

Growth and reproduction of *Rumex maritimus* and *Chenopodium rubrum* under different waterlogging regimes

A. J. M. VAN DER SMAN, O. F. R. VAN TONGEREN* and
C. W. P. M. BLOM

Department of Experimental Botany, Catholic University of Nijmegen, Toernooiveld, 6525 ED Nijmegen, The Netherlands

SUMMARY

The influence of different waterlogging treatments on above-ground development and subsequent flowering and seed production of *Chenopodium rubrum* L. and *Rumex maritimus* L. was studied in a greenhouse experiment.

C. rubrum, a typical occupant of low sandy beaches at times when floods have subsided, appeared to be suppressed by all waterlogging regimes. *R. maritimus*, an inhabitant of wet mud flats of old river beds, was found to be quite tolerant to waterlogging conditions; early waterlogging, during the rosette stage, led to an increase in dry weight and seed production in some cases. In general, seed production changed more than biomass as a result of waterlogging; responses greatly depend on regimes. Intermittent waterlogging generally caused more damage than did continuous waterlogging, especially in the case of *C. rubrum*. Even *R. maritimus* produced less seeds under conditions of intermittent waterlogging. The results demonstrate that adaptations to, and damage from, flooding greatly depend on flooding regimes which vary substantially in the field situation.

Key-words: *Chenopodium rubrum*, growth, reproduction, *Rumex maritimus*, waterlogging.

INTRODUCTION

During the last few decades river forelands of the Rhine-branches in The Netherlands were flooded more frequently in summer, due to a faster rain-water discharge from the upper Rhine-basin into the river. As a consequence, plants were subjected to more frequent and earlier floodings of longer duration, which has a strong influence on flora and vegetation (Van de Steeg 1984; Brock *et al.* 1987). Specific morphological responses on waterlogging under controlled conditions are chlorosis and accelerated senescence of leaves (Jackson & Campbell 1975, 1976; Trought & Drew 1980a). There is often an accompanying reduction in growth of above-ground parts and withering of the root-system (Kramer 1951; Jones & Etherington 1971). Quite common effects of waterlogging

*Present address: Limnological Institute, Vijverhoflaboratory, Rijksweg 6, 3631 AC Nieuwersluis, The Netherlands.

are the formation of adventitious roots and of aerenchyma in these roots and in other plant parts (Iversen 1949; Armstrong 1975, 1978; Etherington 1984; Schat 1984). Regrowth of above-ground parts frequently occurs after adventitious roots are initiated. Jackson (1955) found that these roots have a positive influence on the recovery of some species during waterlogging.

The present study is part of a project aimed at studying the effects of flooding on ecophysiological and population characteristics of some plant species that occur in the marshes along rivers in The Netherlands (Voeselek & Blom 1987; Voeselek *et al.* 1988). Our study concerned a greenhouse experiment on growth and reproduction of two annual species that are common in the Dutch riverine area, i.e. *Chenopodium rubrum* L. and *Rumex maritimus* L. Both species occupy habitats that are infrequently flooded in summer. *C. rubrum* is a common species of sandy beaches, directly adjacent to the river. To a lesser extent this species occupies the mud flats of former river beds, where *R. maritimus* has its optimal occurrence (Salisbury 1942, Tüxen 1979). In these more anaerobic habitats only small individuals of *C. rubrum* are found. Both species are frequently found as pioneer species on clay and or sand pits as well, which are quite common habitats in the Dutch riverine area. Germination of both species can occur from the end of May until late summer, after the floods recede. Plants of *R. maritimus*, that germinate late in the season, will probably not flower the same year but winter as a rosette. The second year flowering occurs unless rosettes succumb to winter flooding (Hejny 1960). *C. rubrum* plants that germinate early in the season grow vegetatively during the summer and can become quite large, whereas late germinating plants remain small. All *C. rubrum* plants flower late in the summer under short daylight conditions (Cumming 1969; Bernier *et al.* 1981). The water regime seems to be an important environmental factor for vegetative and generative development of both species and was, therefore, chosen to be studied in detail in a greenhouse experiment.

