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DIFFERENCES IN GROWTH RATE AND SALT TOLERANCE BETWEEN VARIETIES OF THE HALOPHYTE CENTAURIUM LITTORALE (TURNER) GILMOUR, AND THEIR ECOLOGICAL SIGNIFICANCE

A. H. J. FREIJSEN and A. VAN DIJK

Instituut voor Oecologisch Onderzoek, Biologisch Station "Weevers' Duin", Oostvoorne

SUMMARY

Four varieties of *Centaurium littorale* were cultured on Hoagland's nutrient solution with and without extra NaCl. The varieties investigated were var. *littorale*, var. *iberoides* (two biotypes), and var. *latifolium* from The Netherlands, and var. *minus* from England. The experimental plants were vegetative rosettes. The increase in fresh weight, the shoot:root ratio, the dry matter content, and the mineral composition of the leaves were determined.

There appear to be infraspecific differences in growth rate. These agree with maximal plant size in the field. The growth rate in *C. littorale* is determined by the shoot:root ratio, the dry matter content of the leaves, but also by the leaf morphology. The physiological properties of the varieties investigated were affected in the salt treatments. Growth was reduced by a suction tension of 3.51 atm NaCl. The disturbance of the ionic balance by the accumulation of NaCl is a major factor in this growth reduction. Var. *latifolium* seems to have a low salt tolerance, which is in agreement with its occurrence on almost desalinized salt marshes.

1. INTRODUCTION

In a previous paper (FREIJSEN 1971a) experiments on the growth and mineral nutrition of the halophyte *Centaurium littorale* (Turner) Gilmour were described. This species is a biennial herb belonging to the Gentianaceae family. Vegetative rosette-plants were grown in a sand culture with a nutrient availability as low as in the natural environment of *C. littorale*, and with various concentrations of NaCl. In these experiments only one variety of *C. littorale* namely var. *iberoides*, was used. *C. littorale* proved to have a very low growth rate, resulting in a low consumption of mineral nutrients. The plants were tolerant to salt concentrations with suction tensions of up to 7 atm NaCl. These properties could be related to the natural environment of *C. littorale*. Along the northwestern coast of Europe it occurs in young dune slacks, on sand flats, and on sandy salt marshes. The soils of these habitats are poor in mineral nutrients and brackish (FREIJSEN 1967).

In a preliminary experiment the growth and mineral nutrition of two other varieties of *C. littorale* were studied, viz. var. *littorale* and var. *latifolium*. In this case plants were grown on a nutrient solution without NaCl and at a suction tension of 4.2 atm NaCl, respectively. Var. *latifolium*, despite a lower shoot:

root ratio, had the same growth rate as var. *littorale*, thanks to its thinner leaves. In var. *latifolium* more photosynthesizing area proved to be formed from the same quantity of dry matter. The ionic balance and the growth of var. *latifolium* were severely affected by the salinity of the culture medium (FREIJSEN 1971b).

The experiments described in the present paper were set up to study the growth of the oligotrophic plant species *C. littorale* under the maximal nutritional conditions of culture solution. A second and more important aim was to look for similarities and dissimilarities in growth physiology and salt tolerance between five infraspecific units of *C. littorale*, including the above-mentioned varieties, and to relate the physiological properties of these infraspecific units with their occurrence in the field.

All but one of these units are found along the Netherlands coast, and their occurrence there was studied in particular (FREIJSEN 1967). Adult plants of *C. littorale* var. *littorale* have an erect habit, those of var. *iberoides* (Jonker) Freijsen are characterized by procumbent-ascending stems and branches. Under optimal conditions, plants of var. *littorale* are larger than those of var. *iberoides* or the other varieties.

In The Netherlands plants of the varieties *littorale* and *iberoides* are found together in many places. In some localities one or mainly one of the two is found. Var. *iberoides* possibly prefers a somewhat wetter soil for germination. For the rest, there seems to be no difference in ecological requirements. Besides the typical form of var. *iberoides*, a deviant was studied. This paramorph occurring on the salt marsh Kwade Hoek on the island of Goeree (Zeeland) gives the impression of being intermediate between var. *iberoides* and var. *littorale*. The stems and branches are ascending. Var. *latifolium* (Marsson) Freijsen has a clearly distinguishable habitat, being found in mainly glycophytic vegetations on old salt marsh soils. It is characterized by broad thin leaves, whereas the leaves of the other varieties are somewhat succulent. Var. *minus* (Wittr.) Sterner is one of the varieties of *C. littorale* occurring in Scandinavia and Great Britain. Second-year plants have very short stems owing to closely arranged nodes (STERNER 1940–1941). It was seen by us in sandy dune slacks in England.

2. METHODS

The seeds of the experimental plants were collected in the following localities: var. *littorale* on the salt marsh Boschplaat on the West Frisian island of Terschelling, var. *iberoides* in the dune area near Oostvoorne in the province of Zuid-Holland, the deviating paramorph of var. *iberoides* on the salt marsh Kwade Hoek on the island of Goeree, var. *latifolium* on the salt marsh Oosterkwelder on the West Frisian island of Schiermonnikoog, and lastly var. *minus* in the Ross Links dune system in Northumberland, Great Britain.

