·7	22·1
P	NS	NS	0·021	NS	NS	0·001
Seed size (SS)						
d.f.		2			2	
MS		59·0			30·1	
P		0·007			0·002	
Interactions						
PA × CA						
d.f.	5	4	14	5	4	14
MS	59·5	19·3	354·1	7·6	23·3	85·6
P	0·001	NS	0·000	NS	0·001	0·000
PA × SS						
d.f.		4			4	
MS		16·7			4·6	
P		NS			NS	
CA × SS						
d.f.		4			4	
MS		8·9			1·7	
P		NS			NS	
Error						
d.f.	192	571	125	192	571	125
MS	13·1	11·7	18·6	3·3	4·7	6·1
Total						
d.f.	204	590	149	204	590	149
MS	15·8	16·3	67·1	4·9	5·6	15·7

families. The observed interaction between progeny family and nutrient level for this trait may act to preserve variation for first flowering day in a heterogeneous environment.

Although nutrient conditions have a strong impact on the duration of flowering, peak ovule production per plant is reached at similar intervals after the start of flowering at various nutrient conditions. This synchrony mainly results from the simultaneous initiation of primary and secondary capsules that produce the largest number of ovules.

Qualitative and quantitative variation in seed yield

Within individuals. Up to twofold differences in the potential number of seeds per capsule were observed within individuals, dependent on the position (i.e. ontogenetic age) of the capsule within the inflorescence. Although the percentage of seed-set was not studied in the greenhouse experiments, field-collected capsules showed a decrease in the number of actually produced seeds from primary to tertiary capsules as well. This contrasts with the relatively constant number of seeds per capsule in the dichasia of the related *Silene dioica* (Thompson 1981). Differences in germination and production rate within and among seed batches from these different locations within inflorescences were small, and mainly resulted from differences in seed size. There was no indication that timing of the production of seeds, early or late in the generative phase, had any effect on offspring quality in addition to the effects resulting from differences in seed size.

Between individuals. The most trivial and yet the most pronounced variation in seed yield in the even-aged experimental populations of *Lychnis flos-cuculi* was due to a sharp distinction between individuals that flowered in their first year and those remaining in the vegetative rosette stage. The average percentage of individuals in this monocarpic perennial that showed a delay in generative reproduction varied significantly among progeny groups, but the strong response of each progeny group to varying nutrient conditions was very similar. This similarity may indicate a relative constancy in the perception and minimum requirement of available resources for generative reproduction in even-aged individuals within a species. Long-term field studies are needed to evaluate the consequences of delayed reproduction for life time fecundity and the chance of survival.

Between flowering individuals, a 35-fold difference in potential seed yield was observed. These quantitative differences were determined early in the generative phase, mainly by the number of flower stalks per plant and the number of nodes that develop flowering branches. In the even-aged experimental population, variation in yield components was, to a large extent, environmentally determined, i.e. by the amount of supplied nutrients, though significant twofold variation among overall family means of different progeny groups was found. Reciprocal transplant studies have generally revealed that variation in yield components is largely due to phenotypic plasticity (Kik 1987; Winn & Werner 1987). Although genetic differences in plasticity within populations may occur (Marshall *et al.* 1986), in *Lychnis flos-cuculi* interactions between parent and nutrient supply were low or non-significant for most of the seed yield components, suggesting that progeny groups respond in a similar way to differences in environmental conditions.

The magnitude of the phenotypic response to different nutrient levels varied among seed yield components and decreased in the order: number of inflorescences per plant, nodes with flowering branches per inflorescence, flowers per node, and ovules per flower. Apparently, yield components in earlier reproductive stages show a larger amount of phenotypic plasticity. Similar trends have been shown, for example for *Plantago lanceolata* (Primack & Antonovics 1981), *Lotus corniculatus* (Stephenson 1984) and *Prunella vulgaris* (Winn & Werner 1987).

Correlations among seed yield components were predominantly negative at lower levels of nutrient supply, but no such trade-offs were observed under high nutrient conditions. Environmental correlations are thus positive or non-significant. Similar environmental modifications were shown for correlations between seed number per capsule and a number of other yield components in *Plantago lanceolata* (Primack & Antonovics 1981).

It illustrates on a phenotypic level that negative correlations among yield components may result from developmental plasticity among successive components competing for a limiting resource (Adams 1967; Caswell 1983; Silander 1985). The absence of trade-offs at higher nutrient levels indicates that the total yield in these conditions is not tightly buffered and that adjustment of yield components may occur in the course of the reproductive period.