MATERIALS AND METHODS

Main growth experiment

Plants of *C. rubrum* and *R. maritimus* were grown from seeds that were 2-year-old and dry-stored after being collected from the river habitat near Nijmegen, The Netherlands. Uniform germination was achieved in a growth chamber under a fluctuating temperature regime of 30°C and 15°C during the 12/12 h photo- and dark-period respectively. The young seedlings were transferred immediately to the greenhouse, where they were transplanted into plastic containers (diameter 18 cm), that were filled with an industrial peat/soil mixture. The photo-period was kept at 16 h by means of 400 W high-pressure sodium lamps, which supplemented the normal daylight with a light intensity of 110 $\mu\text{E m}^{-2} \text{s}^{-1}$ at plant level (minimum during the periods without daylight).

The experiment was carried out to study the effects of different waterlogging regimes on growth and reproduction. An additional series of plants was used to obtain extra information about morphological changes and to acquire biomass estimates for growth curves of individual plants in the experiment (see next paragraph).

The experiment was started in the period of exponential plant growth, 6 weeks after sowing. Mean height of the *C. rubrum* plants was 14 cm; *R. maritimus* plants were still in the rosette stage, with rosettes nearly fully expanded. During the following 8 weeks, 80 plants from both species were subjected to different waterlogging treatments in a

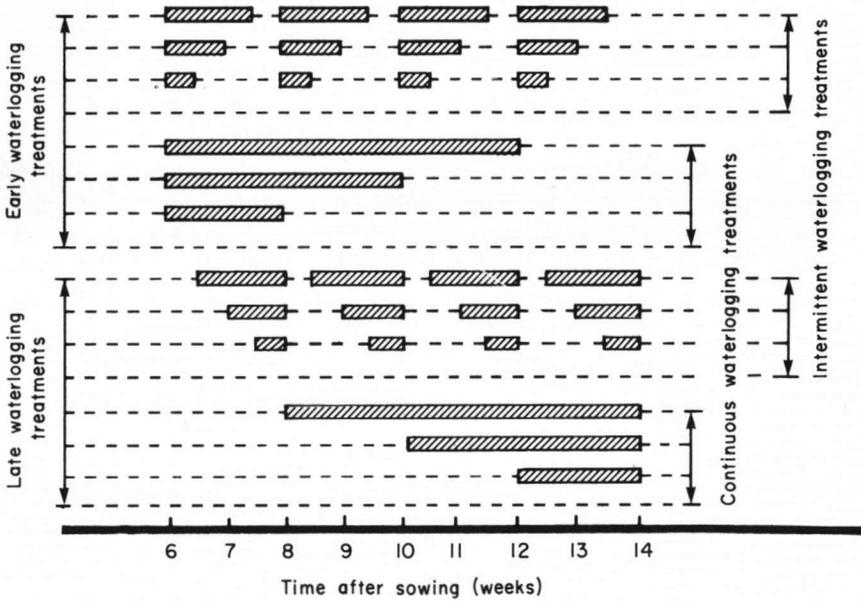


Fig. 1. Scheme to show waterlogging treatments in the full factorial experiment; (—) Waterlogging periods, (---) drained conditions.

completely randomized full factorial design. The different factors of waterlogging that were tested were duration (0, 2, 4 and 6 weeks of waterlogging, either in one extended period or split into shorter periods), frequency ('continuous', i.e. waterlogging in one extended period and 'intermittent', i.e. waterlogging in four equal shorter periods) and time course ('early', i.e. waterlogging beginning 6 weeks after sowing and 'late', i.e. waterlogging ending 14 weeks after sowing). A scheme for the different treatments is presented in Fig. 1. Per treatment five replicates were used.

Non-waterlogged plants were kept under constant moisture conditions (60% by weight), later referred to as standard watering conditions. Waterlogging was achieved by placing the pots in tanks in which the water level was kept 14 cm above the soil level. All waterlogged plants were completely submerged at the start of the experiment. From 14 weeks onwards all surviving plants were kept under standard watering conditions until flowering and seed formation occurred.