The culture experiments were carried out in 1971, experiment 1 between 11 May and 3 August and experiment 2 between 18 June and 6 September. Vegetative rosette-plants of *C. littorale* were used in these experiments. The germination and initial growth of the juvenile plants took place on a sandy substrate. A week before the start of the experiments the plants were transplanted in Hoagland's nutrient solution of half strength. During the experiments, each rosette grew in a plastic pot filled with 1200 ml of the same concentration of Hoagland's solution. Periodic additions of demineralized water compensated for losses caused by evaporation and transpiration. The nutrient solution was renewed regularly at intervals of at most 9 days. In the salt treatments given quantities of NaCl were added to the solution at the start of the experiments. The non-salt treatments comprised 15 plants; the salt treatments were started with more plants, some of which died off in the course of the experiments.

The culture experiments were carried out in a greenhouse with daytime temperatures mostly between 25° and 30 °C and a night temperature averaging 18 °C. The lowest value of the vapour pressure was 40%. The plants of experiment 2 were initially grown in a growth room under conditions with 24 hours artificial light (20,000 Lux on plant level) and a constant temperature of 25 °C. Because the leaves of these plants developed an unnaturally undulated margin, the experiment was continued in the greenhouse after some time (28 July).

Total fresh weights of all plants were determined fortnightly. On the basis of weights of plants which were vital till the end of the experiments, the growth curves were drawn and the values of the relative growth rate calculated.

After harvesting, the plants were dried at 70°C, and the dry weights of rosettes and roots were determined. Two samples of the ground and mixed leaf material of each treatment were taken for tissue analysis. A sample of about 600 mg was wet-ashed with sulfuric acid and hydrogen peroxide (LINDNER & HARLEY 1942). The destruate formed was used to measure the contents of P by colorimetric determination of the phosphomolybdenum-blue complex; Kjeldahl-N, Na, and K by flame photometry (Lange model 6); and Ca and Mg by atomic absorption spectrophotometry (Zeiss PMQ II/FA2). Another tissue sample of about 1000 mg was extracted with 0.5 N acetic acid, and the following minerals were determined in the extract: Cl^- by potentiometric titration (NELSON 1960), NO_3^- by colorimetric determination of nitroxylenol (HARBERTS & THIJSEN 1960), and SO_4^{--} by turbidimetric determination of $BaSO_4$ (LACHICA GARRIDO 1964). It was assumed that in plant tissue all minerals are present in the ionic form, P as $H_2PO_4^-$ (DIJKSHOORN 1969, 1971). These mineral contents were expressed as milliequivalents (meq) per kg dry matter (105 °C) or per l plant water.

3. RESULTS

3.1. Growth curves in experiment 1

In experiment 1 the growth of the following varieties of *C. littorale* was studied: var. *littorale*, var. *iberoides* (Voorne and Goeree), and var. *latifolium*. The varieties were cultured on nutrient solution with and without NaCl. Initially also var. *minus* formed part of this experiment. All salt-treated plants of this

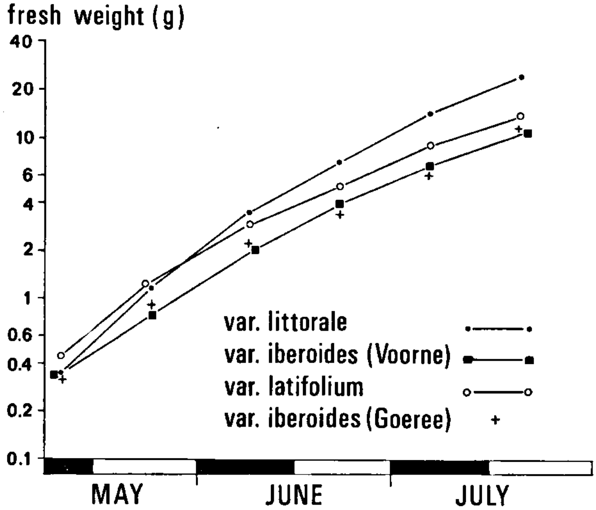

Fig. 1. Growth curves of four varieties of *Centaurium littorale* cultured on nutrient solution without added NaCl (exp. 1).

variety died off in an early stage of the experiment, and gradually also half the number of the non-salt plants.

Fig. 1 gives the growth curves of the plants cultured without added NaCl (non-salt plants). These curves are slightly bent, indicating that the rate of growth diminished in the course of the experiment. In the 2½-month experimental period fresh weights increased from 0.4 to about 15 g. This means that *C. littorale* grew very slowly. The growth curves of the plants from Voorne and Goeree are very similar. (These plants will be treated in this paper often as one category: var. *iberoides.*) Although var. *littorale* and var. *iberoides* had identical initial weights, the former attained a higher weight at the end of the experiment. Var. *littorale* obviously has a higher growth rate. In the initial phase of the experiment the young rosettes of var. *latifolium* grew a little faster than those of var. *iberoides.* Apart from that, the growth curves of these two varieties are parallel. All growth curves have "lows" on 23 June as a consequence of the unfavourable weather conditions in the foregoing period.