Qualitative versus quantitative variation. Qualitative aspects of seed production appeared to be of minor importance for the overall variation in fecundity among individuals. First, due to the regular developmental pattern of the inflorescence, differences in the distribution of capsule types among individuals of corresponding stature are small. As a result, the contribution of this within-plant variation to differences in seed number or in seed size distribution among individuals is low, though the performance of seedlings from a particular capsule position appeared to vary among plants. Second, despite differences in average seed size between individuals, and significant differences in biomass production among their progeny, absolute differences do not account for more than a few per cent of the total biomass in the controlled environment studied. Although qualitative differences may be more pronounced in field situations (Hendrix 1984; Stanton 1984), we conclude that from a population dynamics point of view, quantitative variation has a much greater impact on fecundity than qualitative aspects.

ACKNOWLEDGEMENTS

This study was supported by the foundation for Fundamental Biological Research (BION), which is subsidized by the Netherlands Organization for Scientific Research (NWO).

REFERENCES

Adams, M.W. (1967): Basis of yield component compensation in crop plants with special reference to the field bean, *Phaseolus vulgaris*. *Crop. Sci.* **7**: 505–510.

Blom, C.W.P.M. (1983): Plasticity of life characteristics in two different populations of *Plantago maritima* L. *Acta Oecol./Oecol. Plant.* **4**: 377–394.

Caswell, H. (1983): Phenotypic plasticity in life history traits: demographic effects and evolutionary consequences. *Am. Zool.* **23**: 35–46.

Dolan, W.D. (1984): The effect of seed size and maternal source on individual size in a population of *Ludwigia leptocarpa (Onagraceae)*. *Am. J. Bot.* **71**: 1302–1307.

Ennos, R.A. (1985): The significance of genetic variation for root growth within a natural population of white clover (*Trifolium repens*). *J. Ecol.* **73**: 615–624.

Ernst, W.H.O. (1981): Ecological implications of fruit variability in *Phleum arenarium* L., an annual dune grass. *Flora (Jena)* **171**: 287–398.

Gross, R.S. & Werner, P.A. (1983): Relationships among flowering phenology, insect visitors, and seed-set of individuals: experimental studies on four co-occurring species of goldenrod (*Solidago: Compositae*). *Ecol. Monogr.* **53**: 95–117.

Harper, J.L. (1967): A Darwinian approach to plant ecology. *J. Ecol.* **55**: 247–270.

— (1977): *Population Biology of Plants*. Academic Press, London.

Hendrix, S.D. (1984): Variation in seed weight and its effects on germination in *Pastinaca sativa* L. (*Umbelliferae*). *Am. J. Bot.* **71**: 795–802.

Kawano, S. (1981): Trade-off relationships between some reproductive characteristics in plants with special reference to life history strategy. *Bot. Mag. Tokyo* **94**: 285–294.

Kik, C. (1987): *On the ecological genetics of the clonal perennial Agrostis stolonifera*. Thesis University of Groningen, The Netherlands.

Lee, T.D. & Bazzaz, F.A. (1982): Regulation of fruit and seed production in an annual legume, *Cassia fasciculata*. *Ecology* **63**: 1363–1373.

Lloyd, D.G. (1980): Sexual strategies in plants I. An hypothesis of serial adjustment of maternal investment during one reproductive session. *New Phytol.* **86**: 69–79.

—, Webb, C.J. & Primack, R.B. (1980): Sexual strategies in plants II. Data on the temporal regulation of maternal investment. *New Phytol.* **86:** 81–92.

Marshall, D.L., Fowler, N.L. & Levin, D.A. (1985a): Plasticity in yield components in natural populations of three species of *Sesbania*. *Ecology* **66:** 753–761.

—, — & — (1986): Plasticity of yield components in response to stress in *Sesbania macrocarpa* and *Sesbania vesicaria (Leguminosae)*. *Am. Nat.* **127:** 508–521.

—, Levin, D.A. & Fowler, N.L. (1985b): Plasticity in yield components in response to fruit predation and date of fruit initiation in three species of *Sesbania (Leguminosae)*. *J. Ecol.* **73:** 71–81.

Mazer, S.J. (1987): The quantitative genetics of life history and fitness components in *Raphanus raphistrum* L. (*Brassicaceae*): ecological and evolutionary consequences of seed-weight variation. *Am. Nat.* **130:** 891–914.

