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ECOLOGICAL RESEARCH AT THE PLANTECOLOGY LABORATORY, STATE UNIVERSITY, GRONINGEN

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GENERAL INTRODUCTION

At the Plantecology Laboratory, situated at Haren, a village south of Groningen, activities started in January 1963. Facilities provided for research there are an experimental garden on pleistocene sand and a glass-house with more or less controlled temperature conditions. Moreover, on the Westfrisian island Schiermonnikoog, the laboratory has the disposal of a field station situated in the midst of extensive dune and salt marsh vegetations. Research of the laboratory has been concentrated mainly on the ecology of plants from unstratified vegetations owing to the character of the habitats available for study, viz. hemiparasites, halophytes, hapaxants etc.

In the year of foundation much effort had to be spent in obtaining equipment and personnel. Therefore only a few studies could be set up in 1963, but quite a number of investigations were started since 1964. It will be obvious that only a few results could be gained up to now. From the following studies preliminary reports can be given at present:

1. Hemiparasites by Sina J. ter Borg;
2. Ecological studies on Dutch paramorphs of *Salicornia europaea* L. by D. Otzen;
3. On life forms of hapaxants in the Dutch flora by D. Bakker.

With the exception of the genus *Odontites*, the nomenclature of HEUKELS and VAN OOSTSTROOM (1962) has been followed as to names of plants.

1. HEMIPARASITES

INTRODUCTION

The hemiparasites which are studied in this laboratory all belong to the *Rhinanthoideae*, a subfamily of the *Scrophulariaceae*. So far the main work was concentrated on two species of the genus *Rhinanthus;* the study of some other genera, *Odontites* among other ones, is gradually taken up.

Primarily the morphological variability is being investigated. Next the distribution of different paramorphs is studied as well as their relations to the habitat.

The work is still in progress, and so it should be noted that only preliminary results can be recorded here.

RHINANTHUS

Three species of this genus occur in the Netherlands: *R. minor* L. and *R. glaber* Lamk. (*R. serotinus* (Schönh.) Oborny) are found frequently, the rare *R. alectorolophus* (Scop.) All. is not included in this study.

Von Wettstein and his pupils described the seasonal dimorphism in *Rhinanthus* and some other genera (WETTSTEIN, 1895, 1899; STERNECK, 1901). They distinguished an aestival and an autumnal species. The first is characterized by early flowering, few nodes, long internodes, broad leaves, few or no branches or intercalary leaves (i.e. the sterile leaves between the topmost branch and the lower bract); the autumnal species flowers later, it has many nodes and branches, short internodes, narrow leaves and several intercalary leaves. Originally it was thought that these two groups owed their existence to the haymaking, the aestival species flowering and setting seed before that time, the autumnal one doing so afterwards. VON SOÓ (1926, 1929) classified the two groups as subspecies or races. He stressed the fact that all habitat factors together determine the occurrence of a particular paramorph. He observed that the extreme aestival and autumnal types are connected by a continuous range of intermediates, in which he distinguished several subspecies. Besides, he and other authors described some subspecies with deviating morphological characters, mostly confined to particular habitats (SCHNEIDER, 1962, 1963). A well known example is *R. glaber* ssp. *apterus*, with wingless seeds; this subspecies is found in grainfields.

In the Netherlands the aestival subspecies of *R. glaber* is known to grow in wet meadows, but as a result of the changed agricultural practice this habitat is vanishing. The species seems to be unable to maintain itself in the modern well managed grassland; only locally it is still present, particularly along ditches and in some bad parts of the fields. However, *R. glaber* is growing abundantly along some recently constructed highroads. Here and in other poor and dry habitats autumnal populations can be found.

R. minor seems to be represented in the Netherlands by its aestival paramorph only. It prefers a rather poor and dry soil.

Usually both species grow in large isolated populations. Locally they share the same habitat.

A study of the variability and the distribution of the two *Rhinanthus* species in the northern Netherlands was started in 1963. The variability of *R. minor* appeared to be of minor importance, therefore the work was gradually concentrated on *R. glaber*.

CULTIVATION EXPERIMENTS

Cultivation experiments were carried out in the experimental garden. In 1963 and 1964 plants and seed were collected from ± 50 *R. glaber* populations. 100 seeds of 25 populations each, mixed with seeds of grasses, were sown in september 1963. Several characters were measured to compare the field samples and the cultivated plants, e.g.:

1. node number below the inflorescence
2. number of intercalary leaves (if branches present)
3. number of well developed branches
4. leaf index = $\frac{\text{leaf length}}{\text{leaf width}}$ (one of the middle leaves of the main axis)
5. length (up to the lowest bract)
6. in the experimental garden only: the germination percentage
7. „ „ „ „ „ : the "50% flower date", i.e. the date 50% of the ultimate number of flowering plants had come into bloom.

Table 1 shows a small part of the data. So far a statistical analysis has not been carried out, but it can be noticed that the samples grown in the garden in general show a reasonable resemblance to the field samples; the plants have the same general appearance. Characteristic features are maintained in cultivation, e.g. the exceptionally high number of intercalary leaves in the Schipborg sample and the greater homogeneity of the aestival populations as compared with that of the autumnal ones. These figures give some evidence that the node number, the flowering date, the number of intercalary leaves and the maximum number of branches are genetically controlled. Therefore it was assumed that the variability and the distribution of these characters can be studied in the field; they are phenotypically influenced to a limited degree only.

Furthermore the cultivation experiments showed the correlation of node number and flower date (Fig. 1). The same tendency was observed in the field samples, where early flowering plants of a population have a smaller node number than those flowering at a later date. Several other characters are more or less correlated with these two, all of them show a clinal variation, so that classification becomes difficult. However, because of the wide morphological variation classification seems to be necessary. Recently Schneider published a revision of the German material. She distinguished seven subspecies (SCHNEIDER, 1962, 1963). When arranging the Dutch material according to this German classification, one meets difficulties. When applying Schneiders descriptions the populations would often comprise individuals belonging to different subspecies. Besides many intermediates are found. So far no natural boundaries were discovered in the Dutch

TABLE 1

The table shows some data of the field samples and of the plants cultivated in the garden