The biomass of individual plants was estimated from stem length and maximal leaf length twice weekly. At the end of the different waterlogging treatments (14 weeks after sowing), the biomass of all *R. maritimus* plants was estimated. The regression method for estimating biomass, however, appeared not to be accurate for *C. rubrum*. Regression parameters were found to be different for different treatments (see next paragraph for the method by means of which this was tested). Two plants were harvested per treatment after 14 weeks to obtain more precise biomass values. The remaining plants were kept to provide the information on seed production. The timing of flowering was determined by recording the first appearance of a macroscopically visible inflorescence. Seed was collected, dry stored for a few weeks and weighed (perianth included). A few samples were counted to determine whether differences were due to seed numbers or seed sizes.

Additional measurements

In an earlier study of these species (J.v.d. Sman, unpublished), performed under standard watering conditions, the biomass could be estimated by the formula:

$$\log(\text{dry weight}) = a + b\{\log(\text{stem length})\} + c\{\log(\text{maximal leaf length})\}.$$

We did not, however, know whether such an equation could be applied to waterlogged plants of both species as well. Therefore, additional plants were grown and placed at random between the plants from the experiment. Three more extreme treatments were applied to these plants: (1) standard watering conditions, (2) continuous waterlogging from 6 weeks onwards and (3) intermittent waterlogging (alternate weeks) from 6 weeks onwards. To obtain biomass estimates for the plants in the experiment, each week, in the period between the sixth and fourteenth week after sowing, a plant was harvested from each treatment series. Multiple linear regression was performed (by means of the least squares method) on 30 harvested plants per species with biomass as the dependent variable and stem length and maximal leaf length as independent variables. To distinguish between the treatments, two dummy variables were introduced, representing both the waterlogging treatments. When either of these variables showed a significant effect on biomass, the regression equation was modified accordingly. All tests were performed using the general linear models (GLM) procedure from the SAS-package (SAS Institute Inc. 1985).

In addition, number of leaves, number and length of shoots and dry weight were determined at harvest. In the case of *R. maritimus*, mean petiole length of rosette leaves and stem diameter were also measured.

Root performance of the harvested plants was examined for degeneration of the root-system, and the formation of adventitious roots and aerenchyma. Specific gravity of roots, measured with a pycnometer (Iversen 1949; Schat 1984), was used to indicate root porosity.

Five plants per treatment were kept waterlogged under the same regimes after the fourteenth week to explore the effects on reproduction of prolonged continuous and intermittent waterlogging conditions throughout flowering and seed production.

RESULTS

The first remarkable response of both species upon waterlogging was the change of leaves and stems from a prostrate to a more vertical position. In every case this was noticed within a few days. Differences in response between the two species were apparent shortly afterwards (Table 1 and 2).

Waterlogging of *C. rubrum* plants caused severe chlorosis and shedding of most of the underwater leaves. Stems became weak and started to display strange curvatures; newly formed leaves remained small. Table 1 summarizes some measured above-ground parameters on harvested plants from this species. Growth of most above-ground parts of *R. maritimus*, on the other hand, was stimulated under conditions of waterlogging (Table 2) and, by means of petiole elongation, rosette leaves were being restored to the water surface, resulting in less chlorosis and leaf shedding. Results of regression analysis with the 30 harvested plants per species are summarized in Table 3. Figure 2 presents growth curves, based on estimated biomass values, which separate the three different treatment factors and the most remarkable interaction term: frequency \times time course. The results of both biomass and seed production after 14 weeks are presented for each individual treatment in Fig. 3 (biomass values are from harvested plants in the case of *C. rubrum*). Table 4

Table 1. Influence of continuous and intermittent waterlogging on various above-ground growth parameters of *Chenopodium rubrum*. Values represent the means \pm 1SE of five plants harvested between 10 and 14 weeks after sowing

| | Standard watering conditions | Intermittently waterlogged | Continuously waterlogged |
|------------------------------------|------------------------------|----------------------------|--------------------------|
| Number of leaves \geq 1 mm/plant | 1100 \pm 100 | 400 \pm 100 | 170 \pm 50 |
| Maximal leaf length (cm) | 10 \pm 1 | 8 \pm 1 | 6 \pm 1 |
| Number of branches | 15 \pm 2 | 10 \pm 1 | 9 \pm 2 |
| Stem length (cm) | 51 \pm 4 | 33 \pm 1 | 43 \pm 6 |
| Length of first branch (cm) | 39 \pm 4 | 23 \pm 3 | 26 \pm 5 |
| Dry weight (g) | 23 \pm 2 | 5 \pm 1 | 5 \pm 1 |

