DEMOGRAPHIC STUDIES OF ANTHYLLIS VULNERARIA L. IN THE NETHERLANDS.
II. POPULATION DENSITY FLUCTUATIONS AND ADAPTATIONS TO ARID CONDITIONS, SEED POPULATIONS, SEEDLING MORTALITY, AND INFLUENCE OF THE BIOCENOSIS ON DEMOGRAPHIC FEATURES.

A. A. STERK[1], A. VAN DUIJKEREN[2], J. HOGERVORST[1], and E. D. M. VERBEEK[1]

[1] Hugo de Vries-Laboratorium, Universiteit van Amsterdam, Plantage Middenlaan 2a, 1018 DD Amsterdam
[2] Vakgroep Experimentele Entomologie, Universiteit van Amsterdam, Kruislaan 302, 1098 SM Amsterdam

SUMMARY

During a period of eight years demographic studies were made of a coastal population of *Anthyllis vulneraria* L. var. *langei* Jalas and of an inland population of its var. *vulneraria*. The coastal population was found in open dune vegetation on a sandy soil, whereas the inland population occurs in a relatively dense, calciphilous grassland vegetation on a loamy soil. Intermittent periods of drought occur both along the coast and inland, but the dune biotope is considerably more arid than the inland one. In the interior, the more fertile soil supports a much denser and richer biocenosis than does the dunal habitat, and this has important consequences for the population biology. In the coastal region much more extreme population density fluctuations take place, whilst the correlation between these fluctuations and the fluctuations of the abiotic environment (drought) are more evident than they are inland. The dunal form is obviously better adapted to periodic droughts, *i.e.*, to an abiotic factor which is not dependent on population density. In the interior, such biotic factors as competition and predation have a much greater influence owing to the more complex mutual relations between individuals and to the richer composition of the total biocenosis. There are differences in germination ecology, in mortality of seedlings and juvenile plants, in reproduction strategy, and in seed predation between the two populations studied. The coastal populations and the inland ones are each to a large extent build up by pure lines on account of the almost obligatory autogamy; these lines exhibit genetically controlled differences in pubescence.

1. INTRODUCTION

Demographic studies of Dutch populations of *Anthyllis vulneraria* L. belonging to the varieties *langei* Jalas and *vulneraria* were carried out since 1969 (STERK 1975). The var. *langei* occurs along the coast and a population referable to this taxon was studied at a dune grassland site near Egmond aan Zee in the North-Holland Dune Nature Reserve, province of N. Holland. The other variety is found inland and was studied in a calciphilous grassland in the nature reserve "De Wrakelberg" in the province of Limburg, municipality of Wijlre.

The first author has reported the descriptive aspects of the inquiry extensively (STERK 1975). These concern chiefly the life-span of the individuals, the density fluctuations of flowering specimens, and the fluctuations in biomass- and flower production. The present paper, which concludes the investigation,
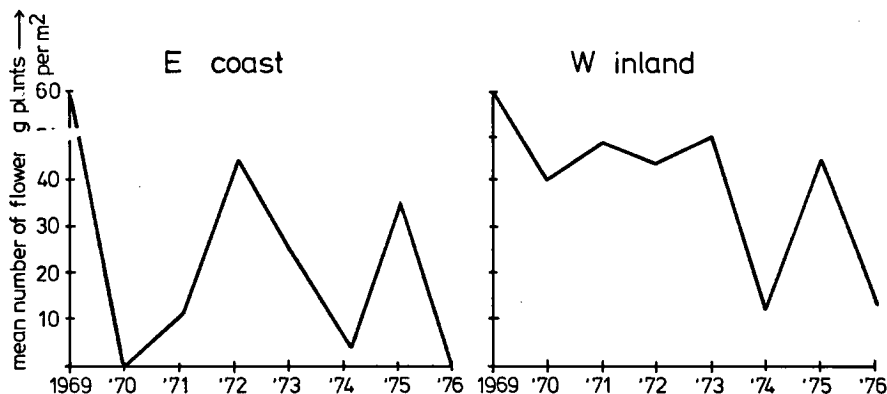
A. A. STERK, A. VAN DUIJKEREN, J. HOGERVORST AND E. D. M. VERBEEK

Fig. 1. Fluctuations in the mean number of flowering plants/m^2 of the coastal population E (var. *langei*) and of the inland population W (var. *vulneraria*).
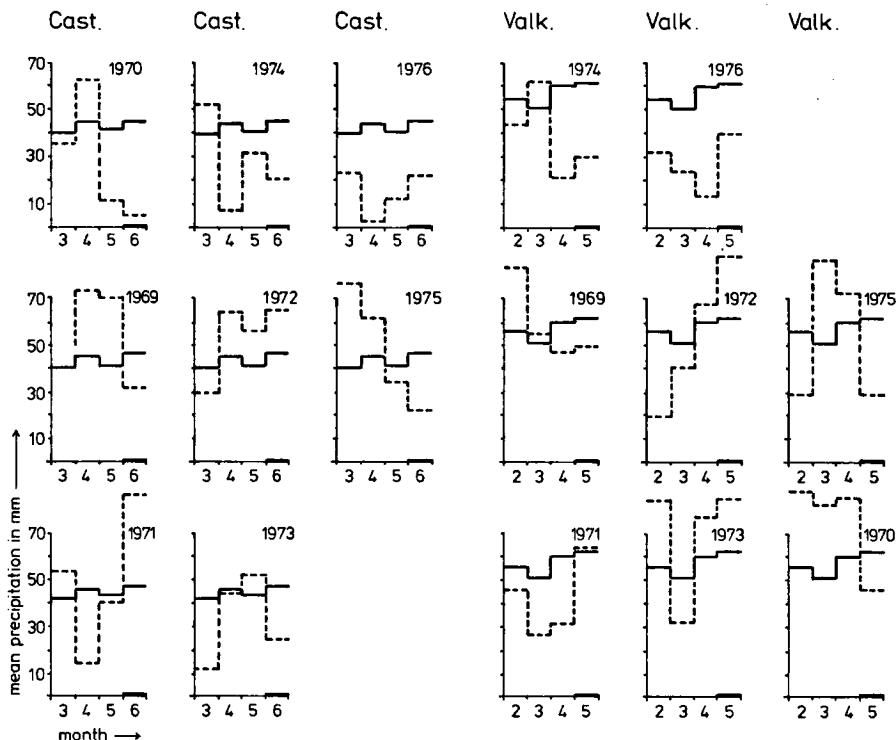

Fig. 2. Means of monthly amounts of precipitation (February–June) in mm in 1969–1976 near Castricum (Cast. situated near E) and near Valkenburg (Valk., situated near W). The upper diagrams are those of the drier years.

———■———: flowering time.

—————— : mean precipitation in the period 1930–1970.

— — — : mean precipitation per month.

enters more profoundly into the connection between fluctuations within the populations and in atmospheric precipitation, into adaptations to arid conditions, into some aspects of the seed population and seed bank and of seedling mortality, and into the effect of the biocenotic complexity on demographic features.

2. FLUCTUATIONS IN POPULATION DENSITY AND IN ATMOSPHERIC PRECIPITATION

Fig. 1 shows the fluctuation in the mean number of flowering plants per m^2 of the coastal population E (var. *langei)* of Egmond aan Zee and of the inland population W (var. *vulneraria)* of "De Wrakelberg".

Population E in particular exhibits an appreciable fluctuation in flowering specimen density, in some years (such as 1970 and 1976) no flowering taking place at all, so that no seed is produced in such inclement years. The fluctuations are far less pronounced in the inland population and no years without any flowering were recorded. As pointed out earlier (STERK 1975) the fluctuations in question are correlated with fluctuations of the mean biomass, and with the mean number of flower heads per plant.

Fig. 2 shows the mean amounts of precipitation per month during the period *Anthyllis* is in flower and during the preceding months of the year. These data were kindly provided by the weather stations of the K.N.M.I. near Castricum (the one nearest the site of population E), and near Valkenburg (nearest "De Wrakelberg"), respectively. A comparison between *figs. 1* and *2* clearly indicates a correlation between flowering individuals density per m^2 and the mean precipitation in the month of flowering and in the preceding month; this correlation is statistically significant, and the effect of drought is such that when the rainfall in the two critical months lies below or at half the average amount (of 40 consecutive years), no plants of the var. *langei* come into flower (as happened in 1970, and in 1976) and the number of flowering individuals of the var. *vulneraria* is much reduced (1974, 1976). It is well-known that the amount of precipitation is one of the major factors in the water economy of plant species and populations (SLATYER 1967). Apart from other factors, the water-retaining capacity of the soil is certainly of importance.

Table 1 shows the moisture content at pF values of 2.0 (= water-saturated soil) and 4.2 (= wilting point), and the resulting potentially available quantity of water of the dune sand soil near Egmond aan Zee, and the *loess* soil on "De Wrakelberg".

In the dunes the moisture-retaining capacity was established at two depths, because the uppermost 0–5 cm layer is manifestly humic, whereas the gravelly *loess* soil does not have any developed horizontal layering.

The table indicates that the *loess* soil exhibits an appreciably higher moisture retention than does the sandy dune soil, and this difference is presumably the reason why at the Wrakelberg site no years were recorded without any flowering individuals, as was noted several times in the dunal habitat. Another impor-

Table 1. pF data and amounts of available water of the dune soil (E) and the loess soil (W).

Locality	Depth in cm	Moisture content in weight % g of water/100 g dry soil		Available quantity of water in g/l soil
		pF 2.0	pF 4.2	
Dunes (E)	0– 5	14.1	5.2	128
	5–20	8.6	1.1	112
Calciphilous grassland (W)	0–20	33.8	17.6	204

tant factor of direct significance for the moisture conditions is the fertility of the soil, which is much higher in the interior than near the coast, so that the stand of vegetation at the W population site is much denser and has a moister microclimate than at the site of the E population. The percentage cover of the herb layer in the calciphile *Mesobromion* at W is 95%–100% as against about 70% in the *Anthyllido-Silenetum* grassland at E (STERK 1975). The greater stand density at W also results in a more stable microclimate than that obtaining in the open dune site near Egmond.

