Investment in survival and reproduction along a semelparity–iteroparity gradient in the *Beta* species complex

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Abstract

The *Beta* species complex shows a gradient of life histories from pronounced semelparity (big-bang reproduction) to pronounced iteroparity (repeated reproduction). Models assume a trade-off between investment in reproduction and survival. Reproductive effort is thought to increase with decreasing life span, and to be invariable in semelparous plants and susceptible to environmental conditions in iteroparous plants. These assumptions and hypotheses were verified by a greenhouse experiment testing six different life cycles at three contrasting nutrient levels. This study suggests that reproductive effort is negatively correlated with mean life span along the life-cycle gradient. Unlike semelparous beets, reproductive effort in iteroparous beets is extremely sensitive to nutrient level. Phenotypic correlation between allocation to reproduction and allocation to survival generally appeared significantly negative in the longest-lived iteroparous beets, nonsignificant in intermediate life histories and obviously positive in semelparous beets (no trade-off control).

Introduction

Annual weeds share with bamboos or Agaves, as well as with many animals such as Pacific salmons or butterflies, a life history characterized by a single massive reproductive episode, followed by the death of the individual. This life history is called semelparity (sometimes referred to as monocarpy in plants, or big-bang reproduction, see Gadgil & Bossert, 1970). Its alternative is iteroparity (polycarpy), i.e. repeated reproduction, which may be accompanied by progressive senescence. Semelparity has a polyphyletic origin in Angiosperms (Young & Augspurger, 1991; Watkinson, 1992). Both strategies may be observed in closely related species (Pitelka, 1977; Primack, 1979; Conti *et al.*, 1999), subspecies (Spira & Pollak, 1986; Huxman & Loik, 1997), populations (Till-Bottraud *et al.*, 1990) or even morphs within one single population (Grosberg, 1988).

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Semelparity, as seen in some weedy annuals, may result simply from lethal environmental factors, such as frost or drought after the reproductive season (Harper, 1977). In very unpredictable environments, it may be a successful strategy to produce offspring continually during the reproductive season until accidental death of the individual (Harper, 1977). Nevertheless most semelparous species die immediately after reproduction without any clear environmental cause, e.g. long-lived semelparous species, such as Yuccas, Agaves (Young & Augspurger, 1991), some bamboos (Keeley & Bond, 1999), Cicadas (Karban, 1997) or Pacific salmons (review in Finch, 1990). This suggests programmed death (Wilson, 1974; Young & Augspurger, 1991), involving internal mechanisms of abrupt senescence (Rose, 1991). In this paper we will refer only to this last category of semelparous taxa.

Many models have been developed to explain the evolution of semelparity. All allow the evolution of programmed death. Some of these models confront semelparous and iteroparous strategies as defined by their demographic parameters (Young, 1990; Young & Augspurger, 1991), e.g. adult and juvenile survival, age

at first reproduction, etc. These models show that any demographic changes decreasing adult, relative to juvenile reproductive value should favour semelparity (Cole, 1954; Gadgil & Bossert, 1970; Bryant, 1971; Charnov & Schaffer, 1973). Although all models assume more or less explicitly costs of reproduction, some other models are called reproductive-effort models (Stearns, 1992), because they are more directly based on allocation patterns. The part of an individual's energy which is allocated to reproduction during a given reproductive episode (the reproductive effort), is no longer available for survival nor future reproduction, and vice versa. As one function decreases and the other increases, this relationship is named trade-off, and reproduction is said to be costly. The optimum reproductive effort here depends on the balance between the benefits of current reproduction (in terms of progeny) and its costs (in terms of mortality or future reproduction), which is also modified by external causes of mortality. If the optimum reproductive effort corresponds to the maximum possible value, semelparity should evolve, whereas iteroparity will be the probable outcome in other cases (Gadgil & Bossert, 1970; Schaffer, 1974; Taylor *et al.*, 1974; Schaffer & Rosenzweig, 1977). The notions of reproductive effort and of reproductive costs gave more recently rise to optimal allocation models in which energy is explicitly divided between reproduction, growth, survival and even maintenance (among many others, see: Perrin, 1991; Perrin & Sibly, 1993; Teriokhin, 1998; Kozlowski & Teriokhin, 1999). As both categories of models assume more or less explicitly the occurrence of trade-offs between current reproduction and survival (or future reproduction) and the influence of external causes of mortality, the main difference arises from the method: contrary to others, reproductive effort models consider a continuum of strategies with semelparity being one extreme, which might be more realistic.

