

# GROWTH-PHYSIOLOGY, SALT-TOLERANCE AND MINERAL NUTRITION OF *CENTAURIUM LITTORALE* (TURNER) GILMOUR: ADAPTATIONS TO ITS OLYGOTROPHIC AND BRACKISH HABITAT

A. H. J. FREIJSEN

Biologisch Station "Weevers' Duin", Oostvoorne

## SUMMARY

*Centaurium littorale* was cultured under various conditions of nutrient availability, salinity and pH. The mineral composition of the experimental plants and of plants from a field site was investigated. The highest relative growth rate observed was  $0.02 \text{ mg.mg.}^{-1} \text{ day}^{-1}$  and the shoot: root ratio was 0.8. Optimal growth occurred at very low nutrient availability. Suction tensions below 7 atm had no strong effect on the growth rate. There was a marked accumulation of NaCl in the tissues without a negative effect on the uptake of nutrient ions. In the pH-range 7.7–4.8 growth was equal. In its growth physiology and mineral nutrition *Centaurium littorale* is well adapted to the habitat: the brackish and poor young dune soil.

## 1. INTRODUCTION

The species *Centaurium littorale* (Turner) Gilmour occurs along the coasts of Northwest Europe and on salty soils in East and Central Europe. In the coastal area the species is found at the margins of young dune slacks, in protected places of sandy beaches, and on the higher parts of salt marshes. The soils of these coastal environments have some characteristics in common.

The soil moisture is brackish (0.02–0.10%  $\text{Cl}^-$ ). The soil material itself consists almost entirely of sand. Only the topmost 1 cm layer contains a little organic matter. Plant nutrients, especially N, are deficient, and this determines the composition and open structure of the vegetation. The soil reaction is about neutral as a consequence of the presence of shell fragments. These data have been taken from a field study on the ecology of *Centaurium littorale* (FREIJSEN 1967).

The present paper describes preliminary investigations on the way in which *Centaurium littorale* is adapted to the three seemingly important environmental factors: moderate salinity, poorness in nutrients, and neutral soil reaction.

## 2. METHODS

The investigations were of three sorts: germination and culture experiments, and tissue analyses. All of them were carried out with plants of *Centaurium littorale* var. *iberoides* (Jonker) Freijsen 1967. The seeds were collected in the dunes near Oostvoorne, S.W. Netherlands. *Centaurium littorale* is a biennial.

forming a rosette during the first growing season and stems during the second. Typical specimens of the variety *iberoides* have decumbent stems. The experimental plants were in the rosette-stage and about 3 months old at the start of the experiments.

Germination and culture experiments were done in the period May–September 1968 in a greenhouse with an average daily temperature of 24°C. Plants were grown in polythene containers with 1700 g (dry weight) clean coarse river sand. The pH was 7.7 and the average moisture content was 110 ml per pot. Germination experiments were carried out with similar pots, but in this case the moisture content was maintained at 300 ml. These moisture levels were chosen because they correspond with the natural water conditions of *Centaureum littorale* during the summer and during the germination period in spring, respectively. Certain quantities of “Hoagland” solution and also NaCl had been mixed with the sand beforehand. For convenience in this paper the nutrient levels are expressed as numbers of milliequivalents (me.) of  $\text{NO}_3^-$  per pot.  $\text{NO}_3^-$  was chosen, because under field conditions this nutrient ion especially is deficient. Every culture and germination experiment was performed in triplicate. At the start of the culture experiments the dry weights of the rosettes and the roots were about equal. For the pH experiments the culture sand was treated with HCl in order to dissolve the lime contained in it. After this the sand was washed with running tapwater. The different pH levels were created by adding increasing quantities of  $\text{H}_2\text{SO}_4$ .

At the end of the culture experiments the rosettes and the roots were harvested, dried at 70°C and weighed. For tissue analyses the plant material was ground. After wet ashing with  $\text{H}_2\text{SO}_4$  and  $\text{H}_2\text{O}_2$  of 600 mg of each sample the following chemical components were determined:

- P – colorimetric determination of the phosphomolybdenum-blue-complex,
- organic N – titrimetric determination after alkaline distillation,
- K, Na and Ca – emission flame photometric determinations,
- Mg – colorimetric determination with titan yellow.

