REMARKS ON THE HALOPHYTE CENTAURIUM LITTORALE

BY

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1. THE GEOGRAPHICAL DISTRIBUTION OF CENTAURIUM LITTORALE

The range of Centaurium littorale (Turner) Gilmour consists of two separate parts. The first is situated along the European northwest coast from Manche (France) in the south to almost the 61st degree of latitude in the Scandinavian countries and Finland. The west and north coasts of Great Britain are in this part of the area. The second part of the area includes some continental European countries: Austria, Hungary, Czechoslovakia, and possibly South Russia. In this part a hairy subspecies occurs: ssp. uliginosum (W. et K.) Rothm. The nomenclature of this subspecies was taken from ROTHMALER (1958). For the species itself van Ooststroom (HEUKELS–VAN OOSTSTROOM 1962) is followed who calls the species Centaurium littorale (Turner) Gilmour.

Between the continental and Atlantic parts of its range, Centaurium littorale occurs in some limited areas in Central Germany, e.g. near Frankenhausen. According to HEGI (1927) the species and the subspecies grow in these localities which form a link between the continental and the Atlantic regions. ROTHMALER (l.c.) stated, that only subsp. uliginosum occurs in these inland areas. STERNER (1940), who gave a detailed description of the infraspecific taxa of Centaurium littorale, reported ssp. uliginosum from Gotland and Öland in Sweden. His paper contains a distribution map of the species as a whole.

2. CENTAURIUM LITTORALE AS A HALOPHYTE

Apart from climatic conditions the distribution of Centaurium littorale depends on the presence of salts in the soil. Centaurium littorale is a halophyte which is restricted to rather humid and saline sandy soils along the north and west coast of Europe. This preference appears from all the floras of this region, e.g. HEUKELS–VAN OOSTSTROOM (l.c.) and HEGI (l.c.). Subsp. uliginosum in eastern and central Europe occurs on soils rich in various salts, e.g. Na_2CO_3 in the neighbourhood of the Neusiedlersee (WENDELBERGER 1950).

For both parts of the area of Centaurium littorale good classifications of local halophytes have been published which include Centaurium littorale. IVERSEN (1936) gave a survey of a number of West European

halophytes. His classification was founded on comparison in the field. His system is therefore relative and subjective but still useful. Iversen placed Centaurium littorale in the following salt and water classes:

oligo-mesohalobious ..... NaCl $I–II_3$
oligo-mesohygrobious ..... H_2O $II–III_4$

The classification of WENDELBERGER (l.c.) for East European halophytes follows for the greater part the system of Iversen. With regard to Centaurium uliginosum his data are:

lowest salt degree I
mesohygrobious, obviously humid places ... III/2

According to Wendelberger, ssp. uliginosum is salt-tolerant and can grow on soils free of salt.

3. AIM OF THE PRESENT STUDY

After this brief survey of the literature the aim of the present study may be stated. It forms part of a more extensive one. It is the author's intention to study the important plant communities in which Centaurium littorale occurs and the physical habitat of this species, especially the influence of the factor NaCl. This seems to be a master factor for Centaurium littorale. In this article the author presents some results of the analysis of the factor NaCl and preliminary conclusions. Further he would like to state, that so far the survey has only been carried out on the Dutch island of Terschelling.

4. NaCl IN THE HABITAT OF CENTAURIUM LITTORALE

Introduction

The salt concentration in the soil moisture is very variable and depends on a number of weather conditions (CHAPMAN 1954). Therefore a single determination of salt and water content in a habitat is of limited value. For the present study the author took monthly samples in the vegetation period of 1963, so that the analyses give a reasonable idea of the fluctuations in NaCl and water content of the sample spot (the first analysis in table I dates from 1962).