Trade-offs may be revealed through the observation of negative correlations between simple phenotypic measures of traits related to reproduction and survival. Unfortunately, using this approach, trade-offs may be masked by environmental variability (Reznick, 1985; Van Noordwijk & de Jong, 1986). Observation of trade-offs may even depend on the quantity of available resources (Van Noordwijk & de Jong, 1986). The search for phenotypic trade-offs therefore means keeping in mind the conditions in which phenotypic correlations constitute good representations of genetic correlations (Reznick, 1985; Cheverud, 1988; Pease & Bull, 1988; Willis *et al.*, 1991; Roff, 2000).

One theoretical prediction resulting from the trade-off assumption is that, whereas reproductive effort in semelparous taxa will be fixed to its physiological maximum (Stearns, 1992), iteroparous taxa may be able to change their reproductive effort in response to environmental factors, such as the quantity of available resources. This plasticity of reproductive effort can be of major importance in iteroparous taxa, which face different environmental conditions from one reproductive episode to the next (Hirshfield & Tinkle, 1975).

Families or genera with taxa differing in life history are ideal for the comparative study of reproductive effort and trade-offs, because such organisms are otherwise similar in many ways. They are quite rare but much sought-after (for examples of interspecific comparisons between two, or rarely more, semelparous and iteroparous taxa, see: Pitelka, 1977; Primack, 1979; Marshall *et al.*, 1985; Young, 1990; for intraspecific comparisons of two morphs or taxa, see: Spira & Pollak, 1986; Grosberg, 1988; Till-Bottraud *et al.*, 1990). The *Beta* species-complex is therefore of particular interest. It includes *Beta vulgaris* ssp. *vulgaris*, the cultivated beet and four wild relatives. All are able to interbreed. Nevertheless such crosses are unlikely in the wild, which explains why some taxa are described as distinct species. The species *Beta vulgaris* includes *B. v. vulgaris*, its closest wild relative *B. v. maritima* and *B. v. adanensis*. The two other species of the complex are *B. patula* and *B. macrocarpa* (Letschert, 1993). Within the *Beta* species-complex, we observed a gradient from pronounced iteroparity to pronounced semelparity. Among populations of *B. v. maritima*, which is iteroparous, the variation of life expectancy is striking: under controlled conditions, mean life spans range from 2 to 10 years (Van Dijk & Desplanque, 1999). *B. patula* is mostly semelparous but some individuals may survive and reproduce at least for 2 years (Letschert, 1993, personal observations). According to our observations the subspecies *B. v. adanensis* is semelparous, although it is sometimes described as possibly iteroparous (Letschert, 1993). *B. macrocarpa* is strictly semelparous, dying immediately after seed maturity. The *Beta* complex is therefore ideal for comparisons between many phylogenetically closely related taxa or populations with contrasting life cycles, such as semelparous vs. iteroparous life cycles, but also with gradual variations between these extreme life cycles. The study of life histories has received considerable attention in the zoological literature but is poor in plant taxa, where most studies concentrate on traits related to reproductive systems. Furthermore, although life-history predictions have been extensively tested through the opposition of semelparous and iteroparous taxa in animals (Calow, 1978; Grosberg, 1988) and in plants (Pitelka, 1977; Primack, 1979), tests in a life-cycle gradient going from annuality to long-lived iteroparity are lacking. To our knowledge, such test has only been done in a fish, *Alosa sapidissima*, for which the shortest life cycle is long-lived semelparity (Leggett & Carscadden, 1978) and this is totally lacking in plant taxa. The *Beta* species complex combines the advantages of allowing tests of predictions in a new plant system, constituted of closely related taxa showing gradual variations in life histories, rather than oppositions.

In a controlled-conditions experiment, involving six different life cycles of the *Beta* species complex (from

long-lived iteroparous to strictly semelparous plants), grown at three contrasting nutrient levels, we addressed the following questions: (1) Does reproductive effort decrease with increasing life span, from the reference maximum value found in strictly semelparous plants to a minimum value found in the longest-lived iteroparous beets? Is reproductive effort more plastic in iteroparous than semelparous taxa? (2) Are there any significant phenotypic correlations between allocation to survival and reproduction along the iteroparity gradient? What is their sign? Are these phenotypic correlations sensitive to the nutritive conditions?

Methods

Experimental design

Six different life cycles were selected to represent the gradient: three mostly semelparous species, *B. macrocarpa*, *B. v. adanensis*, *B. patula* and three iteroparous life cycles of *B. v. maritima* with different life expectancies. To (1) separate life cycle effects from population effects and to (2) increase the probability of observing trade-offs (Van Noordwijk & de Jong, 1986), two origins were chosen per life cycle, except for *B. patula* (an endemic species from Madeira) for which only one population is known (Table 1).