In the salt treatment the plants of var. *littorale* and var. *iberoides* grew at a suction tension of 3.51 atm NaCl (at 27°C), which corresponds with a concentration of 0.25% Cl^-. During the first fortnight the plants were cultured at a suction tension of 1.75 atm to facilitate the osmotic adjustment. The overall picture of the growth curves of the salt-treated plants shown in *fig. 2* closely resembles that of the non-salt plants. The curves of plants from Voorne and Goeree are less congruent, which cannot be explained solely by the small difference in mean initial weight. The increase in fresh weight of the salt-treated plants was reduced by the salinity of the culture medium. At the end of the culture period of the non-salt plants (21 July) the mean weight of the salt plants of var. *littorale* was 28% of that of the non-salt plants, and in var. *iberoides* it was 40%. Although the growth of var. *littorale* was relatively more reduced by

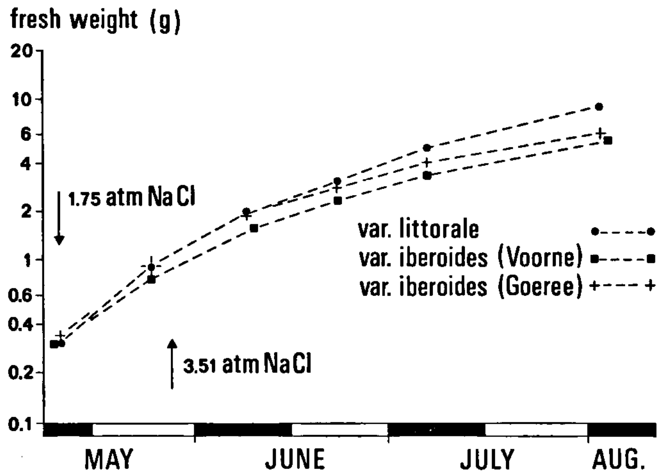

Fig. 2. Growth curves of three varieties of *Centaurium littorale* cultured at a suction tension of 3.51 atm NaCl (exp. 1).

salinity than that of var. *iberoides*, the former attained a higher harvest weight.

Because of its low salt tolerance, known from earlier experiments (FREIJSEN 1971b), var. *latifolium* was cultured at 1.75 atm NaCl suction tension during the whole experimental period. In spite of this modification, the mortality of the salt plants of var. *latifolium* was 53 %, whereas in the other varieties mortality was between 31 and 36 %. The high mortality of var. *latifolium* showed again its rather high salt sensitivity. The growth of the remaining rosettes was reduced by the suction tension of 1.75 atm (see 3.2).

3.2. Relative growth rate in experiment 1

The curves in *fig. 3* show the relative growth rates of three varieties of *C.littorale* in the course of experiment 1, as well as the rates of the non-salt plants and those of the salt-treated plants. The relative growth rate is understood as the mean increase of (fresh) weight per unit of initial weight and per unit of time, calculated over a short period during the lifetime of a plant. Apart from environmental conditions, the growth rate of a plant is determined by the total size of the assimilating area of the plant relative to its total dry weight (= leaf area ratio) and the photosynthetic capacity of the plant (= unit leaf rate). The relative growth rate, which is a parameter for comparison of the growth of plants of different habit, size, and age, can be calculated with the equation $R = \ln W2 - \ln W1 / t2 - t1$, in which W1 is initial weight at time t1 and W2 the weight at the later time t2. For more detailed information, the reader is referred to EVANS (1972) and FOGG (1966). In *fig. 3* the relative growth rate is plotted against fresh weight instead of time, as frequently found in the literature, because in this way the growth rate of the investigated varieties can be compared directly.

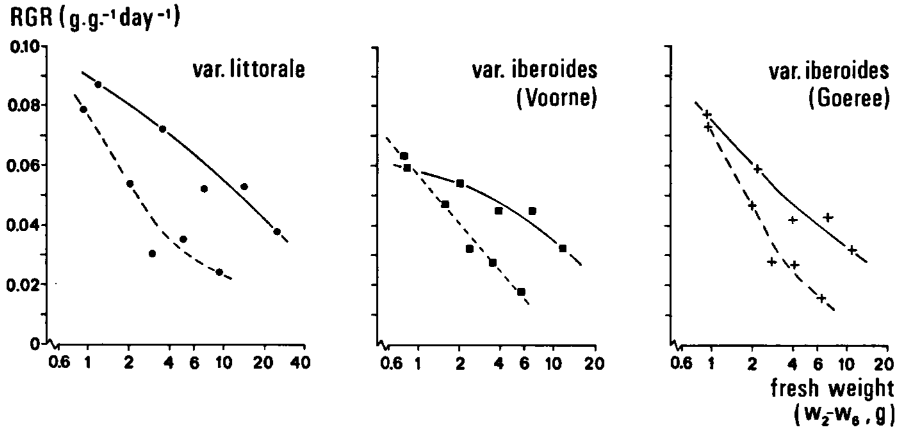

Fig. 3. Relative growth rates of three varieties of *Centaurium littorale* cultured without added NaCl (——) and at a suction tension of 3.51 atm NaCl (- - -) (exp. 1).

The relative growth rates of the non-salt plants decreased strongly during experiment 1, falling to the low value of 0.03 g.g.$^{-1}$. day^{-1}. In the earlier sand culture experiments with *C. littorale* var. *iberoides*, the plants of the least poor nutrient treatment had a relative growth rate of 0.02 g.g.$^{-1}$. day^{-1} (FREIJSEN 1971a). Under non-saline conditions the relative growth rates of both paramorphs of var. *iberoides*, especially that of the Voorne plants in the first phase of the experiment, were lower than in var. *littorale*.

The initial values for the relative growth rate of the salt-treated plants were not (much) lower than the corresponding values for the non-salt plants, because during the first fortnight all plants were cultured at a suction tension of 1.75 atm NaCl. Later, when var. *littorale* and var. *iberoides* were cultured at 3.51 atm, their growth rate decreased much more than in the case of the non-salt treatment. In the last phase of the culture period of the salt plants, e.g. at a plant weight of 5 g, their relative growth rate was reduced to about 50% of that of corresponding non-salt plants. Whereas this percentage is equal in both varieties, the level of the growth rate of the salt plants of var. *littorale* was higher.