(It appeared that Mg figures obtained by this method were distinctly lower than corresponding ones from determinations with atomic absorption spectrophotometry.) 1000 mg of each sample was extracted with acetic acid 0.5 N for the determination of:

- $\text{Cl}^-$  – potentiometric titration,
- $\text{SO}_4^{--}$  – turbidimetric determination as  $\text{BaSO}_4$ ,
- $\text{NO}_3^-$  – colorimetric determination of nitroxylenol.

All values of the tissue analyses are expressed as milliequivalents (me.) per kg of dry matter (dried at 105°C). Organic N and P ( $\text{H}_2\text{PO}_4^-$ ) are treated as monovalent ions. C and A are used as abbreviations for the total contents (in me.) of cations and inorganic anions, respectively. (C–A) is the difference between these two values. In other words, it is the content of the carboxylate anions (see DIJKSHOORN 1969).

## 3. EXPERIMENTS

## 3.1. Growth rate

Experiment 1 was carried out to get general information on growth and behaviour of *Centaurium littorale* under experimental conditions. The rosettes were grown with 2.5 me.  $\text{NO}_3^-$  and without extra NaCl. In this and the following experiments low nutrient levels were applied, because the natural environment of *Centaurium littorale* is poor in nutrients, as already mentioned above. Experiment 1 lasted 118 days: 16 May–11 September. During this period the plants developed from simple rosettes with 12 leaves to large ones with a diameter of 50 mm and secondary small rosettes in the leaf axils. In its typical environment *Centaurium littorale* has the same size and growth habit at the end of the first vegetation period.

Fig. 1 gives the increase of the total dry weight. The rosettes of *Centaurium littorale* exhibited an exponential growth. Such a growth pattern normally occurs in the juvenile stage of herbs and grasses under optimal conditions. The relative growth rate was constant and attained the very low value of  $0.02 \text{ mg} \cdot \text{mg}^{-1} \text{ day}^{-1}$ . (For the calculation of the "relative growth rate" the author used the formula given by WILLIAMS, 1946, Ann. Bot. N.S.10: 41–73 —  $\text{RGR} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$ ). The constant rate of growth shows that the slowness was not

due to nutrient deficiency. In cases of insufficient nutrient supply growth curves tend to decline. Besides, less than half the nutrient supply was consumed by the plants. The low productivity of *Centaurium littorale* is well understandable in the light of its growth physiology. In preliminary determinations (by Dr. Th. Alberda, I.B.S., Wageningen, not published) *Centaurium littorale* appeared to possess a low photosynthetic rate. Furthermore, the harvested plants of experiment 1 had a shoot: root ratio = 0.9. This means that only a small proportion of the continuously produced dry matter was used for building new assimilating tissues. The importance of the dry matter distribution and the total leaf surface for the growth rate of plants is described in the literature (e.g. VAN DOBBEN 1967).

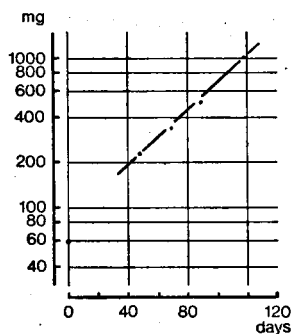


Fig. 1. The increase of dry weight of *Centaurium littorale* in experiment 1. Initial dry weight = 60 mg.

### 3.2. Germination and salinity

The germination of *Centaurium littorale* under saline conditions was tested in a pot experiment. 30 seeds were evenly distributed on the surface of each pot. *Table 1* gives the results of four salt treatments and a control treatment. The two lowest salt levels in this experiment corresponded with the average and the maximal salt concentration, respectively, occurring in the natural habitat of *Centaurium littorale* (FREIJSEN 1967).

*Centaurium littorale* attained the highest germination percentage in the treatment without NaCl. Already the two lowest "natural" salt concentrations had an increasingly negative effect on the germination. A salt level with a suction tension of 7 atm appeared to be critical. At this level only few seeds germinated and the germination process took more time.