Seeds of *B. macrocarpa* (origins VS1 and VS2, Table 1), *B. v. adanensis* (origins LS1 and LS2 from two different Greek localities), and *B. patula* (SI) were provided by L. Frese (BAZ Gene Bank at Braunschweig, Germany, each origin being collected as a bulk). These taxa are essentially autogamous, contrary to *B. v. maritima* which is self-incompatible. The *B. v. maritima* origins LI1 and LI2 (with a mean life span of 2–3 years) and MI1 and MI2 (3–4 years) were part of our laboratory collections (Van Dijk *et al.*, 1997). In the very iteroparous origins (VI1 and VI2, with a mean life span of about 5 years) we had to increase the frequency of the dominant B allele, which suppresses the vernalization requirement, i.e. induction

of flowering by exposure of the bb plants to low temperature during winter (Abegg, 1936; Boudry *et al.*, 1994), and allows the comparison of plants flowering in the first year. This was done by crosses (in VI1, both parent plants had at least one B allele: B– × B–; in VI2, one parent had at least one B allele, contrary to the other: B– × bb), thus obtaining approximately 75 and 50% of plants (depending on the penetrance, see Boudry *et al.*, 1994) without vernalization requirement (B) which were kept for this experiment. All *B. v. maritima* origins were full sibs.

Plants were sown during April and grown in a greenhouse under natural day-length at three different nutrient levels (3 dm^3 pots): a rich and an intermediate medium of enriched turf (respectively, 2 and 0.8 kg m^{-3} of 14:16:18 NPK fertilizer with microelements) and a low nutrient medium of a mix of vermiculite and 0.8 kg m^{-3} fertilized turf in proportions 1:9, thus containing 0.08 kg m^{-3} of fertilizer. Plants were randomized each fortnight during the experiment. Pollen donators were added to the experimental design to avoid seed-set limitation.

This experiment therefore involved 11 origins and three nutritive treatments per origin. To obtain around 10 individuals per treatment, 360 plants were potted at the beginning of the experiment. After elimination of plants requiring vernalization or that had been accidentally damaged, 309 individuals remained for further analysis.

Dry biomass distribution in plants

Iteroparous beets overwinter as vegetative rosettes, which are produced at the end of the reproductive season. Except for the seeds, all other aerial parts (stems, leaves and flowers) dry out. At this unambiguous physiological stage, we harvested plants of all life cycles in their first year. All plants were harvested and divided into seeds, flowers (both aborted and nonfertilized), major roots, leaves, stems, rosette leaves and rosette stems. All those

Table 1 Taxa, life cycles, codes and number of individuals of the various origins of the experiment. Labelling was chosen to obviate future necessity of cross-referencing to this table: long-lived iteroparous life cycles or origins are referred to as VI for 'very' and 'iteroparous', M means 'medium', L 'less' and S simply means 'semelparous'.

Taxon	Origin	Life cycle	Code	Number of individuals
B. v. maritima	French Atlantic coast 1	Iteroparous, 4.7 years ± 1.9	VI1	41
B. v. maritima	French Atlantic coast 2	Iteroparous, 5.5 years ± 2.0	VI2	22
B. v. maritima	Mediterranean 1	Iteroparous, 4.1 years ± 1.5	MI1	29
B. v. maritima	Mediterranean 2	Iteroparous, 2.8 years ± 1.2	MI2	30
B. v. maritima	Agen area 1	Iteroparous, 2.0 years ± 0.9	LI1	28
B. v. maritima	Agen area 2	Iteroparous, 2.0 years ± 1.0	LI2	29
B. patula	Madeira	Semelparous, or rarely iteroparous	SI	20
B. v. adanensis	Greece 1	Semelparous	LS1	27
B. v. adanensis	Greece 2	Semelparous	LS2	30
B. macrocarpa	Cyprus	Strictly semelparous	VS1	27
B. macrocarpa	Tunisia	Strictly semelparous	VS2	26

parts were dried in a 50 °C oven for 7 days (14 for the roots). Dry weight was used as an estimation of carbon allocation to the different parts of the plants.

Estimations of reproductive effort and survival

Reproductive effort is the relative investment of an individual in reproduction, which is expected to compete with future survival and reproduction. In annual plants reproductive effort is expected to be maximum, but this maximum will depend on the efficiency of converting the resources drained from the vegetative tissues into reproduction. This efficiency may depend on the evolutionary stage: in a lineage that is evolving towards semelparity, reproductive effort is expected to continue to increase after the population has become semelparous.