Description of the site

The investigation was performed on a sandy salt marsh called the Boschplaat. For a description of this nature reservation the reader is referred to WESTHOFF (1947). Most soil samples were taken on a small dune near kilometer mark 23. This dune is covered with the following vegetation zones:

Koelerion albescentis Tüxen '37, Weevers '40
Centaurieto-Saginetum moniliformis D.S. et W. '40
Armerieto-Festucetum litoralis Br. Bl. et de L. '36
with some patches of
Saginetum maritimae W., van L. et A. '61

In the beginning of the investigation soil samples were taken three times in different but corresponding places (28–4, 16–5 and 26–6).

It is not only important to sample periodically in a single habitat, but also to sample simultaneously in neighbouring vegetation zones. The results are shown in tables I and II, which give NaCl and H_2O percentages in the previously indicated vegetations on several dates in 1963. As it is the author's intention to describe the vegetation types with Centaurium littorale more extensively in a future paper, only a brief description is given here.

The Koelerion vegetation grows on the top of the small dune and is submerged only by storm-floods in autumn and winter. At its lower border Centaurium littorale reaches its optimal development in a vegetation which may be provisionally placed in the Centaurieto-Saginetum moniliformis. The foot of the dune is covered by a thick sward of Festuca rubra var. litoralis which Centaurium littorale avoids. Spring tides submerge this community, but rarely in summer. The upper soil layer of 4 cm has a silt content of 4 % and the percentage of humus is about 3. All other investigated soils are sandy and poorer in humus. On small and open elevations in the Armerieto-Festucetum and on the transition between Festucetum and Centaurietum occurs the Saginetum. The two plant communities Saginetum and Centaurietum are related. WESTHOFF, VAN LEEUWEN and ADRIANI (1961) gave a provisional discussion of the Saginetum. Centaurium littorale grows also in the Saginetum. The individual plants are smaller and their density is higher. Therefore a comparison of the two communities is interesting.

Some topographical information about the transsect:

length ..... 15 m
difference in elevation ..... 65 cm

Method

Except for the Armerieto-Festucetum, tables I and II distinguish two soil layers: the layer from 0–1 cm and the rhizosphere from 1–20 cm. The uppermost soil layer undergoes the strongest desiccation during spells of dry weather. In the Centaurietum and the Saginetum the superficial layer becomes a stone-hard crust by luting of sand grains (ZUUR 1948). In the discussion of the analyses the author expects to justify the choice of these two layers for his investigation.

For sampling the so-called agricultural drill was used (see DE VRIES

lsnd DECHERING 1960). Each sample was composed of 20 drillings. The ɔəmples were handled in the laboratory of the Biological Station on ⅃'rschelling. The H_2O content was determined after drying and the ʁs concentration was determined with $AgNO_3$ (see ADRIANI 1945).

In table I the results of the NaCl analyses are summarized. The figures give the NaCl concentration in the soil moisture i.e. the actual salinity (WESTHOFF, VAN LEEUWEN and ADRIANI l.c.). The NaCl concentration was derived from the Cl′ concentration by multiplying by the factor 1.648. Properly speaking, 12 percent of the Cl′ in seawater is combined with Mg. The author prefers to express the salinity as NaCl concentration, because the Na-ions too are important for the physiology of the halophyte.

In table II the reader finds the corresponding results of the H_2O determinations. The H_2O content is expressed in percentages of the dry

TABLE I

Concentrations of NaCl

Date	28–4	16–5	5–6	26–6	26–7	22–8	23–9	25–10	27–11
Koelerion									
0–1	<0.05	—	0.50	—	1.00	0.20	3.50	0.10	0.10
1–20	—	0.10	—	—	0.55	0.15	0.20	0.10	1.35
Centaurietum									
0–1	<0.05	—	0.80	0.15	0.25	0.10	0.60	<0.05	0.30
1–20	0.20	0.05	0.20	0.10	0.15	0.10	0.10	0.15	0.85
Saginetum									
0–1	—	—	2.00	0.05	0.90	0.05	0.05	0.05	0.85
1–20	—	—	—	0.05	0.05	0.05	0.10	0.20	0.75
Armeriet.-Fest.									
0–4	0.95	<0.05	0.55	—	1.00	1.70	0.05	0.45	0.75
4–20	0.85	0.10	0.50	—	0.70	0.50	0.10	0.30	0.75