	Field samples 1964						Plants cultivated in the garden, 1964						
Locality	number of plants	number of nodes	number of interc. leaves	length	leaf index	number of branches	% germ.	50% flower date	number of nodes	number of interc. leaves	length	leaf index	number of branches
De Groeve	105	5.8	0.1	33.4	3.9	0.4	55	29/5	5.3	0.3	14.5	—	0.4
		4–8	0–1	24–47	3–6	0–3		25/5–15/6	4–7	0–1	9–27	—	0–3
Lieveren	98	6.7	0.3	19.9	3.8	0.3	59	4/6	6.8	0.4	16.1	3.6	1.2
		5–10	0–2	9–38	2–6	0–3		29/5–18/6	4–8(–12)	0–3	11–25	2–5	0–4
Hemrik	32	6.8	0.1	21.5	3.5	1.6	39	8/6	7.9	1.2	16.1	5.1	1.7
		5–8	0–1	14–31	2–4	0–6		29/5–25/6	5–12	0–4	8–27	3–7	0–5
De Punt	50	7.3	0.1	32.7	4.2	1.1	61	8/6	7.7	0.4	18.4	4.8	1.0
		5–9(–11)	0–2	16–44	3–6	0–3		29/5–25/6	6–11	0–2	11–25	2–6(–8)	0–3
Donderen	107	8.8	0.9	24.9	4.0	1.3	47	11/6	9.3	1.3	19.7	5.0	2.0
		5–13	0–4	16–42	2–7	0–4		1/6–2/7	7–13	0–3	13–27	4–7	0–4
Peize	71	9.4	1.0	24.0	4.4	2.1	26	15/6	10.1	1.8	19.1	5.1	2.6
		6–14	0–3	14–40	2–6	0–5(–7)		11/6–2/7	8–13	0–3	12–26	4–6	0–5
Beilen	54	10.7	0.8	24.8	4.7	3.9	16	18/6	9.0	1.3	23.5	4.8	4.5
		7–14	0–5	14–54	3–6	0–9		15/6–2/7	7–11	0–2	19–27	3–7	2–6
Norg	50	11.4	1.8	26.1	—	2.3	72	11/6	8.7	0.6	20.8	5.0	2.5
		8–15(–17)	0–4(–7)	13–41	—	0–6		1/6–22/6	(4–)7–11	0–3	13–34	3–9	0–7
Erm	45	11.7	0.8	21.3	4.7	2.1	33	22/6	10.8	0.7	21.6	5.6	2.7
		8–17	0–3	11–36	3–7	0–6(–10)		15/6–20/7	8–14	0–2	16–30	2–9	0–7(–10)
Roderwolde	34	12.6	1.4	37.6	—	3.5	51	18/6	11.3	1.4	33.3	7.0	5.8
		9–16	0–5	24–56	—	0–7(–9)		11/6–29/6	9–16	0–4	24–44	5–9(–11)	1–11
Staphorst	192	13.5	1.8	25.3	5.9	2.9	27	2/7	14.2	2.4	30.2	6.2	4.3
		9–20(–23)	0–5	13–47(–55)	3–9(–12)	0–9		29/6–20/7	12–16	1–4	14–38	4–8	2–9
Schipborg	68	14.1	5.1	18.8	4.2	0.8	18	25/6	11.5	4.5	20.2	5.9	2.5
		(6–)10–19	(0–)3–8	12–32	3–8	0–2(–5)		11/6–6/7	8–15	2–8	15–23	4–7(–9)	0–3(–5)
Wezep	84	15.3	2.3	28.2	5.6	3.8	22	20/7	16.1	3.0	41.5	—	5.8
		(6–)9–22	0–6	15–55(–65)	2–8	0–12		9/7–10/8	12–24	1–6	37–52	—	1–11

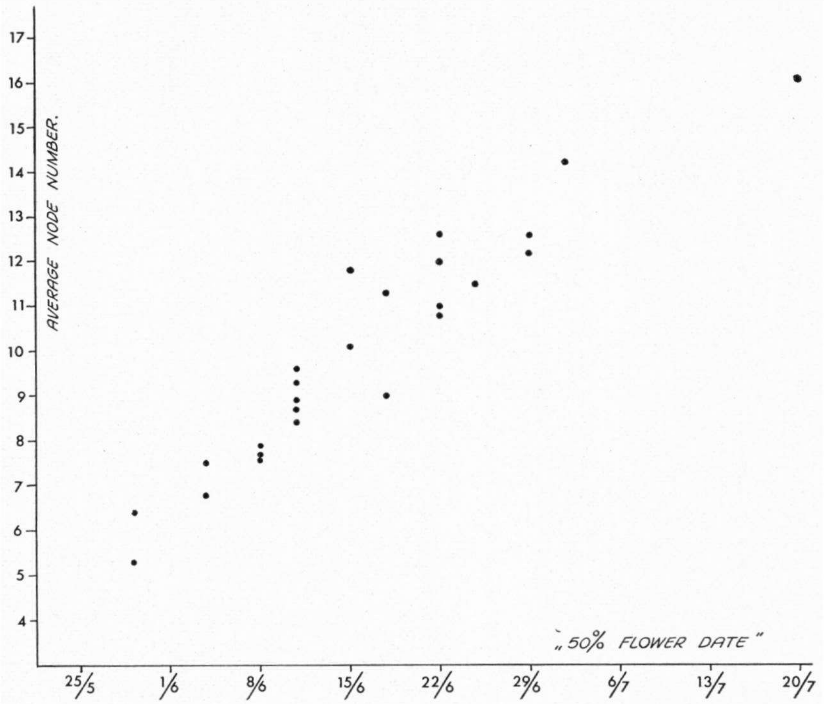

Fig. 1. The average node number of the samples cultivated in the garden in 1964 plotted against their "50% flower date".

material that might justify the delimitation of subspecies. The small gaps that do exist require further examination. Nevertheless this does not alter the fact that large differences in morphological characters exist. For the time being I will use the neutral term paramorph for the different types.

It was observed that different paramorphs often show a preference for different habitats. Now some insight into the morphological variability has been obtained, investigations with regard to the relations between the paramorphs and their habitats can be carried out.

GERMINATION EXPERIMENTS

Germination experiments have been described by HEINRICHER (1898) and SPERLICH (1919), who used seed of *R. alectorolophus*, and by VALLANCE (1952), who examined *R. crista galli* (*R. minor*?). In the following pages some aspects of the germination of *R. glaber* and *R. minor* will be described.

The seed was collected from natural populations. It was stored dry and then put on to moist blotting paper in plastic Petri dishes, 50 seeds per dish. Germinated seeds were counted once a week. Germination was considered successful if the roottip penetrated the seed coat.

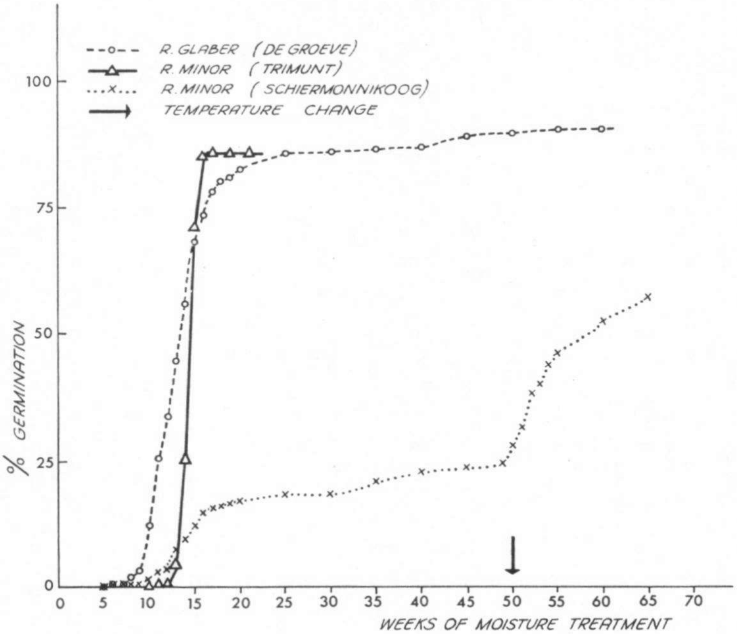

Fig. 2. The normal course of the germination in *R. glaber* (De Groeve, aestival) and *R. minor* (Trimunt, aestival) at low temperatures. A small increase of temperature causes a change of the germination rate in *R. minor* (Schiermonnikoog, intermediate).