The aim here was to compare different taxa and origins differing by their life cycles. We used the only strictly semelparous taxon (e.g. *B. macrocarpa*) as a reference point for maximum reproductive effort in our comparisons. We defined major roots (able to stock resources) and rosette leaves (in charge of photosynthesis during winter) as investment in survival, which was a good compromise for the whole gradient, although the consequence is a potential allocation to survival in semelparous forms (albeit a weak one). Reproductive parts were restricted to seeds and nonseeding flowers. Dry leaves could be considered as devoted to both reproduction and survival because they are responsible for photosynthesis during the growth of both roots and flowering stems. Dry stems only develop when plants bolt for flowering, but they also bear leaves and conduct the products of photosynthesis to the reserve organs. Therefore, we do not consider dry leaves and stems as reproductive structures as suggested by Thompson & Stewart (1981). Furthermore stems could introduce bias in the comparisons of reproductive allocation between species because they highly depend on the architecture of the plants. Thus reproductive effort was estimated as the dry biomass of parts devoted with certainty to reproduction (seeds and flowers) divided by the dry biomass of parts devoted with certainty to survival and reproduction (major roots plus rosette leaves and seeds plus flowers).

In this way, what will be called reproductive effort later on reflects the trade-off between current reproduction and future survival and reproduction and allows the comparison among all taxa of the *Beta* species complex. Obviously we checked that this method does not change the qualitative results compared with a classical reproductive effort (reproductive biomass divided by total biomass), and that it only enhances their clarity.

Survival was indicated by the production of rosette leaves at the end of the reproductive season. As all plants were harvested, estimations of mean life spans per origin (Table 1) were obtained from previous experiments (method in: Van Dijk & Desplanque, 1999).

Statistical analyses

A mixed-model ANOVA (GLM procedure, SAS Institute, 1988) was applied to compare reproductive effort between life cycles, origins within life cycles and nutrient levels (treatments). Life cycle and treatment were fixed effects, all others were random. This model was a partially nested mixed-model ANOVA:

$$Y_{ijkn} = \mu + \alpha_i + B_{ij} + \delta_k + (\delta\alpha)_{ik} + (\delta B)_{ijk} + e_{ijkn}$$

where Y_{ijkn} is the reproductive effort of the nth individual of the jth origin nested in the ith life cycle and cultivated in the kth treatment. μ is the mean, α_i is the fixed effect of the ith life cycle, δ_k is the fixed effect of the kth treatment, B_{ij} is the random contribution of the jth origin of the ith life cycle. $(\delta\alpha)_{ik}$ and $(\delta B)_{ijk}$ are, respectively, the life cycle × nutritive treatment interaction effect and the origin × nutritive treatment interaction effect, and e_{ijkn} is the error term. Test denominators were mean squares of origin (life cycle) for life cycle effect, of treatment × origin (life cycle) for treatment and treatment × life cycle effects and of the error term for other effects. F-tests used type III sums of squares. This analysis of variance was first conducted for all origins and second for the semelparous (VS1, VS2, LS1, LS2, SI) and the iteroparous origins (LI1, LI2, MI1, MI2, VI1 and VI2) separately. Reproductive effort data were arcsine transformed to meet the normality and homoscedasticity requirement of ANOVA (Sokal & Rohlf, 1995). In the analysis of variance conducted for all origins, a planned contrast (d.f. = 1) opposing semelparous to iteroparous life cycles (with origin within life cycle as an error term) was conducted (Sokal & Rohlf, 1995).

Among-origins, correlations between reproductive effort and life span were calculated for each treatment.

To investigate phenotypic trade-offs, data of the two origins from a same life cycle were pooled to increase genetic variability, thus increasing the probability of observing trade-offs (Van Noordwijk & de Jong, 1986). As this confounds correlation because of covariance within and between origins, we partitioned the covariance within life cycles into within and between origins covariances (using PROC NESTED, SAS Institute, 1988): we observed that correlations were mostly caused by the within-origins covariances. Pairwise Pearson correlations were therefore calculated among the seven types of biomass data (dry stems, flowers, seeds, dry leaves, major roots, rosette leaves and stems) for each combination of life cycle and treatment (PROC CORR, SAS Institute, 1988). Tests were considered significant at $P < 0.05$. Significance levels were adjusted to multiple inferences by a sequential Bonferroni test (Rice, 1988), with $\alpha = 0.05$, 21 tests in iteroparous plants, and 10 tests in semelparous plants (because they do not have any rosette leaves nor stems). Semelparous life cycles were considered as control ones in which only positive correlations are expected.

In order to estimate consistency of correlation patterns among pairs of treatments, Mantel tests (Mantel, 1967) were conducted (using Genepop 3.2 Raymond & Rousset, 1995) among pairs of correlation matrices in a same life cycle (i.e. three tests per life cycle).

