DEMOGRAPHIC STUDIES OF ANTHYLLIS VULNERARIA L. IN THE NETHERLANDS

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SUMMARY

In the course of 4 to 6 years demographic studies were made of several coastal populations of *Anthyllis vulneraria* L. var. *langei* Jalas and of an inland population of the var. *vulneraria*. Fluctuations in the population density, in the biomass and in the rate of flowering were recorded, and in addition the relation between life span and flower production was investigated.

Coastal populations appear to exhibit a far greater fluctuation in density, annual biomass production and rate of flowering than the inland population studied. These different degrees of fluctuation are associated with differences in the environment. In the interior, fewer flowers are produced per plant and the plants more often flower only once, whilst more plants start flowering at a later age than is the case in coastal populations. The differences in the pattern of flowering are most probably correlated with the denser stands of vegetation at the site in the interior where the mutual competition among the plants is stronger. The total life-span of the plants appears to be about the same near the coast and in the interior.

1. INTRODUCTION

Anthyllis vulneraria L. is an extremely variable taxon which has already been studied mainly by descriptive taxonomic methods (SAGORSKI 1908; BECKER 1910, 1912; MARSDEN-JONES & TURRILL 1933 a, b; ROTHMALER 1941; JUZEPCZUK 1945; JALAS 1950, 1957; CULLEN 1961, 1968). The species occurs all over Europe and is found in a great variety of ecological situations. CULLEN (1968) recognises 24 subspecies in western Europe which are connected by intermediate forms in nature. The geographical ranges of several subspecies exhibit an appreciable overlap. Biotaxonomic investigations of the aggregate species have only recently been attempted (COUDERC 1971).

A. vulneraria is found in the Netherlands near the coast and in the interior (HEUKELS-VAN OOSTSTROOM 1970), but in this country its taxonomy has not been sufficiently studied. According to Dr. J. Cullen (Edinburgh), whose kind co-operation is gratefully acknowledged, specimens belonging to the coastal populations studied are referable to *A. vulneraria* L. ssp. *vulneraria* var. *langei* Jalas, and those of the inland population to the ssp. *vulneraria* var. *vulneraria*. The coastal populations do not belong to the ssp. *maritima* Schweig. as stated by BOERBOOM (1957) and by WESTHOFF & DEN HELD (1969); the ssp. *maritima* is related with the East-European ssp. *polyphylla* (DC.) Nyman and is restricted in its distribution to the southern coastal zones of the Baltics.

In the course of 4–6 years demographic studies were carried out with several Dutch coastal populations of the var. *langei* and with an inland population of the var. *vulneraria.* The reason was the consideration that for an ecogeographic analysis of closely related populations of a population complex comparative studies of the population dynamics may yield important data. This can be deduced from the fact that seed production, the rate of survival, age groups, and other characteristics of populations usually have a high adaptive value, so that comparative studies may indicate the causes of the niche differentiation of related populations.

The population dynamics of *A. vulneraria* have never been studied as far as can be ascertained. Generally speaking one may accept that the inquiry into the dynamics and in a broader sense, the biology of populations has not been much developed in plant ecology. For surveys concerning population dynamics in botany the reader is referred to HARPER (1967), HARPER & WHITE (1970) and SARUKHÁN & HARPER (1973).

Populations of the var. *langei* are found along the coast in a number of different environments (BOERBOOM 1957, DOING 1964, WESTHOFF & DEN HELD 1969, WEEVERS 1940, FREIJSEN 1967).

The present investigation was carried out on a number of dune slopes near Egmond-aan-Zee (province of N.-Holland) and on the low dunes of the nature conservation area "De Boschplaat" in the island of Terschelling. These two areas differ in ecology, the differences in environmental conditions including, among other things, unequal water- and salt relations.

The populations on "De Boschplaat" are situated relatively close to the ground water level and become submerged by the sea during very high spring tides (KLIJN 1972), whereas the populations near Egmond are not affected by changes in the ground water level and never become flooded by sea water.

The var. *vulneraria* occurs in the interior in calciphile grass land vegetation in Zuid-Limburg (province of Limburg), compare DIEMONT et al. 1953, WEST-HOFF & DEN HELD 1969, WERKHOVEN 1969. The population studied occurs in het nature reserve "De Wrakelberg" (municipality of Wijlre).

The present paper reports mainly the outcome of field surveys of the populations; the results of ecological and experimental studies will be published elsewhere.

2. METHODS

The populations were studied by means of systematic samples taken in permanent plots. At the site a quadrangular grid was placed on the surface, which grid was subdivided in squares (of usually 1 m² surface area). At the points of intersection of the grid lines poles with a square cross area were driven into the ground, and when a sample was to be selected open squares of aluminium (usually measuring 30 cm × 30 cm) were fitted with an inner corner around a pole and subsequently individual plants were studied in each square. Usually about 60 squares were investigated.

In three areas population samples were studied in this way three times in each growing season and the phenological condition of each plant was noted. In the two coastal populations E1 and E2 (see below) the counts were done at the beginning of May, August and October (by the beginning of August the main flowering period is just over). The inland population W was sampled for the second time at the end of June because the plants come to flower 4–5 weeks earlier than they do near the coast. The other plots were sampled only once immediately after the principal flowering period.

The biomass (estimated as the dry weight of the parts of the plants above the ground) and the seed production were determined of samples of 50–75 plants collected in the same vegetation type in sites immediately adjacent to the permanent plots. These plants were systematically sampled, plants at a distance of 1 m from one another being gathered. The life-span and the number of years in which plants bear flowers was determined by marking individual specimens with pieces of plastic-covered copper wire, a different colour of the plastic coat being used each year.

In order to obtain data regarding the changeability of the environment and the stands of vegetation, every year a relevé was made according to the France-Swiss school during the sampling in the main flowering period. The estimation of dominance was made according to DOING KRAFT (1954). For the nomenclature of the taxa recorded HEUKELS-VAN OOSTSTROOM (1970) was followed, for that of the syntaxonomic units WESTHOFF & DEN HELD (1969).

3. SOME ECOLOGICAL DATA RELATING TO THE PERMANENT PLOTS

The plots E1, E2, E3 and E5 are situated immediately to the S of Egmond-aan -Zee in the dune nature reserve of N. Holland under management of the provincial water board of N. Holland (see *fig. 1, a, b, c*). E1 lies near the so-called "Verkade Bunkers" close to the outermost row of dunes; E2 lies more inland in the so-called "Vossendal"; E3 lies on the other side of the high dune on which E2 is situated; and E5 is not very far away from "De Kaap" in the innermost dune ridges.