Table 1: The germination of *Centaurium littorale* under saline conditions

NaCl conc. in %	suction tension of NaCl in atm	Mean number of seedlings after	
		13 days	28 days
0	0	23	26
0.08	0.7	21	22
0.17	1.4	18	18
0.84	7.0	3	9
1.68	14.0	0	0

### 3.3. Salt tolerance

In experiments 2, 3 and 4 rosettes of *Centaurium littorale* were cultured at three nutrient levels, 1.5; 0.5, and 0.1 me.  $\text{NO}_3^-$ , respectively. Each experiment consisted of eight NaCl-treatments forming a salinity range from 0 to 14 atm suction tension. Experiments 2 and 3 lasted 82 days (29 May–19 August and 7 June–29 August) and the initial dry weight of the juvenile plants was 60 mg. In experiment 4 which lasted 89 days (12 June–9 September) the initial weight was 300 mg. (At the start of experiment 4 only sufficient plants of this size were still available). The results are shown in *figs. 2 and 3*, in which the total yield in mg has been plotted against the salinity expressed in atm suction tension and in me.  $\text{Cl}^-$  added per pot (on the logarithmic x-axis). These two parameters for salinity were given bearing in mind two possible effects of added salts. It is generally accepted that high salt concentrations have a non-specific osmotic effect, concentrations below 2 atm a specific one (STEINER & ESCHRICH 1958).

There was a distinct reduction in vitality and in yield at the two highest salt levels of all three experiments. Suction tensions of 7 atm and higher were apparently unfavourable for the growth of *Centaurium littorale*. Below that limit the rosettes had equal vitality. As a consequence of the great non-systematic variation in yield of these plants it was impossible to draw conclusions on the effect of the salinity treatments between 0 and 7 atm. An exception was

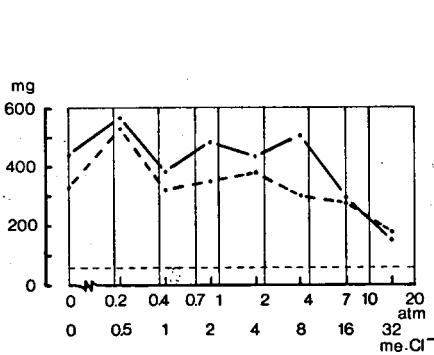


Fig. 2. The total dry weight attained by *Centaurium littorale* after 82 days at increasing degrees of salinity in experiments 2. —, and 3. - - - - - .  
- - - - - = initial dry weight.

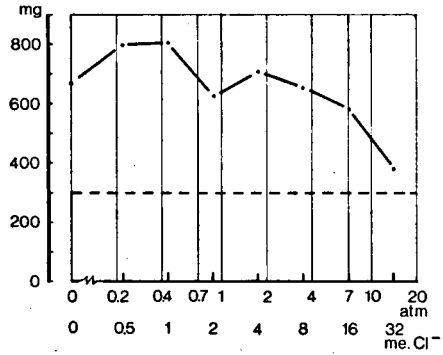


Fig. 3. The total dry weight attained by *Centaurium littorale* after 89 days at increasing degrees of salinity in experiment 4. - - - - - = initial dry weight.

formed by the plants of the 0.5 me. Cl<sup>-</sup> treatment which attained notably higher dry weights in all experiments. However, a possibly positive effect of low quantities of NaCl was not found in a water culture experiment (Freijsen, in preparation).

### 3.4. Response to nutrient levels

The growth of the plants in the experiments 2, 3, and 4 was clearly affected by the applied nutrient levels. At 1.5 me. NO<sub>3</sub> the average growth rate of the plants up to the two highest Cl<sup>-</sup> steps was similar to the growth rate in experiment 1. A relatively great decrease of nutrient availability from 2.5 me. to 1.5 me. NO<sub>3</sub> per pot had no influence on the growth. In other words, a nutrient supply of 1.5 me. NO<sub>3</sub> appeared to be sufficient for optimal growth. On the average the yield of the plants in experiment 3 was 100 mg lower. Here, at 0.5 me. NO<sub>3</sub>, *Centaurium littorale* apparently grew under suboptimal nutritional conditions. The results of experiment 4 cannot simply be compared with the foregoing ones. The plants of *Centaurium littorale* attained a higher absolute terminal weight. This, however, was only 2.5 times the initial weight. The growth rate was sharply depressed by nutrient stress. However, more dry matter could be formed because of a 5 times higher amount of assimilating tissues at the start of the experiment. Furthermore, part of the shortness of nutrients was compensated by the minerals taken up before the experiment began. This initial capital was also about 5 times higher.