—, Snow, A.A. & Stanton, M.L. (1986): Fertilization dynamics and parental effects upon fruit development in *Raphanus raphistrum*: consequences for seed size variation. *Am. J. Bot.* **73:** 500–511.

Nie, N.H., Hull, C.H., Jenkins, J.G., Steinbrenner, K. & Bent, D.H. (1975): *Statistical Package for The Social Sciences*. 2nd edn. McGraw-Hill, New York.

Primack, R.B. (1978): Regulation of seed yield in *Plantago*. *J. Ecol.* **66:** 835–847.

— & Antonovics, J. (1981): Experimental ecological genetics in *Plantago*. V. Components of seed yield in the ribwort plantain *Plantago lanceolata* L. *Evolution* **35:** 1069–1079.

Sarukhán, J., Martinez-Ramos, M. & Piñero, D. (1984): The analysis of demographic variability at the individual level and its populational consequences. In: Dirzo, R. & Sarukhán, J. (eds): *Perspectives on Plant Population Ecology*. 83–106. Sinauer Associates, Sunderland.

Schaal, B.A. (1980): Reproductive capacity and seed size in *Lupinus texensis*. *Am. J. Bot.* **67:** 703–709.

Schmitt, J. (1983): Individual flowering phenology, plant size, and reproductive success in *Linanthus androsaceus*, a Californian annual. *Oceologia* **59:** 135–140.

Silander, J.A. (1985): The genetic basis of the ecological amplitude of *Spartina patens*. II. Variance and correlation analysis. *Evolution* **39:** 1034–1052.

Snaydon, R.W. (1985): Aspects of ecological genetics in pasture species. In: Haeck, J., Woldendorp, J.W. (eds.): *Structure and Functioning of Plant Populations* **2:** 127–152. North-Holland Publishing Company, Amsterdam.

Sokal, R.R. & Rohlf, F.J. (1981): *Biometry*. 2nd edn. Freeman, San Francisco.

Solbring, O.T. (1981): Studies on the population biology of the genus Viola. II. The effect of plant size on fitness in *Viola sororia*. *Evolution* **35:** 1080–1093.

Stanton, M.L. (1984): Seed variation in wild radish: effect of seed size on components of seedling and adult fitness. *Ecology* **65:** 1105–1112.

Stephenson, A.G. (1984): The regulation of maternal investment in an indeterminate flowering plant (*Lotus corniculatus*). *Ecology* **65:** 113–121.

Thompson, P.A. (1981): Variation in seed size within populations of *Silene dioica* (L.) Clairv. in relation to habitat. *Ann. Bot.* **47:** 623–634.

Thompson, J.N. (1984): Variation among individual seed masses in *Lomatium grayi* (Umbelliferae) under controlled conditions: magnitude and partitioning of the variance. *Ecology* **65:** 626–631.

Van Andel, J. & Ernst, W.H.O. (1985): Ecophysiological adaptation, plastic responses, and genetic variation in annuals, biennials and perennials in woodland clearings. In: Haeck, J. & Woldendorp, J.W. (eds.): *Structure and Functioning of Plant Populations* **2:** 27–49. North-Holland Publishing Company, Amsterdam.

—, Wesselingh, R.A. & Van Donk, R. (1988): The performance of progeny groups from two populations of *Phyteuma nigrum*, with particular reference to the chance of survival or extinction. *Acta Bot. Neerl.* **37:** 165–169.

Van Groenendael, J.M. (1985): *Selection for different life histories in Plantago lanceolata*. Thesis University of Nijmegen, The Netherlands.

Werner, P.A. (1985): Phenotypic variation and implications for reproductive success. In: Haeck, J. & Woldendorp, J.W. (eds.): *Structure and Functioning of Plant Populations* **2:** 1–26. North-Holland Publishing Company, Amsterdam.

Westhof, V. & Den Held, A.J. (1975): *Planten gemeenschappen in Nederland*. 2nd edn. Thieme, Zutphen NL.

Willson, M.F. & Price, P.W. (1979): Resource limitation of fruit and seed production in some *Asclepias* species. *Can J. Bot.* **58:** 2229–2233.

Winn, A.A. & Werner, P.A. (1987): Regulation of seed yield within and among populations of *Prunella vulgaris*. *Ecology* **68:** 12245–1233.

Wulff, R.D. (1986): Seed size variation in *Desmodium paniculatum*. II. Effects on seedling growth and physiological performance. *J. Ecol.* **74:** 99–114.