Details concerning soil conditions, topography and vegetation are given in *table 1;* the plots are not grazed and hardly tread upon. The stands of vegetation on the plots E1, E2, E3 and E5 belong to the *Anthyllido-Silenetum*, which association is chiefly found on northfacing slopes and in dry dune valleys in the calciferous dunes between Bergen and Scheveningen. In the so-called "Waddendistrict" (HEUKELS-VAN OOSTSTROOM 1970) this association does not occur; and outside the Netherlands it has not been recorded either (BOERBOOM 1957). This association belongs to the alliance *Galio-Koelerion* of which *Anthyllis vulneraria* is a characteristic species. This alliance includes vegetation types of dry and stabilised but not very much leached-out (and, accordingly, fairly lime-rich to rather acid) parts of the coastal dunes, and occurs along the coasts of W. Europe from southern Norway to NW Spain and also in the British Isles (WESTHOFF & DEN HELD 1969).
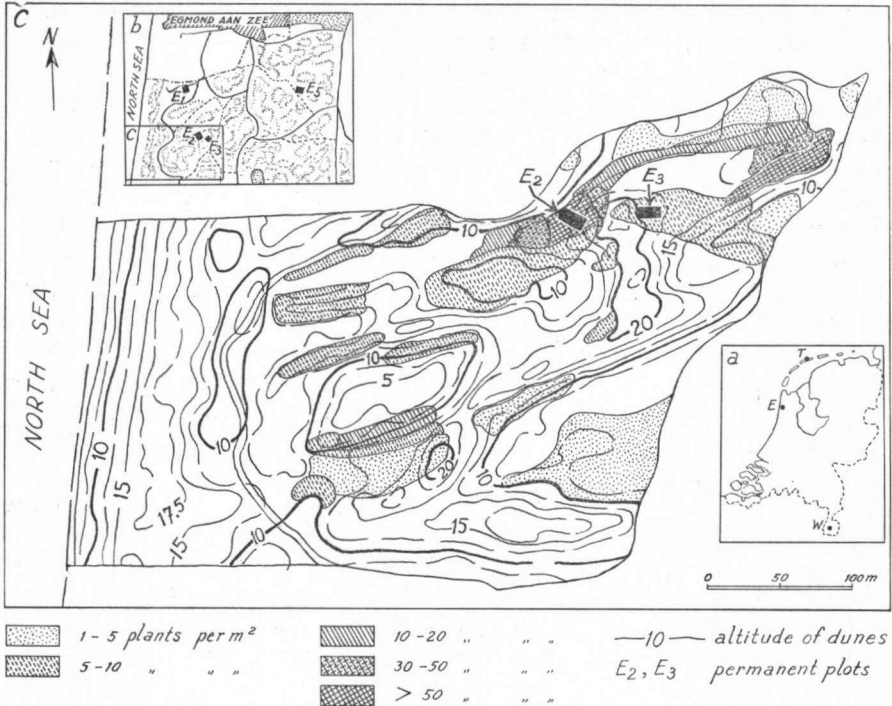
Fig. 1. Distribution of *Anthyllis vulneraria* in a dune area south of Egmond-aan-Zee in 1971.
Fig. 1a: T = Terschelling, E = Egmond-aan-Zee, W = "De Wrakelberg".

Plot T is situated on a low dune in the nature reserve "De Boschplaat" in the island of Terschelling (see *fig. 1a*). This dune lies at the height of beach mark no. 24, about 140 m S of the artificial dune ridge (see KLIJN 1972). In this area *Anthyllis* grows in an association closely allied to the *Centaurieto-Saginetum moniliformis*, more particularly to the "dry" variant of this association (WEST-HOFF 1947, FREIJSEN 1967). This *Centaurieto-Saginetum* is found on moist and slightly brackish beach planes isolated from the beach by dune ridges and in still rather barren primary dune valleys; on "De Boschplaat" especially in horizontal zones girdling the food of dunes. The association is known from coastal areas along the North Sea.

Plot W is situated in the reserve "De Wrakelberg" (see *fig. 1a*) which contains mainly a hillside covered with calciphilous grassland vegetation. The highest point of this reserve lies at 170 m above Dutch standard sealevel (NAP), the plot at about 150 m above NAP; the sloping angle is here about 15°. The reserve was purchased by the Dutch Forestry Service in 1961 and kept under management as a nature sanctuary ever since, but before that time the slopes were partly used as arable land and partly for grazing cattle. It is now only mowed once a year during the cold season. The subsoil consists of Cretaceous

Table 1. Ecological data pertaining to the populations studied.

Relevé nr	E1	E2	E3	E5	T	W
Locality	coast	coast	coast	coast	coast	inland
Date	18-7-69	18-7-69	20-8-71	7-8-72	15-8-71	10-7-69
Slope	C. 3°	C. 11°	C. 20°	C. 3°	C. 5°	C. 15°
Exposition	NW	NW	E	E	SE	S
Soil	dune sand	dune sand	dune sand	dune sand	dune sand	loam
Coverage: herb layer	30%	70%	60%	80%	50%	95%
moss layer (incl. Lichens)	90%	60%	50%	40%	5%	10%
Anthyllis vulneraria						
var. langei	02	02	a	02	01	–
Silene nutans	p	01	02	01	–	–
Koeleria cristata	a	01	01	a	–	–
Silene otites	a	a	p	–	–	–
Erophila verna	a	p	–	–	–	–
Galium mollugo	a	a	p	a	–	–
Rhinanthus serotinus	a	a	a	a	–	–
Carex arenaria	p	–	–	r	–	–
Cerastium semidecandrum	a	–	–	p	–	–
Plantago lanceolata	a	–	r	–	–	–
Thymus pulegioides	–	a	–	01	–	–
Helictotrichon pubescens	–	a	–	–	–	– .
Aira praecox	–	a	–	–	–	–
Cerastium arvense	–	p	–	a	–	–
Polypodium vulgare	–	p	p	a	–	–
Poa pratensis	–	a	–	a	–	–
Luzula campestris	–	a	p	p	–	–
Hypochaeris radicata	–	a	r	–	–	–
Sedum acre	m	r	–	a	a	–
Hieracium umbellatum	a	p	a	–	01	–
Ammophila arenaria	r	p	a	–	a	–
Arenaria serpyllifolia	a	–	–	–	a	–
Festuca rubra	–	–	–	–	01	–
Trifolium campestre	–	–	–	p	–	–
Trifolium arvense	–	–	–	p	01	–
Corynephorus canescens	–	–	–	–	a	–
Jasione montana	–	–	–	–	a	–
Leontodon nudicaulis	–	–	–	–	p	–
Calamagrostis epigeios	–	–	r	–	a	–
Sagina nodosa	–	–	–	–	r	–
Ononis repens	–	–	r	p	–	–
Picris hieracioides	p	a	a	a	–	02
Galium verum	–	–	r	a	–	–
Achillea millefolium	–	a	–	–	–	a
Senecio jacobaea	–	–	p	–	–	–
Daucus carota	–	r	p	p	–	a
Polygala vulgaris	–	a	r	–	–	p
Rubus caesius	–	p	03	03	–	–

Anthyllis vulneraria
        var. vulneraria   –   –   –   –   –   02

Sanguisorba minor	–	–	–	–	–	01
Knautia arvensis	–	–	–	–	–	01
Origanum vulgare	–	–	–	–	–	01
Hieracium pilosella	–	–	a	–	–	02
Centaurea scabiosa	–	–	–	–	–	a
Carlina vulgaris	–	–	–	–	–	a
Lotus corniculatus	–	–	–	p	–	a
Euphrasia officinalis	–	–	–	–	–	a
Chrysanthemum leucanthemum	–	–	–	–	–	a
Centaurea pratensis	–	–	–	–	–	a
Hypericum perforatum	–	–	–	–	–	p
Briza media	–	–	–	–	–	p
Linum catharticum	–	–	–	–	–	p
Agrimonia eupatoria	–	–	–	–	–	p
Satureja acinos	–	–	–	–	–	r
Fragaria vesca	–	–	–	–	–	p
Gentianella germanica	–	–	–	–	–	r
Scabiosa columbaria	–	–	–	–	–	p