### 3.5. Shoot : root ratio

In a preceding part of this paper attention was given to the consequence of the low shoot : root ratio of *Centaurium littorale* for its growth rate. Table 2 summarizes values for the shoot : root ratio from all culture experiments. It appears

that there was very little variation. Within the tested range of nutrient levels there were no differences. With respect to the degree of salinity it may be said that a slight increase of the shoot : root ratio occurred at 7 and 14 atm. These salinity levels had a stronger detrimental effect on root growth than on the growth of the plant as a whole.

Generally speaking, plants show a tendency to form relatively larger root systems under nutrient stress, or water stress in saline mediums (BROUWER 1963b and 1968). *Centaurium littorale* did not use this adaptational mechanism to cope with the unfavourable experimental conditions.

Table 2: Shoot: root ratio of *Centaurium littorale* at various combinations of nutrient and salinity (NaCl) levels

Suction tension in atm	Me. NO <sub>3</sub> <sup>-</sup>			
	2.5	1.5	0.5	0.1
0	0.9	1.1	0.8	0.8
0.2	-	0.8	0.9	0.8
0.4	-	0.8	0.8	0.8
0.9	-	0.8	0.8	0.8
1.8	-	0.8	1.0	0.8
3.5	-	0.9	0.7	0.9
7.0	-	1.0	1.0	1.0
14.1	-	1.0	0.9	1.1

### 3.6. The influence of the pH

The germination of *Centaurium littorale* under acidic conditions was investigated in the same way as the germination on saline substrates. Three pH values were tested: 5.9–5.4–4.8. There was no significant drop in the germination percentage with decreasing pH. However, more recently germination was tested on a heath-subsoil of pH = 4. Root growth of the seedlings was completely inhibited and the seedlings died off soon after emergence.

The influence of different pH values on the growth of *Centaurium littorale* was determined in a culture experiment with a pH range from 7.3 to 4.0. The results were compared with those of control plants and of plants cultured on soil to which CaCO<sub>3</sub> was added after acidification. The pots contained 1.5 me. NO<sub>3</sub><sup>-</sup> and 1 me. Cl<sup>-</sup>. The initial plant dry weight was 150 mg and the experimental period was 71 days (3 July–12 September). Table 3 gives the results. pH = 4.0 appeared to be lethal for *Centaurium littorale*. Above that value there was no systematic variation in growth. The average relative growth rate was as high as in experiment 1 and 2. However, the plants possessed much higher shoot : root ratios. This phenomenon is difficult to explain, just as the lower yield of the control plants. At the end of the experiment pH values in the acid pots were considerably higher as a consequence of the exchange of bicarbonate for nitrate (DIJKSHOORN 1969).

Table 3: The influence of the pH on the growth of *Centaurium littorale*

initial pH	terminal pH	yield in mg	shoot : root ratio	treatment
7.7	7.1	425	1.0	control
7.7	7.0	628	1.5	acid + CaCO <sub>3</sub>
7.3	7.0	596	1.2	acid
5.9	6.6	604	1.5	acid
5.4	6.7	570	1.6	acid
4.8	6.1	679	1.5	acid
4.0	4.4	died off	-	acid

#### 4. MINERAL COMPOSITION

##### 4.1. Accumulation of Cl<sup>-</sup> and Na<sup>+</sup>

The leaf material of experiment 3 (0.5 me. NO<sub>3</sub><sup>-</sup>) was analysed to find the interaction of accumulation of Cl<sup>-</sup> and Na<sup>+</sup>, and total ionic balance. As a consequence of the low dry weight of the plants, material of different treatments had to be combined in three samples: 0-0.5; 1-8; 16-32 me. Cl<sup>-</sup>. In *fig. 4* the contents of the main elements of the ionic balance (in me. per kg of dry material) are plotted against average Cl<sup>-</sup> values of the medium, expressed as me. Cl<sup>-</sup> per pot.