When the seeds were set germinating at 1–5° C germination started after some months. The rate of germination was usually higher in *R. minor* than in *R. glaber*. In both species, but particularly in *R. glaber*, germination could go on for a year at least. In Fig. 2 the samples *R. minor* (Trimunt) and *R. glaber* (De Groeve) show the normal course. The *R. minor* (Schiermonnikoog) sample shows the high sensitivity for slight temperature changes: when after a year the temperature of the refrigerator was raised from ± 1° C to 2 à 3° C, the rate of germination showed a sharp increase.

Furthermore the effect of dry storage at three different temperatures has been investigated. After storage at low temperatures during more than a year the eventual percentage of germination that was reached at 3° C had decreased only slightly. The length of the dormancy period had been halved in samples that had been stored at 2–8° C, it had been decreased with 65% in samples stored at freezing temperatures. In samples kept at room temperature the germination had been slightly accelerated, but the number of viable seeds showed a sharp decrease after one year's storage.

Data about the effect of varying periods of moist and chill pretreatment are given in Fig. 3. Seed samples were pretreated at 3° C during 3–10 weeks, afterwards they were transferred to a growth cabinet

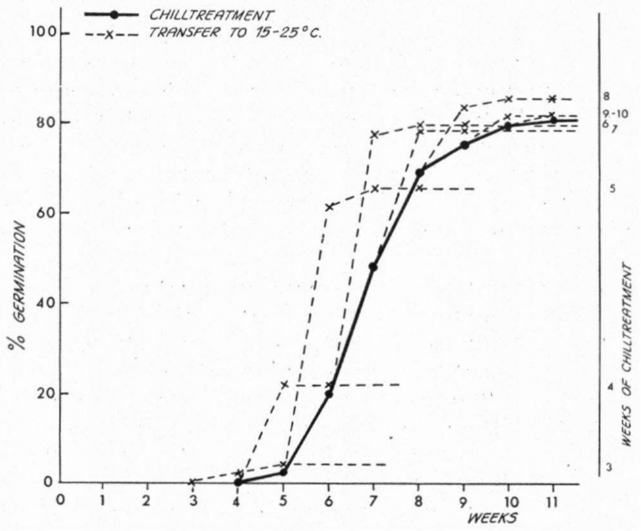

Fig. 3. Percentage germination of *R. glaber* seeds at low temperatures (——•——); ——×—— denotes germination after transfer to a growth cabinet (12 h light, 25°C – 12 h dark, 15°C) after a preceding chilltreatment of 3–10 weeks. Seed sample from De Punt, an aestival population.

(12 h light, 25° C – 12 h dark, 15° C). A certain minimal time of pretreatment appeared to be necessary; high temperatures accelerated only the last phase of the germination process. Other experiments showed that seeds of different populations need a different period of pretreatment.

R. glaber seeds that were kept in the garden, buried in soil, since september 1964, were digged up at regular intervals. Remarkably the germination of the De Groeve seeds had started in December already; seed emergence was observed from the middle of January. In three samples the number of germinated seeds was counted:

De Groeve (aestival):	21/12	36%	4/1	55%	25/1	78%	15/2	85%
Trimunt N (intermediate):		1%		2%		19%		31%
Wezep (autumnal):		—		—		0.5%		20%

Seeds from soil-samples collected in the field 14-1-'65 also showed a certain percentage of germination, up to 34%, particularly in the aestival populations. No doubt these figures are above normal because of the mild weather conditions during this winter.

Although no exact data have been collected yet, the impression was gained that seeds of aestival paramorphs germinate some time before those of autumnal populations.

ODONTITES

According to literature (PEDERSEN, 1963) *Odontites verna* (Bell.) Dum. is represented in the Netherlands by the following subspecies: ssp. *litoralis* (Fr.) A. Pedersen, an aestival paramorph in the upper salt marshes, ssp. *verna*, an aestival paramorph in ryefields and quarries, ssp. *pumila* (Nordst.) A. Pedersen, an intermediate paramorph in salt marshes, and ssp. *serotina* (Wettst.) E. F. Warb., a variable autumnal paramorph, growing along roads and in fields and in the upper salt marshes.

So far the study of *Odontites* was concentrated on Schiermonnikoog, where the local populations were investigated by SWEERS-MEIJERING (1964). In this area the ssp. *verna* does not occur. The ssp. *litoralis* could be clearly distinguished by its morphological characters and flowering time. However, the delimitation of ssp. *pumila* and ssp. *serotina* appeared to be impossible. Although distinct morphological differences between the extremes exist, variation is clinal. For the time being these two subspecies will not be separated.

Cultivation experiments, carried out at the moment, show that many of the characters are genetically controlled, in a similar way as recorded for *Rhinanthus*.

On Schiermonnikoog *O. verna* ssp. *litoralis* and ssp. *serotina* usually grow in well separated and probably somewhat different places; but here again the morphological variability needs further investigation before the study of the ecological requirements can be started.

SUMMARY

The morphological variability of two hemiparasitic species, *Rhinanthus glaber* and *Odontites verna*, was examined. With the exception of *Odontites verna* ssp. *litoralis* and ssp. *verna* a clinal variation was observed, so that the delimitation of subspecies was found to be difficult.

The study of ecological differences is gradually taken up. So the germination of *R. minor* and *R. glaber* was investigated. The seed of both species needs a moist chill pretreatment before germination takes place. The seed keeps its viability when stored dry at low temperatures.

2. ECOLOGICAL STUDIES ON DUTCH PARAMORPHS OF SALICORNIA EUROPAEA L.

INTRODUCTION

Salicornia europaea of the Dutch Floras contains a number of paramorphs. Each paramorph seems to be adapted to a particular habitat. Therefore they are interesting objects of eco-taxonomical studies. Ecological research on those paramorphs is attractive since they grow under almost complete abiotic influences. From this latter point of view *Salicornia* plants present excellent objects of autecological field observations.

Nevertheless, it should be noted, taking *Salicornia* as a subject for taxonomical studies, that the reduced morphology and succulent structure offer difficulties with regard to the description and preservation of the material. Furthermore, growing populations under experimental conditions, which is done usually in biosystematics, is difficult. Transplantation in the field is also difficult since the water movement threatens the transplants and seedlings.

This paper does not aim at reviewing all publications on the taxonomy of *Salicornia*. Only some directly related work will be briefly summarized here.