Results

Reproductive effort along the iteroparity – semelparity gradient

Iteroparous plants generally have a small reproductive effort compared with the maximum value reached in the present study by annuals (Fig. 1). The planned contrast between semelparous and iteroparous life cycles reveals a highly significant difference between semelparous and iteroparous life cycles for reproductive effort ($F_{1,5} = 23.27$, $P < 0.01$). The analysis of variance reveals significant effects of life cycle ($P < 0.05$, Table 2a), origin, treatment and life cycle × treatment interaction ($P < 0.001$).

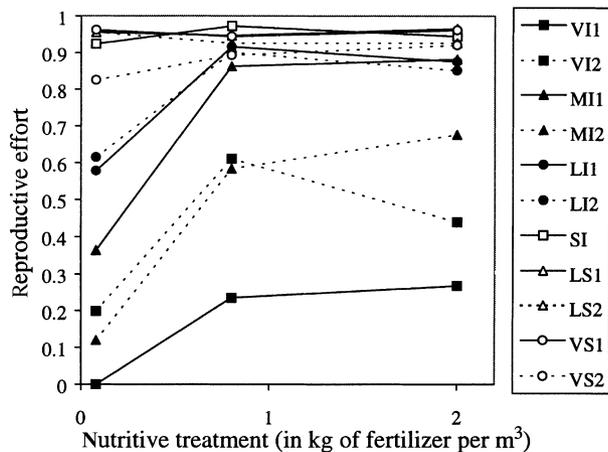The correlation between reproductive effort and mean life span among origins is significantly negative whatever

Fig. 1 Reproductive effort with respect to treatment for the 11 origins.

the treatment (low: $r = -0.893$, $P < 0.001$; medium: $r = -0.757$, $P < 0.001$; high: $r = -0.844$, $P < 0.001$, $n = 11$).

Plasticity of reproductive effort

The analysis of variance of reproductive effort for all life cycles (Table 2a) reveals a significant effect of treatment). The life cycle × treatment interaction is highly significant, whereas the origin × treatment interaction is not. Semelparous life cycles have a constant reproductive effort among treatments (Fig. 1, Table 2b), whereas in iteroparous life cycles reproductive effort increases significantly with treatment (Fig. 1, Table 2c). Origin × treatment interactions are not significant when semelparous and iteroparous life cycles are analysed separately (Table 2b and c).

In VI1, all individuals of the low nutrient treatment stayed at rosette stage and did not flower. Similarly, two MI2 individuals did not flower in this treatment. Three individuals of *B. patula* (SI) maintained basal leaves after seed maturation in the low nutrient treatment. These leaves may be considered as rosette leaves, allowing individuals to survive in low nutrient environments. No surviving structure has been observed after seed maturation in *B. v. adanensis* nor in *B. macrocarpa*.

Phenotypic correlations within life cycles

After a sequential Bonferroni test, significant negative correlations among individuals within life cycles were found exclusively between dry stems, flowers and seeds vs. dry leaves, roots, rosette leaves and stems (Table 3a and b). Correlations between dry stems, flowers and seeds or between dry leaves, roots, rosette leaves and stems, were either positive or non-significant after a sequential Bonferroni test (Table 3b).

All negative correlations (significant at $\alpha = 0.05$) were obtained in iteroparous life cycles (Table 3a), and the sequential Bonferroni test supported negative correlations in the very long-lived iteroparous life cycle. The significant negative correlations became less numerous with decreasing iteroparity. On the other hand, positive correlations become progressively more numerous and

Table 2 Mixed model analysis of variance (GLM) on arcsine transformed reproductive efforts. A first analysis has been conducted on all life cycles (a), two others have been conducted on semelparous life cycles (b) and on iteroparous life cycles (c) separately.

Source	(a) All plants			(b) Semelparous life cycles			(c) Iteroparous life cycles		
	d.f.	MS	F	d.f.	MS	F	d.f.	MS	F
Life cycles (L)	5	5.81	8.52*	2	0.04	0.32	2	5.35	5.06
Origin [O(L)]	5	0.68	37.93***	2	0.12	10.99***	3	1.06	46.05***
Treatment (T)	2	2.06	74.01***	2	0.01	0.6	2	4.19	112.83***
L × T	10	0.39	14.08***	4	0.02	1.43	4	0.14	3.67
O(L) × T	10	0.03	1.55	4	0.01	1.26	6	0.04	1.62
Error	276	0.02		115	0.01		161	0.02	

*$P < 0.05$; ***$P < 0.001$.

more significant (Table 3a). Figure 2 illustrates the general tendencies of the phenotypic correlations between reproduction and survival.

