

Life span in *Beta vulgaris* ssp. *maritima*: the effects of age at first reproduction and disturbance

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Summary

- 1 Life span, an essential component of fitness, can be affected by traits such as age at first reproduction, as well as by the mortality regime imposed by the environment. In a long-term experiment under controlled conditions, we studied life span in an iteroparous plant species, the sea beet *Beta vulgaris* ssp. *maritima* (L.), from 104 wild populations sampled in France, Belgium, Great Britain and the Netherlands. We estimated the intensity of selective pressures on life span and the specific effects of age at first reproduction (first or second year, depending on vernalization requirement) and of environmental disturbance.
- 2 Mean life span (measured in glasshouse conditions) increases with latitude from about 2 years in inland habitats of south-western France to at least 11 years in north Brittany, before decreasing to about 5 years in the northernmost populations.
- 3 Comparison of spatial autocorrelograms for life span and cytoplasmic neutral markers showed there is strong selection for life span.
- 4 Within populations the effect of age at first reproduction on life span proved to be marginal. No causal relationship was detected among populations, although, in the southern part of the study area, a strong association between reproduction in the first year and short life span suggests common selective pressures.
- 5 Life span appeared to be highly associated with habitat type, as defined by mortality regimes. Populations with the longest-lived individuals occurred in the most stable habitats and populations with the shortest-lived individuals in the most disturbed locations.

Key-words: age at maturity, life history, longevity, long-term experiment, mortality regime

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Introduction

Life span appears to be one of the major life-history traits of an individual. It has obvious effects on the number of reproductive episodes in organisms that reproduce repeatedly, on brood size or quality (via trade-offs between investment in survival and reproduction), and on demography (Schaffer & Rosenzweig 1977; Roff 1992; Stearns 1992). Longevity is therefore subject to natural selection as a major component of individual fitness (Kirkwood & Rose 1991; Partridge & Barton 1993).

The direction of selection on life span will depend on the optimal compromise (in terms of total fitness) in the trade-offs between current reproduction and survival (Williams 1966; Schaffer & Rosenzweig 1977;

Kirkwood & Rose 1991; Roff 1992; Stearns 1992). This is dependent not only on the intrinsic relationship between these traits, but also on any external factors that influence them. Mortality due to external causes, e.g. herbivory, disturbance or drought, may shift the optimal compromise towards shorter life spans, annuality being the extreme possibility (Hamilton 1966; Edney & Gill 1968; Gadgil & Bossert 1970; Bryant 1971; Charnov & Schaffer 1973; Charlesworth 1980; Stearns 1992). Any between-population differences in mortality regime will therefore induce variation in life span (there is little empirical evidence but see Reznick *et al.* 1990; Till-Bottraud *et al.* 1990; Reznick *et al.* 1996).

In the *Beta* species-complex, the sea beet, *Beta vulgaris* ssp. *maritima* (L.) Arcangeli, has a particularly variable life cycle (Letschert 1993), from long-lived iteroparous (repeated reproduction, see Gadgil & Bossert 1970) in the northern part of its distribution area (Atlantic coasts of France, Belgium, the Netherlands, Great-Britain and of the western Baltic sea) to

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annual (short-lived semelparous) in the Mediterranean area (Letschert 1993).

Ssp. maritima shows marked variability in its vernalization requirement (i.e. exposure to low temperature during winter) for flowering (Van Dijk *et al.* 1997), which is mainly determined by the recessive genotype at the B/b locus (Boudry *et al.* 1994). Individuals requiring vernalization are quite rare in Mediterranean populations, but are the rule in northern populations, with the two types coexisting at various rates in the intervening regions (Van Dijk *et al.* 1997). Unless germination occurs very early, a vernalization requirement delays flowering until the second year and in semelparous plants this has obvious consequences for life span as death is also delayed. The delay of flowering may also increase life span in iteroparous plants, such as the Atlantic sea beetle, because of trade-offs between reproduction and survival (Hautekète *et al.* 2001), but this is poorly documented. Coexistence in the same population of sea beetle of plants flowering in their first or second year may, however, provide information about the relationship between age at first flowering and life span.