3. ADAPTATIONS TO ARID CONDITIONS

The established relation between the fluctuation in numbers of flowering individuals and the amount of precipitation renders it probable that the available amount of water is an important ecological factor in the population dynamics of *Anthyllis*, especially in the coastal areas where the periods of water shortage in spring and summer are of paramount ecological importance.

Plant taxa may exhibit structural and physiological adaptations to arid conditions. Two of the adaptive features, *viz.*, the pubescence and the stomata density were investigated more closely.

3.1. Density of pubescence

Both varieties of *A. vulneraria* studied have pubescent leaves and stems, but the upper surface of the leaflets is usually glabrous or bears only a few scattered, long hairs. The lower leaf surface is densely covered with unicellular adpressed hairs directed towards the apex *(fig. 3b)*. The density of the pubescence is not uniform but is greater along and on the midrib and towards the edge of the leaflets. The degree of hairiness was always estimated of a leaf inserted near the stem base (which is usually pinnate, and in this case the apical leaflet was used). By means of a net micrometer in a square area of 1.25×1.25 mm^2 situated in the middle of the leaf or leaflet surface and exactly between midrib and leaf-edge (see *fig. 3a*) all visible hairs were counted, *i.e.*, also those inserted outside of the square area but protruding into the square.

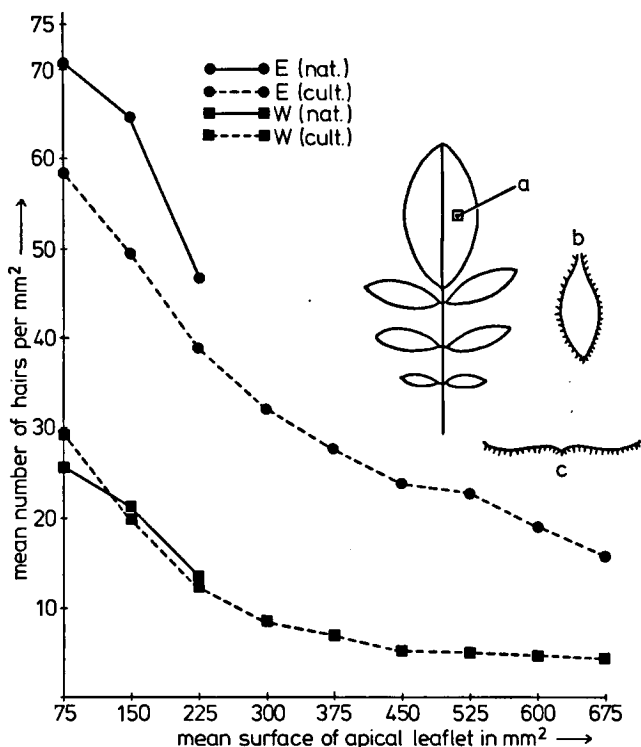Already at a first glance there appears to be a relation between leaf size and

Fig. 3. Mean number of hairs per mm² of lower surface of apical leaflets in random samples of natural populations (nat.) and in random samples of populations reared from seed (cult.) of the coastal area (E) and from the interior (W). The cultivated plants were grown under identical conditions. a = place where hairs were counted, b = infolded leaflet from E under dry conditions, c = open leaflet from E.
E cult.: n = 148; E nat.: = 127;
W cult.: n = 152; W nat.: n = 210.

density of pubescence. In order to obtain comparable population samples it proved to be necessary to examine leaves with corresponding leaf surface areas. To this end the apical leaflets were referred to the following classes of surface area: class 75 (with a surface area from 38 mm² to 112 mm²), 150 (113 mm² to 188 mm²), etc. The mean pubescence density is plotted against the mean leaf surface area in *fig. 3*. The relation between these two parameters is manifest: the pubescence becomes sparser as the surface area increases. This figure also indicates that the overall picture is the same in E and W populations, although in nature the mean density of leaf pubescence in E is about three times that in W. In specimens raised from representative seed samples of natural populations in our experimental garden, the density of pubescence of the W progeny remained almost the same as in the natural W population but in the E progeny the density was about 20% lower than in the parent population. Since the plants were grown under similar conditions in the garden, the difference in pu-

bescence between the var. *langei* (E) and the var. *vulneraria* (W) must be geneti-
cally determined.

A preliminary study was made of the variation in leaf pubescence between indi-
viduals of the same population (see *table 2*).

Table 2. Differences in pubescence between plants raised from seed of the E (var. *langei*) and of
the W (var. *vulneraria*) population.

Origin	Mean number of hairs per mm² class 150	Number of leaflets
E plant 1	70	20
plant 2	53	20
W plant 1	35	20
plant 2	21	20

Table 2 clearly shows that there are consistent differences in leaf pubescence
density within the E and the W populations; the differences between plants 1
and 2 proved to be statistically significant. The leaf size distribution within the
150 class is the same in E and in W individuals, so that the difference in degree
of pubescence cannot be ascribed to leaf size variation within class 150. Since
the plants studied were reared in the experimental garden, these differences
must be genetically determined. The corollary is that within both the E-popula-
tion and the W-population there are genetical differences in pubescence be-
tween the individuals.

3.2. Trichome length
Apart from the density of pubescence the length of the trichomes is of impor-
tance in connection with adaptation to arid conditions. *Table 3* shows the tri-
chome lengths in representative samples of the natural populations E and W.
Per apical leaflet 3 hairs were measured at the place indicated in *fig.* 3 by a.

Table 3. Trichome length on apical leaflets of individuals of the natural populations E (var. *langei*)
and W (var. *vulneraria*).

Leaf class in (mm²)	Number of trichomes		Trichome length (mm)					
				E			W	
	E	W	min.	mean	max.	min.	mean	max.
75	42	75	0.25	0.37	0.55	0.20	0.35	0.55
100	96	171	0.20	0.37	0.65	0.15	0.37	0.60
125	81	108	0.25	0.38	0.55	0.20	0.39	0.70
150	69	78	0.20	0.38	0.55	0.20	0.37	0.60
175	66	96	0.25	0.38	0.60	0.20	0.37	0.65
200	24	54	0.25	0.41	0.60	0.25	0.43	0.65

Table 3 indicates that the hairs are somewhat longer on the larger leaflets than on smaller ones, but the differences are not very great. There were no significant differences in trichome length between the E and the W populations. The difference in adaptive capacity of the pubescence between these two populations is, therefore, attributable to a different density of pubescence rather than to a difference in trichome length.

3.3. Stomatal density

An important structural adaptive feature against excessive transpiration is the distribution, density and size of the foliar stomata. The number of stomata was counted at the place indicated in *fig. 3a* in a circular field of vision covering 0.07 mm² of leaf surface; per apical leaflet two such fields were examined.

The *Anthyllis* leaf is amphistomatic (STÅLFELT 1956), *i.e.,* there are stomata on either leaf surface. The stomatal density was established in a single cultivated plant raised from seed of an E population and a plant raised from W seed and grown under the same conditions. *Fig. 4* shows the results of the counts: it appears that the stomatal density depends on the leaf size, smaller leaves exhibiting a higher density than larger ones. This rule applies to both the upper and the lower leaf surface, but does not as manifestly apply to the lower surface of E-plants.

The upper leaf surface contains an appreciably greater number of stomata than does the lower one (epi-amphistomatic condition: STÅLFELT 1956); the difference is upon the average a factor of 1.5–2 times in both the E and the W plant. The stomatal density is clearly higher in the W individual than in the E plant, but the diagram showing the relation between stomatal density of the upper leaf surface and the leaf surface area has about the same course in the case of E and W plants. However, the lower surfaces of E and W leaves exhibit
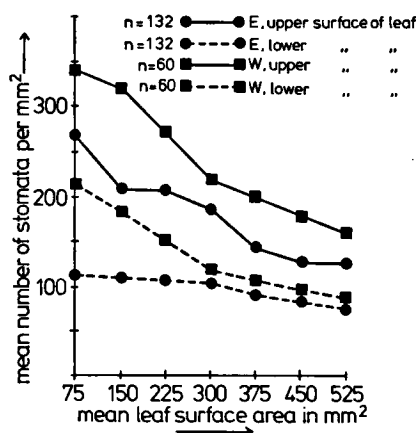

Fig. 4. Relation between mean number of stomata and mean leaf size. The upper and lower surfaces of the apical leaflets of a single plant grown from a seed of the E population and of a single plant reared from the W population were studied. The plants grew up under the same conditions.
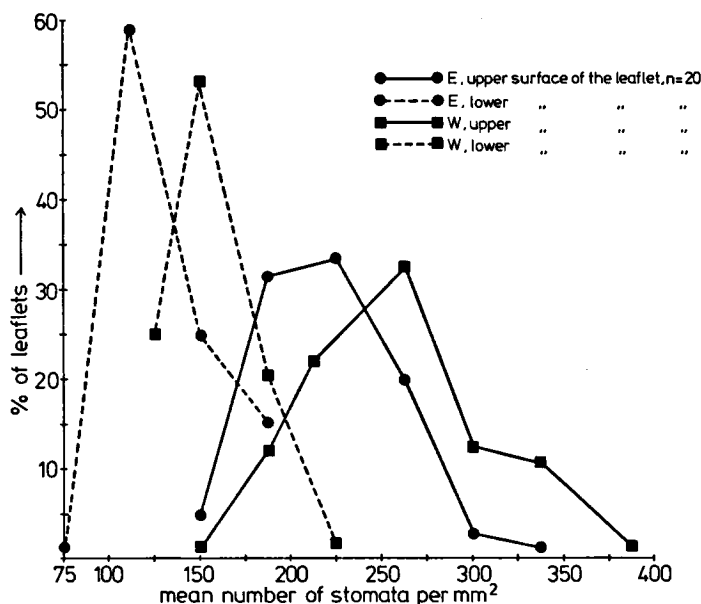
Fig. 5. Mean number of stomata of the upper and the lower surfaces of the leaflets of cultivated populations reared from seeds of E and W. The apical leaflets of the leaf class 225 mm² were studied.

a difference. *Fig. 5* shows the stomatal densities (per mm²) of the upper and the lower surfaces of class 225 leaves of plants raised in the experimental garden from seed of natural E and W populations. The density of the upper leaf surface is appreciable greater than that of the lower surface in both E and W plants. The figure also indicates that the stomatal density per mm² is smaller in the E plants than in the W plants, the difference is statistically significant. The lower stomatal density of the E plants may be taken as an adaptation to the drier dunal habitat.