FEEKES (1936) studied *Salicornia* in the first Zuyderzeepolder, the Wieringermeer, both taxonomically and ecologically. So did KÖNIG (1960) in the coastal area of north-western Germany. BALL and TUTIN (1959), DALBY (1962) and BALL (1964) have given detailed descriptions, mainly taxonomical, of the *Salicorniae* along the coast of Great Britain. WIEHE (1935) studied the effect of the duration of tidal submergence on the mortality of *Salicornia* seedlings.

It follows from taxonomical data of the above mentioned investigators that the paramorphs in our region may be roughly divided into two groups: long-spiked, little-branched, tetraploids ($2n = 36$) and short-spiked, strongly branched, diploids ($2n = 18$). The tetraploids seem to have a more pronounced pioneer character; they are usually found in coastal areas below mean high water mark (MHW) and rarely on bare saltish areas free from daily tidal inundation. The diploids occur mostly at MHW or even at a somewhat higher level in habitats that are still saltish. They usually grow together with other salt-marsh species among which are *Puccinellia maritima* and *Suaeda maritima*.

INVESTIGATIONS

It is the intention to make detailed ecological studies of the paramorphs of *Salicornia* in the northern Netherlands. Until now a few orienting observations have been taken. ALINGH PRINS (1964) studied the taxonomy and ecology of *Salicornia* on the isle of Schiermonnikoog. In his opinion most of the occurring paramorphs may be classified according to KÖNIG (1960). Nevertheless, the delimitation of the paramorphs offers difficulties, both taxonomically and ecologically. Furthermore, Alingh Prins transplanted sods with plants from different habitats vice versa, in June 1963. The different paramorphs did not show any preference to one of the habitats studied after transplanting in that time. This result is not in contradiction with FEEKES' (1936) supposition that habitat selection occurs in a very early stage of plant development.

In 1964 the author took soil-samples from the upper layers, viz. 0–5 and 5–20 cm, on 7 sample-plots on Schiermonnikoog. In addition green parts of *Salicornia*, if the plants were not too small, were sampled. The performance of the plants was roughly estimated by measuring the length of the highest plants. The percentage of soil moisture was determined; in addition the osmotic value of the soil solution was calculated from the concentration of Cl'-ions, using a regression curve which was obtained by measuring a great number of sea- and creek-water samples from the area concerned. The osmotic value of the *Salicornia* samples was cryoscopically estimated in expressed sap.

Sampling took place on several days in June, August and September (unfortunately personal circumstances made it impossible to take samples during the month of July).

A brief description of the sample-plots follows below:

A. Sandy tidal flat. Below MHW. Long-spiked *Salicorniae* of the slender type occur almost exclusively.
B. Like A.
C. Silty salt marsh. About MHW. Lower side of the *Puccinellietum maritimae*, with a lot of *Suaeda maritima*. Short-spiked *Salicorniae* dominate here.
D. Silty mud on creak edge, about 100 m upstream. Almost exclusively long-spiked *Salicorniae* of the slender type.
E. Like D, about 1000 m upstream.
F. Bare sandy plain behind artificial range of fore-dunes. The plain is in open contact with the sea, but its level is above mean spring high water mark (MSHW). Only incidentally submerged by sea water. Here long-spiked *Salicorniae* dominate, which have a bushy or windswept appearance.
G. Like F, but a little dryer. Here growth of Salicornia (same type as in F) was delayed strongly and therefore in June the plants were still too small to be sampled. *Agrostis stolonifera* occupied this plot.

DISCUSSION OF RESULTS

The results of this preliminary investigations are summarized in Fig. 4. Since sampling took place rather infrequently the fluctuations may not be considered significant. During the period 17 June–12 August the graphs are interrupted to avoid the suggestion that no fluctuations occurred in this period.

It follows from the figures that the osmotic value in the plant tends to increase during the growing-season. This tendency was not found in the soil solution, which can be explained by supposing that the osmotic value of this solution is much more weather dependent than season dependent. Mainly rainfall, evapotranspiration and submergence by sea water determine the moisture- and salt-balance. Hence one would expect that in June, when evaporation is often at its maximum, whereas rainfall is relatively low, high extremes in the osmotic value of the soil solution are likely to occur in places where submergence is short or

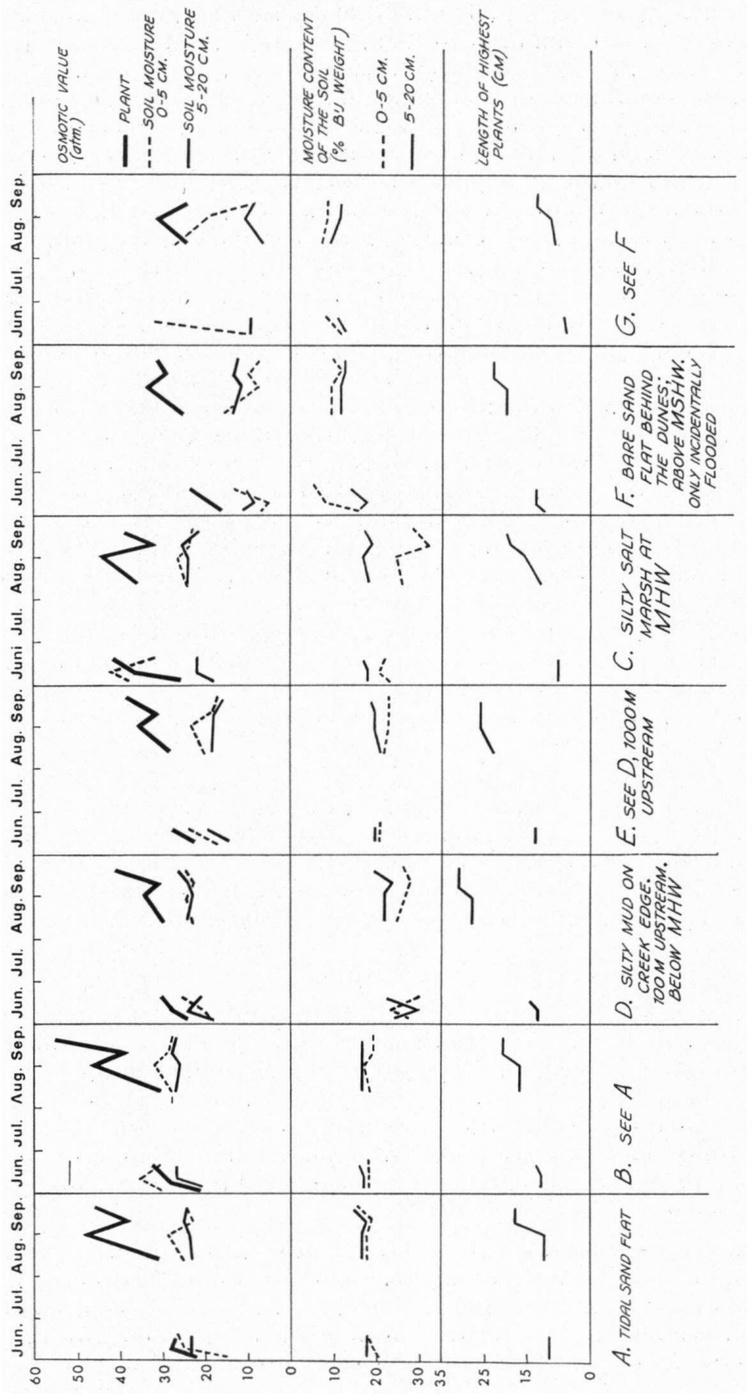

Fig. 4. Osmotic value and growth of Salicornia as related to soil salinity and moisture content.

occurs irregulary (plots C, F and G). This assumption is confirmed by the observations taken in the 0–5 cm layer at C and G.