Sea beetle occurs in various habitats with contrasting disturbance regimes: its natural habitat is high water margins along the sea shores, but wild populations are also found in man-disturbed habitats, e.g. in the inland area of southern France (Van Dijk *et al.* 1997; Desplanque *et al.* 1999). As disturbance is thought to greatly influence life span, through its modification of the mortality regime (Murphy 1968; Charnov & Schaffer 1973; Michod 1979; Bulmer 1985; Orzack & Tuljapurkar 1989; Charnov 1990; Benton & Grant 1999), we assess the impact of disturbance as well as vernalization requirement on the distribution of life span in *ssp. maritima*.

To gain insight into the importance of natural selection, relative to random genetic drift, in shaping the life cycle patterns, we use spatial autocorrelation analysis to compare the genetic structure of neutral cytoplasmic markers (cytotypes and mitotypes) with the distribution of life span in *ssp. maritima*.

We address the following questions:

- What is the range of variation in life span in *ssp. maritima*? How is this trait geographically distributed?
- Does the delay of reproduction to the second year of life influence life span?
- Is life span influenced by habitat, i.e. does life span decrease with disturbance?
- What is the relative influence of selective pressures and random genetic drift on the distribution pattern of life span in *ssp. maritima*?

Materials and methods

STUDY SPECIES

Beta vulgaris ssp. maritima is self-incompatible and mostly wind-pollinated. Groups of two to eight flowers

form glomerules whose seeds mature as a seedball, perianths forming a corky pericarp firmly attached to the seeds (Letschert 1993). This appears to be an adaptation to transport by seawater (Dale & Ford-Lloyd 1985) or possibly to surface spread by wind (valuable both along coasts and in disturbed locations).

Sea beetle occurs along the Atlantic coasts of western Europe and of western North Africa, as well as along coasts of the Mediterranean basin. Its distribution area ranges from Sweden to the Azores (Letschert 1993). Inland wild beetles are also known, e.g. in the south-western part of France (Desplanque *et al.* 1999).

SAMPLING AND CULTURE

Seeds were collected in 1989 (see Van Dijk *et al.* 1997). One hundred and four populations were sampled, mostly along French coasts and inland (see Fig. 1), but also on Jersey and Guernsey, along Belgian and Dutch coasts and along the English coast in Kent. In each population, seeds were collected as half-sibs. Sample size (one to 30 half-sib families) varied according to population size.

Plants were grown in the University of Lille experimental glasshouse using seeds from these 104 populations. New seedlings were generated each year from 1990 to 1999 to minimize sowing-year (cohort) effect, when possible using a different family in each year. In total 1715 individuals were grown (i.e. a mean of 16.49 individuals per population \pm s.d. 8.02).

Seeds were sown each year in September after 3 months with a long photoperiod (16 h, additional light being provided by 400 W high pressure sodium lamps) and non-vernalizing temperatures (20 °C), plants were grown in conditions avoiding external causes of mortality, under natural photoperiod and seminatural temperatures (from 5 °C to 25 °C). Plants were randomly distributed under spatially homogeneous glasshouse conditions and randomised twice a year. To replenish nutrients, plants were re-potted each year with new compost (3-L pots).

The same individuals, and hence the same experimental design, were used to estimate both life span and vernalization requirement.

LIFE SPAN

As death could not be observed for all individuals, especially in the later cohorts, we estimated life span using a linear regression model. We firstly calculated survival percentage to age x per population (x going from 1 to 10 years), as the number of x -year-old individuals relative to the number of individuals potted x years before. We did this separately for each cohort and then calculated the unweighted mean, thus minimizing any effect of accidentally unbalanced numbers of individuals per cohort. Survival percentage was arcsine transformed for normalization. For each population, these data were fitted to a linear regression model,