3.4. Size of stomata

The rate of stomatal transpiration does not depend on the stomatal density alone but also on the size of the stomatal openings. In *fig. 6* the lengths of the stomatal slits of the same leaf areas as examined for the data shown in *fig. 5* are given. *Fig. 6* does not indicate any appreciable differences in slit length between the upper and the lower leaf surfaces, and indicates that the stomatal slit length of leaves of E individuals differs not significantly from that of W plants.

As regards the stomatal features there is another important difference between E and W individuals. In E plants the stomata are more deeply sunk into the leaf blade than in W plants. It follows that as far as differences in adaptive capacity with regard to the factor aridity are concerned, the differences between the E and the W populations are not attributable to differences in size
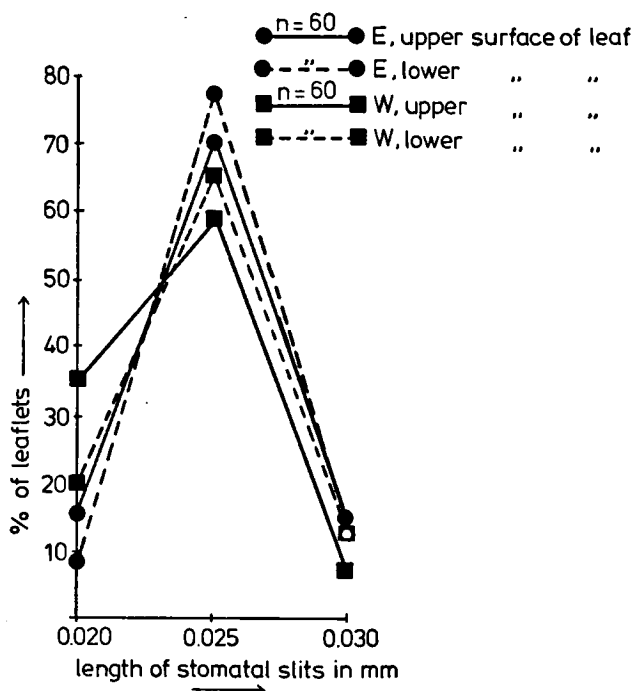
Fig. 6. Length of stomatal slits (in mm) of the upper and lower surfaces of leaflets of the leafclass of 225 mm^2 of plants grown from seed collected from the natural populations at E and W.

of the stomatal slits but to differences in stomatal density and to the greater or lesser degree of immersion of the stomatal apparatus into the leaf blade.

A comparison between the stomatal density and the degree of pubescence (compare the *figs. 3* and *5)* reveals that the former is highest on the glabrous upper surface of both E and W individuals. On this surface the rate of transpiration may become much higher than on the lower leaf surface with a lower stomatal density and a relatively dense pubescence. The plants have, accordingly, an important regulation capacity by reducing the upper leaf surface transpiration by infolding the leaf with the upper surface turned inside and the hairy surface on the outside (see *figs. 3a* and *3b)*. Especially E plants in the dunes exhibit this infolding during periods of drought, the transpiration almost entirely taking place through the pubescent lower leafblade surface. The leaves of E plants have also a thicker cuticle and are firmer and more rigid than those of W plants which, therefore, cannot infold their leaves as effectively as E plants can do.

4. THE SEED POPULATION

The viable seeds present on or in the soil form an integral part of the population. The seed bank in the soil is of special importance for the maintenance of
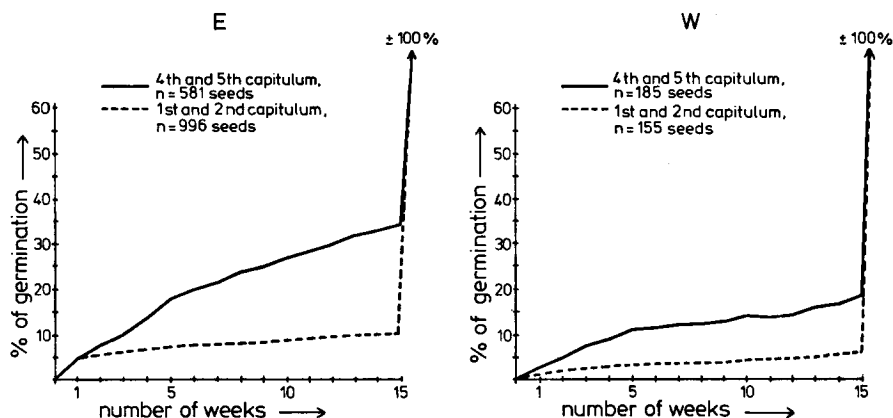
Fig. 7. Germination of seeds formed by earliest capitula (1st and 2nd) and by the last (4th and 5th) collected from cultivated E and W individuals. After 15 weeks seeds were sand-papered and a 100% germination followed. Germination at 25°C, 12 hrs. light/12 hrs. darkness on filterpaper in distilled water.
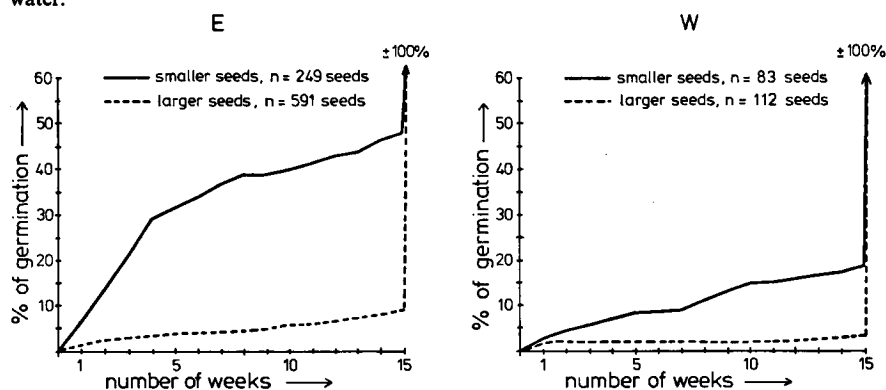

Fig. 8. Germination of larger seeds (diam. 2.3–2.4 mm) and smaller seeds (diam. 1.9–2.0 mm) collected from cultivated E and W plants. After 15 weeks seeds were sand-papered and a 100% germination followed. Germination at 25°C, 12 hrs. light/12 hrs. darkness on filterpaper in distilled water.

annuals and short-lived perennials with a greatly fluctuating annual seed production; this certainly also holds true for the kidney vetch (see *fig. 1*). Generally speaking the seed production per plant of *Anthyllis vulneraria* is low, each flower producing only a single seed (or very rarely two seeds). In favourable years, as in 1972 (see *fig. 1* and STERK 1975), E plants produce an average of 20 flower heads per plant of which usually 13 per head are seed-forming, so that the seed production averages 260 seeds per individual. In the inland W population, in favourable years, as in 1973 (see *fig. 1* and STERK 1975), an average of 4–5 heads per plant with per head 10 productive flowers yields a production of about 50 seeds per individual.

The production of flowers per m² and the subsequent maximum seed fall

per m^2 may in the dunal E population fluctuate from year to year, from zero (in 1970 and 1976) to 11210 (1972). In the lime grassland of W the fluctuation is not by far so excessive and the yields vary from 222 in 1974 to 2228 in 1973 (STERK 1975: 330). As the result of predation and parasitism the number of viable seeds produced per m^2 may be far less than the amount of seed-setting flowers per m^2, see p. 25.

The seeds have no visible adaptation to dispersal. It is unknown whether zoochory (birds, ants) plays any role, and anemochory is of little importance, so that most probably the great majority of the seeds remain within the local population and hardly lead to any gene flow. Some aspects of the seed population dynamics have been studied, *viz.,* germination, seed (or ovule) predation on the parent plants, and, finally the fate of the shed seeds.

4.1. Some data concerning delayed germination

The seeds have a hard testa and an extended germination (see *fig. 10)*, a high proportion of the seeds exhibiting a longlasting so-called "innate" dormancy (HARPER 1977). This dormancy can be broken by a light abrasion of the seed-coat to render it permeable; after this treatment germination takes place readily *(fig. 7)*.

All germination experiments to be discussed presently were carried out as follows: seeds were put out in petri dishes to germinate on filter paper in distilled water at 25°C with a 12 hrs light/12 hrs darkness regime. Per experiment 100–300 seeds were used.

The germination ecology is rather intricate, even the seed size and the site of its formation on the plant being of significance. *Fig. 7* shows that the first-formed seeds (of the first and second capitula) germinate more slowly than those formed later on (4th and 5th capitula), and *fig. 8* indicates that smaller seeds germinate at a faster rate than larger ones. *Fig. 9* shows the size-distributions of the seeds of the first-formed (1st and 2nd) heads and of those of the younger (4th and 5th) heads. *Fig. 9* indicates that the first-formed flower heads
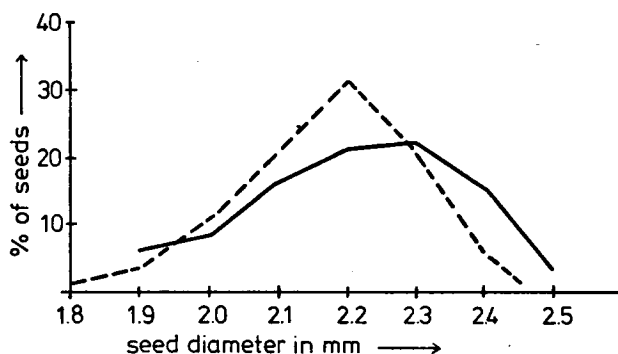

Fig. 9. Size distribution of seeds formed by the oldest heads (1st and 2nd) and by the youngest (4th and 5th) of cultivated E plants.

produce a somewhat higher proportion of large seeds than the last-formed capitula, but it is clear that the size distribution is practically the same in both cases. Any difference in germination time between "early" and "late" seeds can obviously not be ascribed to a size difference.