Fig. 4 gives the curves of the relative growth rate of var. *latifolium*. In the first part of the experimental period the growth rate of the non-salt plants was intermediate between those of the varieties *littorale* and *iberoides*. Afterwards it dropped to the level of var. *iberoides*. The plants growing at a suction tension of 1.75 atm NaCl exhibited a slower growth.

3.3. Growth curves and relative growth rate in experiment 2

Because the plants of var. *minus* died off in experiment 1, a second experiment was set up to study the growth of this variety in relation to that of the varieties *iberoides* (Goeree) and *latifolium*. In this experiment too, the plants were grown

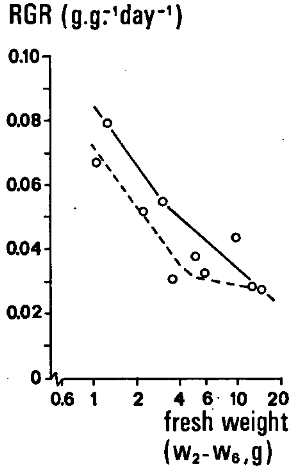

Fig. 4. Relative growth rate of *Centaurium littorale* var. *latifolium* cultured without added NaCl (——) and at a suction tension of 1.75 atm NaCl (- - - -) (exp. 1).

on nutrient solution with and without addition of NaCl. Because the salt sensitivity of var. *minus* seemed to be rather high in experiment 1, a lower suction tension, i.e. 0.88 atm NaCl, was applied in experiment 2. This suction tension corresponds with 0.06% Cl^-.

The growth curves of all of the non-salt plants in experiment 2, shown in *fig. 5*, resemble those obtained in experiment 1 (see *fig. 1*). In the latter the growth curves of var. *iberoides* and var. *latifolium* are parallel, in the former they almost coincide. The first parts of the curves of the varieties *iberoides* and

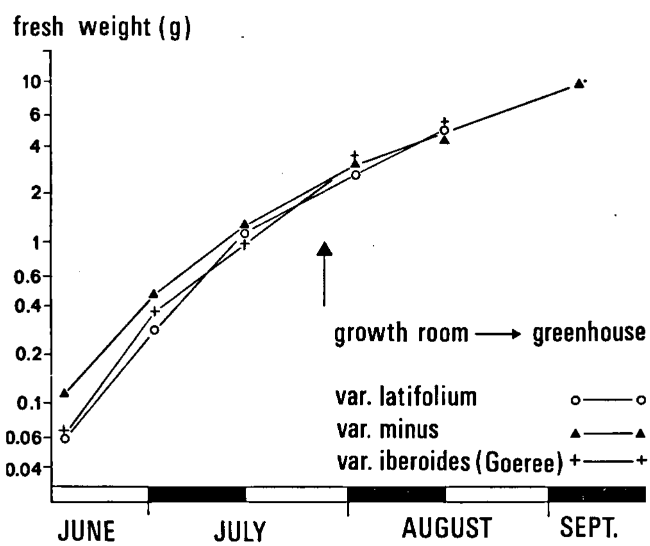

Fig. 5. Growth curves of three varieties of *Centaurium littorale* cultured on nutrient solution without added NaCl (exp. 2).

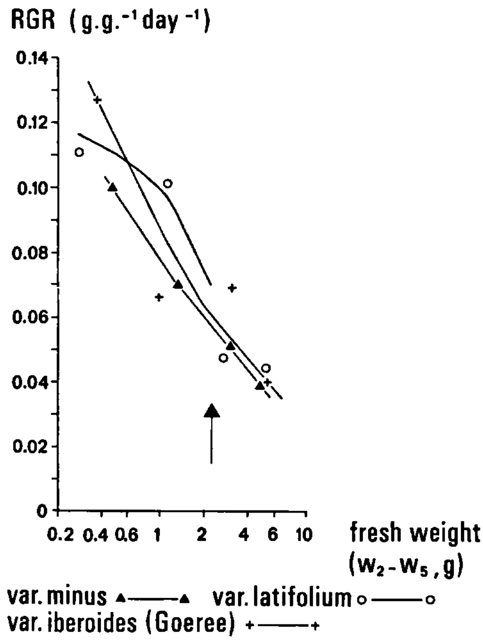

Fig. 6. Relative growth rates of three varieties of *Centaurium littorale* cultured without added NaCl (exp. 2).

latifolium are rather steep, indicating a rapid initial growth of the experimental rosette-plants. This may be related to their small size (about 6 times smaller than in experiment 1). Having been started with bigger plants, var. *minus* maintained the highest fresh weight for a long time, but at the end of the experiment all of the varieties had similar weights.

The salt-treated plants in experiment 2 did not show any measurable growth reduction. Their growth curves are similar to those of the non-salt plants. Although var. *latifolium* proved to be rather sensitive to intermediate salt concentrations and in experiment 1 var. *minus* also seemed to have a low salt tolerance, they were not unfavourably affected by a suction tension of 0.88 atm NaCl any more than var. *iberoides*.