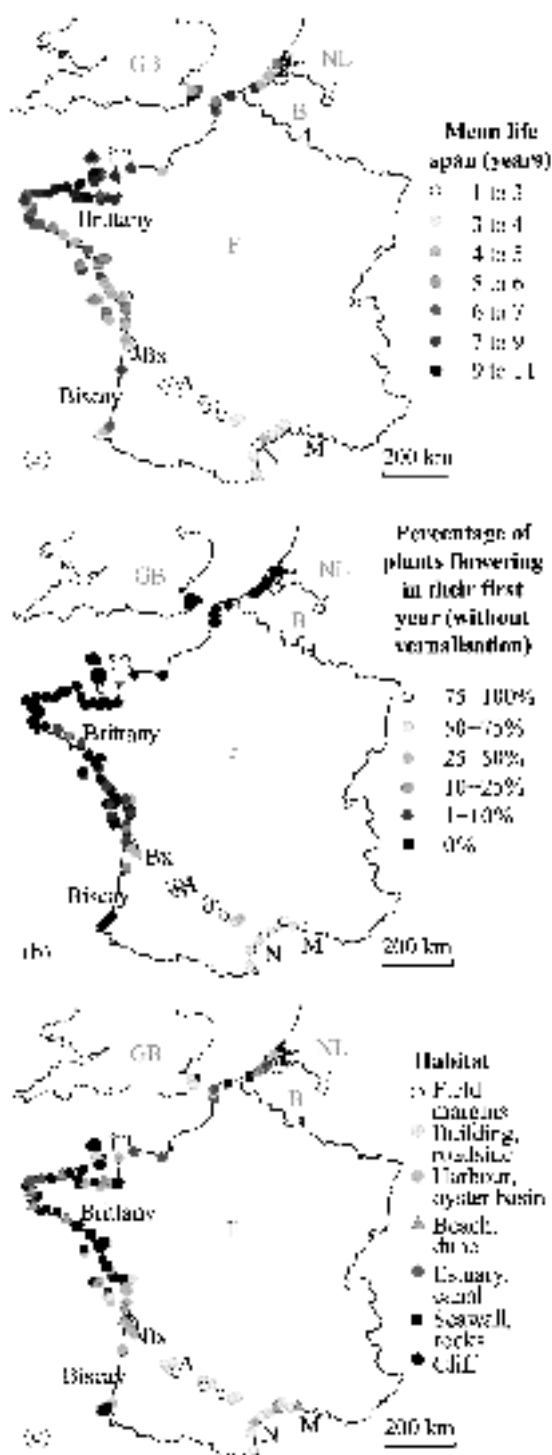


Fig. 1 Distribution of traits in studied sea beetle populations: (a) life span; (b) percentage of plants flowering in their first year (i.e. without vernalization); (c) habitats. F = France; B = Belgium; NL = the Netherlands; GB = Great Britain; Bx = Bordeaux; A = Agen; C = Carcassonne; N = Narbonne; M = Marseille.

with age as an independent variable and the arcsine-transformed survival percentage as the dependent variable, both weighted by the number of participating cohorts. Ages where survival stayed constant at 0 or 100% were excluded from the regression. We then estimated a mean life span for each population, as the age at which

50% of the individuals were still alive. Three populations showed very low mortality over the 10-year period and their mean life span was fixed by default to 11 years.

VERNALIZATION REQUIREMENT

Vernalization requirement was easily characterized as the three first months of growth occurred at long days and non-vernalizing temperatures: thus plants that did not flower in their first year were considered vernalization-dependent. Percentages of individuals requiring, or not, vernalization were calculated per population. As latitudinal variation in vernalization requirement has been reported in a previous paper (Van Dijk *et al.* 1997), we will here only focus on the impact of this trait on life span.

HABITAT TYPE

Each of the 104 populations was characterized for the presence of 11 habitat types: roadside, near-building area, margin of fields, harbour, oyster basin, beach or dune, rocks, canal, estuary, seawall and cliff, ranging from the least (natural granite cliffs) to most disturbed (margins of fields, where beets are regularly mown or eliminated by hand or by herbicide treatments).

CYTOPLASMIC HAPLOTYPES

Neutral markers, such as chlorotypes and mitotypes, have previously been assessed in, respectively, 40 and 38 populations with *c.* five individuals per population by non-radioactive RFLPs using total genomic DNA extracted following Saumitou-Laprade *et al.* (1991). The use of the entire chloroplast genome as a probe on *Hind*III, *Sma*I and *Eco*RV DNA digests revealed nine chloroplastic haplotypes (Forcioli *et al.* 1998) and three diagnostic probes on *Eco*RI DNA digests distinguished 10 mitochondrial haplotypes (Cuguen *et al.* 1994). The populations for which those data were available constituted geographically representative subsamples of our 104 populations, and can therefore be used to test correlation with life span. These previously described data therefore enabled us to assess the importance of selective pressures on life span within an entirely new context.