Figs. 7 and *8* show that seeds of E plants from the dunes under the conditions employed germinate at a faster rate than those of W plants from the inland; this holds for both the first-formed and the late seeds, and for both the large and the small seeds of each population. The seeds used were produced by plants raised from seed of natural populations and were simultaneously grown in the experimental garden; they were stored and put to germinate under identical conditions, so that the recorded differences in innate dormancy must have a genetical basis.

4.2. Germination under natural conditions

For a proper cognisance of the meaning of the life cycle in the biocenosis and the climatic conditions some data concerning germination under natural conditions in the field are essential. In *fig. 10* the germination of seeds of the E population (var. *langei*) in the dunes and of those of the inland W population (var. *vulneraria*) during the months of February up to and including September 1975 are shown (HOGERVORST 1978).

The germination of the E seeds began on about the 8th of March to attain its maximum in April and the beginning of May; from the end of May onward hardly any additional germination takes place. The germination of the W population is markedly different. The rapid increase in germination rate sets in sooner, most probably on account of the more southernly and less exposed site,
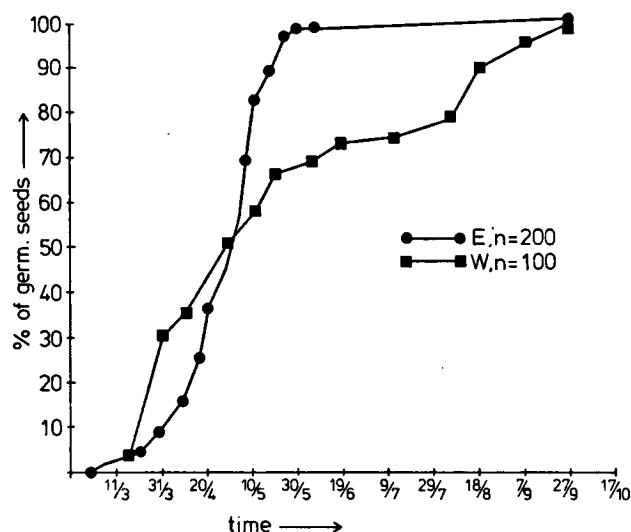

Fig. 10. Germination of seeds of the E population in the dunes and of the W population in the calcareous grassland in 1975 on 3 m².

and commences already in March. A fast rate of germination follows during March, April and May, to fall off towards the beginning of June, but germination continues at a slower rate till August, to increase a little again in August and September. During the cold season no germination occurs in either population.

In the W population germination apparently takes place throughout the spring and summer, but in the E population this is not the case. The difference is easily explained by the fact that at the calciphile grassland habitat (W) the conditions for a successful germination of the seeds and the establishment of the young plants remain favourable throughout, whereas at the more arid dune site with a more open vegetation cover the dry summer period does not permit any germination, and also the growth ceases altogether.

For a comparative study of the seed population of the different varieties in different biotopes it is not only necessary to establish the course of the germination rate during the growing season, but also to estimate the percentage of seeds germinating in this time-span. In order to investigate this two experiments were carried out. In the first place, quantities of seeds obtained from the E and the W populations were studied for the incidence of germination during one year. The lots of seed of either variety used appeared to be capable of 99% germination after the dormancy had been broken by rubbing the seed-coat with an abrasive. During this long-lasting experiment the distilled water was regularly replenished. Previously to the experiment the lots of seed had been dry-stored for 1 1/2 years at 20°C.

In *fig. 11* the results are shown. It is clear that the spreading of the germination is very great in both the E and the W seeds. It also appears that during the period of observation a much higher percentage of the E seeds germinated than of the W seeds. Especially in the first few weeks many E seeds germinated which, accordingly, had a weakly developed innate dormancy (or none at all). It follows that the innate dormancy is much stronger developed in W than in E seeds. The results of this germination experiment agree with those shown in *figs. 7* and *8*. In a second experiment seeds of the E and the W populations were sown in a natural vegetation, and the germination recorded by periodic
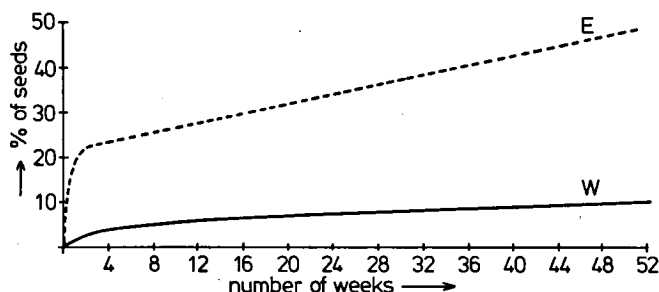

Fig. 11. Germination of seeds from the dune population E and from the interior population W during 12 months in distilled water at 25°C, 12 hrs. light/12 hrs. darkness.

controls. This experiment was carried out during the same time span as in the laboratory study shown in *fig. 11*. The rate of the germination agrees with that carried out under laboratory conditions, but the corresponding field germination curve of E lies at a lower level (that of W seed about coincides with the laboratory experiment). The final result after 44 weeks of observation was that about 20% of the E seed and 15% of the W seed has germinated (as compared to 50% and 10%, respectively, in the laboratory experiment). That the percentage was much lower in the case of the E seed can be explained by, among other things, the different conditions for germination which were much more favourable in the laboratory experiment than in the field; this holds especially for the dunal site where during the experiment periods with low temperatures and periods of drought occurred. An additional complication is that in the field a less frequent recording was made, so that some of the seedlings may have been overlooked. In W the conditions were much moister in the closed vegetation cover, so that the difference with the laboratory tests were smaller. Summarising, one may conclude that the principal period of germination of both the E and the W seeds lies in the spring. During the dry summer time there is hardly any germination in E, but in the W population germination continues throughout except during the coldest winter months, with a marked maximum in the spring and a smaller one in the autumn. Most of the E seeds have a less pronounced innate dormany than the W seeds, which feature is apparently adaptive. The reason is that in the relatively dry summer the dunal environment is not suitable for a successful germination, so that it is of importance that during the favourable spring season many seeds can germinate owing to the low degree of innate dormancy. For the W seeds, which can germinate throughout the growing season, it is of importance that the greater hazards in the much more diverse vegetation with a greater variety of predators than in E are being met with by a wider time-span of germination, accomplished by a higher degree of innate dormancy.

4.3. Predation of seeds on parent plant

When seed was collected in the field for our germination experiments it was noted that in many pods there was a hole, in particular at the W site. Such pods did not contain viable seeds and often the seed had disappeared completely. This observation instigated as study of the responsible predators of the ovules and developing seeds, carried out by D. Gillissen, Dr. A. Veerman and the second author at the Laboratory of Experimental Entomology, University of Amsterdam during the years 1975–1977 near Egmond aan Zee and on De Wrakelberg. Only the principal results will be mentioned here as far as they are relevant to the population dynamics of *Anthyllis,* for details and pertaining references the reader is referred to VAN DUIJKEREN & GILLISSEN (1979). The principal questions to be answered were: (1) what animals attack the ovules and/or young seeds, (2) how does predation proceed, and (3) are there any appreciable differences in rates of parasitisation between the E-locality and the W-locality as regards both the predator species involved and the amount of damage

caused. The answer to the first question is that a number of insect species attack the ovules and seeds of the kidney vetch. They will be discussed below.

1. *Tychius schneideri* Herbst. (*Curculionidae*)

An important predator appeared to be the snout beetle *Tychius schneideri*. The first record in N. Holland of this presumably rare beetle dates from 1973 and was made by Dr. A. Veerman. The imagines appear by the middle of May and are found in copulation on the flower heads. About four days after having been fertilised the females start laying their eggs, about 20 in all and 3–4 per capitulum. The eggs are deposited inside the ovarial cavity, one to each ovule, and subsequently the female gnaws a hole with its snout in the ovary wall, always at a certain spot near the attachment of the ovarial stalk. This hole gets closed again later by the growing ovarial tissue. The eggs hatch after about 12 days under laboratory conditions and the larvae start devouring the developing seed and their growth keeps step with that of the young seed. After 1 to 1 1/2 month the larva is full-grown and gnaws a hole in the wall of the pod and drops down. In the laboratory the larva pupates at once and the young beetle emerges from the pupal skin after about a month. In the field the larva presumably digs into the soil and pupates subterraneously. The imagines hibernate. *T. schneideri* was never found on other *Papilionaceae* (such as *Lotus corniculatus* and *Trifolium pratense*) growing at the E and/or W sites. Also in experiments in which beetles in copulation were placed on flowers of *Lotus* and *Trifolium* did this not result in predation of the latter. Most probably *T. schneideri* is a monophagous parasite of *Anthyllis vulneraria*. In 1976 *T. schneideri* had no chance to predate on *Anthyllis* seed near Egmond aan Zee, because no *Anthyllis* flowers were produced (see *fig. 1*). It was, therefore, remarkable that already in 1977 a relatively large number of this curculionid was found on *Anthyllis* again. This strongly suggests that the beetle is perennial; hibernation experiments in the laboratory showed that it can attain an age of at least two years. Apparently *T. schneideri* survive such unfavourable (dry) years as occurred in the dunes in 1970 and 1976 (see *fig. 1*), but how this is achieved is not clear; conceivably the beetle can use an alternative source of larval food in years when *Anthyllis* does not flower.

T. schneideri is an important seed predator of the kidney vetch. The following *table 4* shows the rate of predation of quantities of pods collected in the field.

Table 4. Rate of attack of pods of the kidney vetch by the snout beetle *Tychius schneideri*.

	Date	No. of pods	% attacked pods	% undamaged pods
Egmond	July 1974	500	4	96
Egmond	July 1975	250	3	97
Wrakelberg	26-6-1975	60	38	62
Wrakelberg	6-7-1975	1387	54	46
Wrakelberg	20-8-1976	335	58	42

The table clearly shows a much higher degree of parasitisation of the pods in the inland population in the time-span studied than in the dunal population.