In the early part of experiment 2 the non-salt plants of the three varieties investigated had high (although slightly divergent) relative growth rates (*fig. 6*), because the experimental plants were small. These high values decreased sharply in the course of the experiment. In consequence, var. *iberoides* and var. *latifolium* rather soon reached a growth rate of the same order of magnitude as that in experiment 1. The rosettes of var. *minus*, which were larger almost until the end of the experiment, had the lowest growth rate.

3.4. Shoot: root ratio

Fig. 7 gives the values of the quotient of the dry weights (70 °C) of the rosette and the root of *C. littorale* in experiments 1 and 2. This measure for the dry matter distribution in the plant is called the shoot: root ratio.

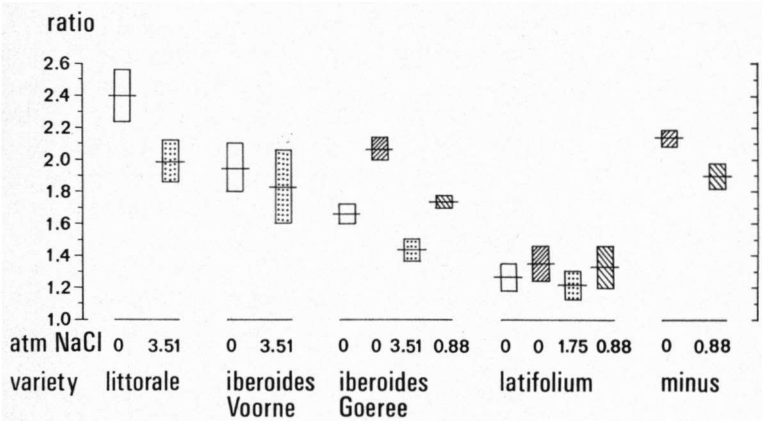

Fig. 7. Shoot:root ratios of the varieties of *Centaurium littorale* investigated in experiments 1 and 2. Hatching applies to experiment 2. Mean values and 95% confidence intervals.

There are relatively large differences in shoot: root ratio between the varieties of *C. littorale*. The non-salt plants of var. *littorale*, var. *iberoides*, and var. *latifolium*, in that order, exhibit progressively decreasing values. The same sequence, with very similar levels of the shoot: root ratio, was found for these varieties in the earlier water-culture experiment (FREIJSEN 1971b). Var. *minus*, too, is characterized by a rather high shoot: root ratio.

Salt-treated plants of all varieties of *C. littorale* have lower shoot: root ratios than the corresponding non-salt plants. Due to the increased suction tension of the environment, the plants obviously used more dry matter for the formation of roots. This effect of salinity was largest in var. *littorale*. Although the salinity level in experiment 2 was rather low, the shoot: root ratios of var. *iberoides* and var. *minus* were distinctly lowered by the salt.

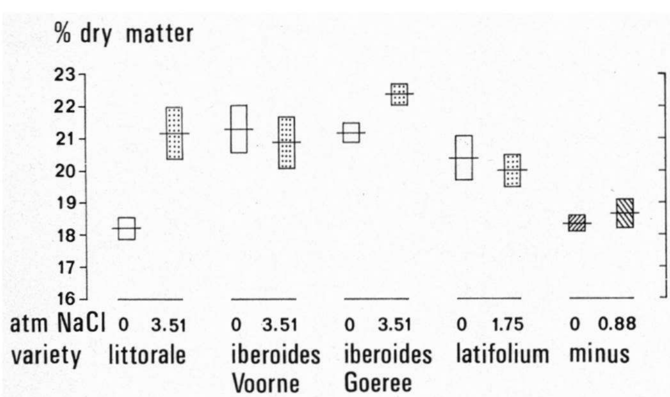

Fig. 8. Dry matter contents of the rosette-leaves of varieties of *Centaurium littorale* investigated in experiments 1 and 2. Mean values and 95% confidence intervals.

3.5. Dry matter contents of rosette-leaves

The dry matter contents (at 70 °C) of the leaves of *C. littorale* are given in *fig. 8*. In experiment 2 only the fresh weights and the dry matter content of var. *minus* were determined. The overall picture indicates that about 20% of the rosette-leaves of *C. littorale* consists of dry matter. The dry matter percentages of the non-salt plants of var. *littorale*, and of all plants of var. *minus* are significantly lower than those of the other plants. From a certain quantity of dry matter, these two varieties were able to form larger rosettes, and thus more leaf tissue, than the others. The dry matter content of the salt plants of var. *littorale* is as high as those of the varieties *iberoides* and *latifolium*.

3.6. Mineral composition of the leaves

The mineral composition of rosette-leaves of *C. littorale* from experiments 1 and 2 was investigated. The levels of all macro-nutrient ions, including Na^+ and Cl^-, were determined. The columns in *figs. 9, 10*, and *11* indicate the total content of cations and anions, each section of a column representing the content of a single ion. The difference in height between a cation and an anion column of a pair represents the content of organic anions, which are formed as a result of the assimilation of NO_3^- in the leaf cells. In addition to their other functions these anions endow the plant with electroneutrality (DIJKSHOORN 1969, 1971). Plant taxa are characterized by specific values of the organic anion content,