Coverage: mosses and lichens
Relevé E 1: *Hypnum cupressiforme* L. var. *elatum* B.S. 70%,
           Dicranum scoparium Hedw. 20%;
Relevé E 2: *Hypnum cupressiforme* L. var. *elatum* B.S. 20%,
           Dicranum scoparium Hedw. 20%,
           Cladonia impexa Harm. p,
           Cladonia pityrea (Flörke) Fr. a,
           Cladonia rangiformis Hoffm. p,
           Cladonia furcata Schrad. a;
Relevé E 3: *Hypnum cupressiforme* L. var. *elatum* B.S. 50%;
Relevé E 5: *Hypnum cupressiforme* L. var. *elatum* B.S. 40%;
Relevé   T: *Cladonia furcata* Schrad. p,
           Cladonia rangiformis Hoffm. p,
           Peltigera spuria (Ach.) DC. r,
           Cladonia chlorophaea Spreng. p,
           Ceratodon purpureus Brid. p,
           Tortula ruralis Ehrh. p;
Relevé   W: *Fissidens taxifolius* Hedw. 02,
           Camptothecium lutescens (Hedw.) B. and G. a,
           Campylium chrysophyllum (Brid.) Lange a,
           Pseudoscleropodium purum (Hedw.) Fleisch. a,
           Weissia controversa Hedw. p,
           Brachythecium rutabulum (L.) B.S.

limestone or marl directly underlying a so-called rendzina soil, i.e., a lime- and humus-rich loamy topsoil.

Anthyllis grows here in a plant community included in the alliance of the *Mesobromion* (WERKHOVEN 1969, WESTHOFF & DEN HELD 1969, see *table 1*). The vegetation types of this alliance are grassy associations on relatively dry and somewhat basic to calcareous, loamy soils; the alliance has a distributional range from southern Scandinavia to Spain including England and Ireland. *A. vulneraria* ssp. *vulneraria* is a characteristic species of the *Mesobromion* alliance.

4. FLUCTUATIONS IN POPULATION DENSITY

In *fig. 2A* the mean number of flowering individuals per m² on the E plots near Egmond-aan-Zee in the years 1969–1974 is shown. This diagram indicates a strong fluctuation in the annual density of the flowering specimens: very high densities were recorded in E1 and E2 during 1969 and not a single flowering individual was seen at the same sites in the year 1970; this was followed by a partial recovery in 1971–1973 in E1 and another decline in 1974. The fluctuation pattern of E3 and E5 resembles that of E1 to some extent, but there were also marked quantitative differences especially in 1973 and 1974.
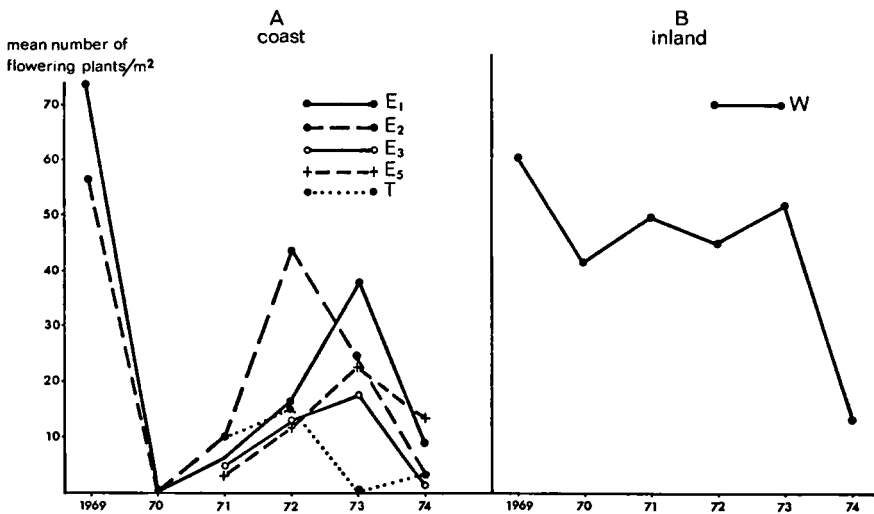

Fig. 2. Fluctuations in the mean number of flowering plants per m² of the coastal populations (E1-E5 and T) and of the inland population W from 1969 to 1974.
For the localities see *fig. 1*.
E1 and E2: mean is based on 60 squares of 0.09 m²
E3 and E5: mean is based on 60 squares of 0.25 m²
T: mean is based on 160 squares of 0.25 m²
W: mean is based on 60 squares of 0.045 m²

E2 differs from the other E plots in that an appreciable increase in population density occurred in 1972 which exceeded by far the increases in the other E sites, whereas in 1973, in contrast to the other plots, a considerable decline was noted. In 1974 the number of flowering plants per m^2 was very low (2) and the population apparently suffered from another depression comparable with that of 1970.

These data indicate that the E plots exhibit a certain degree of individuality as far as the annual density of flowering specimens is concerned. This individuality is a characteristic of the local population of each plot. What is meant here by the term "local population" is explained by means of a mapping survey of *Anthyllis* carried out in the Egmond area some years ago. A part of the distribution map shown in *fig. 1c* clearly shows that the kidney vetch is not evenly distributed over the area but is only found in certain parts of the accidented landscape and seems to have a marked preference for N- and NW-facing slopes with a relatively mild and humid microclimate. In such sites the species occurs in the highest densities and it is here that the *Anthyllido-Silenetum* attains its optimum development (DOING 1964). In this area *Anthyllis* is found, according to the map, as a complex of more or less continuous groups of plants, each group under favourable conditions developing in a more or less discrete, local habitat. These groups are called local populations. They show an individual stand density and population dynamics, good examples of which are the populations in E2 and E3 (compare *figs. 1c* and *2A*) both situated on the same dune hill not more than 30 m apart, but the one on the NW-facing slope and the other one on the E-facing side (see *table 1*). These two local populations exhibit appreciable differences in the fluctuation of stand densities of specimens in anthesis. In point of fact this is not so much a fluctuation in the density of the generative component of the local population, as a fluctuation in the number counted in the smaller sampling plots. It is evident from *fig. 1c* that on slopes the densities show a kind of gradient; in such cases the samples lay at sites where the density attains a maximum value (compare, e.g., E2). The figure also shows that the local populations have a certain degree of spatial connection, so that the indication of the limits of a local population is arbitrary. The shifting limits of such a population in time also cause difficulties. This is attributable to the spread in the time of germination of the seeds which may extend over several years, so that the plants of a local stand of *Anthyllis* may have originated from seeds produced in several (and not always consecutive) years. The distribution pattern of the local populations on "De Boschplaat" is very similar to that observed in the Egmond area (see KLIJN 1972).

The interconnections and the identity of the local populations is to a large extent determined by the rate of seed migration, apart from the ecological characteristics of the habitat. There are indications that the horizontal displacement of the seeds is very limited; this point is now under investigation. More is known about the gene flow between the local populations by pollen transfer. Cross-pollination does not occur to an appreciable extent because *Anthyllis* is extremely autogamous, the mature pollen already becoming released

in the closed flowerbud and self-pollination thus easily taking place (see also COUDERC 1971).