Tychius schneideri is parasitised, both near Egmond and on De Wrakelberg, by the chalcidid *Habrocystus sequester (Chalcoidea, Pteromalidae);* on De Wrakelberg in 1976 about 27% of the snout beetle larvae were parasitised.

2. *Hypera trilineata* Mrsh. *(Curculionidae)*
The curculionid beetle *Hypera trilineata* is known to parasitise several papilionaceous taxa such as *Anthyllis vulneraria, Lotus corniculatus* and *Ulex nanus.* At the Wrakelberg site where *Anthyllis* and *Lotus corniculatus* occur sympatrically and flower simultaneously, *H. trilineata* was only found on *Anthyllis.*

By the middle of May the larvae are found in the flower heads. The imagines which laid the eggs are not present any longer and presumably stay on the flowers only for a short time when flowering commences. Per flower head a maximum of 4–5 larvae is found. The larvae are ectophagous and move about a great deal and each larva attacks several pods. After about 3 weeks the larvae are full-grown and they start spinning a transparent, fine-meshed cocoon attached to the host plant by means of a sticky substance. Under laboratory conditions the young beetles emerge from the cocoons after about 6 days and hibernate in the soil. Hyper-parasites of this species were not encountered. Quantitatively *H. trilineata* is not an important *Anthyllis* predator.

3. *Tychius junceus* Reich *(Curculionidae)*
This snout beetle was found only once on flower heads of *Anthyllis vulneraria* at Egmond and only once on De Wrakelberg. It is highly probable that this beetle has hardly any influence on the seed production owing to its scarcity.

4. *Aproaerema anthyllidella* Hübn. *(Lepidoptera, Gelechiidae)*
The caterpillars of this about 10 mm long moth were found near Egmond on the flower heads of kidney vetch; it was not encountered on De Wrakelberg. Normally there is only one caterpillar per capitulum which tunnels through the rather numerous (6–7) flowers and destroys the young pods completely. The caterpillars mature in July or in August and spin a cocoon between a group of partly devoured flowers, thus rendering the latter a compressed aspect. The larva pupates inside the cocoon and the adult moth hatches about two weeks later. In 1977 9% of 839 flowers examined had been attacked. The damage starts by the end of June and is initially not extensive, only a few flower heads being predated, but later in the season the damage increases to reach a peak in the second half of July and first half of August. At this time some samples contained up to 30% heads with *Frass*, but after the middle of August the infestation declines rapidly. The late flowers are not attacked by the caterpillars.

A. anthyllidella is parasitised during the larval and pupal stages by *Agathis tibialis* Nees *(Braconidae).*

5. *Bruchophagus spec. (Eurytomidae)*

Parasitic wasps of this genus were encountered in both areas studies. The identification was made by M. J. Gijswijt. The larvae were found in small numbers in developing pods, so that this wasp is hardly of significance as a seed predator.

6. *Gall midges (Cecidomyiidae)*

Of these 1.5 mm long gall midges the larvae were found in flower heads in both areas studied. Adult midges were reared from these larvae but could not be identified to the genus. The predation of *Anthyllis* by these cecidomyiids is negligible. The preliminary corollary of our findings is that in the inland De Wrakelberg locality seed predation is chiefly by the curculionid *Tychius schneideri*, and along the coast near Egmond principally by the microlepidopteron *Aproaerema anthyllidella* which may locally cause appreciable damage. It is also evident that seed loss by insect predation is very much higher on De Wrakelberg than it is near Egmond.

4.4. The fate of shed seeds

It was tried to gain some insight into the fate of viable seeds shed by the parent plant, more particularly as regards the rate of disappearance of these seeds in the course of the season. This last question is of primary importance because the surviving seed bank must establish a new generation after a year in which no flowers were produced and the mortality among the plants was high.

To study this point, quantities of seed were sown in natural stands of vegetation and the fate of the seeds was followed for 44 weeks (see VERBEEK 1977). Per m² 3000 seeds were sown by dividing the surface in small squares of 10 × 10 cm² and by placing 30 seeds on each small square by means of a tube (diam. 5.7 cm) placed vertically in the middle of the square. In each area under study 3m² were sown in in this way. The seeds used for these experiments had been tested for their germination capacity beforehand and 99% appeared to be capable of germinating. After the seeds had been sown a net was placed over areas sown in during two weeks, so as to preclude seed predation of superficially lying seeds by birds. During the experiment all flower heads of *Anthyllis* were removed from neighbouring plants up to a distance of 2 m from the experimental plots so as to avoid an influx of seed. Periodically soil samples were taken in each m² sown in by means of a soil drill of 7.9 cm diam. placed in the centre of each dm² and to a depth of 3 cm. Per day of sampling 45 soil cores were drilled (*i.e.*, 15 per m² sown in). In all, four times samples were taken, after 2, 9, 18, and 44 weeks, respectively, the first on 14-5-1975. The seeds were recovered from the samples by sieving. The samples from the dune habitat were loose enough to sieve them when dry, but the samples from De Wrakelberg had to be rinsed through the sieve under a tap. The seeds are large and conspicuous enough to be recognised on sight. All whole seeds recovered were put out to germinate; when after an incubation period of 6 weeks still no germination had occurred the seeds were tested for vitality by means of the tetrazolium reagent (ROBERTS 1972).

The recovered seeds were referred to one of the following categories:

(1) seed in enforced dormancy (HARPER 1977: 65) *i.e.*, the seeds germinated when the conditions were favourable (in petri dishes on filter paper drenched in distilled water at 25°C and with a 12 hrs light/12 hrs dark illumination regime);

(2) seed in innate dormancy (HARPER, l.c.), *i.e.,* the seeds were dormant as from the moment of shedding and seed in induced dormancy (HARPER, l.c.): such seeds became dormant as the result of the action of unfavourable environmental factors; the categories innate and induced dormancy do not germinate when exposed to favourable laboratory conditions, but the seeds react positively with the tetrazolium reagent and, accordingly, contain viable embryos;

(3) seeds with fungal infestation: the seeds are infected by pathogenic fungi which attack the young seedling immediately after germination;

(4) non-viable seed, including partly eaten seeds often exhibiting a characteristic *Frass* pattern.

Categories 1–3 together constitute the living fraction of the seed bank. *Fig. 12* shows the decrease in number of the viable seed fraction recovered from the sown seed population in the course of the season. It appears that the loss of seed proceeds rapidly during the first few weeks but in the course of time the decrease continues at a much slower rate to become very small after about 18 weeks. It is rather striking that after 44 weeks the differences between the surviving numbers of viable seeds appeared to be practically the same in the E and
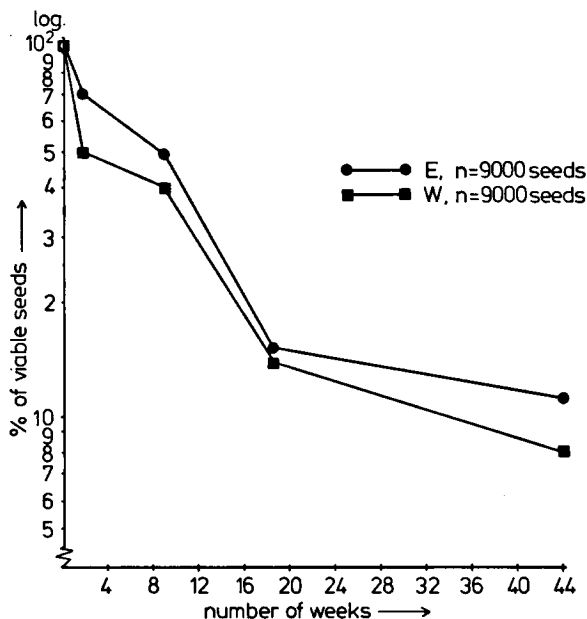

Fig. 12. Decrease of fraction of viable seeds of the seed population of E and of W in the course of 44 weeks.

the W populations, *viz.*, 10% and 14%, respectively; it follows that after 44 weeks about 90% of the seeds had disappeared. The question arises through what causes the fraction of viable seeds decreases in number. The principal ones must be the following:

(1) Germination. When a seed has germinated the seed skin is cast off, and although such remains are recognisable they disintegrate at a fast rate. On the basis of laboratory experiments and observations of emerging seedlings in the field it can be estimated that 25–30% of the E seeds and 10–15% of the W seeds disappear by germination (see p. 24). Especially the initial, rapid decrease in the number of viable seeds is largely attributable to germination, since the seeds in enforced dormancy as the result of dry storage start germinating as soon as natural conditions permit. The noted different rates of decrease between the E and the W population is to a large extent also the result of a difference in dormancy, the innate dormancy of W, as had been established already, being greater than in E.

(2) Predation. Not only of intact seeds but also of freshly germinated ones, seedlings and young individuals. After predation usually but little remains or nothing at all. Several kinds of predators play a role: seed-eating birds and small rodents, insects, snails and slugs. Direct observations are wanting, with the exception of the beetle *Harpalus rupripes* Dftz. *(Carabidae)*. This beetle was found alive in a soil sample, and when placed in a container with intact *Anthyllis* seeds the animal appeared to devour the germ from the seed skin. The *Frass* was of a characteristic type already noticed previously.

It is more than likely that there is a relation between the relative density of the seed per unit of surface area of the soil and the rate of predation in the sense that the predation is higher as the density is higher. The course of the diagrams in *fig. 12, viz.*, a very rapid, initial decrease in number which decreases later, is also attributable to predation expecially in the first two weeks. The population density of 3000 seeds/m^2 is high, but in favourable years the seed fally may attain or even exceed this number in the E population (when up to 11,000 flowers are produced per m^2: STERK 1975, *table 2*); this is not the case in the W population, however.

(3) Mortality and decay. This may occur, among other things, when seeds ultimately come to lie in unsuitable microhabitats. As in the case of (2) no remains are recovered. It is estimated that in the E habitat (dunes) about 60% of the seeds produced by the E population, and in the W population (chalk grassland) about 75% of the seed, disappeared by predation and through untimely mortality. The rate of predation at the W site was in any event higher than it was at the E locality.