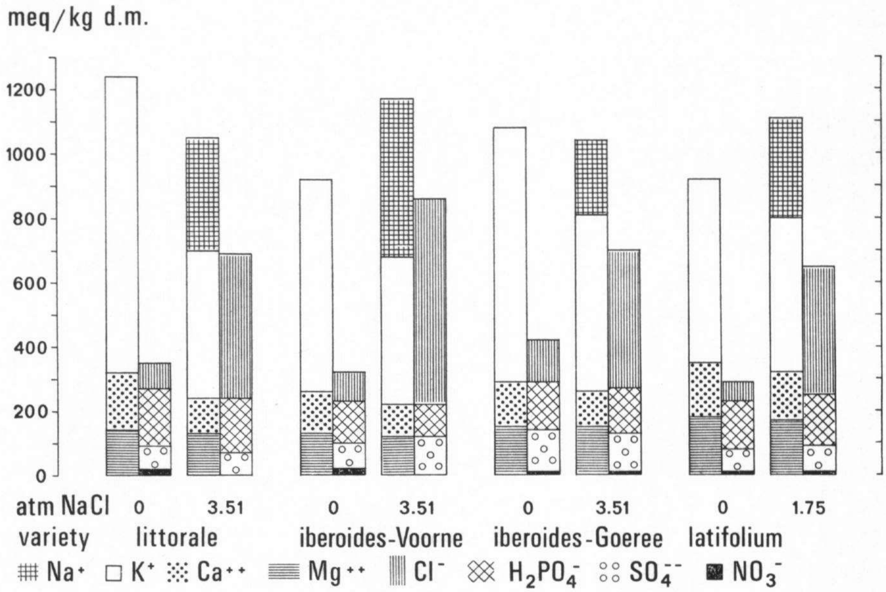

Fig. 9. Mineral composition of rosette-leaves of varieties of *Centaurium littorale* cultured without added NaCl and at a suction tension of 3.51 (1.75) atm NaCl (exp. 1). Contents expressed as milliequivalents per kg dry matter.

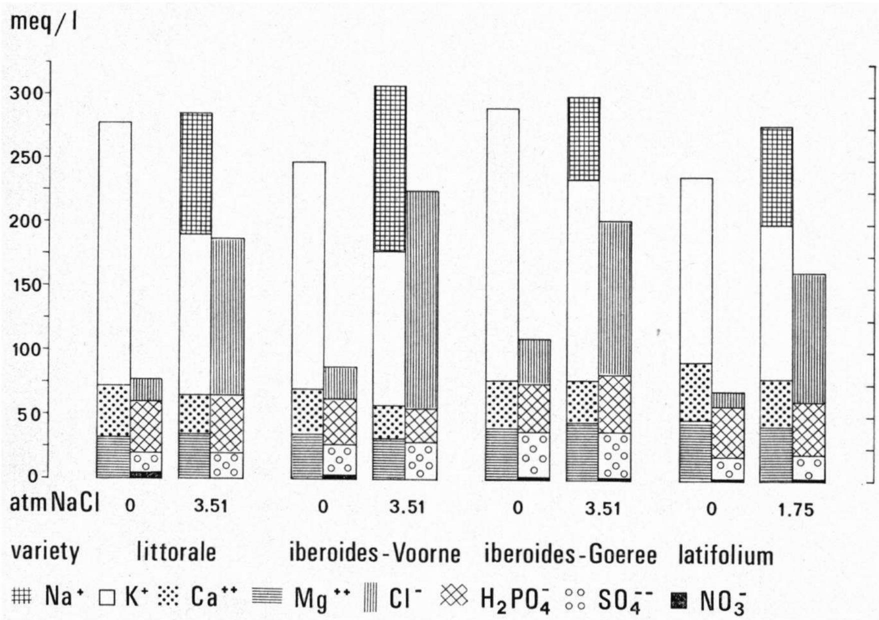

Fig. 10. Mineral composition of *Centaurium littorale* in experiment 1, in milliequivalents per 1 plant water.

which can shift in dependence on changing environmental conditions (DE WIT et al. 1963).

Fig. 9 shows the mineral composition of the varieties of *C. littorale* investigated in experiment 1. The ionic contents are expressed as milliequivalents (meq) per kg dry matter, as in our earlier investigations and in the above-cited literature. The ionic composition of non-salt plants of var. *iberoides* is similar to that found at a much lower nutritional level in the sand-culture experiments already referred to (FREIJSEN 1971a). An increase in the availability of minerals above a certain low level appears to have no effect on the mineral composition of *C. littorale*. The very low content of NO_3^- is remarkable. The oligotrophic *C. littorale* is typified by this low level. The ability of plant species to accumulate nitrate is proportional to the richness of nitrate of their natural environments (SCHNURBEIN 1967).

In *fig. 10* the ionic contents are expressed as concentrations in the water of the experimental plants of *C. littorale*. The non-salt plants of the varieties of *C. littorale* exhibit only small differences in mineral composition. (The greater infraspecific differences in *fig. 9* originate from the differences in dry matter content). The variety *littorale* is typified by the highest content of organic anions. Var. *latifolium* possesses somewhat higher levels of Ca-ions and Mg-ions, together with the lowest measured content of K-ions. The mineral compositions of the two paramorphs of var. *iberoides*, both non-salt and salt-treated plants, are not identical in all respects.