Mantel tests among pairs of correlation matrices reveal a significant consistency of correlation patterns among pairs of treatments ($P < 0.05$), except comparisons of low vs. medium or low vs. high nutritive treatments in the LS life cycle and of low vs. medium nutritive treatments in the VS life cycle (i.e. 13 comparisons of 16 are significant at $\alpha = 0.05$).

Discussion

Reproductive effort in the semelparity–iteroparity gradient

Our results show that reproductive effort ranges between the obvious high value found in semelparous taxa and a relatively low value found in the longest-lived iteroparous beets. To our surprise, there was no significant difference among life cycles within semelparous or iteroparous beets. *B. macrocarpa* and *B. v. adanensis* seemed to be truly semelparous but *B. patula* produced rosette leaves in low nutrient conditions, which reveals its capacity to invest in survival. Within the iteroparous taxon *B. v. maritima*, analysis of variance did not reveal any effect of life cycle. We can nevertheless note that reproductive effort was negatively correlated with mean life span. This observation of reproductive cost is consistent with life-history theory (Roff, 1992; Stearns, 1992).

Many authors revealed that reproductive effort is higher in semelparous taxa than in iteroparous ones (Pitelka, 1977; Calow, 1978; Primack, 1979; Grosberg, 1988), but, to our knowledge, such evidence of negative relationship between reproduction and survival along a life-cycle gradient is only given by Leggett & Carscadden (1978) for the fish *Alosa sapidissima*.

It is worth noting that our estimate of reproductive effort does not include expenditure in pollen. That might cause a problem for the comparison of the reproductive effort between semelparous plants, which are all selfers here, and iteroparous plants, which are outcrossers. In selfing semelparous plants indeed, the smaller investment in pollen might allow a higher investment in flowers and seeds than in outcrossing iteroparous plants, even with a similar reproductive effort (including pollen). This is not probable in terms of biomass (because of the so small biomass of stamens compared with seed biomass in wild beets), but might be investigated further in terms of energy amount.

The hypothesis of a higher reproductive effort in semelparous taxa relative to iteroparous taxa can be tested by using several semelparous and iteroparous related species, provided there is enough taxonomic diversity within each life cycle to randomize differences between taxa within life cycles (in order to eliminate the possibility of a phylogenetic constraint on the trait). Here the actual iteroparous origins belong to the same subspecies, *B. v. maritima*, which would decrease the interest of comparing reproductive efforts of semelparous vs.

Table 3 Phenotypic correlations per life-cycle. (a) Number of significant* negative and positive correlations between dry stems, flowers and seeds on the one hand, and dry leaves, roots, rosette leaves and rosette stems on the other. (b) Number of significant† negative and positive correlations: other tests.

	Significant negative correlations			Significant positive correlations		
Life-cycle	Low nutrient treatment	Medium nutrient treatment	High nutrient treatment	Low nutrient treatment	Medium nutrient treatment	High nutrient treatment
(a)						
VI	3 (2)	10 (3)	6 (4)	0	0	0
MI	3 (0)	1 (0)	2 (0)	0	0	0
LI	1 (0)	2 (0)	1 (0)	3 (0)	1 (0)	4 (4)
SI	0	0	0	2 (0)	1 (1)	1 (0)
LS	0	0	0	4 (4)	3 (2)	6 (6)
VS	0	0	0	1 (1)	4 (4)	6 (6)
(b)						
VI	0	0	0	4 (4)	4 (1)	7 (5)
MI	0	0	0	6 (1)	4 (2)	5 (1)
LI	0	0	0	1 (0)	1 (1)	3 (3)
SI	1 (0)	0	0	2 (1)	1 (0)	0
LS	0	0	0	3 (2)	2 (1)	4 (3)
VS	0	0	0	2 (0)	2 (2)	3 (3)

*Significance is tested for $\alpha = 0.05$. Significant correlations after a sequential Bonferroni test are in parentheses. The total number of tested correlations were 12 in life cycles 1–3, as well as in life cycle 4, poor treatment, and six in all others, as a result of missing parts (rosette stems and leaves) in annual plants.