Table 2. Influence of continuous and intermittent waterlogging on various above-ground growth parameters of *Rumex maritimus*. Values represent the means \pm 1SE of four plants harvested between 11 and 14 weeks after sowing

| | Standard watering conditions | Intermittently waterlogged | Continuously waterlogged |
|------------------------------------|------------------------------|----------------------------|--------------------------|
| Number of leaves \geq 1 mm/plant | 220 \pm 70 | 190 \pm 50 | 170 \pm 30 |
| Maximal leaf length (cm) | 30 \pm 2 | 30 \pm 3 | 39 \pm 3 |
| Stem length (cm) | 100 \pm 8 | 116 \pm 9 | 135 \pm 6 |
| Stem diameter (cm) | 1.3 \pm 0.05 | 1.5 \pm 0.05 | 2.2 \pm 0.1 |
| Petiole length (cm)* | 8.7 \pm 0.8 | 14.5 \pm 0.8 | 14.7 \pm 0.6 |
| Dry weight (g) | 24 \pm 4 | 21 \pm 2 | 28 \pm 4 |

*Mean petiole length of the five largest rosette leaves per plant.

Table 3. Parameter estimates \pm 1SE for the equation $\log(\text{biomass}) = a + b\{\log(\text{L.L.})\} + c\{\log(\text{S.L.})\}$ * with all 30 harvested plants of *Chenopodium rubrum* and *Rumex maritimus*

| Parameter | <i>C. rubrum</i> | | | <i>R. maritimus</i> | | |
|-----------|-------------------|-------|-------|---------------------|-------|-------|
| | Estimate | F | P < | Estimate | F | P < |
| a | -7.7 \times 1.9 | | | -0.9 \pm 3.7 | | |
| b | 1.7 \pm 0.4 | 14.40 | 0.001 | 1.4 \pm 0.7 | 4.47 | 0.050 |
| c | 1.5 \pm 0.2 | 47.82 | 0.001 | 0.4 \pm 0.1 | 35.24 | 0.001 |

*Biomass in milligrams and leaf length (L.L.) and stem length (S.L.) in millimetres.