No indications were found that *Salicornia* is less successful in maintaining an osmotic value above the osmotic level of the soil solution as the season advances, which was a conclusion KÖNIG (1960) drew from his results. König seems right in doubting whether a decrease of the ability of the plant to regulate its internal salt-balance towards the end of the flowering time is relevant for the seed production.

In the investigations the lowest osmotic values in the plants were always found at the beginning of the observation period (early June). This might give an indication that, as in many species, the critical phase for a successful establishment lies at the beginning of the life cycle. Then the young plants are entirely dependent on the thin upper soil layer, where considerable fluctuations in the osmotic value occur as a result of rainfall and evaporation. No doubt the range of fluctuations exceeds the one in the rather thick layer from 0–5 cm. Moreover, the capillary suction tension as a result of incidental desiccating of upper layers of sites above MHW may be expected to add to high osmotic values. Especially on the plots F and G this will have been the case. The diagrams of the soil moisture data are presented "upside down" to suggest the possibility of a cumulative effect of osmotic value and capillary suction tension.

In the plots A–E the 5–20 cm layer is mostly drier than the 0–5 cm layer. This may be explained by a gradient in the soil-texture, with decreasing silt content downwards.

Briefly summarizing we can state that the following habitat types were involved in this observations:

1. Typical tidal flats and creek-edges below MHW (plots A, B, D and E). The regular submergence acts as a buffer for the water- and salt-balance of the soil. The moisture content is mostly above or about field capacity. The salt concentration in the soil solution is, at least in the summer halfyear, usually above that of the sea-water, as a result of evaporation during low tide. This is the typical habitat of the long-spiked slender *Salicorniae.*
2. Sites at MHW (plot C). Regular salt supply by submergence. In dry periods the concentration of the soil solution may increase strongly as a result of evaporation. Water content in upper layers is below field capacity at times, but capillary suction tension presumably still of little interest for the plants. On an average salinity does not exceed that of habitat 1, but there are high extremes during dry periods. Typical habitat of the short-spiked *Salicorniae.*
3. Bare sandy plains above MHW (Plots G and F). Only incidental supply of salt water. Strong fluctuations with high extremes in osmotic value and in capillary suction tension occur, dependent on surface-texture and relative altitude, in co-operation with rainfall and evaporation. Small differences in altitude and surface-texture

may determine differences in leaching and capillary rising. Only during high tides the plants are exposed to moving water. At times they may be attacked by blowing sand. The microclimate is probably different from that on the other habitats (higher temperatures and lower air humidity during sunny days). This is a habitat of long-spiked *Salicorniae*, which develop a bushy or windswept appearance and look less fresh and green and are less shiny. Cultivation experiments, which are in progress, seem to show that this characters are genetically controlled.

As mentioned above, in this investigation only a few aspects of the ecology concerning *Salicornia* were touched superficially. In future the attention will be concentrated on the germination and the development of seedlings first of all. In addition it will be tried to get a better understanding of the salt- and moisture-balance of the soil, especially concerning the daily fluctuations under extreme conditions. Furthermore a great number of measurements of osmotic values in expressed saps of some well recognizable *Salicornia*-paramorphs will have to be made, in order to examine whether there exists a statistically reliable difference in osmotic value between these types in their natural habitat as well as under similar conditions in cultivation experiments.

In my opinion the investigations of *Salicornia* should be extended over several years, including cyto-taxonomy.

Summary and conclusion

Some results of an ecological investigation concerning paramorphs o *Salicornia europaea* are given. Indications of differences in salt- and moisture-balance between some typical habitats were obtained. Comparison between the osmotic values (measured at various times) in the soil and in the plants did not solve the problem how selection of the paramorphs adapted to the habitats takes place, nor did transplantation tests. Further investigations will concentrate on germination and development of seedlings, since it is supposed that habitat selection takes place especially during these stages.

3. ON LIFE FORMS OF HAPAXANTS IN THE DUTCH FLORA

Introduction

This paper has been based on the empirism that the vegetation should be considered the most susceptible "registration apparatus" of the habitat, for the response of a plant to the habitat conditions finds expression in its life forms, as a matter of course within the framework of its genetical potency. Consequently, the conditions of a given habitat will be reflected by the life form spectra of the plants composing the vegetation of this habitat.

The application of the life form spectra as the "registration apparatus" for the habitat conditions cannot be possible at present owing to our limited knowledge of the relationship between life forms and habitat. Viewed in that light the investigations have been concentrated on a detail of this problem, viz. mainly on the question to what extent macroclimatological habitat conditions affect the life forms of hapaxants (*sensu* WARMING, 1908).

The results, shown in the provisional life form system of Table 2 have been founded on a study of literature, field observations and a limited number of experiments. For some time the criteria recorded in Table 2 have been tested in experimental conditions on many hapaxants of the Dutch flora. The first results already suggest some changes in the groups, but they will not be introduced before a clear insight into these phenomena has been gained. It must be emphasized that the system may only be valid for habitat conditions prevailing in the Netherlands.

HAPAXANTS

WARMING (1908) understands by hapaxants: herbaceous, autotrophic anthophytes flowering only once in the course of their life cycle; after flowering and seed production the plants die. It follows that annuals, biannuals and pluriannuals belong to the hapaxants.

As a rule, a rather distinct boundary occurs between hapaxants and plants with at least two flowering periods during their life cycle, the so-called pollakants or perennials. In some instances, however, this boundary does not seem to be well marked and it needs further investigation, as will be discussed below.

Some individuals of hapaxantous species may flower twice during the same growing season. Especially plants flowering in early summer may show a strong reduction of the aerial vegetative parts in dry summers, followed by die back of the inflorescences. When the moisture content ceases to be the limiting factor in late summer, vegetative development starts anew, followed by flowering. This phenomenon was observed among others for *Erodium cicutarium* and *Senecio aquaticus* and proved to be brought about phenotypically, in other words those plants belong to the hapaxants. Due to grazing and mowing, moreover, hapaxants may flower anew in the same season. Furthermore, it is an open question whether or not this bipartite flowering time is genetically controlled in some species.