The diagram shows that the stand densities of the local populations exhibit differences almost every year, but apparently the influence of a complex of factors may sometimes be so great in a certain area that the local populations in that whole area react in exactly the same way, as was the case in 1970 when during an unusual period of drought in the spring and summer so many older plants died that none reached the flowering stage. The "new" population replacing the exterminated one was built up by dormant seeds present in the soil. The amount of atmospheric precipitation, or, more generally speaking, the moisture relations, appear(s) to be one of the most important factors causing fluctuation in the number of plants, more particularly by setting the lower limits. This will be reported in extenso later on. *Fig. 2A* demonstrates that plot T on "De Boschplaat" in Terschelling also exhibits marked number fluctuations. There is no manifest correlation between the fluctuations of the E-populations and that of the T-population, however. In 1973, for instance, the population densities of the E-populations were high, whereas in the sampled T-population not a single flowering specimen was encountered. As pointed out already, the "*Anthyllis* environment" of the dunes near Egmond-aan-Zee differs appreciably from that on "De Boschplaat", the latter one being subjected to different moisture and salt conditions associated with the action of the tides. Conceivably, these differences are responsible for the different behaviour of the populations in the two areas. As is the case in the Egmond plots, the T-population exhibits appreciable differences is population density over relatively short distances. In plot T near beach-mark 24 no plants in anthesis were seen in 1973, but at a site near beach-mark 22, situated at 2 km from plot T in the same year the relatively high number of 19 flowering individuals per m² was recorded.

In *fig. 2B* the density fluctuations of the inland W-population (on "De Wrakelberg", see *fig. 1a*) is shown. The variation in number was relatively insignificant in the period 1969–1973, but in 1974 a marked decline occurred as compared to the preceding four years.

There are considerable differences in the rate of fluctuation between the W-population on the one hand and the coastal E-populations on the other. Along the coast the fluctuations are much more pronounced, which must be interpreted as an expression of the much broader spectrum of environmental dynamics as compared to the more stable sites in the interior. This applies particularly to the moisture relations: in the top layer of the well-drained dune slopes consisting of rather coarse sand the moisture content shows greater and more frequent oscillations than it does in the heavier and better moisture-retaining loess soil of "De Wrakelberg". The greater environmental stability of the latter site is also manifest from the denser and higher herbaceous vegetation (compare *table 1*). It is, furthermore, noteworthy that when the coastal populations are compared with the inland one, the W-population comes into flower about one month earlier than the E-populations. The flowering time of

the T-population in turn lags behind that of the E-populations by about a fort-
night. Details will be published later. As is the case in all populations of peren-
nials, the stands of *Anthyllis* consist, in dependence on the season, of different
components, viz., of dormant seeds in the soil, seedlings, vegetative individuals,
and generative plants. The above-mentioned considerations only refer to the
latter category, but some data were compiled about the vegetative specimens.
It is important, in this connection, that seed germination chiefly takes places
in the spring, and that the ensuing (younger) plants remain in the vegetative
stage throughout the growing season, hibernate and usually attain the flowering
stage in the second season. The number of flowering and fruiting individuals
can most accurately be determined as a population component, but this is by no
means the case with the ephemerous seedlings. The precise number of seedlings
can be determined in a single sample at a certain time it is true, but a seedling
may be very short-lived. Especially in intermittent periods of rainy weather
and droughts large quantities of seedlings may emerge during the wetter spells
to perish during a subsequent dry period.

One count in the spring does not yield more than a temporary impression.
In E2 the following numbers of seedlings per m^2 were recorded in the month
of April in the consecutive years 1970–1974: 228, 24, 40, 353, 102, respectively;
in W these figures, recorded in the same years and in the same month, were:
512, 41, 91, 32, 274. It is clear that these numbers may attain very high values.

As may be expected, there is no fixed relation between the number of genera-
tive specimens and of vegetative plants in the summer. This is attributable to
the fact that the number of non-flowering individuals is also decided by the
amount of new seedlings emerged in the spring whose mortality rate is extremely
variable. In E2 the ratio between the mean numbers of vegetative and repro-
ductive plants per m^2, determined anually in the month of August from 1969 to
1974, was as follows:

$$\frac{34 \text{ veg.}}{57 \text{ gen.}}; \frac{56 \text{ veg.}}{0 \text{ gen.}}; \frac{44 \text{ veg.}}{9 \text{ gen.}}; \frac{56 \text{ veg.}}{42 \text{ gen.}}; \frac{98 \text{ veg.}}{24 \text{ gen.}}; \frac{138 \text{ veg.}}{2 \text{ gen.}};$$

in W these figures were:

$$\frac{558 \text{ veg.}}{42 \text{ gen.}}; \frac{209 \text{ veg.}}{51 \text{ gen.}}; \frac{175 \text{ veg.}}{46 \text{ gen.}}; \frac{104 \text{ veg.}}{52 \text{ gen.}}; \frac{289 \text{ veg.}}{14 \text{ gen.}}$$

Generally speaking the vegetative individuals by far outnumber the generative
ones, but their ratio varies appreciably. In some years their ratio is reversed
because there are more generative than vegetative individuals (as in E2 in 1969,
see above).

Upon the whole three counts per season do not give a sufficient insight into
the changing numbers of non-flowering specimens in populations of *Anthyllis*.
It has become clear, however, that these populations exhibit an enormous
dynamism, appreciable numbers of seedlings emerging and vegetative plants
dying off every year, both in coastal and in inland populations.

5. FLUCTUATIONS IN THE BIOMASS OF THE FLOWERING INDIVIDUALS

Fig. 3 shows the fluctuations of the mean biomass (the mean dry weight of the parts of the plant above the ground) of the flowering specimens of the populations E2 and T (coastal) and W (inland) in the years 1970–1974. In E2 the biomass fluctuates appreciably. In 1972 the plants were upon the average more than twice as heavy as they were in 1971, whereas in 1973 the plants weighed about 1/3 of the mean weight of 1972 and in 1974 even only 1/6 of the 1972 average. The picture of the T population agrees rather closely with that of E2. The W population, on the other hand, did not exhibit such extreme oscillations in weight in the period 1969–1974 as the other two.

It is striking that the W plants have upon the average a much lower biomass than the E2 and the T plants. Both the smaller rate of fluctuation in biomass and the lower mean weight of the plants are associated with the greater vegetation density in the habitat and the smaller environmental dynamics in W (compare *table 1*). In W the vegetation cover was almost closed in the consecutive years, which resulted in a mutual influence of the plants and in competition. A mutual influence inhibits the growth of the plants, so that they do not attain the size of the plants of E2 and T where the stands of vegetation are sparser and the mutual influence of the plants accordingly far smaller. In favourable years the plants can grow out to a considerable extent in E2 and T, whereas the dense plant cover in W prevents any excessive growth.

The mutual influence between the plants in natural stands is also expressed in their growth form: in the sparser vegetation cover of E2 the individual plants usually branch profusely from the basal parts of the stem, so that a more or less manifest rosette habit develops, whereas in the much denser stands at the W site such basal offshoots hardly occur and the plants form one single branch or only a few shoots which grow upwards through the local vegetation.