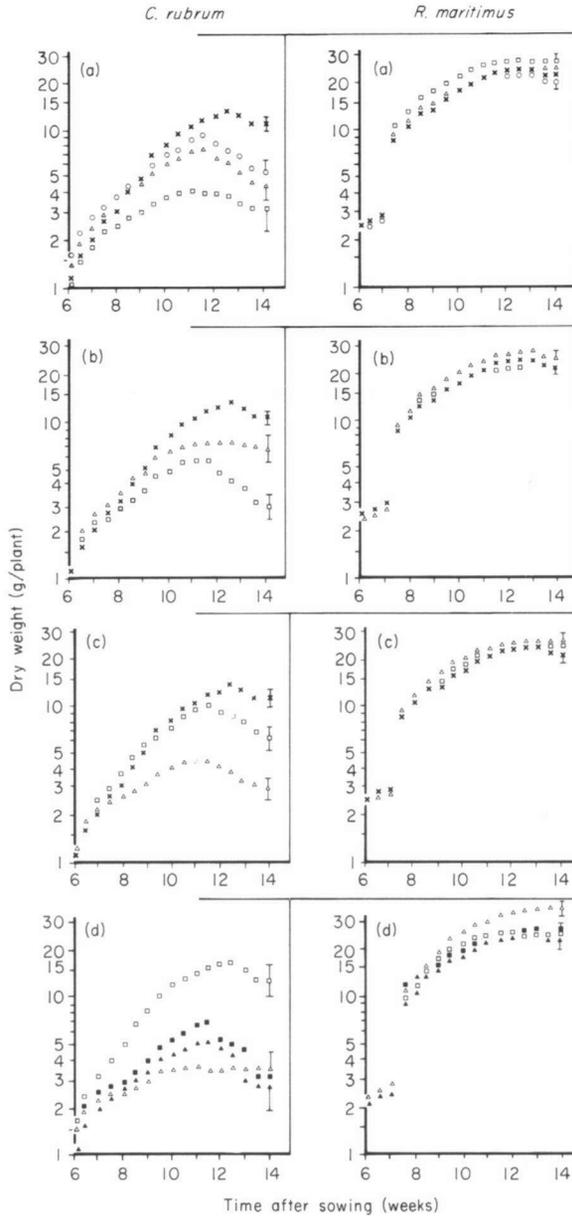


Fig. 2. Growth curves of *Chenopodium rubrum* and *Rumex maritimus*, representing the main effects of: duration (a), (×) non-waterlogging, (O) 2 weeks waterlogging, (Δ) 4 weeks waterlogging, (□) 6 weeks waterlogging; frequency (b), (×) non-waterlogging, (Δ) continuous waterlogging, (□) intermittent waterlogging; time (c), (×) non-waterlogging, (Δ) early waterlogging, (□) late waterlogging; and the interaction frequency × time (d), (Δ) early continuous waterlogging, (□) late continuous waterlogging, (▲) early intermittent waterlogging, (■) late intermittent waterlogging of waterlogging in the period between 6 and 14 weeks after sowing.

summarizes the statistical significance of these results. It is apparent that growth and seed production of both species are significantly influenced by the different treatment factors.

A more detailed examination of the growth curves and the results of the analysis of variance on biomass after 14 weeks indicates that *C. rubrum* suffers from waterlogging,

whereas the biomass of *R. maritimus* seems to be increased slightly by prolonged waterlogging (main effects of duration and frequency). Repeated waterlogging in short periods damages *C. rubrum* but not *R. maritimus*. This effect is found as an interaction effect, indicating that longer, repeated inundations can be more damaging than the same number of days inundation in one prolonged period. This is, however, dependent on the time of waterlogging. If *C. rubrum* is older at the time of the first inundation, this species is damaged less (main effect of time). This effect can also be seen for *R. maritimus* (Fig. 3) but it is not significant for biomass values (Table 4). The interaction term duration \times time course indicates that the effect of longer periods of waterlogging is larger for younger *C. rubrum* plants than for older ones. The frequency \times time course interaction for both species indicates that younger plants are less capable of coping with frequently changing conditions than older ones.

The effects of waterlogging on flowering and seed production are even more pronounced. All surviving *C. rubrum* plants flowered but the time of flowering was influenced by the treatments. Flowering was delayed in relation to the frequency and duration of waterlogging (Table 5). A delay of more than 2 months was caused by prolonged waterlogging throughout flowering and seed formation. All *R. maritimus* plants flowered between 13 and 15 weeks after sowing and differences in the time of flowering did not appear to be related to the waterlogging treatments.

The influence of the applied treatments on seed production of *R. maritimus* was significant (Table 4), including all twofold interactions. Seed production increased by continuous waterlogging but decreased due to intermittent waterlogging. The interaction terms in Table 4 are of special interest. The effect of duration and of frequency was much larger in the case of early waterlogging, as can be seen in Fig. 3.

Seed production of *C. rubrum* was severely reduced because of waterlogging (Fig. 3) but only the duration and time course (as distinguishable factors) showed significant effects (Table 4). The data on seed production of the ten additional plants per species that experienced prolonged periods of waterlogging, confirm the above results (Fig. 3). These data quite elegantly show the tendency of adaptation to prolonged waterlogging conditions. Possible mechanisms to avoid the less preferable conditions during waterlogging are found in the additional information on above-ground parameters and the root system; these were collected on the plants that were harvested for regression analysis. While growth of stems and leaves is inhibited in *C. rubrum* (Table 1), the stem and petiole lengths of *R. maritimus* plants increased during waterlogging (Table 2).

After a few weeks of waterlogging *R. maritimus* plants developed a secondary root system below the soil surface. This consisted of very white and thick roots. Within 5 days of waterlogging, adventitious roots were initiated above-ground. These roots possessed tiny laterals over the entire root length. A few weeks later a mat of roots was formed over the soil surface; these could attain a length of about 30 cm.

As soon as stem growth advanced (about 8 weeks after sowing), adventitious roots without secondary laterals started to grow from nodes just under the water level. Plants that were waterlogged after stems were initiated developed this latter root type only. When drained conditions were restored, most adventitious roots dried out; some of them survived by growing into the soil. Intermittently waterlogged plants, therefore, were unable to produce as many adventitious roots as continuously waterlogged ones.