TABLE II

Water contents

Date	28–4	16–5	5–6	26–6	26–7	22–8	23–9	25–10	27–11
Koelerion									
0–1	—	—	<1	—	<1	1	<1	4	5
1–20	—	3	—	—	1	4	2	4	5
Centaurietum									
0–1	—	—	1	3	1	5	1	12	13
1–20	19	9	3	3	2	5	3	12	13
Saginetum									
0–1	—	—	2	22	2	18	21	39	54
1–20	—	—	—	8	7	12	8	23	26
Armeriet.-Fest.									
0–4	57	78	49	—	42	47	55	62	72
4–20	28	27	18	—	21	23	24	30	31

weight of the soil. Table I should be read against the background of table II.

All numbers in table I have been rounded off on 5/100 for two reasons. Theoretically there is little point in expressing concentrations in 1/100 exactly if the differences between the determinations exceed 1/10. In practice the table is more readable. Moreover we should not pretend to have attained a high exactitude with the above mentioned method which yields only an average. The analysis employed can only give an approach to the true NaCl condition in the soil. For similar reasons the concentrations of 1 % or more are rounded off on 5/10 and the figures in table II are rounded off too.

Discussion of tables I and II

a. Centaurietum: optimal habitat of Centaurium littorale on the Boschplaat.

layer from 1–20 cm = rhizosphere of Centaurium littorale.

The NaCl content fluctuates between 0.20 and 0.05 %, except on November 27 in consequence of at least three storm-floods during that month. The last of these was on Nov. 23, just before the day of sampling. The author supposes that this high figure of 0.85 % NaCl did not influence Centaurium littorale because at the time it was in a dormant state.

layer from 0–1 cm.

In summer the NaCl concentrations are mostly higher because of the low water content. Especially the topmost layer of several millimeters may dry out completely and become very hard. It is interesting that in this very layer the salinity reaches very low values in spring and autumn, accompanied by a high water content. The factors leading to this situation are:

lower evaporation
higher phreatic level
rainfall.

This is very important for the germination of the summer and winter annuals in the Centaurietum. Centaurium littorale itself germinates in April–May. In the following pages it will be shown that the plant is susceptible for a high degree of salinity. Other species, e.g. Cerastium atrovirens and Cochlearia danica, germinate from the end of August.

b. Saginetum: Here Centaurium littorale is of smaller stature, but reaches a higher density.

layer from 1–20 cm.

The NaCl content is lower than in the Centaurietum. This is understandable in view of the higher H_2O content of the habitat. On the

average the phreatic level is 20 cm higher. The potential salinity (WESTHOFF, VAN LEEUWEN and ADRIANI 1961) is distinctly higher, but the effect of the higher NaCl as well as of the higher H_2O content is an even lower actual salinity. Tables I and II inform us that this rhizosphere shows fewer fluctuations in NaCl and H_2O content than the one of the Centaurietum.

layer from 0–1 cm.

This layer possesses some silt and is therefore able to hold a greater quantity of water. An unfavourable circumstance is that this soil habitat may lose very much water by evaporation. The fluctuations in moisture are considerable and the NaCl content is very variable.

c. Koelerion: without Centaurium littorale.

The potential salinity, i.e. the absolute amount of NaCl in this milieu, is very low. Because of the low average humidity, especially in the upper soil layer, very high actual salinities may be found in the samples. These can be even higher than in the lower zones. The NaCl concentrations on Sept. 23 in the upper layers of the Koelerion and the Centaurietum, 3.50 % and 0.60 %, respectively are plainly consequences of desiccation. The other soil layers were not influenced by the dry weather.