*Centaurium littorale* showed a tendency to accumulate relatively large quantities of Cl<sup>-</sup> in its leaves, even when little or no extra (see below) Cl<sup>-</sup> was added to the pots. The difference between the Cl<sup>-</sup> content and the total anion content was constant. The rather low levels of other inorganic anions did not show any variation. In leaves of low salinity plants the Na<sup>+</sup> content was small. At higher

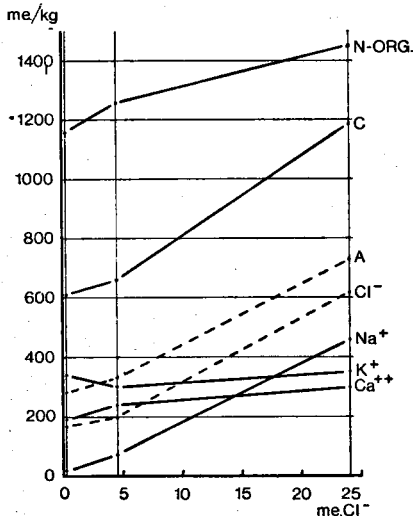


Fig. 4. The mineral composition of rosette leaves of *Centaurium littorale* at three salt concentrations in experiment 3. (C = total content of cations; A = total content of anions)

salinity levels of the culture medium this content increased in proportion to the  $\text{Cl}^-$  content. Contrary to the leaves, the root material contained more  $\text{Na}^+$  than  $\text{Cl}^-$ . Also the uptake of cations was not influenced by the salinity of the culture environment. The important element  $\text{K}^+$  had about the same concentration in all samples.

The total ionic concentrations in the leaf water were used for a rough calculation of osmotic values. In this way an average value of 8 atm was found for the first and the second sample, and one of 13 atm for the third sample. The internal suction tensions of plants grown at salinity levels below 7 atm were distinctly higher than the corresponding external suction tensions. Above a salinity of 7 atm there was apparently no sufficient gradient between the internal and external osmotic values. In this case the growth of *Centaurium littorale* was impeded by an insufficient osmotic adjustment.

#### 4.2. Ionic balance

The effect of the nutrient levels applied in experiments 1, 2, 3 and 4, i.e. 2.5, 1.5, 0.5 and 0.1 me.  $\text{NO}_3^-$ , on the mineral composition is shown in *fig. 5* (for the below-mentioned discussion of the  $\text{K}^+$  contents also the  $\text{K}^+$  levels of the medium are given on the x-axis). Analyses were carried out in samples composed of leaf material of the treatments 0–8 me.  $\text{Cl}^-$ . In experiment 1, i.e. at 2.5 me.  $\text{NO}_3^-$  no extra  $\text{NaCl}$  was added.

The richness of the culture treatments was reflected by the organic N content of the tissues of *Centaurium littorale*. The slight decline in N content in the plants of the 2.5 me.  $\text{NO}_3^-$  treatment cannot be explained by exhaustion of the substrate. The amount of  $\text{NO}_3^-$  in the tissues was always extremely low. It ranged from 5 to 16 me. per kg dry matter. Contrary to the organic N content

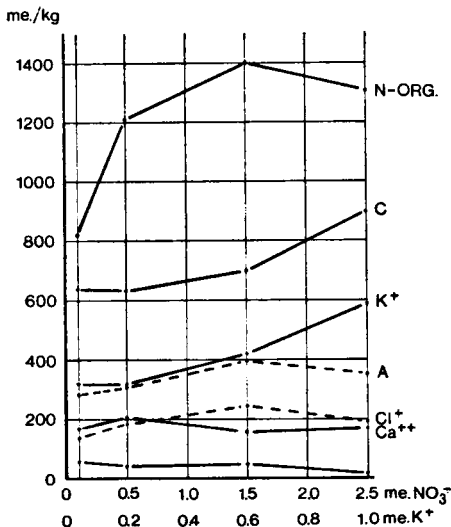


Fig. 5. The mineral composition of rosette leaves of *Centaurium littorale* at four nutrient levels. (C = total content of cations; A = total content of anions)