STATISTICAL ANALYSIS

Life span data were sorted by six major geographical areas: (i) Netherlands and Great Britain to north Brittany; (ii) south Brittany; (iii) Biscay (from Bordeaux to Spain, see Fig. 1); (iv) the inland area of southwestern France (around Agen and Carcassonne); (v) the Mediterranean coast; (vi) sublittoral populations: non-coastal populations contiguous to Atlantic and Mediterranean populations (the number of populations per geographical area is given Table 1). A Levene's test for the homogeneity of variances was performed on

Table 1 Life span of *Beta vulgaris* ssp. *maritima* in various geographical habitats

Geographical area	Mean life span	Variance	Coefficient of variation	Number of populations
Netherlands and Great Britain to North Brittany	7.16	3.28	25.45	39
South Brittany	5.88	1.22	19.20	12
Biscay	5.37	1.05	19.23	29
South-western France (inland)	2.12	0.10	15.71	8
Mediterranean	3.09	0.64	26.46	10
Sublittoral	3.27	0.87	29.64	6

ln-transformed life span data to test whether or not variances vary simply as a function of means.

To test for the effect of age at first flowering, we selected populations in which plants flowering in their first and second years coexisted (28 populations). We estimated mean life spans for the two categories, per population, before conducting a paired comparison between them (two-way ANOVA without replication: Sokal & Rohlf 1995; using PROC GLM, SAS Institute 1988).

A one-way ANOVA with habitat as a factor was performed to assess the effect of disturbance level on life spans. Multiple comparisons among means were conducted following a Student-Neumann-Keuls procedure (Sokal & Rohlf 1995).

Macrogeographical patterns of life span, percentage of flowering in the first year and cytotype frequencies distribution were assessed using spatial autocorrelation analysis, which expresses differentiation between populations as a function of distance.

The sea is thought to transport seedballs among coastal populations and human influence may have a similar effect in inland areas. Distances were calculated linearly after exclusion of non-continental populations according to the linear distribution of *Beta vulgaris* ssp. *maritima* continental populations in the investigated area (Desplanque 1999). To understand the relative contribution of southern populations in the life history and cytotype spatial structuring, separate analyses were performed for populations from the Netherlands to Biscay (path 1) and for populations from the Netherlands to Marseille via Bordeaux, Agen and Narbonne (path 2). Spatial autocorrelation analyses were performed using SAAP 4.3 (Wartenberg 1994) for life span and percentage of flowering in first year and AutocorG 2.0 (Hardy & Vekemans 1999; Hardy *et al.* 2000) for cytotypes. Moran's *I* statistics (Sokal & Oden 1978) were computed in all analyses and significance was determined by two-tailed tests (Sokal & Rohlf 1995).

Distance classes were defined for life span analyses to contain equal numbers of comparisons, and then used in all other analyses of the same path. Upper distance bounds were 113, 228, 347, 487, 625, 770, 946, 1174, 1482 and 2232 km (path 1), and 102, 207, 317, 441, 569, 709, 850, 1055, 1354 and 2081 km (path 2). Analyses for life span and percentage of first-year flowering involved 57 and 70 populations (paths 1 and 2, respectively), whereas analyses for cytotypes

involved 19 and 24 populations (each about five individuals), depending on how many populations were common to our three data sets. This did not change the balance between distance classes for the number of comparisons.

Results

LIFE SPAN

Mean life spans range from 2 years in the inland area of south-western France to 11 years in several populations in north Brittany and the Channel Islands (Fig. 1a). This upper value is an underestimate as several individuals sown in the early 1990s are still alive.

A very high variance of the trait is found in the northernmost geographical area between the Netherlands and North Brittany compared with much lower values in inland and Mediterranean areas (Table 1). Unbiased coefficients of variation (Sokal & Rohlf 1995) are, however, similar among geographical areas (Table 1), confirmed by a Levene's test for homogeneity of variances performed on ln-transformed data (Levene's statistic = 0.608, $P = 0.699$).