†Significance is tested for $\alpha = 0.05$. Significant correlations after a sequential Bonferroni test are in parentheses. The total number of tested correlations was nine in life cycles 1–3, as well as in life cycle 4, poor treatment. It was equal to four in all others.
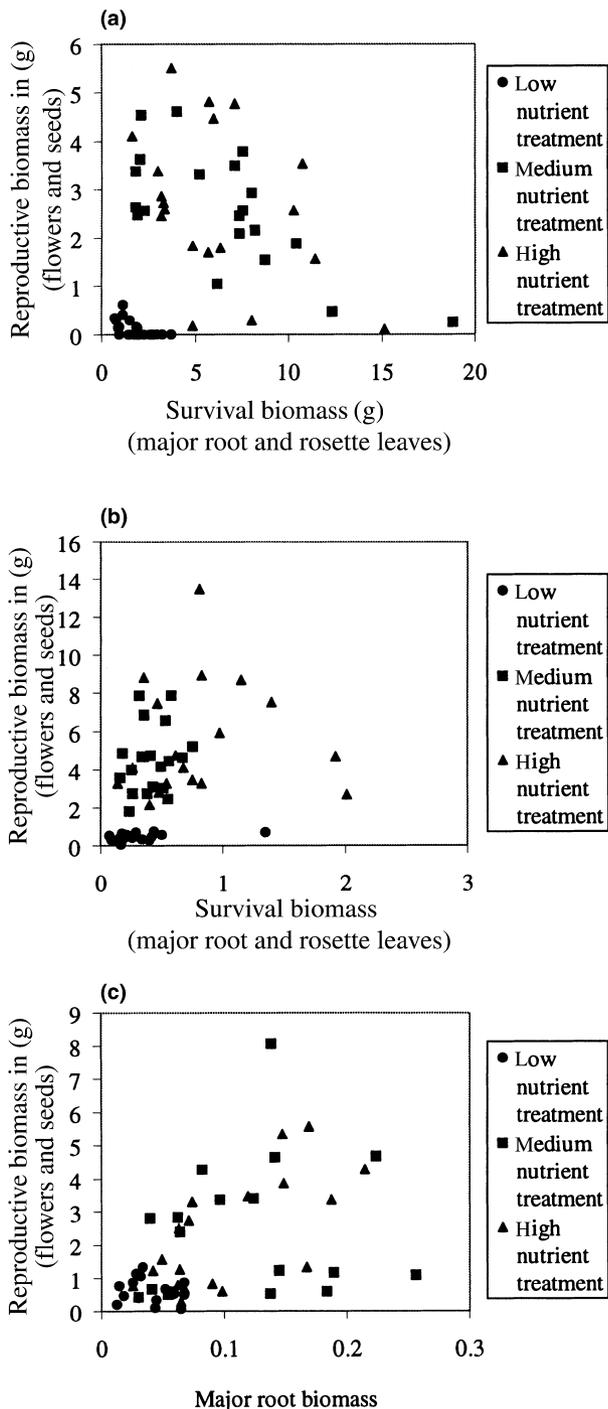
Fig. 2 Reproductive biomass vs. survival biomass in two extreme and an intermediate life cycle. Both origins of each life cycle are represented altogether. (a) Long-lived iteroparous life cycle. (b) Short-lived iteroparous life cycle. (c) Strict semelparous life cycle.

iteroparous taxa. However the most important result is the decrease of reproductive effort with increasing life span, which is observed in the overall life-cycle gradient and is

therefore not dependent on phylogenetic constraints. Furthermore the most important source of variance for reproductive effort is not the taxonomic level but the origin, especially within *B. v. maritima* (Fig. 1).

Plasticity of reproductive effort

The analysis of variance in iteroparous beets revealed a significant effect of nutrient level on reproductive allocation: investment in reproduction is lower when resource level is low. The most striking example was one longest-lived iteroparous origin (VI1), in which no plant flowered in the low nutrient conditions. This is also true for one moderately iteroparous origin (MI2), in which two individuals of 10 did not flower in the low nutrient conditions, and for *B. patula*, which survived after reproduction in the low nutrient treatment. In the most semelparous beets, treatment has no significant effect on reproductive effort: the allocation to reproduction is at its maximum whatever the availability of resources. A similar pattern was observed by Grosberg (1988) in the colonial ascidian *Botryllus schlosseri*.

This suggests that, in low nutrient environments, iteroparous *Beta* invest in survival rather than in reproduction. The longest-lived iteroparous ones may even skip a reproductive season in bad years. On the other hand, in good conditions, survival is more or less guaranteed and surplus resources are invested in reproduction. Two mechanisms of delaying first reproduction have been proposed. First is the occurrence of a threshold size. Some plants have to reach a certain size before being able to flower (Tissue & Nobel, 1990; Wesselingh *et al.*, 1997). Secondly, growth rate may also determine flowering. Smit (1983) showed that bolting rate (the percentage of plants that bolt and flower) is related to growth rate in cultivated beet, *B. v. vulgaris*. The phylogenetic proximity to *B. v. maritima* suggests that flowering in wild beets may also depend on growth rate.