the  $K^+$  content continued to rise in the plants of the 2.5 me.  $NO_3^-$  treatment. The values of the other ions did not show much variation. Although no extra NaCl was added to the pots, the plants in experiment 1 accumulated as much NaCl as the salt treated plants in the other experiments. (This justified including the analyses from experiment 1 in fig 5.) *Centaurium littorale* grew under widely different nutritional conditions in the experiments 2, 3 and 4, ranging from marginal to optimal, as was discussed above. In spite of this the (C-A) content was always about 325 me. In experiment 1 where nutrient availability was still higher than in experiment 2, but the relative growth rate was not enlarged, the (C-A) content attained a value of 550 me. Further investigations are necessary to decide if these facts are indeed in contradiction with the general idea about the relationship between (C-A) content and optimal growth of plants stated by DE WIT, DIJKSHOORN & NOGGLE (1963). According to these authors optimal growth of plants would be characterized by a particular value of the (C-A) content.

#### 4.3. Mineral composition in the field

Plants of *Centaurium littorale* were collected in the field. The leaf material was used in the chemical analyses. The site was a beach near Oostvoorne, the soil of which contained some silt. Both first-year plants, i.e. rosettes, as well as second-year specimens of the biennial *Centaurium littorale*, were sampled in 1969. On the x-axis of figs. 6 and 7 the samples are arranged as if they referred to a complete two-year life-history.

Generally speaking these plants possessed ionic levels as high as or even higher than those of the plants of *Centaurium littorale* cultured with 2.5 me.  $NO_3^-$ . The content of organic N, the total anion content, and the quantities of  $H_2PO_4^-$  and  $SO_4^{2-}$  were higher in the beach plants. Other ions including  $NO_3^-$  were present in equal amounts. These facts show the relative richness of the habitat caused by the silt in the beach soil.

There were fluctuations and changes in the mineral contents. The ionic levels

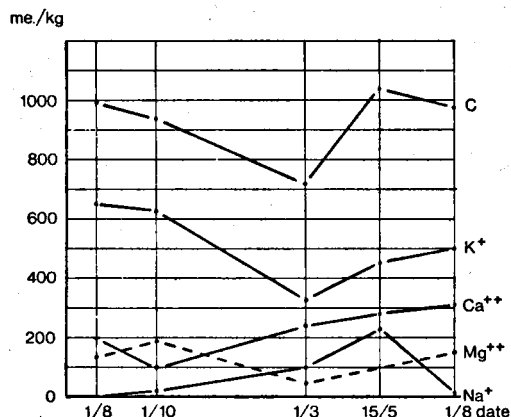


Fig. 6. The mineral composition of *Centaurium littorale* during its life-history in the field. 1 Cations. (C = total content of cations)

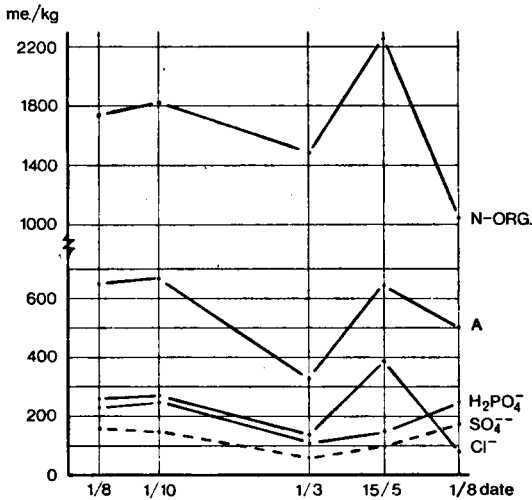


Fig. 7. The mineral composition of *Centaurium littorale* during its life-history in the field. 2 Anions and organic N. (A = total content of anions)

of e.g.  $K^+$  dropped during the winter. Perhaps as a consequence of internal dilution organic N attained its lowest value in the second summer season, when stem elongation and formation of inflorescences took place. The  $Ca^{++}$  content increased in the course of the life-history, which is a normal phenomenon. Notable were the "peaks" for  $Na^+$  and  $Cl^-$  in May which could be related to the dry weather and high salt concentrations in the soil moisture characteristic for this month (see FREIJSEN 1967). Overall the (C-A) content increased from 300 to 500 me.