(4) Fungal infestation. An idea of the severity of fungal attack can be obtained when seeds are incubated in the laboratory. Of the seed samples of the W population collected in May 5% had an infestation of 0.5%; seeds collected in July, September and February were free from fungal infection. Of the seed samples of the E population collected in May 5% was infected, of the lots collected in July 11%, in September 0.5% and in February 0%. Especially in the
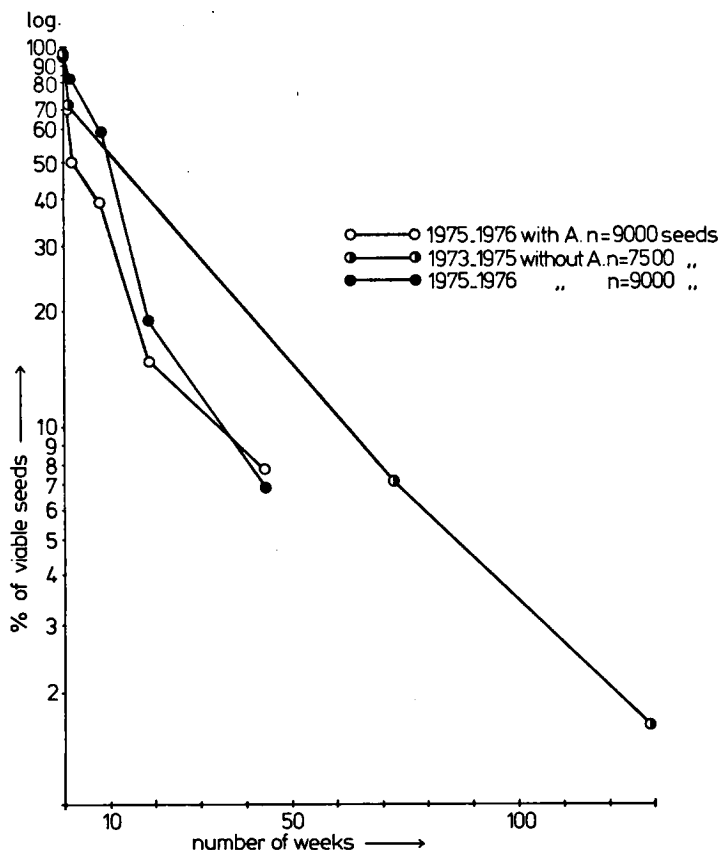
Fig. 13. Decrease of percentages of viable seeds in seed populations near E in a vegetation with and without plants of *Anthyllis*.

dunes many seeds are infected by pathogenic fungi in the period May–August. When infected seeds survive and germinate the seedling is immediately attacked and killed. The following pathogens were recorded: *Alternaria alternata* (Fr.) Keissl., *Botrytis cinerea* Pers. ex Fr., *Fusarium oxysporum* Schlecht and *F. sambucinum* Fuck. It is estimated that during the period of study within the total area covered by the dunal E population 5–10% of the seedlings perished from fungal blight whereas this cause of death is negligible in the W population.

(5) Emigration (and immigration) of seeds. This factor is presumably of little importance.

An impression can be gained of the long-term fate of seeds by a glance at *fig. 13* which shows the results of another sowing experiment similar to that described above, but with a sowing density of 25 seeds per dm² instead of 30. The selected site lies in the vicinity of the E population near Egmond but at the time *Anthyllis* hardly occurred there. Sowing took place on 7-11-1973 and

the recoveries of soil samples on 15-11-1973, 27-3-1975 and 27-4-1976, *i.e.,* after 1, 72 and 128 weeks, respectively. In the same stand of vegetation almost devoid of *Anthyllis* a sowing experiment as described above and shown in *fig. 12* was carried out; the results are also shown in *fig. 13* in which the curve of the E population of *fig. 12* is re-drawn as a basis of comparison.

The uppermost curve of *fig. 13* indicates that after 128 weeks about 1% of the seed had survived, *i.e.,* about 25 seeds per m^2. It is also clear that the decrease in number of viable seeds proceeded at a more rapid rate in the period 1975–1976 than in 1973–1975, but when the density per dm^2 becomes low the decrease likewise continues much more slowly: in 1974/1975, when the density is higher, the decrease is several times higher. A possible complication is that the soil samples were taken to a depth of 3 cm, so that not only the superficially situated seeds were included but also seeds that already lay buried in the soil. A preliminary study in dunal vegetation without *Anthyllis* had shown that the soil does not contain any seeds of the kidney vetch, which is not surprising because passive migration of seed from neighbouring localities is a negligible factor. Vertical seed migration did not occur at the selected sites with an undisturbed soil profile and absence of rabbit holes.

A comparison of the curves obtained from the experiments at sites without *Anthyllis* (1975–1976) with those in stands of vegetation with *Anthyllis* (1975–1976) shows that the loss of seed follows the same trend but in the second case proceeds at a faster rate presumably on account of the more favourable conditions for germination in the stand of vegetation in which *Anthyllis* feels at home. The ultimate result is about the same, however: after 44 weeks about 7% of the seeds had survived. The seeds remaining in the soil longest will have the strongest innate dormancy. From this experiment the conclusion may be drawn that a single dry summer, or even two dry ones in succession, when no seed is produced, do not seriously threaten the kidney vetch population in the dunes, but three consecutive dry years or more may be disastrous because after that time-span the seed bank will be practically exhausted in the greater part of the area. Such a calamity is hardly likely to occur in the present Dutch climatic zone.

5. MORTALITY OF YOUNG INDIVIDUALS

When the seeds have survived all hazard on the parent plant and on or in the soil and have germinated, there is still an appreciable mortality of seedlings and young individuals. A study of this mortality was carried out in E (var. *langei)* and in W (var. *vulneraria)*. An area of 3 m^2 was studied for such a mortality by labelling newly germinated seeds by placing a plastic marker near each young plant and by following the fate of the labelled individuals by means of a fortnightly recording of the surviving plantlets. The latter were classified in one of the following phenological stages:
(1) newly germinated seeds: the radicle is visible;
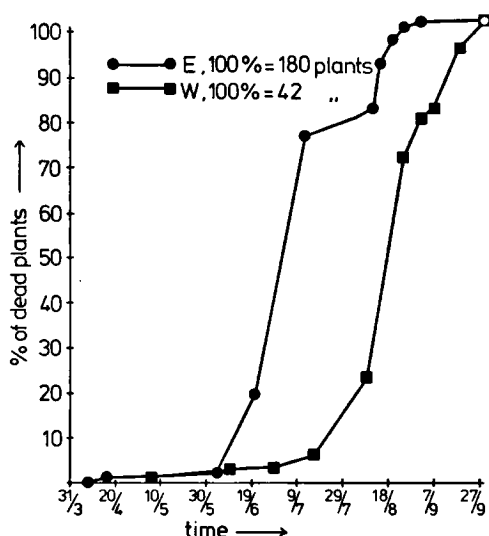(2) seedlings with developed cotyledons;

Fig. 14. Mortality in young plants in 1975 in the coastal population E and in the inland population W.

(3) juvenile specimens with one functional leaf (cotyledons shrivelled);
(4) juvenile plants with two leaves;
(5) plants with three leaves, etc.

In *fig. 14* the incidence of juvenile mortality in E and in W is shown. In the dunes the greatest mortality falls in the time-span June 20th–July 13th; it is attributable to the greatest aridity prevailing there at the time. At the inland site the greatest mortality occurred later, between the 8th and the 20th of August when the stand of vegetation had attained its greatest density and height, but aridity was here also an important factor. The striking difference in maximum mortality between the two habitats (during the period of observation 91% in the dunes as against only 39% in the interior) is attributable to the difference in density of the respective stands of vegetation: in the denser inland stands the seedlings are much better protected against drought than in the open sandy dune habitat where 91% already perished in a relatively short time after a relative short period of drought.

The accurate system of registration enabled us to establish in which phase of the life cycle the young individuals perish; for the recording a difference was made between the actual and the phenological age at death. The phenological age is the phenological stage (see above) in which the plants die off. In *fig. 15* the true and the phenological age at the time of death are indicated. It appeared that the mortality in the E population is highest among plants 75–90 days old; in this age class the mortality is about normally distributed. A relatively great number of plantlets died when they had two functional leaves; the mortality was markedly lower in plantlets with only one functional leaf or with 3–4 such leaves.
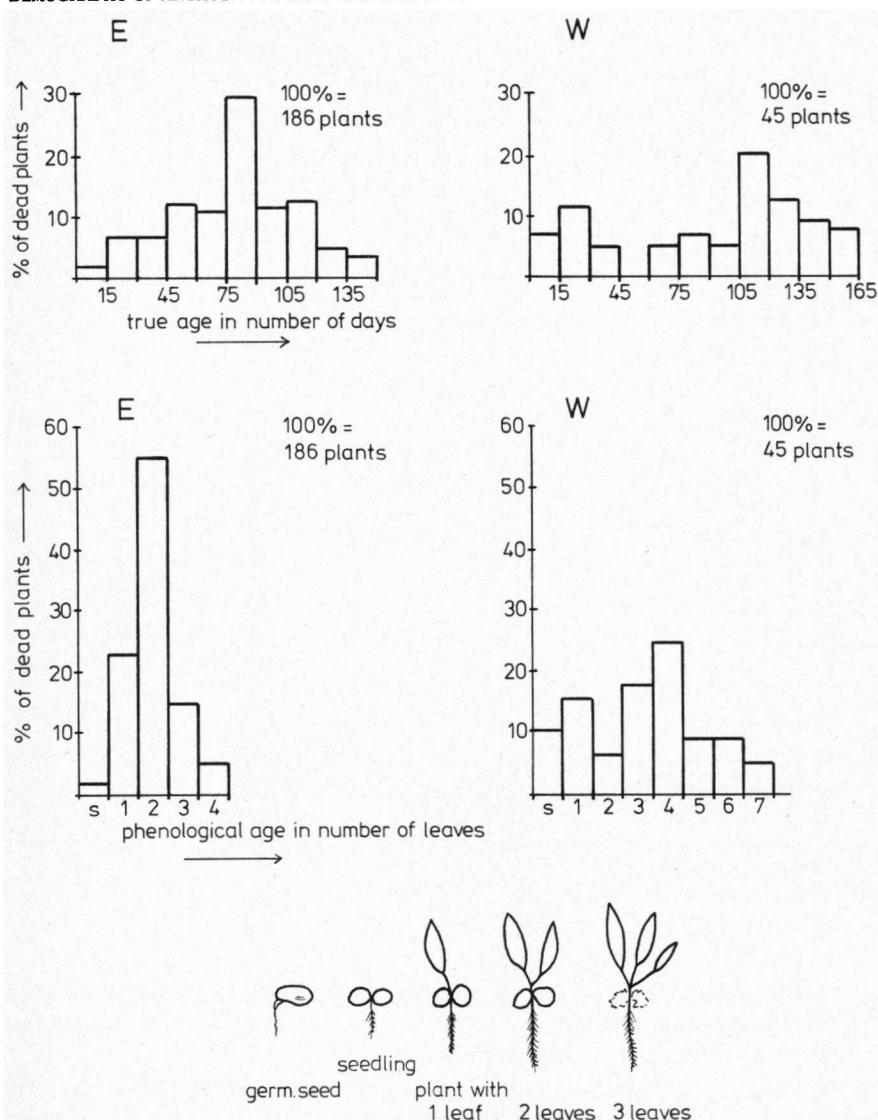
Fig. 15. True and phenological ages of plants in the coastal population E and in the inland population W caused by dying off in 1975. s = seedling with cotyledons.