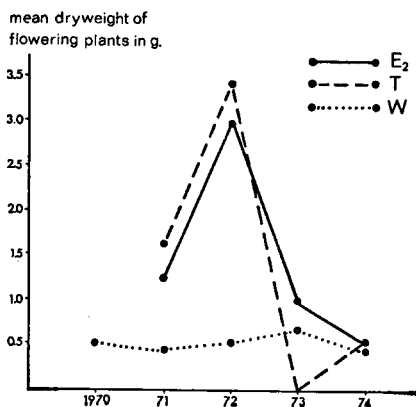Plants well spaced out in the experimental garden exhibit a manifest rosette

Fig. 3. Fluctuations in mean biomass (as dry weight in g) of plant body above the ground of the flowering specimens of the coastal populations E2 and T and of the inland population W from 1970 to 1974.

habit. When plants were reared from seeds of the E2 and W populations in the garden they did not show appreciable differences in habit form, which indicates that the differences between the individuals of the E2 and W populations are directly habitat-induced.

There is a certain amount of correlation between the course of the fluctuation in biomass and the population density both in E2 and in T (compare *fig. 3* with *fig. 2*). In years of a lower density the plants tend to remain smaller in stature and lighter than in years of high densities. As regards the relation between stand density and plant size in E2 in the years 1971 to 1974 it must be borne in mind that the density of the vegetative individuals of *Anthyllis* was so high in the months of October in the years 1970 to 1973 (viz., 42, 60, 89, and 54 plants per m², respectively) that the difference in the growth conditions in the following winter, spring, and summer seasons may well explain the correlation between plant size and stand density: in a favourable winter, spring and summer season the low mortality rate will cause many plants that were present in the vegetative state in October to develop into generative individuals, and these are likely to be on the large side, whereas in less favourable years the high mortality prevents the development of many plants into their generative phase during the next year, and those which become reproductive tend to remain smaller (1973 and 1974). It is noteworthy that the cold season was mild in the years 1970 to 1973, which resulted in a low rate of mortality of the hibernating plants; predation and parasitism did not take place to an appreciable extent either. It is highly probable that a marked relation between stand density and plant size, as found in E2, can often be observed in coastal areas.

Fig. 4 shows the relative frequency distributions of the dry weight of flowering individuals collected in E2 (*fig. 4A*) and in W (*fig. 4B*) in the years 1972 and 1973. The frequency distributions in the W populations appear to be oblique and extend towards the right-hand side of the diagrams. In more favourable years (compare the results of 1973 with those of 1972) the percentage of larger individuals in the population increases and that of the smaller ones decreases. This phenomenon is even more manifest in the distribution found in the E2 population when the years 1972 and 1973 are compared. This difference in the frequency distributions of the biomass in the E2 and W populations in years with more favourable and with less suitable growing conditions is also connected with the vegetation density. In the open E2 stands a large number of plants can develop profusely, so that some may even grow very large (compare *fig. 4A*, 1972), whereas in W the denser stand and the concomitant growth-inhibiting action of the surrounding plants prevent any excessive outgrowth. Apparently the size variation is smaller according as the stands are denser, and vice versa.

Generally speaking the frequency distribution of the plant dry weights is not a normal one in the *Anthyllis* populations studied, but oblique, smaller individuals being relatively better represented than the larger size groups. SALISBURY (1942) has demonstrated that this kind of frequency distribution also occurs in other species such as *Cardamine hirsuta* and *Silene conica*.
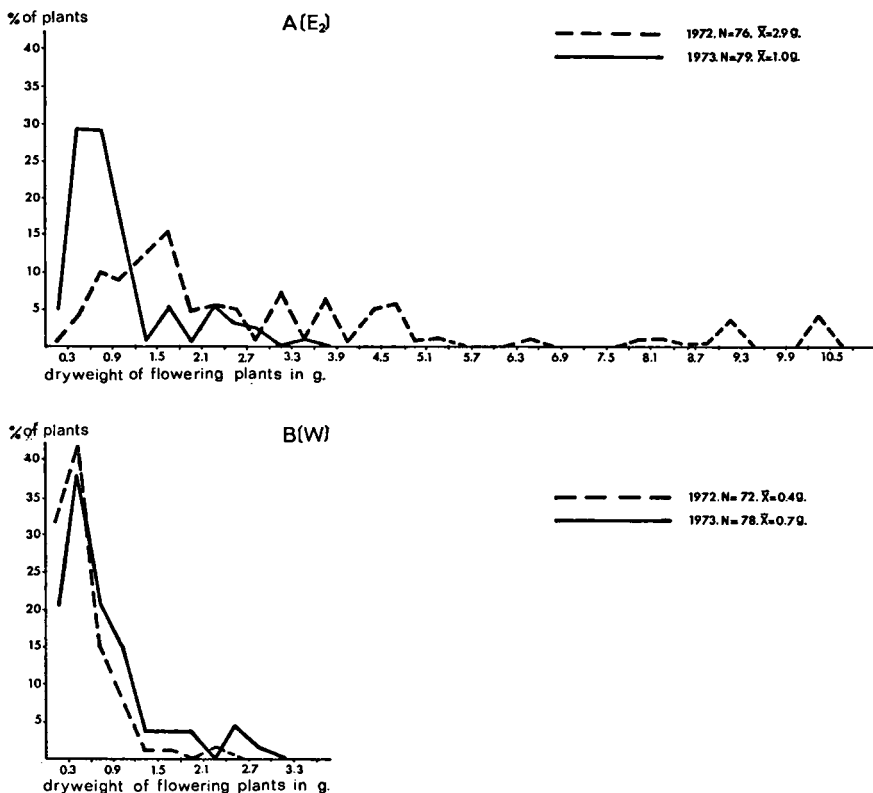
Fig. 4. Frequency distribution of dry weight of parts above the ground (in g) of flowering specimens of the coastal population E2 (*A*) and the inland population W(*B*) sampled in 1972 and 1973.
N = number of plants, $\bar{x}$ = mean.

6. FLUCTUATIONS IN FLOWERING RATE

For the assessment of the flower production the following method was employed. Of every individual plant of each population sample one stem of average length was used for counting the number of flower heads and the number of flowers in each head. From these data the mean number of flowers per inflorescence in the total sample was calculated (*a*). Subsequently the number of flower heads occurring on all plants was determined to find the mean number of heads per plant in the population sample (*b*). The mean number of flowers per plant in the sample is thus calculated as $a \times b$.

Fig. 5 shows the fluctuations in the mean number of flowers per plant of the coastal population E2 and the inland population W in the years 1970 to 1974. It appears that this number varies appreciably in E2: in 1972 it was more than 2.5 times higher than it was in 1971, in 1973 it was about the same as in 1971 to
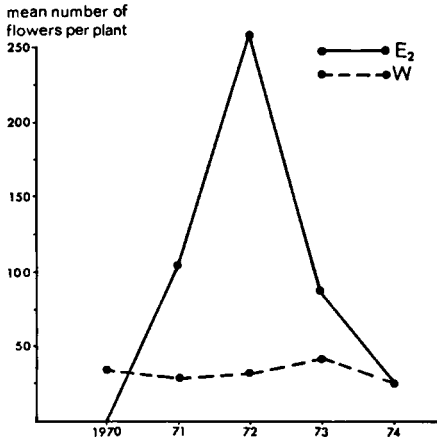
mean number of
flowers per plant

Fig. 5. Fluctuations of the mean number of flowers per plant of the coastal population E2 and the inland population W during 1970–1974.

decrease to less than onetenth of the 1972 number in 1974. In 1970 not a single flowering specimen was encountered. The number of flowers per plant is a complex entity and depends on the number of flowering shoots produced by the plants, on the number of heads per stem, and on the number of flowers in each inflorescence. *Fig. 6* shows the frequency distribution and the mean numbers of flowering stems per plant, the number of flowers per inflorescence, and the number of heads per plant of the E2 population samples. A comparison of this figure with *fig. 5* indicates that when plants produce a large number of flowers, the following correlations are manifest: (1) such plants produce a relatively high number of flowering shoots, (2) these shoots produce an appreciable number of flowerheads, and (3) the number of flowers per head is also relatively high. These data obtained from samples gathered in the field do not permit the assessment of more reliable numerical relations.