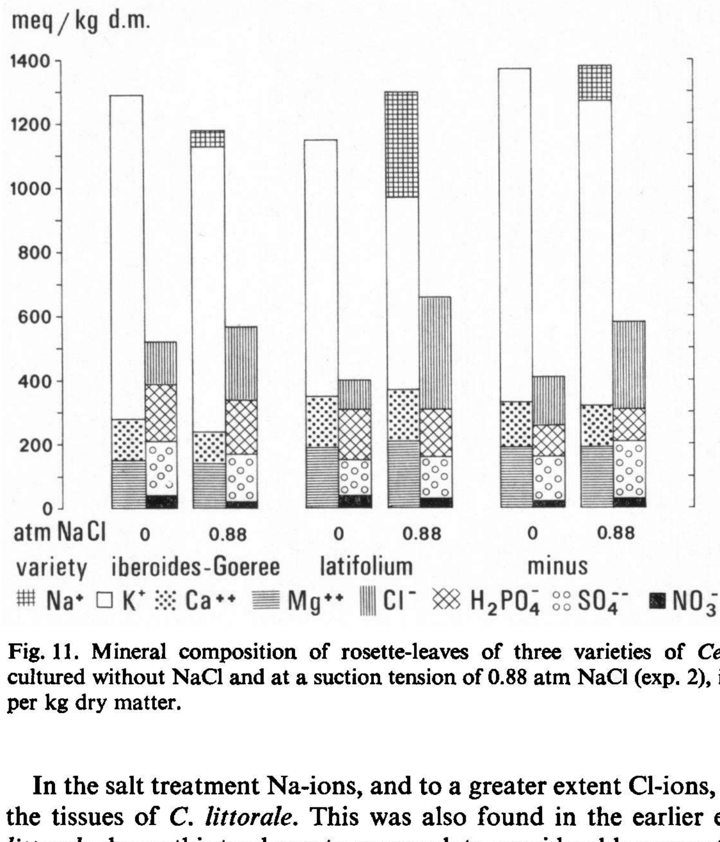

Fig. 11. Mineral composition of rosette-leaves of three varieties of *Centaurium littorale* cultured without NaCl and at a suction tension of 0.88 atm NaCl (exp. 2), in milliequivalents per kg dry matter.

In the salt treatment Na-ions, and to a greater extent Cl-ions, accumulated in the tissues of *C. littorale*. This was also found in the earlier experiments. *C. littorale* shares this tendency to accumulate considerable amounts of NaCl with other halophytes (FREIJSEN 1971a, b). Certainly as a consequence of the preferential uptake of Na^+ and Cl^- the internal concentrations of K^+ and organic anions are greatly reduced (DE WIT et al. 1963). The reduction of these two elements of the ionic balance is greatest in var. *littorale*. It may be supposed that the salt-treated plants of *C. littorale* had a higher suction tension than the corresponding non-salt plants due to the increase of the total ionic concentration and especially to the substitution of monovalent Cl-ions for polyvalent organic anions (BERNSTEIN 1961).

The mineral composition of the three varieties of *C. littorale* cultured in experiment 2 is given in *fig. 11*. The ionic contents of the non-salt plants of var. *iberoides* and var. *latifolium* are higher than in experiment 1, e.g. the levels of K^+ and NO_3^-. The salt plants of both experiments are not fully comparable, because the NaCl suction tension was lower in experiment 2.

Plants of var. *latifolium* accumulated more salt, especially Na-ions, than the rosettes of the other varieties. In experiment 1, in which var. *latifolium* was cultured at 50% of the NaCl concentration used for the other varieties, its uptake of NaCl was of the same order of magnitude as that of the others. Var.

latifolium is typified by an extremely high salt accumulation.

The organic nitrogen contents of the leaves of *C. littorale* are given in *table 1*. Under the favourable nutritional conditions offered by the Hoagland culture solution, the organic nitrogen level is on an average twice as high as under the sand-culture conditions of previous experiments (FREIJSEN 1971a). The nitrogen availability of the culture medium had more effect on the organic nitrogen content of the plants than on their nitrate content. Under the various saline conditions applied in experiments 1 and 2, organic nitrogen levels were lowered.

Table 1: Organic nitrogen content (in mmol/kg dry matter) of rosette-leaves of *Centaurium littorale*

variety	experiment nr.	treatment (NaCl in atm)			
		0	0.88	1.75	3.51
littorale	1	2543	–	–	2495
iberoides-Voorne	1	2423	–	–	2172
iberoides-Goeree	1	2744	–	–	2735
	2	2807	2795	–	–
latifolium	1	3037	–	2767	–
	2	2882	2653	–	–
minus	2	2846	2772	–	–

4. DISCUSSION

The growth rate and the shoot:root ratio – an important factor for the growth rate – of *C. littorale* var. *iberoides* in a nutrient-rich solution are only twice as high as in a sand culture with poor nutrient availability. This supports the impression that the growth rate of the oligotrophic plant species *C. littorale* only responds feebly to richer nutritional conditions (FREIJSEN 1971a).

In the early rosette-stage of *C. littorale* the pairs of opposite leaves are spirally arranged, and they do not cover each other. In bigger rosettes the leaves are very densely packed, and there is much self-shading. It stands to reason that the photosynthetic capacity of many leaves is lowered. This seems to be the main reason for the sharp decrease in the relative growth rate of the growing rosette.

Under non-saline conditions the variety *littorale* appears to have the highest growth rate. This must certainly be related to its high shoot:root ratio and its low dry-matter percentage. A relatively high proportion of the dry matter is invested in the photosynthetic system. The size of this photosynthetic system, i.e. the biomass of the leaves, is increased by the uptake of a greater quantity of water than in other varieties. The effect of such a strategy on the growth rate was stressed by VAN DOBBEN (1962, 1967). Moreover, var. *littorale* is characterized by relatively long rosette-leaves. In a comparative study on the morphology of the varieties of *C. littorale* occurring on the West Frisian island of Terschelling, BRINK (1964) found that the mean length and width of 250 rosette-leaves were 26.4 mm and 4.8 mm, respectively. These relatively long leaves mean that there is less self-shading in the periphery of the rosette, and there is less interference with photosynthesis than in rosettes with a smaller diameter. The larger size of plants of var. *littorale* in the field is in agreement with the high growth rate.