More complicated is the situation in species with a part of the individuals distinctly hapaxant, whereas other individuals flower during two or more growing seasons. It is recorded for 40 species in the Dutch flora (HEUKELS and VAN OOSTSTROOM, 1962), but only a few examples will be mentioned. As to *Senecio congestus* it must be pointed out that the species belongs to the hapaxants. Under exceptional conditions, however, summer annual plants of this species flowering late in autumn may develop inflorescences the next spring as well, at least if several leaf-rosettes are present. Only those rosettes, which did not come to the generative phase during the preceding autumn can produce flowers in spring.

On the other hand, the hapaxantous *Senecio jacobaea* is capable of flowering during several seasons after the vegetative parts have been damaged by frost, ploughing or grazing. It was found that *Daucus carota* and *Melandrium album* may behave likewise. On the contrary, *Aster tripolium* might be as well facultative as obligate pollakant (FEEKES, 1936). But further investigations showed that in the Netherlands the majority of the *Aster* populations at least belongs to the facultative hapaxants, whereas it appeared that pollakantous plants come into being as a phenotypical response to the habitat conditions.

In spite of FEEKES' (1936) suggestion with regard to *Aster tripolium*, it is still an unsolved problem whether or not in the Dutch flora species are to be found with obligate hapaxantous and pollakantous populations. If this distinction can be made in the area under observation, the question arises to what extent it depends on selection by the habitat conditions.

CRITERIA

The criteria of the proposed provisional life form system are mainly connected with the effect of macroclimatological conditions on the pattern of genetical pecularities, viz. the life span, the stage of development during the winter, the absence or presence of a dormancy period of the seed, the season in which dormancy occurs, the influence of low temperatures on the initiation of the flowering process and the flowering date. Moreover, attention will be paid to the question how far the life forms are adapted to non-macroclimatological conditions. Now the criteria will be discussed.

The life span should be considered the shortest time going by from the moment of seed dissemination until the stage of die-off after seed production. In order to exclude the considerably prolonged life span which may occur under influence of certain non-macroclimatological conditions, the emphasis has been laid on the "shortest time". Some examples: owing to burial in the soil the seed may be dormant during several years, but it may germinate if brought in an environment favourable to germination, e.g. near the soil surface (BRENCHLEY and WARINGTON, 1930); due to the density of the vegetation or the damage caused by animals some hapaxants are capable of staying in the rosette stage during several growing seasons; in open vegetations some species germinate in the autumn of the year of seed dissemination, but in continuous vegetations germination takes place in the next spring, in the last case the life span is somewhat lengthened.

With regard to the way of overwintering four groups are distinguished, characterized by respectively: seed stage, rosettes or short shoots, buds on the root apices and "summer dress" *sensu* SISSINGH (1952). According to Table 2 those species overwintering exclusively or facultatively in the seed stage belong to the ephemerals (A2, A3) and annuals (B1, B2, B4), but the biannuals remain in the seed stage during the first winter of their life cycle too. Rosettes or short shoots are shown by ephemerals and annuals germinating in late summer, in autumn or in winter (A2, B3, B4, B5), moreover rosettes are exhibited in the second winter of two groups of biannuals (C1, C2). Buds on the root apices occur in the biannual group C3 during the second winter, the rosettes having died off in the autumn. Ephemerals overwintering in "summer dress" are to be found in the vegetative and generative phase throughout the year (A1); however, they may perish in severe winters without snow cover.

Freshly shed seed of hapaxants may show a dormancy period. Breakage of dormancy rather often requires certain temperature conditions, especially in winter (B2, C2) and in summer (B3). Fluctuations in temperature are probably the most important in this respect. However, even within a population the seeds don't always have the same temperature requirements. Many species show a periodicity of germination; it depends on changes in temperature, on day-length or on factors within the seeds (Thurston, 1960). Besides, within some species a variability may occur with regard to the dormancy period of the seed, which offers difficulties in determining the shortest duration of the life span. On the other hand, several species overwinter in the seed stage exclusively owing to low temperatures in autumn and in winter, unfavourable to germination, in other words a dormancy period does not occur (A2, A3, B1, B4, C1, C3).

Moreover, the system of Table 2 calls attention to two aspects covering the field of vernalization requirements and flowering times. The vernalization requirements are connected with the phenomenon of the initiation of the flowering process in response to low temperature during germination or later stages of development. The qualitative or quantitative effect of vernalization may vary considerably, even within a species or population. In many instances, these inductive temperature effects interact with photoperiodic stimuli (Salisbury, 1963). Besides, temperature and day-length may work in a direct way, viz. owing to increasing day-length and rising temperature growth and flowering is realised. Experiments in controlled conditions are needed to form a good notion of the two aspects mentioned above. The scarce data available in this respect suggest a great diversity with regard to the hapaxants in the Dutch flora. Hence, the vernalization requirements in the table have only been indicated approximately (+, ±, —), whereas the influence of day-length and temperature in a direct way have been expressed as flowering times. That means, a plant capable of flowering throughout the year will be neutral to day-length and it will show no special requirements to temperature. On the contrary, a hapaxant germinating in autumn or in winter and flowering in spring exclusively may have a pronounced vernalization requirement. It grows and flowers under rather low temperature conditions. With respect to day-length, it must be regarded as a day-neutral or as a short-day plant.

TABLE 2

Provisional life form system of hapaxants in the Dutch flora (for discussion of criteria see text)

	Life span	Stage of development during the winter	Occurrence of seed dormancy	Vernalization requirements	Flowering times
A	1 ½–4 months (ephemerals)	1. "summer dress"	—	—	entire year
		2. seed, leaf-rosette	—	—	May–November
		3. seed	—	—	May–October
B	1 year (annuals)	1. seed (summer annual)	—	—	June–September
		2. seed (summer annual)	winter	—	June–October
		3. leaf-rosette (winter annual *s.s.*)	summer	+	March–June
		4. seed, leaf-rosette (partly winter annual *s.l.*)	—	±, —	May–September
		5. leaf-rosette (mainly winter annual *s.l.*)	—	+	May–August
C	2 years (biannuals)	1. 1st year seed, 2nd year leaf-rosette	—	+ 2nd year	June–September
		2. ,,	winter	+ 2nd year	June–August
		3. 1st year seed, 2nd year buds on root apices	—	+ 2nd year	July–September

PROVISIONAL LIFE FORM SYSTEM

The life form system summarized in Table 2 and discussed below comprises 426 indigenous anthophytes recorded as hapaxants in the Dutch flora, on a total number of 1300 species (HEUKELS and VAN OOSTSTROOM, 1962). It must be noted that those numbers have a somewhat arbitrary character as a result of the subjective criterion applied to separating indigenes and adventives.

A. All representatives of A are considered ephemerals owing to their short life span not exceeding four months. A dormancy period of the seed does not occur, neither does a vernalization requirement.

A1. The ephemerals overwintering in "summer dress" may flower throughout the year. With regard to *Poa annua* and *Senecio vulgaris*, two representatives of this group, SALISBURY (1963) states that they must be placed in the category of day-neutral plants, with no causative temperature effect as far as their flowering goes. There is evidence that this may be true for the other A1 species as well. Nevertheless, several typical representatives of A1 exhibit some peaks of floral development, in all probability depending on a certain interaction of temperature and soil moisture highly favourable to germination, e.g. *Poa annua*, *Stellaria media* and *Senecio vulgaris* in spring and in autumn.