In the inland calciphile habitat (W population) the mortality is relatively low (42 plantlets) and the overall picture is less reliable in view of the small number of plantlets per age class. Most plantlets died in the period between 105 and 120 days and the periods immediately before and after. In the W population a relatively great number perished but in the period of 30–75 days there is relatively little mortality. The plants upon the average attain a greater age in W than they do in E. There is an appreciable difference in phenological age at
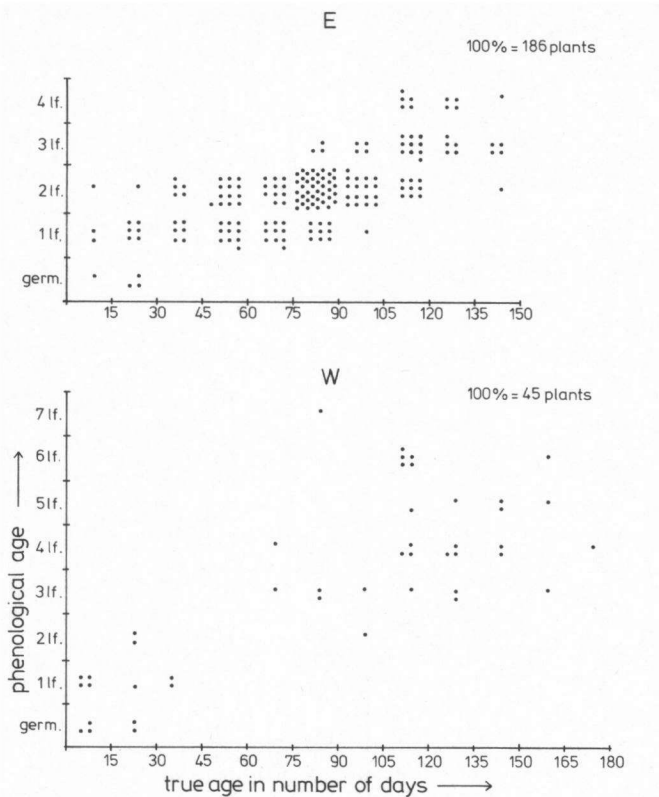
Fig. 16. Comparison of the true and the phenological ages of dead plantlets in the coastal population E and the inland population W.

death between the E and W populations. In the W population there is no evident phenological age when the mortality is high, but in W a relatively greater percentage of seedlings perish than in E.

In *fig. 16* the true age is compared with the phenological age at death. It is clear that the seedlings grow at a faster rate in the calciphile grassland (W population) than they do in the dunal E population. A greater growth rate means that the W plants produce more leaves in the same time-span than do E plants; in other words: the phenological age of W plants is higher than that of E plants of the same true age. This is explicable by the slow growth rate of the E plantlets during the dry summer period in the open stands of dune vegetation, whereas in the moister calciphilous grassland (W) the plantlets can keep growing. The recorded difference between the phenological and the actual ages of the E and the W population is, accordingly, mainly attributable to the different moisture conditions prevailing in the two biotopes.

6. EFFECT OF THE STRUCTURE OF THE BIOCENOSIS ON DEMOGRAPHIC CHARACTERISTICS

The structure of the biocenosis appears to exert an appreciable influence on the demographic particulars of plant populations (HARPER 1977), and this certainly holds good for the kidney vetch. An important structural feature of the biocenosis is the construction and the density of the stand of vegetation. The interaction between individuals of the same species becomes greater as the vegetation density increases, which has an appreciable bearing upon the phenotypical appearance of the individuals and upon the properties of the populations. *Fig. 17* is a diagrammatic representation of the life cycle of groups of labelled plantlets of the E and the W populations in cultivation and in their natural habitats in the years 1970 and 1971 (for the composition and percentage cover of the stands of vegetation in the two habitats, see STERK 1975: table 1). The cultivated plants of both varieties, amply spaced and growing in a fertile garden soil, proved to be strictly biannual; they remain in a vegetative stage during the first year and produce a sizeable rozette; they develop strongly and flower profusely in the second year, after which all plants die off. There is no interference from other plants. In their natural habitat the E plants remain vegetative in their first year and during the second season many (68%) come into flower; in the third year 56% of the plants flower, and in the fourth the flowering ceases almost completely (only about 2% of the plants still flower). The plants form
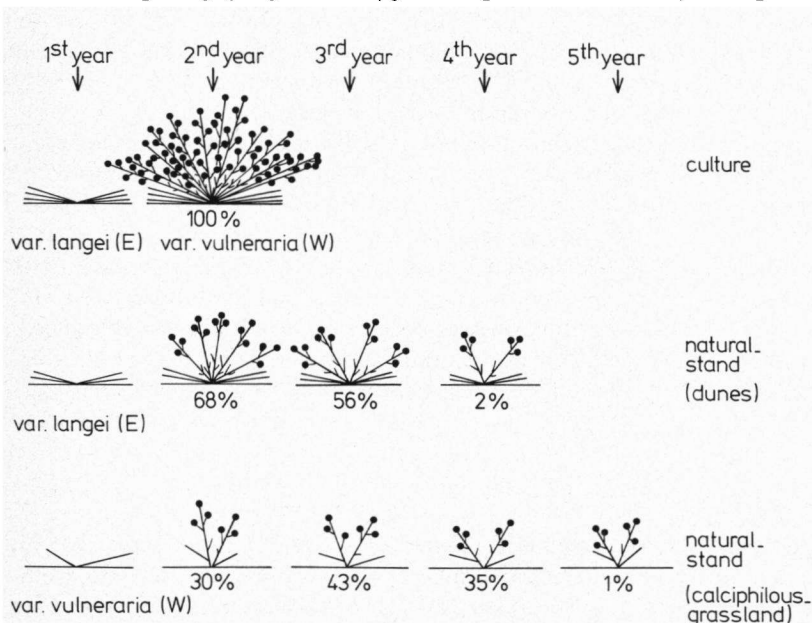

Fig. 17. Diagram of life history of groups of labelled seedlings of var. *langei* (E) and of var. *vulneraria* (W) in cultivation experiments and under natural conditions. The percentage of plants coming into flower is related to the total number of generative individuals.

rosettes, but never develop so strongly as they do when cultivated and produce much fewer flowering stems and flowers.

The stand density is relatively low in the dunes, but some interference (competition) between individuals is present and this is presumably the reason why the differences between the plants in the natural habitat and cultivated ones are so great. In the much greater stand density on "De Wrakelberg" the plants of the var. *langei* have acquired a different phenotype and produce weaker rosettes than they do in the dunes and their flowering stems are more erect. Relatively speaking, the plants are smaller and produce fewer flowers per plant.

The biomass and flower production of the W population remains about the same throughout, in contrast to the dunal (E) population whose biomass and flower production fluctuates from year to year (STERK 1975). As is the case in the E population, W plants remain vegetative during the first year partly to come into flower the second year but in lower percentage (30%) than in the E population. In the third year the highest percentage of individuals flowers (43%), and in the fourth 35% of the plants flower. Especially this last feature is in contrast with the situation in the E habitat where flowering practically ceases in the fourth year. Even in their fifth year some W plants come into flower (1%). These manifest differences in flowering strategy between the E and the W populations are not the only ones. As previously reported (STERK 1975) 36% of the labelled E plants came into flower as against 18% of the W plants. In the W habitat 90% of the individuals flower only once, and only 9% twice; in the dunes these percentages are 73% and 26%, respectively. The percentage of individuals flowering for the first time in the 2nd, 3rd, 4th and 5th year is in the dunes 68%, 32%, 0% and 0%, respectively and in the W habitat 30%, 39%, 27% and 1%, respectively. Summarising, one may conclude that flowering behaviour and seed production of the E population in the course of time differs from that of the W population. In the denser vegetation stand, owing to the stronger interaction and competition, the individuals do not come into flower so easily as they do in the sparser vegetation cover in the dunes.

In terms of r- and K-selection, the W population (var. *vulneraria*) exhibits more K traits in the denser vegetation type, whereas the E population (var. *langei*) has more r-traits in the more open dune habitat. This difference is induced, however, and only an environmental modification since the two varieties behave similarly when grown under the same conditions in an experimental garden.