It is questionable whether high values in the upper layer of the Koelerion have any influence on plant life, since the water content falls below the minimum which plants can utilise. Furthermore shallowly rooting plants are sparse in summer.

d. Armerieto-Festucetum: without Centaurium littorale.

layer from 4–20 cm.

The NaCl concentration fluctuates between 0.10 and 0.85 %. Higher concentrations occur also in the summer, with a constant high humidity.

layer from 0–4 cm.

This silty layer shows the strongest fluctuations: from 0.05–1.70 % NaCl. The high value found on Aug. 22 is perhaps a consequence of three high tides in August which reached the lower limit of the Armerieto-Festucetum.

Allthough the NaCl conditions themselves may form a difficulty for the occurrence of Centaurium littorale in this community, it is probable that other factors in the Armerieto-Festucetum are even more unfavourable:

silt content – Centaurium littorale only grows on sand
density of vegetation – Centaurium littorale is heliophilous
too high humidity.

The author intends to investigate the influence on Centaurium littorale of the separate factors in this habitat as far as possible.

Conclusions

The analyses in the Centaurieto-Saginetum moniliformis and the Saginetum maritimae show that Centaurium littorale on the Boschplaat grows on a saline substratum. In accordance with the ecological definition of Stocker (ADRIANI 1958), we may conclude that Centaurium littorale – at least the plants of the population of the Boschplaat – is a halophyte. This is in accordance with the literature.

The Saginetum of the Boschplaat as a saline substratum is not unfavourable to Centaurium littorale. On the island Goeree (WESTHOFF, VAN LEEUWEN and ADRIANI l.c.) the soil of the Saginetum contains more salt; there Centaurium littorale occurs only in places where the salinity does not reach the maximum values. The reader can draw this conclusion by comparing the vegetation record with the soil analyses in this paper.

The difference in density and development of the plants of Centaurium littorale in the Centaurietum and the Saginetum seems to be a consequence of the different soil water conditions, rather than of different saline conditions in these communities. A habitat of Centaurium littorale outside the Boschplaat with gradually descending phreatic level exhibits the same gradient in density and height of plants.

5. INUNDATION EXPERIMENT

In the summer of 1963 a small spot of open dune vegetation was inundated with a watery solution of 3 % NaCl. The site was a plot of 1 × 1 m in an artificial dune slack in the vicinity of the Biological Station Terschelling. The vegetation, the species of which are enumerated in table III, belongs to the community Centaurieto-Saginetum moniliformis D., S. et W. 1940.

Method

The site was watered three times with 30 l of NaCl solution and during four weeks the reaction of the vegetation was studied. As the surface of the site was somewhat concave, all fluid penetrated the soil of the site. The amount of 30 l corresponds with a solution-layer of 3 cm on the surface of the site.

Before and after each inundation soil samples were taken for H_2O and NaCl determination. These samples were gathered in the layer 0–15 cm and handled according the method described.

Discussion of table III

In the first place table III shows the behaviour of water and NaCl in the soil of the site during the experiment. The water content is expressed as percentage of the dry weight of the soil and NaCl as percentage of the soil moisture. In consequence of the inundations with salt water on

TABLE III
Inundation experiment

Date		18–7	25–7	2–8	9–8
Inundation		x	x	x	.
H_2O % after inundations		. 15	. 15	. 11	.
H_2O % before inundations		.	3 .	2 .	3 .
NaCl % before and after inundations		. 3	3 . 3	7 . 3	2 .
Centaurium littorale:					
adult plants	fl	25	—	(+)	(+)
rosettes	juv	30	.	—	.
seedlings	k	± 180	— +	+	+
Sagina nodosa	fl/k	2.4	—	—	— +
Festuca rubra arenaria	fr/v	1.2	—	—	— +
Sonchus arvensis	v	1.1	—	— +	— +
Leontodon nudicaulis	fl/v	1.1	—	—	+
Juncus articulatus	fr/+	x.2	.	+	— +
Poa pratensis	v	x.1	— +	+	+
Taraxacum spec.	v	x.1	—	+	+
Salix repens	juv	r	— +	+	+
Holcus lanatus	v	r	+	+	+
Calamagrostis epigejos	v	r	—	—	.
Bryum angustirete	v	r	.	— ?	+ ?