About 0.6% of the hapaxants in the Dutch flora is characterized by this life form, especially *Lamium* and *Veronica* species. Nearly all the representatives of this group frequently appear on arable land in root crops (*Chenopodietalia*).

Finally, it is worth noting that some hapaxants, belonging to other groups, may display flowers in mild winters, such as *Aphanes microcarpa*.

A2. In the Dutch flora only *Ranunculus sceleratus* can be placed with certainty in A2, as to the classification of *Filago minima*, *Myosotis arvensis* and *Urtica urens* further investigation is required. Plants of *Ranunculus sceleratus* overwintering in the rosette stage produce seeds in June, which may germinate immediately and develop flowering plants in August. The same sequence was observed after establishment from seed in April. The rosette plants did not exhibit any flowering response to different temperature treatments, that means the vernalization requirement should be small or absent.

A3. The vegetative stage of the representatives of A3 is highly sensitive to frost. Consequently, they overwinter in the seed stage, whereas establishment from seed usually occurs in spring after rising of the temperature, followed by the development of flowering plants within two months. Seeing that the seed does not pass through a dormancy period and the flowering stage is achieved independent of low temperatures, a second generation may grow up in the same season, sometimes even a third one. As to daylength they seem to be neutral or slightly sensitive.

The plants of A3, B1 and B2 are usually considered summer annuals. But it should be clear that the A3 species do not belong to the annuals in consequence of their ephemerical nature.

As far as is known nearly 0.4% of the Dutch hapaxants have the life cycle described for A3. Partly, the representatives of this group belong to the neophytes, originating from tropical and sub-tropical areas. Apparently, they are capable of flowering under long-day conditions, i.e. *Galinsoga parviflora*, *G. ciliata*, *Impatiens parviflora* and *Coronopus didymus*. Furthermore, *Chenopodietalia* and *Nanocyperetalia* species belong to A3, *Anagallis arvensis*, *Euphorbia helioscopia*, *Solanum nigrum*, *Senecio viscosus* and *Gnaphalium uliginosum*, *Centunculus minimus*, *Juncus bufonius* respectively.

B. The B groups are characterized by a life span of about twelve months, in other words they have a typical annual life cycle. In view of the fact that the aerial vegetative parts of B1 and B2 are highly sensitive to frost, the plants of those groups can only overwinter in the seed stage, the so-called summer annuals. On the other hand, the groups B3–B5 overwinter usually (B3, B5) or frequently (B4) in the rosette or shoot stage, the winter annuals *sensu stricto* (B3) and the winter annuals *sensu lato* (B4, B5).

B1. Just like A3 the seed of B1 species does not exhibit a dormancy period, low temperatures prevent germination during winter only. It was found that the floral initiation is brought about independent of low temperatures, but long-day conditions usually promote flowering. Only *Camelina sativa* and *Salicornia* paramorphs can be recorded with certainty as representatives of B1 in the Dutch flora.

B2. Those summer annuals are characterized by an innate dormancy period of the seed. As far as known breakage of dormancy proceeds under influence of winter temperatures, e.g. it has been found for *Atriplex*, *Bidens*, *Chenopodium*, *Galeopsis*, *Rhinanthus* and *Polygonum*. But a diversity seems to occur as to the temperature range in which breakage takes place. Besides, a change in temperature response with storage has been observed for some species of this group, while Miss Ter Borg (see the paper on hemiparasites) has shown that the aestival *Rhinanthus glaber* populations are already capable of germinating in the soil after a treatment with winter temperatures during some months, although the seedlings do not emerge before late winter and early spring.

Furthermore, with regard to the duration of the dormancy period, it was found that even within populations a diversity may come to the fore. Taking *Atriplex*, *Chenopodium* (WILLIAMS, 1963), *Bidens* and *Polygonum* (CAVÉ, 1958) as examples, it can be said that part of the seed of those species exhibits the ability to germinate immediately after shedding, the other part however remains dormant for a shorter or a longer time. It will be clear that seedlings arising from seed in late summer or in autumn are unable to survive our climatic conditions during winter. It follows that the dormancy in this group may be considered a protection against the unfavourable season.

As to the vernalization requirement no direct effect of temperature has been observed. Most species are quantitative long-day plants, germinating mainly in spring during strong temperature alternations and more or less short-day conditions. Vegetative development may proceed slow in this time of the year, e.g. *Bidens*, *Chenopodium* and *Polygonum*. On the contrary, *Centaurium pulchellum* and *Odontites verna* ssp. *litoralis* exhibit a rapid growth in spring. At least for *Chenopodium rubrum* the sequence of climatic conditions in spring and in summer is of paramount importance with respect to the normal course of the life cycle. For this species develops flowering and fruiting dwarfs after germination in summer.

About 25% of the hapaxants in the Dutch flora has been assigned to group B2. In all probability further investigations will show that B2 should be subdivided, e.g. with respect to the sensitivity to day-length and temperature.

Several B2 representatives must be considered weeds of cereals (*Galeopsis* and *Linaria* species) and root crops (*Echinochloa crus-galli* and *Setaria* species). Moreover, in waste places and on soils submerged during winter B2 species frequently appear as well (*Bidentetalia* species). Finally, it must be stated that they usually occur on marine fore-lands (*Atriplex hastata*, *Centaurium pulchellum*, *Odontites verna* ssp. *litoralis*) and on young dunes, like *Cakile maritima* and *Salsola kali*. It should be obvious now that this group mainly dominates in habitats with unstable environmental conditions, extreme especially during winter as a result of ploughing, submerging, sand-storm etc.

B3. A winter annual *sensu stricto* is a plant which shows a dormancy period of the seed in summer, germinates in autumn or in early winter, passes the winter in the vegetative stage (rosettes or short shoots), and flowers, sets seed and dies in the following spring or early summer. In my opinion the seed state in summer should be considered the most characteristic peculiarity of winter annuals *sensu stricto*.

Ability to germinate has been studied by NEWMAN (1963) for two winter annuals, especially with respect to germination in natural conditions. His results show clearly that timing of germination for *Aira praecox* and *Teesdalia nudicaulis* is normally controlled by an interaction of soil moisture, temperature and changing temperature response of the seed. The germination of *Teesdalia*, however, seems to be relatively more affected by soil moisture than that of *Aira*. But from Newman's work the conclusion may be drawn that the response of dormant seed to storage under field conditions needs a closer investigation.