The spatial autocorrelogram for life span (path 2) is shown in Fig. 2(a). Moran's *I*-values are significantly positive ($\alpha = 0.05$) for the first four distance classes (0–487 km) and significantly negative for the last four (769–2232 km). Moran's *I*-values decrease to distance class 1173 km and thereafter. This pattern is also observed when only northern populations (path 1) are included (Fig. 2b): significant positive Moran's *I*-values ($\alpha = 0.05$) are found in the first three and the last distance classes (0–317 km and 1354–2081 km) and significant negative ones in the seventh to ninth distance classes (709–1354 km).

VERNALIZATION REQUIREMENT

There was a very high rate of first-year flowering in the inland area (75–100% of individuals in most populations), but all individuals in populations from south Brittany to the Netherlands and Great Britain required vernalization for flowering (Fig. 1b).

Although mean life spans are slightly higher of plants flowering in their second rather than their first year (Fig. 3), this effect was not significant in a paired comparison ($F_{1,27} = 2.70$, $P = 0.11$).

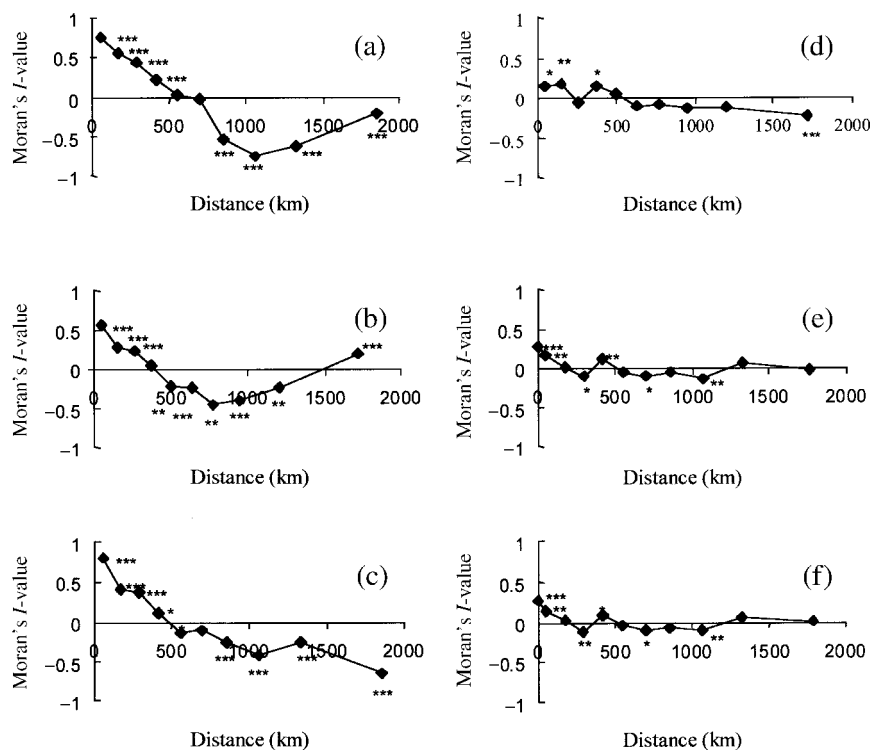


Fig. 2 Spatial autocorrelations: (a) life span, from the Netherlands to the Mediterranean coast; (b) life span, from the Netherlands to Biscay; (c) vernalization requirement, from the Netherlands to the Mediterranean coast; (d) vernalization requirement, from the Netherlands to Biscay; (e) chlorotypes, from the Netherlands to the Mediterranean coast; (f) mitotypes, from the Netherlands to the Mediterranean coast. *Significant at $\alpha = 0.05$; **significant at $\alpha = 0.01$; ***significant at $\alpha = 0.001$.