7. DISCUSSION

A comparative study of populations of the vars. *langei* (E) and *vulneraria* (W) of *Anthyllis vulneraria* has revealed a number of autecological and demographic differences between the two taxa. Although periodic droughts are a feature of both their respective habitats, the E biotope is appreciably drier than the other one. The E plants of coastal dunes are better adapted to arid periods than the W plants of the interior. The adaptations involve a number of well-known

characteristics. In the first place the E plants are more densely pubescent, have a lower stomatal density, and their stomata are more deeply sunk in, and the leaves have a markedly thicker cuticle than the W plants. The leaves of both varieties are epi-amphistomatic with the greatest number of stomata in the upper leaf epidermis. The transpiration through the glabrous upper leaf surface can be regulated by infolding of the leaf (or the leaflets), but owing to their smaller and firmer leaflets the E plants are better adapted in this respect than are the W plants.

Epi-amphistomatic leaves are but rarely found as an adaptation to aridity of the environment, most plant species being hypostomatic and the amphistomatic ones predominantly hypo-amphistomatic (*i.e.*, with a greater number of stomata in the lower leaf epidermis, see STÅLFELT 1956). The difference in arid conditions between the E and the W habitats is brought about by a combination of several climatological and edaphic factors. There are differences in mean annual precipitation and different wind velocities: the evaporation and transpiration rates are much higher along the coast owing to the much higher wind velocities. The different edaphic conditions are of great importance in connection with the available supply of water. The sandy soil of the dune habitat cannot retain so much water as does the *loess* soil of the W environment. The *loess* is also much more fertile and supports an appreciably denser vegetation cover. Especially the stand density is responsible for the more favourable microclimate of the W site. In a denser stand of vegetation not only the water economics of a population (and the concomitant characteristics of that population) may be different, but also the interactions and relations within the biocenosis, both between conspecific individuals and with other taxa including animals, fungi, and other micro-organisms, may be more complex. The stronger and more varied mutual relations in a denser vegetation have a considerable bearing upon the characteristics of the individuals and of the population as a whole, so that a number of recorded differences between the populations is attributable to the above-mentioned differences in density, complexity, and dynamics of the biocenosis.

The following conclusions could be drawn:
1. Generally speaking the direct effect of the climate upon a population does become more strongly modified in a denser stand of vegetation than in an open habitat. Accordingly, the direct effect of the precipitation is much greater in the dunes than it is in the inland habitat with its denser vegetation cover. The greater direct influence is reflected in the stronger correlation between fluctuations in the rain-fall on the one hand, and fluctuations in the density of flowering individuals, in the biomass produced and in the rate of flowering of the E population on the other. The coastal population is better adapted to arid conditions, i.e., to a complex of density-independant abiotic factors.
2. In the coastal population there is a greater incidence of calamities from which the population must recover than in the inland population. The regeneration is to a large extent brought about by the presence of a seed reservoir in the soil consisting of seeds with innate dormancy. This form of dormancy is

largely dependant on the permeability of the seed-coat to water and is, further-
more, correlated with the seed size and the place of origin in the parent plant,
the seeds of a single individual exhibiting appreciable differences in the degree
of dormancy. This innate dormancy is less pronounced in seeds of the E popu-
lation than it is in the W population, which may be taken as indicative of an
adaptation associated with a relatively short period favourable for germination
in spring during which many seeds germinate and a rapid regeneration of the
population becomes possible. The W population is less prone to disasters than
the E population and favourable conditions for germination may obtain
throughout the growing season. In the W population there is a greater range
of lethal environmental factors, so that the seeds and juvenile specimens stand
a greater risk of perishing throughout the year because of density dependant
factors such as competition, predation and infestation. In such a denser biocen-
osis it is of importance that the risks are spread over the growing season, e.g.,
by a more evenly extended rate of germination through a greater variation in
the degree of innate dormancy. The E and the W population evidently exhibit
a different regeneration strategy (compare GRIME 1979). Generally speaking,
species which must be capable of repeated recovery from calamities have prin-
cipally the characteristics of r-selected taxa.
3. That biotic density-dependant factors act more strongly on the W popula-
    tion than they do on the E one can be deduced from the fact that the rate of
seed predation on the mother plant is much higher in the W population. It is
of importance that the stability of the W population is higher, whilst the con-
sistently produced seeds as a source of food form a sound basis for the survival
of the seed predators. The unpredictable fluctuations in seed production in the
dunes do not provide a reliable mode of existence to specialised seed predators.
4. It is striking that the decrease in number of shed seeds fallen unto the soil
    surface was about the same in the E and the W populations, at least after the
period of observation of 44 weeks, viz., ultimately the percentages of surviving
seeds were about the same (10–14%). The main causes responsible for the dis-
appearance of seed are (a) germination, (b) predation, (c) fungal infestation,
and (d) various and partly unknown causes, e.g., perishing in unsuitable micro-
habitats. In the E population the density-independant factors are somewhat
more important, and in the W population the biotic density-dependant factors
such as predation. The higher rate of seed predation in the W habitat is indica-
tive of better developed insect populations with their parasites and predators
as a result of the richer biocenosis.
5. The perishing of seedlings and juvenile individuals follows a somewhat dif-
    ferent course in E than it does in W. In the E population many more seedlings
perish through drought during the period of observation than in the W popula-
tion. The mortality in E is distributed normally, with a highest rate of death
among 75–90 days old plants. In the W population there is no such normally
distributed mortality and most plants die when 105–120 days old. The plants
of the W population appear to attain a greater age and have a higher life expect-
ancy than plants of the E population. Most of the E individuals die when they

have produced 2 functional leaves, but in the W population there is no apparent phenological stage with a high rate of mortality. W plants upon the whole grow at a faster rate than E plants, *i.e.* W plants have a greater phenological age than E plants of the same true age. All differences in mortality are clearly correlated with biotopic differences. At the E site more seeds germinate in spring and the mortality is higher during periods of drought, whilst growth is inhibited when arid conditions obtain, whereas at the W site the conditions are less extreme, so that there is no maximum of mortality at either a true or a phenological age; moreover, the plants do not cease growing.

6. The structural differences between the E and the W biocenoses, in particular the vegetation density, appear to have a considerable bearing upon their respective demographic characteristics. In the dense vegetation cover at W the reproductive strategy is altogether different from that at E: fewer plants come into flower for the first time, so that flowering is extended over several consecutive years, a greater number of individuals flower only once and/or flower at a greater age. Through the stronger interactions in the denser vegetation cover at W the plants cannot come into flower so readily, and the W population exhibits more K-selection traits than the E population which has more r-selection traits.

Some workers have suggested that different populations of the same species may occupy different positions along an r-K continuum (see, *e.g.* GRIME 1979), and this might also hold true for *Anthyllis vulneraria* if this recorded difference between the E and the W populations were not a habitat-induced modification. Generally speaking, in the more complex W biocenosis the *Anthyllis* population is more variable in several of its features than the dune population: in its germination and reproductive strategy, in the age class distribution of juvenile plants, and in the occurrence of phenological stages.

An important adaptation to arid conditions, which presumably has an appreciable hazard-spreading effect, is the difference in pubescence between individual plants. These genetically determined differences render it possible that the population may adapt itself genetically to drier or to moister periods. Fluctuations in the abiotic environment (principally the rain-fall) may be concomitant with fluctuations in the genetic make-up. *Anthyllis vulneraria* is a predominantly autogamous species (see COUDERC 1971) and its populations are most probably often mixtures of pure lines, so that the character of degree of hairiness is persistently inherited. Autogamy prevails among pioneer species and among species of extreme, open habitats. This system of reproduction is, among other things, characterised by a low or altogether negligible genetic recombination, by a relatively high, immediate short-term fitness of the individuals, and by a strong genetic isolation. These properties enable, *e.g.,* a relatively rapid adaptation to a given habitat at a local scale (JAIN 1976).Autogamy is said to have a greater adaptive significance in habitats suitable for r-selected species, but this generalisation is presumably and exaggeration (LLOYD 1980). It is almost certain that there is a relation between the taxonomic diversity of *Anthyllis vulneraria* and its predominant autogamy. The diversity is manifest

from the appreciable amount of subspecies recognised in W. Europe by the latest monographer (CULLEN 1968). Also in The Netherlands this diversity is expressed in the occurrence of two varieties, *viz.,* the vars. *langei* of the coastal area and *vulneraria* of the interior.

REFERENCES

COUDERC, H. (1971): Etude expérimentale de la réproduction de l'Anthyllis vulneraria L. *Bull. Soc. Bot. Fr.* **118**: 359–374.
CULLEN, J. (1968): Anthyllis. In: *Flora Europaea* **2**: 177–182.
DUIJKEREN, A VAN en D. GILLISSEN (1979): Zaadpredatie van Anthyllis vulneraria L. door insecten. *Verslag Lab. voor Exp. Entomologie, Universiteit van Amsterdam.*
GRIME, J. P. (1979): *Plant strategies and vegetation processes.* New York. 222 pp.
HARPER, J. L. (1977): *Population biology of plants.* London. 892 pp.
HOGERVORST, J. M. W. (1978): Onderzoek naar de mortaliteit van kiemplanten van Anthyllis vulneraria L. in de duinen bij Egmond aan Zee en op de Wrakelberg bij Etenaken. *Intern Rapport Hugo de Vries-Lab.* 52, 62 pp. + bijlagen.
JAIN, S. K. (1976): The evolution of inbreeding in plants. *Ann. Rev. Ecol. Syst.* **7**: 469–495.
LLOYD, D. G. (1980): Demographic factors and mating patterns in Angiosperms. In: O.T. SOLBRIG (ed.) (1980): Demography and evolution in plant populations. *Bot. Monogr.* **15**: 67–88.
ROBERTS, E. H. (1972): *Viability of seeds.* Chapman and Hall. 448 pp.
SLATYER, R. O. (1967): *Plant-water relationships.* London. 357 pp.
STÅLFELT, M. G. (1956): Die stomatäre Transpiration und Physiologie der Spaltöffnungen. *Handb. Pflanzenphysiol.* **3**: 350–426.
STERK, A. A. (1975): Demographic studies of Anthyllis vulneraria L. in the Netherlands. 1. Fluctuations and survivorship in natural populations. *Act. Bot. Neerl.* **24** (3): 315–337.
VERBEEK, E. D. M. (1977): Dynamika van zaadpopulaties van Anthyllis vulneraria L. *Intern Rapport Hugo de Vries-lab.* 33. 53 pp. + bijl.