Under saline conditions *C. littorale* has a lower shoot:root ratio. The decrease in the availability of water, which results from the higher suction tension of the environment, is partially neutralized by the enlargement of the uptake system (BROUWER 1963a, b). This adaptation was not found in plants of *C. littorale* var. *iberoides* cultured under the poor nutritional conditions of the sand-culture experiments. The shoot:root ratio of these plants already had an extremely low value as a consequence of a deficient supply of nutrients. Obviously they could not react adequately to the additional problem of salinity (FREIJSEN 1971a). Generally speaking, reduced shoot:root ratios will affect growth rates of plants. In experiment 1 the salt treated plants indeed showed slower growth. However, in experiment 2 the salt-plants grew as rapidly as the non-salt plants in spite of lower shoot:root ratios.

The salt-treated plants of *C. littorale* took up large quantities of Na^+ and Cl^-, and the internal suction tension of the leaves was increased. This is a second adaptation to effect withdrawal of sufficient water from the saline root medium. However, the accumulation of NaCl results in lowered levels of K^+ and organic anions. Reduced contents of these two important elements of the ionic balance were considered responsible for growth reduction of crop plants by DE WIT et al. (1963). The influence of the accumulated NaCl on the ionic balance and toxic effects on physiological processes in plants seem to be more important causes of growth reduction under saline conditions than the disturbance of the water economy (WAISEL 1972, GREENWAY 1973).

The shoot:root ratio, the dry matter content, and elements of the ionic balance of var. *littorale* were more strongly affected by a suction tension of 3.51 atm NaCl than the same properties of var. *iberoides*. This could indicate that the former variety has a lower salt tolerance. However, in both varieties the relative growth rates of the salt plants were reduced to 50% of the values of the non-salt plants. Because the growth rate of the non-salt plants of var. *littorale* was higher than in var. *iberoides*, the salt-treated plants of var. *littorale* grew more rapidly than those of var. *iberoides*.

As compared with var. *littorale*, the shoot:root ratio of var. *iberoides* is lower. The latter variety is also characterized by a higher dry matter content and shorter rosette-leaves. According to BRINK (1964), on Terschelling the leaves of var. *iberoides* measure on an average 21.3×4.9 mm^2. These properties explain why var. *iberoides* has a lower growth rate than var. *littorale*.

The investigations show that there are physiological differences between the varieties *littorale* and *iberoides*, but these are apparently not of great ecological importance. As mentioned above, both infraspecific forms of *C. littorale* occur intermingled in many places. Because var. *iberoides* has a lower growth rate than var. *littorale*, it seems to be better adapted to the nutrient-poor, young dune soil. However, the dunes of Voorne, where only var. *iberoides* occurs, certainly do not represent a more extreme habitat than the salt marsh Boschplaat, where var. *littorale* is the only variety present (FREIJSEN 1967).

In spite of a lower shoot:root ratio the growth rate of var. *latifolium* is very similar to that of var. *iberoides*. This can be explained by the thinner leaves, which permit var. *latifolium* to form more photosynthesizing leaf area from the same quantity of dry matter. The leaves are also broader; according to the mean dimensions given by BRINK (1964), the width is 6.3 mm and the length 20.2 mm.

Under saline conditions, var. *latifolium* exhibits a higher mortality than the other Netherlands varieties of *C. littorale*. Besides the NaCl accumulation of this variety is much more pronounced. In the grasses *Festuca rubra* and *Agrostis stolonifera*, the less salt tolerant populations are characterized by the highest uptake of NaCl (HANNON & BARBER 1972, TIKU & SNAYDON 1971). According to comparative investigations of salt-sensitive and salt-tolerant races of economic plants, the salt accumulation of the former category is much higher (GREENWAY 1973). It is clear that plant taxa with low salt tolerance cannot sufficiently control the uptake of salt. The excessive uptake of NaCl by var. *latifolium* and the higher mortality of this variety show that its salt tolerance is lower than that of the other Netherlands varieties of *C. littorale* as was already found in earlier experiments (FREIJSEN 1971b).

There is a clear correspondence between the rather low salt tolerance of var. *latifolium* and the salinity of its natural environment. In the humous topsoils of old salt marshes, where it grows, only low and little-fluctuating salt concentrations occur (FREIJSEN 1967).

Plants of var. *iberoides* from Voorne and Goeree have identical growth curves, but differ somewhat with respect to the shoot:root ratio and the mineral composition, e.g. the $Na^+:K^+$ ratio under saline conditions. Because of the divergent behaviour of the Goeree plants in the experiments, and also because of their ascending habit in the field, we are inclined to consider these plants as an apart biotype within the variety *iberoides*.

Var. *minus* has a low dry matter content and a high shoot:root ratio under non-saline conditions in common with var. *littorale*, but the shape of the rosette is completely different. Var. *minus* has short and densely packed leaves. With respect to the growth rate, therefore, favourable and unfavourable factors occur together in this variety. In experiment 2 its growth rate was a little lower than those of var. *iberoides* (Goeree) and var. *latifolium*. This low growth rate is in agreement with the small size of the adult plants in the field.

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