The oscillations in mean flower production per plant are much smaller in W than in E2 judging by the diagrams shown in *fig. 5*. The greatest difference recorded was between 1971, with a mean number of 27 flowers per plant, and 1973, with a mean of 44, i.c., the maximum value is only about 1.6 times the minimum during the five years of sampling.

The frequency distributions and means of the flower production in the W population are shown in *fig. 6D, E, F*. These diagrams also point to, comparatively speaking, small differences in the frequency distributions in W. A comparison with *fig. 6A, B, C* shows that the differences in the frequency distributions in the consecutive years were much greater in E2 than they were in W, and also that usually the means of the E2 samples and the ranges of variation of the frequency distributions of the number of heads per plant were appreciably higher than in the W population. The range of variation in the number of heads and the number of flowering stems per plant also increases in W in years with suitable growing conditions, but not by far so much as it does in E2. These marked differences in rate of flowering and in the correlated charac-
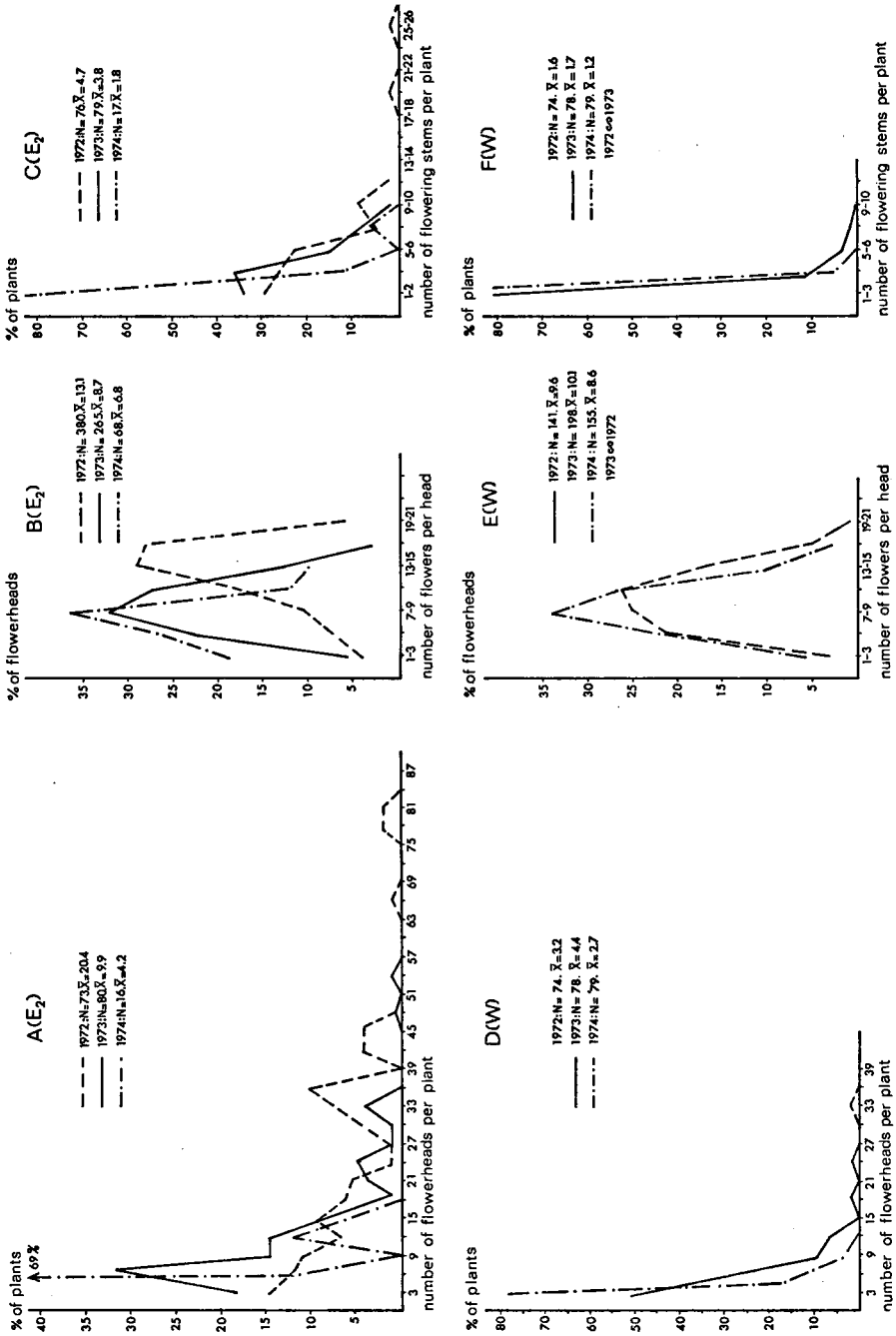
Fig. 6. Frequency distributions and mean numbers of inflorescences per plant and flowers per head, and number of flowering shoots per plant of the E2 (coastal) and W (inland) populations in different years.

N = number of plants or flowerheads, x̄ = mean.

Table 2. The mean number of flowers per m² of the populations E2 (coast) and W (inland) in 1970–1974.

Year	Mean number of flowers per m²	
	E2	W
1970	0	1470
1971	963	1377
1972	11210	1426
1973	2064	2288
1974	58	222

teristics between E2 and W are, like the differences in annual biomass production, clearly attributable to the greater environmental dynamics at the E2 site and the resulting sparser stand density concomitant with a lesser degree of competition.

The frequency distributions of the number of heads and of the number of flowering shoots produced per plant are distinctly oblique, as was also found in the case of the frequency distribution of the dry weights (see *fig. 4*). The frequency distributions of the mean number of flowers per inflorescence are practically normal. Oblique frequency distributions of numbers of flowers and of fruits borne per plant were reported to occur in *Ranunculus repens, R. bulbosus* and *R. acris* by SARUKHÁN & HARPER (1973).

The differences in the rates of flowering between the populations E2 and W are also evident if the flower production is calculated as mean number of flowers per m².

For the interpretation of the data shown in *table 2* it is important that each flower can only produce a single seed, so that the seed production per plant is relatively low. The germination rate is high: 98–100%.

7. REPRODUCTION AND LONGEVITY

No reliable data were available concerning the longevity and rate of reproduction (and the relation between the two) in *Anthyllis vulneraria*. Generally speaking the relation between the age and the reproduction of plants has not been studied to an appreciable extent (HARPER 1970). As far as *A. vulneraria* is concerned, HEUKELS en VAN OOSTSTROOM (1970) report that this taxon is perennial, but CULLEN (1961) and HEGI (1931) state that the species is annual to perennial.

By means of an investigation of the life-span of plants marked as seedlings the age the plants can attain was recorded and it was thus also possible to ascertain when they start flowering and during how many (consecutive) years they may be reproductive. The results are shown in *table 3*.