Iteroparous plants, especially wild beets which live mainly at high water margins, will experience varying environmental conditions from one reproductive episode to another. Hirshfield & Tinkle (1975) suggested the possibility of fluctuating reproductive effort in variable environments in iteroparous plants. This strategy may evolve in seasonal environments with unpredictable conditions from year to year (Stearns, 1976). Such iteroparous plants thus optimize reproductive effort not only as a function of the mean environment but also of its short-term variation. On the other hand, semelparous plants, which are not able to survive, have to invest maximally in reproduction whatever the environmental conditions.

Phenotypic correlations within life cycles

Phenotypic trade-offs between dry stems, flowers and seeds on the one hand, and dry leaves, roots, rosette

leaves and rosette stems on the other, are exclusively found in the iteroparous plants, especially in the longest-lived iteroparous life cycles. Phenotypic correlations are strongly positive in pronounced semelparous taxa. In those plants, major-root biomass is fixed to a minimum not devoted to survival: in semelparous plants the principal root is the architectural link between roots (devoted to foraging and fixation) and aerial parts. Major-root biomass is therefore positively correlated to the size of the plant and variations in traits are the result of variations in total biomass, resulting in positive correlations. Between these two extreme positions (long-lived iteroparous life cycles with trade-offs and strict semelparous life cycles with positive correlations), intermediate life cycles show mostly nonsignificant correlations of both signs.

Van Noordwijk & de Jong (1986) proposed a statistical model predicting the sign of a phenotypic correlation between traits linked by genetically determined trade-offs, based on an acquisition–allocation balance. They showed that negative correlations are observed in populations with a high genetic variability for resource allocation and a low variability in resource acquisition (for environmental reasons). Low genetic variability for resource allocation compared with a high variability in resource acquisition will result in positive correlations. Genetic differences in capacity for acquiring resources would lead to positive genetic correlations (de Laguérie *et al.*, 1991). In the very iteroparous life cycles of this experiment, genetic variability for the allocation to reproduction and survival probably dominates the weak environmental variability. In the very semelparous life cycles, allocation to survival is fixed to zero, all parts are related to reproduction, resulting in positive correlations due to environmental variation and genetic differences in resource acquisition and photosynthesis. Finally, in intermediate life cycles (LI and SI), investment in survival is weak and genetic variability for allocation to reproduction and survival becomes dominated by variability in resource acquisition, even in controlled conditions. Long-lived iteroparous beets add new evidence to the occurrence of trade-offs between reproduction and survival, whereas the life-cycle gradient gives further empirical information about possibility of observing phenotypic trade-offs in controlled experiments.

Some authors predict more negative correlations in the most limiting condition (Reznick, 1985), in which reproductive and survival parts physiologically compete for limited resources. On the contrary, according to Van Noordwijk & de Jong (1986), for mathematical reasons, the average quantity of acquired resources has to be high to demonstrate variation in resource allocation and thus trade-offs. de Laguérie *et al.* (1993) showed that negative genetic correlations between fitness components are more likely to appear in intermediate environments because of saturation of response curves in very rich environments. Multi-environment experiments are

therefore a good solution for this complex problem (Piquot *et al.*, 1998). An experiment in *Lychnis flos-cuculi* (Biere, 1995) showed more trade-offs in limiting conditions, whereas limiting and intermediate conditions revealed more trade-offs in *Sparganium erectum* (Piquot *et al.*, 1998). Our experiment suggests that trade-offs may be more numerous or more significant in rich environments although present at all resource levels, because phenotypic correlations appear very consistent among environments.

Reproductive cost has been demonstrated in many plant species, e.g. increased mortality rate with fruiting (Sohn & Policansky, 1977), reduced probability of subsequent reproduction or reduced growth with fruit production (Snow & Whigham, 1989; Worley & Harder, 1996; Primack & Stacy, 1998). Trade-offs also appeared between rhizome and seed and between rhizome and corm in the grass *Amphibromus scabrivalvis* (Cheplick, 1995) and between several sexual and asexual traits in *S. erectum* (Piquot *et al.*, 1998). Animal species also show various costs of reproduction: reduced subsequent reproduction in birds (Gustafsson & Sutherland, 1988; Nilsson & Svensson, 1996), reduced immune response (Ots & Hórak, 1996; Deerenberg *et al.*, 1997; Oppliger *et al.*, 1997; Nordling *et al.*, 1998), weight loss in some male lizards (Abell, 2000), reduced survival in insects (Tatar & Carey, 1995; Tanaka & Suzuki, 1998) and birds (escape performance: Lee *et al.*, 1996). Our experiment shows decreasing survival (or future reproduction) with increasing investment in current reproduction, by means of two different approaches (reproductive effort decreases with increasing life span, and phenotypic trade-offs have been found in the longest-lived iteroparous plants), both being connected with a potential decrease in survival or a decrease in future fecundity via the decrease in reserve organs.

Acknowledgments

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