## 5. CONCLUSIONS

The juvenile rosette of *Centaurium littorale* grows very slowly. The low growth rate of this species can be explained by a combination of specific properties:

1. *Centaurium littorale* has a relatively low photosynthetic rate.
2. It has a very low shoot: root ratio. A small proportion of the dry matter formed by the plant is used for assimilating tissues.
3. Its mineral uptake is low. Above a certain low nutrient availability the growth rate is not increased by more nutrients.

As a consequence of a slow growth, together with a low mineral uptake, *Centaurium littorale* has a modest need of mineral nutrients. It can grow healthily under conditions of low nutrient availability, as prevailing in its dune habitat.

Relations between growth rate, mineral nutrition and fitness for the natural environment, postulated here for *Centaurium littorale*, were previously described by HIGGS & JAMES (1969). In their paper grass species from eutrophic and oligotrophic habitats were compared with each other. Also BRADSHAW *et al.* (1958) investigated the growth physiology and mineral nutrition of grass species. In both investigations it appeared that grasses from poor soils were characterized by a low growth rate, grasses from rich soils by a high productivity. The ecolo-

gical significance of the relative growth rate and the potential uptake of minerals by the plant is a main point in the theoretical dissertation by RORISON (1969).

Because all experiments were carried out with rosettes, the above discussion holds in a strict sense only for first-year plants of *Centaurium littorale*. In nature the formation of stems and inflorescences of second-year plants is linked with the death of the rosette. Probably the formation of these new above-ground parts of the plant is possible also by redistribution of minerals. It is not known whether the root system becomes larger in the second season.

It was mentioned above that the low shoot : root ratio partially determines the slow growth of *Centaurium littorale*. Apart from this, the low ratio, in other words the relatively extensive root system, is also directly important. It is a necessary means for the uptake of the scarce minerals and of water from a dune soil which can strongly desiccate in summer. Like the growth rate, the shoot : root ratio is correlated with the degree of soil fertility of the habitat; e.g., species from eutrophic environments have high ratios (see VAN DOBBEN 1967, HIGGS & JAMES 1969, BRADSHAW *et al.* 1958).

Below a maximum concentration of about 0.84% NaCl, which corresponds with a suction tension of 7 atm, the growth of the rosettes of *Centaurium littorale* is not strongly affected by salinity. This salt tolerance is explained by two important adaptations with respect to the uptake of minerals.

*Centaurium littorale* accumulates  $\text{Cl}^-$  and  $\text{Na}^+$  in its tissues, also under non-saline conditions. As a consequence of the high concentration of accumulated ions the suction tension of the cells is higher than that of the brackish rooting medium. The difference in suction tension ensures a sufficient water uptake. This is a requirement for normal growth processes (BROUWER 1963a). The salt accumulation process is considered to be an important feature of halophytes (WALTER 1960 and 1961, STEINER & ESCHRICH 1958, ADRIANI 1956, BINET 1966).

Secondly, *Centaurium littorale* is able to extract sufficient quantities of all nutrient ions necessary for normal growth from a substrate with an excessive NaCl concentration. The uptake of nutrient ions is not hindered by the competition of  $\text{Na}^+$  and  $\text{Cl}^-$ . *Centaurium littorale* apparently possesses specific uptake mechanisms for nutrient ions, which appeared to occur in halophytic species (EPSTEIN 1969 and BLACK 1960). By its tolerance for moderate salinity levels *Centaurium littorale* can grow very well in the young dune slack with its brackish soil moisture.

The germination of *Centaurium littorale* is negatively influenced by salinity. The same holds for most halophytes (e.g. UNGAR 1967). In nature *Centaurium littorale* germinates especially in spring when the soil moisture content is highest and the salt concentration is negligible (FREIJSEN 1967).

Contrary to the two environmental factors discussed above, namely poorness in nutrients and soil salinity, the neutral soil reaction of the habitat does not correspond with special eco-physiological properties of *Centaurium littorale*. Down to  $\text{pH} = 4$  the growth of *Centaurium littorale* did not vary. Such a seeming discrepancy between the ecological preference and the physiological indifference occurs in many plant species (ELLENBERG 1958).