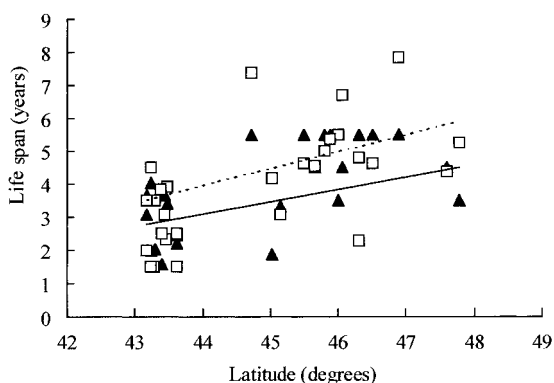


Fig. 3 Mean life span of plants requiring vernalization or not (populations with both categories of plants). \square and dotted regression line, plants requiring vernalization; \blacktriangle and full regression line, plants without vernalization requirement.

When southern populations were included in a spatial autocorrelation for percentage of plants requiring vernalization (Fig. 2c), Moran's I -values decrease regularly with distance, changing from significantly positive to significantly negative. When only northern populations are considered, Moran's I -values still decrease regularly, but fewer values are significantly different from zero (Fig. 2d).

CYTOPLASMIC HAPLOTYPES

The two cytoplasmic markers gave the same autocorrelation pattern, each other in either path (Fig. 2e,f

for chlorotypes and mitotypes, respectively, path 1). Moran's I -values are significant and positive ($\alpha = 0.05$) for the first and fourth distance classes (0–113 and 347–487 km) and significant and negative for the third, sixth and eighth distance classes (228–347, 625–770 and 946–1174 km).

HABITAT TYPE

In the inland part of south-western France and along Mediterranean coasts, almost 100% of the populations occur at margins of fields, roadsides and near buildings (Fig. 1c). Populations along the Atlantic coast around Bordeaux are mostly located in harbours and oyster basins, whereas south Brittany and northern populations are generally found along estuaries, along canals, in rocks or on seawalls, and cliff habitats are very common in north Brittany and in the area between Bordeaux and south Brittany. The range of habitats is very large in the northern part of the sampled area, as well as between Bordeaux and south Brittany.

A one-way ANOVA with habitat as factor gives a significant effect of habitat on life span ($F_{10,93} = 5.97$, $P < 0.001$), with habitat types falling into three non-exclusive clusters (Table 2). Field margins are significantly different from all other habitat types except roadsides, while roadsides and near-buildings areas have intermediate values and all other habitats types show similar, high life spans.

Table 2 Effect of habitat on life span: Student-Neumann-Keuls test

	Number of populations	Mean life span	Clusters
Cliff	15	7.49	a
Seawall	6	6.92	a
Canal	4	6.14	a
Rocks	15	5.77	a
Estuary	7	5.76	a
Beach or dune	11	5.74	a
Harbour	14	5.48	a
Oyster basin	7	5.40	a
Near buildings	12	4.69	a, b
Roadside	10	2.97	b, c
Field margins	3	2.11	c

Discussion

LIFE SPAN

The range of life spans among populations of *ssp. maritima* is very large (from 2 to more than 11 years), which suggests very different selection pressures or histories. No strictly annual population was found in our sample, contrary to some previous descriptions (Letschert 1993). The shortest-lived plants (two years) were usually plants that do not require vernalization and therefore flower twice in their lifetime.

The life span map (Fig. 1a) shows a very marked spatial patchiness at a large geographical scale: the highest values are clustered in north Brittany, Jersey and Guernsey, and the lowest values in the inland area. Spatial autocorrelograms for life span (Fig. 2a,b) show that differentiation between populations is significantly dependent on distance and confirm the macrogeographical patch structure.

Populations separated by short distances (less than 500 km) show similar life spans (Fig. 2b), corresponding to the two patches in Brittany and the inland area of south-western France and the Mediterranean (Fig. 1a). Populations separated by 700–1300 km are, however, significantly different, particularly if they are about 900 km apart (Fig. 2b) (as for north Brittany to Biscay, and north Brittany to northern France, Belgium and the Netherlands, Fig. 1a) or about 1100 km (Fig. 2a, north Brittany vs. southern populations). Populations from the Netherlands, Belgium, Great Britain and northern France have life spans similar to those of populations from Biscay (Figs 1a and 2b). This pattern is inconsistent with the occurrence of selection by a simple unidirectional environmental gradient (e.g. climatic factors varying with latitude: drought, length of the growth season, light), such as described in some other species (Cooper 1963; Leggett & Carscadden 1978), but supports the existence of two gradients from north Brittany (to the south and to the north-east). These two gradients may be caused by a single environmental factor, increasing from the south to north Brittany and then decreasing to the Nether-

lands (e.g. disturbance), or by the combination of two factors or more (e.g. length of the growth season and disturbance).