July 18 and 25 and August 2, the water content of the soil rose suddenly to a high amount. In connection with this it should be stated that the dune soil of Terschelling contains 25 % H_2O just above the phreatic level. This means that the inundations in this experiment gave a sufficiently high water content in the soil. In the intervening periods the water content fell, to a degree normal for the experimental layer.

The NaCl content was constant in the first half of the experimental period: 3 %. The influence of desiccation was counteracted by washing out by rain. The NaCl concentration probably underwent slight oscillations. In the warm week from 25–7 to 2–8 a strong increase in salt content was brought about by the desiccation of the soil.

In the second place table III shows the behaviour of the vegetation during the experiment. The phenological stage of the species before the experiment is stated. The figures in column 1 indicate the quantitative data after the scale of Braun-Blanquet[1]). This was the situation on July 18. The three following columns show the deterioration of the vegetation, observed on the three dates. The symbol — indicates that the unfavourable influence of the salt was visible, at least in a notable number of plants of the species mentioned. This is visible by the turning yellow or brown, the partial dying off etc. of the plants. The sign + indicates that all individuals of the species are dead; — + means that some plants are

[1]) For Centaurium littorale numbers of plants are mentioned.

dead and others injured. Especially after the high NaCl concentrations in the period from 25–7 to 2–8 a number of or all specimens of most species are at least superficially dead. On August 9 nearly all plants are dead or injured.

Calamagrostis epigejos seems to have undergone the NaCl influence without injury. Sagina nodosa, Festuca arenaria, and Sonchus arvensis, too, are not wholly dead at the end of the experiment. This conforms with their behaviour on the Boschplaat where they grow in the Centaurietum.

Centaurium littorale in table III has been divided into three stages. The adult plants possess stems and are already in their second season. The effect of NaCl on these plants is difficult to observe, as under normal conditions, too, they turn yellow in this stage of their lives. The only thing to observe is an acceleration of the colour change. Actually it was possible to establish more or less subjectively a difference in this respect between the plants within and outside the site. The vegetation of the slack was used as a means to check the whole experiment. For the adult plants the symbol + has been placed between brackets in view of the subjective character of the observations.

The group of the seedlings comprises rosette-plants smaller than 1 cm. In this group a variation from true seedlings to small rosettes is found. This group reacts immediately to the high salt content of the soil moisture. It appears that the youngest stages of Centaurium littorale cannot tolerate a concentration of 3 % NaCl, at least not within the scope of the experiment. It was readily observable that small plants in the hollows of the microrelief of the surface die first. The cause of this phenomenon is a difference in water household between hollows and elevations. The soil of the hollows is penetrated first, to the greatest degree, and for the longest time. The plants growing there get the highest dose of H_2O and NaCl. Each soil sample was composed of drillings in hollows and elevations. The analyses give average results.

The rosettes with a diameter of 1 cm or more tolerated the experiment very well. The largest individuals among them suffered no visible damage during the experiment, nor did the specimens in the hollows. It may be concluded that normal rosettes of Centaurium littorale tolerated high NaCl concentrations during their growth. The smaller individuals of the group, especially those in hollows, sometimes died (see August 2). It was not possible to give exact numbers of plants belonging to this group during this experiment, because members of the seedling group passed into it by their growth and numbers of plants alone would give an incorrect idea.

6. Summary

From soil analyses it appears that Centaurium littorale grows in a saline habitat. From the ecological viewpoint Centaurium littorale is a

halophyte. This agrees with information in the literature. The salt concentration fluctuates. In spring low concentrations occur. This is important for the germination of Centaurium littorale.

From a field experiment it appeared that rosette-plants of Centaurium littorale can withstand high concentrations of NaCl, but that seedlings die under such conditions.

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