## ACKNOWLEDGEMENTS

I should like to thank Dr. W. H. van Dobben (director of the Institute for Ecological Research, Arnhem) who suggested to me to initiate eco-physiological investigations. Furthermore, he read critically the manuscript. I am much indebted to Dr. W. Dijkshoorn (Institute for Biological and Chemical Research of Field Crops and Herbage, Wageningen). He gave me hospitality in his laboratory, where I got familiar with his special approach in the research of the mineral nutrition of plants. Dr. A. W. Davison (Newcastle-upon-Tyne) was kind enough to correct the English text. Thanks are also due to Mr. A. van Dijk who did the chemical analyses, and Miss A. Dekker for typing the manuscript.

## REFERENCES

- ADRIANI, M. J. (1956): Der Wasserhaushalt der Halophyten. In: W. RUHLAND (ed.), *Hdb. Pflanzenphysiol.* 3: 902–914, Springer, Berlin.
- BINET, P. (1966): Études d'écologie expérimentale et physiologique sur *Cochlearia anglica* L. I – Études dans l'estuaire de l'Orne. *Oecol. Plant.* 1: 7–37.
- BLACK, R. F. (1960): Effects of NaCl on the ion uptake and growth of *Atriplex vesicaria* Heward. *Aust. J. Biol. Sci.* 13: 249–266.
- BRADSHAW, A. D., R. W. LODGE, D. JOWETT & M. J. CHADWICK (1958): Experimental investigations into the mineral nutrition of several grass species. I. Calcium level. *J. Ecol.* 46: 749–757.
- BROUWER, R. (1968): Morphological and physiological adaptations to external conditions. *Acta Bot. Neerl.* 17: 78–80.
- (1963a): The influence of the suction tension of the nutrient solutions on growth, transpiration and diffusion pressure deficit of bean leaves (*Phaseolus vulgaris*). *Acta Bot. Neerl.* 12: 248–261.
- (1963b): Some aspects of the equilibrium between overground and underground plant parts. *Jaarb. I.B.S.* 1963: 31–39.
- DOBBERN, W. H. VAN (1967): Physiology of growth in two *Senecio* species in relation to their ecological position. *Jaarb. I.B.S.* 1967: 75–83.
- DIJKSHOORN, W. (1969): The relation of growth to the chief ionic constituents of the plant. In: I. H. RORISON (ed.), *Ecological aspects of the mineral nutrition of plants* (symp. B.E.S. 1968): 201–204, Blackwell, Oxford.
- ELLENBERG, H. (1958): Bodenreaktion (einschliesslich Kalkfrage). In: W. RUHLAND (ed.), *Hdb. Pflanzenphysiol.* 4: 638–708, Springer, Berlin.
- EPSTEIN, E. (1969): Mineral metabolism of halophytes. In: I. H. RORISON (ed.), *Ecological aspects of the mineral nutrition of plants* (symp. B.E.S. 1968): 345–355, Blackwell, Oxford.
- FREIJSEN, A. H. J. (1967): *A field study on the ecology of Centaurea vulgare Rafn.* Thesis, Utrecht.
- HIGGS, D. E. B. & D. B. JAMES (1969): Comparative studies on the biology of upland grasses. I. Rate of dry matter production and its control in four grass species. *J. Ecol.* 57: 553–563.
- RORISON, I. H. (1969): Ecological inferences from laboratory experiments on mineral nutrition. In: I. H. RORISON (ed.), *Ecological aspects of the mineral nutrition of plants* (symp. B.E.S. 1968): 155–175, Blackwell, Oxford.
- STEINER, M. & W. ESCHRICH (1958): Die osmotische Bedeutung der Mineralstoffe. In: W. RUHLAND (ed.), *Hdb. Pflanzenphysiol.* 4: 334–354, Springer Berlin.
- UNGAR, I. A. (1967): Influence of salinity and temperature on seed germination. *The Ohio J. Sci.* 67: 120–123.
- WALTER, H. (1960): *Einführung in die Phytologie*. Band 3/1, *Standortslehre*: 477–491, Ulmer, Stuttgart.
- (1961): The adaptation of plants to saline soils. In: *Salinity problems in the arid zones. Arid zone research* 14 (Proc. Teheran symp.): 129–134. Unesco publication.
- WIT, C. T. DE, W. DIJKSHOORN & J. C. NOGGLE (1963): Ionic balance and growth of plants. *Versl. Landbouwk. Onderz. Wageningen* 69: 15.