Furthermore, attention should be paid to the vernalization requirements. From the study made by RATCLIFFE (1961), it is known that temperatures below 15° C in the rosette stage lead to the development of the generative phase in spring, but only below 10° C the plants have the same appearance as in the field. As to day-length RATCLIFFE (1961) states that it generally does not affect the flowering process, although long-day conditions appeared to promote flowering for *Arenaria serpyllifolia* and *Veronica arvensis.*

About 12% of the hapaxants in the Dutch flora has the pecularities of winter annuals *sensu stricto*. They dominate in mediterranean and sub-mediterranean areas, characterized by summer drought and so this life form is usually considered a protection from desiccation. According to RATCLIFFE (1961), however, the dormancy of the seed may prevent the plants from perishing after germination during wet periods, which occur only incidentally in their typical habitats.

In the Netherlands winter annuals *sensu stricto* frequently occur in open, dry habitats, like southern slopes of dunes and dams with *Aira praecox*, *Saxifraga tridactylites*, *Phleum arenarium* among other ones. Besides, on arable fields they may play a part as well, especially in cereals on sandy soil, such as *Anthoxanthum puellii*, *Arnoseris minima* and *Veronica triphyllos.*

Especially with regard to the winter annuals *sensu stricto*, it must be emphasized that the species may exhibit races, belonging to different life forms. Taking *Arabidopsis thaliana* as an example: LAIBACH (1951) found that this species contains summer and winter annual races.

B4. The representatives of B4 show a distinct difference from B3 in the short or absent dormancy period of the seed. It germinates as soon as the conditions become favourable in this respect, that means mainly in late summer and in spring. Consequently, the B4 species may overwinter in the rosette stage or as seed. The rosette plants occurring in winter (winter annual *sensu lato*) are probably exposed to vernalization since they show a greater flower production than the summer annual individuals of the species. Flowering mostly starts in June, exceptionally in May, when long-day conditions are prevailing.

About 25% of the hapaxants belongs to group B4. They frequently grow on arable land and in waste places, viz. *Centaurea cyanus*, *Erigeron canadensis*, *Lithospermum arvense*, *Matricaria chamomilla*, *Sisymbrium altissimum* etc.

On the score of recent investigations, putting the criteria of B4 in practice some difficulties are met with, e.g. *Papaver argemone* and *P. rhoeas* are known to overwinter in the rosette stage (mainly in mild winters) and as seeds. The classification in group B4 does not present difficulties in this respect. However, in contrast with the B4 representatives the seed of those *Papaver* species passes through an innate dormancy period. When sown in soil, seed of these species shows an intermittent and long drawn out sequence of seedling emergence (McNaughton and Harper, 1964).

Nevertheless, the data available offer insufficient evidence to classify the two *Papaver* species in a new group. For it is not known whether or not the overwintering rosette plants may arise from seed produced in the year of germination. If seed from preceding years exclusively is concerned, they might be assigned to group B2, with the restriction: capable of overwintering with rosettes in mild winters. Supposing it appears to be possible for *Papaver* seed to germinate in the year of shedding, a new group must be set up.

B5. The species of B5 are unable to attain the generative phase without a preceding vernalization of the germinating seeds or the rosettes. They mainly germinate in late summer or in autumn (winter annual *sensu lato*), exceptionally in early spring, flowering and seed shedding proceeding in the next summer. Plants germinating in spring mostly exhibit a smaller flower production than the winter annuals *sensu lato*. B5 is closely related to B4 and it remains to be seen whether these groups must be separated. In this connection it is worth mentioning that within a population of *Alopecurus myosuroides* a great variability with regard to the vernalization requirements was shown.

In the Dutch flora only two examples of B5 are known, viz. *Alopecurus myosuroides* and *Senecio aquaticus*.

C. The C-groups belong to the so-called biannuals. A biannual is a plant which passes the first winter in the seed stage, germinates in the next spring, develops the first summer leaf-rosettes, maintains itself during the second winter with rosettes or/and buds on the root apices and finally flowers, sets seed and dies off in the second summer.

From Table 2 it can be read that in the C groups the dormancy period of the seed varies considerably. Some C1 species demonstrate a rather great plasticity with respect to the life form, in the first place depending on the short or absent dormancy period of the seed. So they may accept B1, B4 or B5 life forms as well, especially in mild years and growing on bare soils with a high fertility, like *Cirsium vulgare* and *Echium vulgare*. In the experimental garden, it was observed that fresh harvested seed of *Cirsium vulgare* sown in July produced leaf-rosettes during both winters of its life cycle, although the life span did not exceed two years.

As to vernalization there is some evidence that the inductive promotion of flowering at low temperatures takes place in the second winter. Contrary to what was found for the groups B3–B5, it leads to the conclusion that low temperatures might be unable to induce flowering in the germination and the seedling stage, but it appeared that among some C1 species there is only a quantitative difference in this respect. Furthermore, it must be stated that biannuals display flowering under long-day conditions.

Finally, the distribution of the C representatives will be dealt with. From literature it is known that they dominate under arid and semi-arid conditions of S. and S.E. Europe (*Onopordetalia* species). According to SISSINGH (1950), the frequent occurrence of *Onopordetalia* species in arid areas should be attributed to the high nitrate content of the soil. Apparently, leaching of nitrates is hampered as a result of low rainfall and high evaporation rate during summer months and the impermeability of the soil. The rather scarce occurrence of most biannuals in the Netherlands might be explained by the rapid leaching of nitrates. For in this country rainfall and evaporation rate in summer should be considered high and low respectively if compared with arid regions, while the soils usually show a high permeability. In this connection attention should be paid to the phenomenon that in the Netherlands biannuals grow in the dune and river district mainly, in habitats having a more or less high nitrate level and relatively high soil temperatures during the summer season, like road sides, flood marks, dams and dunes.

C1. The species of C1 are characterized by the absence of a dormancy period of the seed and the occurrence of more or less developed leaf rosettes in the second winter of their life cycle. The C1 life form is found for about 10% of the Dutch hapaxants, e.g. *Barbarea stricta, Centaurium vulgare, Cirsium eriophorum* and *Onopordum acanthium.* Owing to certain edaphic conditions they may easily change into annual life forms, as recorded above.

C2. Group C2 is closely similar to C1, differing from C1 in having a pronounced domancy period of the seed. Only two examples can be recorded with certainty, viz. *Anchusa officinalis* and *Cynoglossum officinale,* but further investigations will undoubtedly show that some species of C1 should be transmitted to C2.

C3. As can be read from Table 2, C3 species are marked by the absence of leaf-rosettes in the second winter. In that stage of development buds are found on the root apices below the soil surface, e.g. for *Arctium* species, the most pronounced biannuals of the C groups.

SUMMARY AND CONCLUSION

The provisonal life form system of hapaxants, summarized in Table 2, has been based mainly on phenotypical characteristics. Hence, it can only be a working hypothesis for experimental studies, started recently. On the score of these studies, it is expected that a clear insight into the response of hapaxants to the habitat conditions may be gained. In the future it might develop into a life form system, comprising the entire Dutch flora and becoming the most susceptible "registration apparatus" of the habitats, characterized by means of life form spectra.

In view of the fact that a number of hapaxants could not be classified in the system owing to incomplete information, the total number of the different life forms discussed amounts to 80% of the Dutch hapaxants.

Finally, it must be stated that pluriannuals were not observed in the area studied.

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