It must be remembered that the germination of the seeds takes predominantly place in the spring. The young plants remain vegetative for the rest of the year and hibernate to flower for the first time in the second year. The table shows

Table 3. Reproduction of the populations E2 (coast) and W (inland). The data are based on the life histories of plants marked in the field in the seedling stage during 1970 and 1971.

Population	E2	W
No. of labelled seedlings	701	416
Percentage of plants that attain the flowering stage	36	18
Percentage of plants flowering once*	73	90
do. twice	26	9
do. three times	1	1
Percentage of plants flowering in 2nd year*	68	30
do. 3rd year	56	43
do. 4th year	2	35
do. 5th year	0	1
Percentage of plants flowering for the first time in 2nd year*	68	30
do. 3rd year	32	39
do. 4th year	0	27
do. 5th year	0	1
Percentage of plants remaining vegetative in 2nd year**	21	35
do. in 3rd year	2	11
do. in 4th year	0	4
do. in 5th year	0	1
Percentage of plants remaining vegetative in both 2nd and 3rd year**	1	21
do. 2nd, 3rd and 4th year	0	3
do. 2nd, 3rd, 4th and 5th year	0	1

* percentages are calculated of the number of plants that attained the flowering stage.
** percentages are calculated of the number of marked specimens.

appreciable differences in the life histories of the plants of the two populations including:
1. a lower percentage of plants attaining the flowering stage in W;
2. a much higher percentage of W plants flowering only once, and a lower percentage of W plants flowering twice;
3. a much lower percentage of W plants flowering in their second year, and also a lower percentage of W plants attaining anthesis in their 3rd year; however, a very much higher percentage of W plants flowering in their 4th year;
4. a much lower percentage of plants of the W population flowering for the first time in their 2nd year, about equal percentages of E and W plants first attaining anthesis in their 3rd year, and a relatively high percentage of plants first coming into flower in their 4th year as against complete absence of flowering in the 4th of 5th in the E2 population;
5. a much higher percentage of W plants remaining unproductive in their 2nd and also of plants still vegetative in their 3rd year, and the complete absence of E2 plants that did not flower before the 5th or 6th year (in contrast to the W population); and
6. a relatively highly percentage of W plants remaining unproductive in both their 2nd and 3rd year as against 1 % of the E plants (in the W population,

although in low numbers, plants were recorded which remained vegetative for four years and 1 % even stayed unproductive till the end of their 5th year).

Summarising this evidence, we may conclude that it is "more difficult" for the plants to reach the flowering stage in W than it is in E2. The causes of the differences must be sought in the much denser stand of the plant community of which *Anthyllis* forms a component. The mutual influence of the individuals in the standing community or "density stress" (HARPER 1967) must be an important reason why *Anthyllis* flowers less and also later in W than it does in E2. Several other species are known to remain unproductive for some time in special ecological situations, e.g., when nutrient and light conditions are unfavourable (RABOTNOV, cited in HARPER & WHITE 1970).

Also the longevity of the *Anthyllis* plants was studied and is shown in *fig. 7*. In W (*fig. 7A*) the chances of survival appear to differ from year to year; these differences are manifest if plants of the 1971 and the 1973 populations are compared: in 1971, 12 months after having been labelled, 38 % of the marked individuals proved to be still alive, whereas in 1973 only 18 % had survived. Also in the E2 population unequal survival rates were noted in different years (see, e.g., the figures for 1970 and 1972 in *fig. 7B*).

The survival diagrams of the W population decline rather regularly as a "smooth" curve, the numbers falling off rather steeply in the beginning owing to the high seedling mortality, and gradually levelling off during the 2nd and 3rd years to become almost horizontal after the 3rd or 4th year. The diagrams of the E2 population are rather similar to those of the W population but they are not so regular. When drawn on the same scale, the E2 diagrams lie above those of the W population in the 2nd and 3rd year of growth (i.e., there are more survivors in E2 than in W), but they do not level off so much during the consecutive years as the W diagrams because of the shorter average longevity of the E2 individuals. The sudden change of direction of some the diagrams in the months 5, 6, 7 or 8 is rather striking and the explanation is apparently a higher mortality rate during that period. About the causes of mortality of *Anthyllis* plants very little is known, but both abiotic factors (moisture relations, frost) and biotic ones (predation, parasitism) seem to be of importance. Details will be given in a forthcoming publication. It can be stated that generally speaking very few detailed data have been recorded regarding the causes of mortality in plants (SARUKHÁN & HARPER 1973). When the data pertaining to W and to E2 are summarised, the conclusion can be drawn that the longevity of the W plants agrees approximately with that of the E2 plants, but a small percentage of W plants grows older than the E2 plants and the dying off proceeds somewhat more regularly in the W population.

The longevity of a population can be recorded rather accurately by means of the so-called half-life (HARPER 1967). Many compiled data have shown that if one starts from a given population size, the annual decrease in number of individuals is nearly constant, which constant decrease is described by the half-life, the half-life being the time in which that population is reduced to half its size by mortality. The half-life calculated from the data obtained from *Anthyllis*
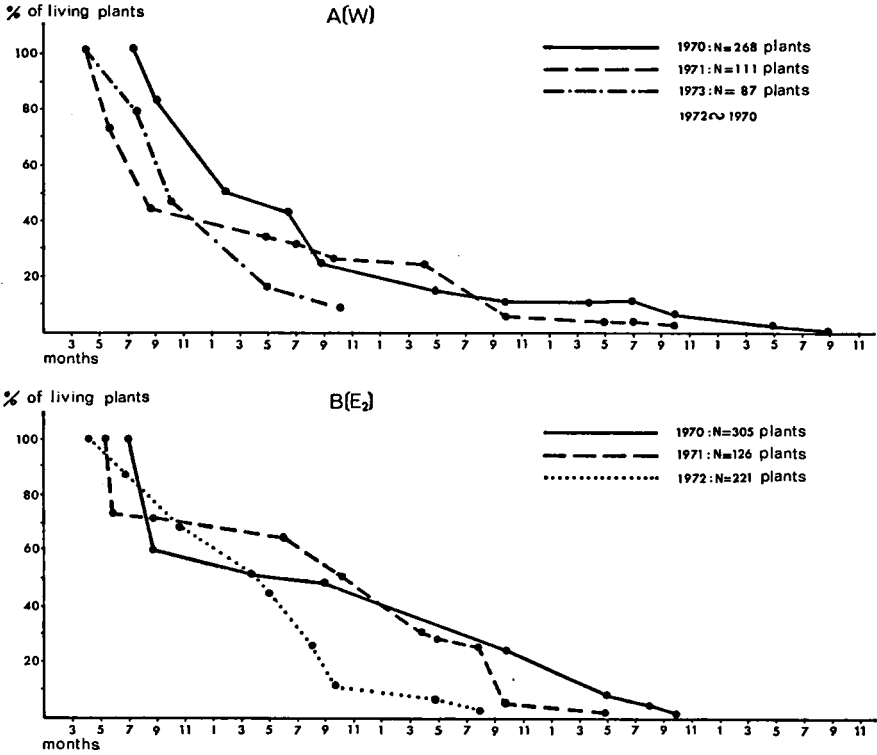
Fig. 7. The life-span of plants of the inland population W (fig .A) and the coastal popula-
tion E2 (fig. B). The data are based on seedlings labelled in the years 1970–1973.
~ = agrees with

plants labelled in 1970 and 1971 is in E2 and W about 9 months (mean value:
this value is somewhat higher in W than it is in E2 because a small percentage
of its individuals attains a somewhat greater age). As pointed out before, the
mortality rate is in fact not the same throughout the different phases of the life
cycle: younger plants have a smaller survival chance owing to the high seedling
mortality, and the mortality seems to be higher in the period April-July than
during the rest of the year apparently on account of seasonal differences. It is
also clear that the half-life of the same population differs from year to year
(compare the year classes 1970 and 1973 in *fig. 7A*). Such phenomena are known
to occur in populations of other species (SARUKHÁN & HARPER 1973).
    When the longevity is related to the reproductive capacity, the flower pro-
duction per plant is usually lower in W than it is in E2, which is to be ascribed
to two causes: (a) the mean number of flowers per plant is lower (see *fig. 5*),
and (b) the mean number of times a single individual comes into bloom during
its life-span is also lower in W than it is in E2. As regards the natural selection

in relation with reproduction there is a different situation in E2 and in W.