Our estimates of life history traits were made in controlled conditions and in a common environment and are thus intrinsic (genetically determined) values, which are extremely difficult to obtain in natural conditions. Environmental effects are eliminated, which is enabling comparison of traits among individuals from different geographical and ecological origins. However, individual mean life span and age at maturity under local conditions may differ from that observed in the glasshouse (as vernalization, water stress or nutritive richness may differ). Our next step should be to replicate this experiment at various latitudes. It has already been shown that the gradient of vernalization requirement is similar in common-environment and multisite experiments (Boudry *et al.*, unpublished results).

VERNALIZATION REQUIREMENT

The effect of age at first flowering on life span within populations is not significant, in spite of a tendency to an increased life span when reproduction is postponed. The difference in life spans between plants flowering in their first or second year (1 year, Fig. 3) may simply be too low to be statistically significant with this sample size.

Plants requiring vernalization for flowering will benefit from one season without spending resources on reproduction, which might be expected to result in increased vegetative growth or accumulation of more reserves for survival or future reproduction (Fisher 1958; Williams 1966; Gadgil & Bossert 1970; Calow 1973; Reznick 1992). There is much evidence for a cost of reproduction in terms of subsequent growth, reproduction or survival in plants (see, among others: Sohn & Policansky 1977; Snow & Whigham 1989; Worley & Harder 1996; Primack & Stacy 1998; Nicotra 1999; Hautekèete *et al.* 2001). The tendency for life span to increase when flowering is delayed suggests that the number of reproductive episodes is independent of age at first flowering, and plants flowering in their second year at least compensate for the first year without flowering. When the length of the natural growing season is too short for an individual to complete reproduction in the same year as germination (e.g. reproductive size is not reached), postponing reproduction might confer an advantage in reproductive output or survival (Reinartz 1984) on individuals in the field that would not be observed in controlled conditions. Mixed populations of plants flowering in their first and second years might be found where the length of the growing season varies between years.

Life span varies between northern populations, while the percentage of individuals requiring vernalization is constant at 100% and the percentage of plants flowering in their first year cannot therefore explain life span variation in these populations (Fig. 1a,b).

The major effect of the introduction of inland and Mediterranean populations in the spatial autocorrelation analysis (Fig. 2c,d) supports Van Dijk *et al.*'s (1997) suggestion of a particularly strong selection for flowering in first year in this area, and short life span may be simultaneously selected by the same environmental factors. In the inland area, producers of seeds of cultivated beet regularly eliminate wild beets to prevent hybridization (Desplanque 1999), usually during the reproductive season when flowering stems make the plants more visible. This should select for weedy characteristics, e.g. rapid growth and flowering, which is clearly not compatible with a vernalization requirement, and high seed output, implying a high reproductive investment, which trades off with life span. Similarly, mowing (along roadsides) increases adult mortality and may also select for both short life span and flowering in first year (Charnov & Schaffer 1973; Michod 1979; Charnov 1990).

CYTOPLASMIC HAPLOTYPES

The similarity between the autocorrelograms for mitotypes and chlorotypes (Fig. 2e,f) is probably a result of migration and of their common maternal inheritance, rather than a result of recurrent homoplastic mutations (Desplanque *et al.* 2000).