The results of the longevity studies agree in so far with those of HEUKELS & VAN OOSTSTROOM that both varieties of the kidney vetch found in the Netherlands viz *Anthyllis vulneraria* L. ssp. *vulneraria* var. *vulneraria* (inland population) and the var. *langei* Jalas (coastal populations) are perennial. It has been shown that the plants usually attain an age of 2–3 years and but rarely of 4, and very rarely of 5 years.

8. DISCUSSION

The field studies of populations of the vars. *langei* and *vulneraria* of *Anthyllis vulneraria* ssp. *vulneraria* have revealed a number of differences in their population biology. In the open plant communities along the coast appreciable annual fluctuations in the population density and in the biomass production of the generative individuals were recorded which were markedly greater than those observed in the more closed inland communities. The causes of the greater fluctuations in the coastal populations must be sought in the much more pronounced environmental dynamics in the dunes compared with the inland. The differences in dynamics recorded in the two regions are to a large extent attributable to the different degrees of fluctuation of the abiotic environmental conditions, more particularly of the moisture relations. In the interior, where the soil consists of loam, the habitat is more stable in this respect than in the sandy dune soil of the coastal environment, and the vegetation cover is denser and contains a much better developed plant community. The greater importance of the moisture conditions near the coast may be reflected in the denser pubescence of the leaves and a smaller number of stomata per unit of leaf surface of the plants of coastal populations, to be reported in detail elsewhere. The higher degree of pubescence of the coastal populations is in fact one of the diagnostic characters used to distinguish between the vars. *langei* and *vulneraria*.

In spite of the greater environmental stability, the inland populations exhibit, like the coastal ones, an appreciable "turn-over" in that large numbers of seedlings and vegetative individuals arise and disappear. It is highly probable that the mortality factors are different near the coast and in the interior. The impression was gained that in the open stands of vegetation along the coast the lack of moisture is a more important factor causing mortality, whereas in the denser vegetation stands in the interior mainly biotic factors, in particular competition and predation, are more important.

The fluctuations in population density and in the phenological condition of the plants are of such a nature that in unfavourable years not a single individual attains the generative stage in the coastal populations; the survival is in such a case largely dependent on dormant seeds present in the soil. The biology and dynamics of the seed population and the causes of fluctuations are at present under investigation. It is to be expected that there are regulation mechanisms for the rate of germination preventing the wholesale exhaustion of the total stock of seed present in the soil (compare KÖLLER 1969). The delayed germi-

nation, caused by an extended dormancy of a part of the annual seed crop, may
be regarded as one of the principal regulating factors.

The relationship of the demographic parameters of a population to its ecologi-
cal niche constitutes one of the central problems of population biology (GADGIL &
SOLBRIG 1972). These authors mention r- and K-selection as mechanisms leading
to adaptations to, respectively, open and closed communities (compare also
MCARTHUR & WILSON 1967). The conceptual basis of the so-called r- and K-
selections is that populations of stable and closed vegetation types with a high
and density-dependent rate of mortality use a larger part of their biomass and
energy production for the development of vegetative parts than for reproductive
purposes (K-selectionists), whereas the plants growing in open and less stable
habitats with a lower density-dependent mortality use a larger portion of their as-
similates and energy for reproduction at the cost of the development of vegetative
organs (r-selectionists). GADGIL & SOLBRIG (1972) have demonstrated that r- and
K-selection is of importance in different biotypes of the *Taraxacum officinale* com-
plex. In open disturbed sites with a low degree of competition the plants exhibit a
lower power of competition and a larger portion of the biomass consists of seed as
compared to biotypes of less disturbed habitats. Both characteristic phenomena
are heriditary. The possible role of these selection mechanisms in causing popu-
lation diversity in *Anthyllis* will be studied by means of competition experiments.

Plant species can also adapt themselves to the environmental dynamics by
means of their reproductive strategy. Many taxa found in unstable habitats
(pioneer species) exhibit a high degree of autogamy. It is often assumed that
autogamy provides a greater direct fittness which has an appreciable adaptive
significance in unstable environments where a rapid build-up of the population
is of paramount importance. Allogamy results in a greater genetic variation but
this advantage falls away against the fact that the progeny of the genotype
already present in the habitat is directly adapted.

According to COUDERC (1971) in France the *Anthyllis* populations are obli-
gately autogamous and allogamy does not take place, but although according
to MARSDEN-JONES (1933a) autogamy prevails in Britain, also allogamous races
occur which form hybrid swarms. A detailed study of the mode of reproduction
of coastal and of inland populations in the Netherlands has been initiated.

A reduction in the rate of genetical recombination can, in conjunction with
natural selection, lead to a genetic uniformity of a population. Such a dimin-
ished genetic variation is sometimes compensated by a greater phenotypic
plasticity of the genotypes. There are indications that this also applies to
Anthyllis, the plasticity being expressed in *e.g.*, the degree of pubescence of the
plants, the growth habit, the biomass production and the reproductivity. There
is apparently also a great deal of plasticity in the longevity and the number of
reproductive seasons. When plants reared from seed collected in the natural
habitat were grown in the experimental garden they remained vegetative in the
first year, they flower, set seed and die off in the second. This applies to plants
cultivated from seed hailing from both coastal and inland populations; in other

words, under cultivation all indivials are typically biannual with a "big-bang" kind of reproduction (compare HARPER 1970). In nature the plants behave altogether differently as we have seen, some growing older than two years and flowering more than once. There are also characteristic differences between the longevity (mortality rate) and mode of flowering of the coastal and the inland populations (compare *table 3*). The variation in longevity and in rate of reproduction are apparently habitat-induced and has an appreciable adaptive significance for the maintenance of the species. It is quite clear that data concerning longevity and mode or time of flowering obtained from plants cultivated in an experimental garden may deviate considerably from the situation prevailing in nature.

The longevity of inland plants differs slightly from that of the coastal form, a small percentage of the population attaining a somewhat greater age than do the plants of coastal populations. This is in contrast with data obtained from other species occurring in both closed and sparse vegetation. Individuals of *Spergularia media* attain a markedly higher age when growing in close stands than they do in open communities (STERK 1969). This phenomenon has also been recorded for other species (SALISBURY 1942, HARPER & WHITE 1970). A greater longevity in more closed plant communities clearly has an adaptive significance, and the fact that individuals of *Anthyllis vulneraria* do not live longer in a closed stand indicate that this species cannot successfully settle and in the long run maintain itself in closed plant communities.

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