Assuming negligible maternal and environmental effects on traits in the conditions of the present experiment, the comparison of spatial autocorrelation analyses for neutral markers (mitotypes and chlorotypes) and selected traits (life span and vernalization requirement) may indicate selection pressures acting on patterns of trait distribution. Maternally inherited markers generally show a higher genetic differentiation than do nuclear markers (as drift is twice as high for haploid genomes and as only seed dispersal contributes to cytoplasmic gene flow, whereas both seed- and pollen-dispersal contribute to nuclear gene flow, Ouborg *et al.* 1999). If gene flow is restricted, maternally inherited markers should therefore show a stronger spatial structuring than nuclear markers, but spatial structuring is still much higher for our life history traits than for these conservative neutral markers (Fig. 2a–d vs. 2e–f). This suggests that environmental selection is responsible for the macrogeographical patterns observed, i.e. selective pressures play a more important role than genetic drift or seed migration in shaping trait distribution.

HABITAT TYPE

Disturbance may be regarded as 'any relatively discrete event in time that removes organisms or otherwise disrupts the community by influencing the availability of space or food resources, or by changing the physical environment' (Begon *et al.* 1996, p. 802). The habitats described appear to differ in their disturbance rate, especially man-made disturbance, which seems to be extremely high in the south.

Spatial distributions of life span and habitats have roughly similar patterns (Fig. 1a, c). Short-lived and highly man-disturbed populations are found in inland and Mediterranean areas, whereas the patch in north Brittany has long-lived populations and a high proportion of cliffs compared with other areas, and other populations are intermediate for both characteristics.

Inland and Mediterranean populations appear to be very different from Atlantic and northern populations for many traits (life span, vernalization requirement and habitat). Desplanque *et al.* (1999) showed that the closest relatives of inland sea beets are in the Mediterranean, despite the closer proximity to Biscay. In fact, in spite of very fine scale exploration, no wild beet population is geographically known between inland and Atlantic populations. Clausen *et al.* (2000), in a study on two species having the same habitat and distribution area as the sea beet (i.e. *Eryngium maritimum* and *Cakile maritima*), argued that presumed distributions of these species during the Würm glacial and post-glacial migrations might explain differentiation between Mediterranean and Atlantic populations and similar explanation might apply to *ssp. maritima*. On the other hand, north Brittany is very different from other areas in terms of beet life span without any known historical explanation. A general tendency to more stable (granite cliffs, rocks, pebbles) and less man-disturbed habitats in this region, revealed by a fine-scale exploration conducted in 2000 (data not shown), might explain such differentiation. Finally, gene flow between populations probably reduces any fine-scale differences due to contrasting habitats, and this could explain the higher homogeneity for life span than for habitats (Fig. 1a,c).

A habitat effect is detected (one-way ANOVA) but is, in fact, hardly distinguishable from effects related to latitude, such as climate; some habitat types are not found at all latitudes. At high latitudes, few populations are found in highly disturbed habitats and their rarity unfortunately prevents any statistical test. Nevertheless, some sublittoral Atlantic populations are found in highly disturbed habitats and are much shorter-lived than their fully littoral and less disturbed neighbours (Fig. 1a,c), supporting our hypothesis of disturbance effects on life span. Furthermore, the pattern of distribution of life span is inconsistent with the occurrence of selection by a simple unidirectional environmental gradient, such as climatic factors varying with latitude.

The general tendency for the co-occurrence of short-lived and highly disturbed populations vs. long-lived and more stable populations indicates that disturbance related to habitat type and human influence may select for short life span. However, additional selective pressures (other causes of disturbance, e.g. frost or drought) might be implicated and will need to be considered in future ecological studies in *ssp. maritima*.

Habitats, defined by their putative disturbance regime, seem to have the greatest influence on life span. Vernalization requirement may simply be selected by

the same environmental factors as life span. Nevertheless, herbivory (Michod 1979; Klinkhamer *et al.* 1997) and parasitism (Bazzaz *et al.* 1987; Sheldon & Verhulst 1996; Oppliger *et al.* 1997; Zangerl *et al.* 1997; Nordling *et al.* 1998) may both have considerable influence on life history traits and hence constitute additional major selective forces, as may cold (Pohl-Orf *et al.* 1999) and drought via mortality. A better knowledge of the history of *ssp. maritima* populations (migrations or local disturbance regimes in the past) would also allow us to assess the selective forces that have acted on life span. Precocious reproduction and short life span may both be selected by external mortality, and factors related to latitude, such as length of growth season, are currently being tested in an allocation model for a similar response.

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