The specific gravity of primary roots decreased from 1.00 (± 0.01) g cm⁻³, under non-waterlogged conditions, to 0.95 (± 0.01) g cm⁻³ under waterlogged conditions. The specific gravity of the adventitious roots of the rosette stage was 0.93 (± 0.01) g cm⁻³

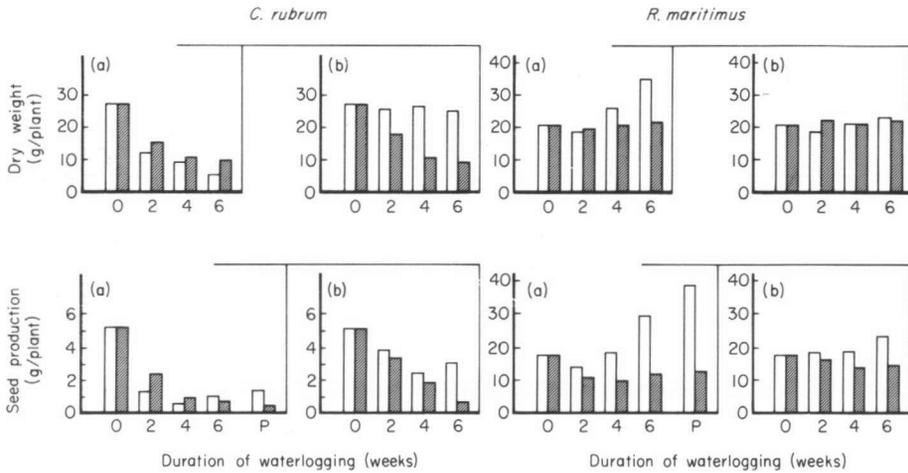


Fig. 3. Effect of waterlogging treatments on biomass and seed production of *Chenopodium rubrum* and *Rumex maritimus*. Horizontal axis: total duration of waterlogging (duration = p: prolonged waterlogging throughout flowering and seed formation); (a) early waterlogging; (b) late waterlogging; (□) continuous waterlogging; (▨) intermittent waterlogging. See Fig. 1 for the different applied treatments.

Table 4. Influence of different factors of waterlogging treatments in the full factorial experiment on dry weight and seed production per plant of *Chenopodium rubrum* and *Rumex maritimus*. Analysis of variance performed on log-transformed values

| | <i>C. rubrum</i> | | <i>R. maritimus</i> | |
|--------------------------------|------------------|------|---------------------|------|
| | Biomass | Seed | Biomass | Seed |
| Duration | *** | *** | *** | *** |
| Frequency | NS | NS | NS | *** |
| Duration × frequency | * | NS | NS | *** |
| Time course | *** | * | NS | ** |
| Duration × time c. | ** | NS | NS | ** |
| Frequency × time c. | *** | NS | * | * |
| Duration × frequency × time c. | ** | NS | NS | NS |

Significance levels: NS = not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

and of the adventitious roots on the stems, $0.85 (\pm 0.01) \text{ g cm}^{-3}$. Light microscope studies of sections showed that most aerenchymatic tissue was located in the latter root type. Aerenchyma developed in the shoots as well and was connected to an increase in stem diameter (Table 2).

The tap-root system, with delicate branching side roots of *C. rubrum*, disappeared during both intermittent and continuous waterlogging. Root degeneration, starting at the bottom of the containers, was complete after 4 weeks of waterlogging. Under intermittent waterlogging conditions a secondary root system, consisting of relatively thick and

Table 5. Flowering of *Chenopodium rubrum* in relation to waterlogging treatments. See Fig. 1 for the different applied treatments

| Duration of waterlogging in weeks | | | | Week number in which the first and last plant per treatment started to flower after sowing* |
|-----------------------------------|------|------------|------|---|
| Intermittent | | Continuous | | |
| Early | Late | Early | Late | |
| 2 | | | 2 | 13-16 |
| | | 2 | | 14-18 |
| 4 | | | 4 | 14-18 |
| | | | | 15-18 |
| 6 | | | | 15-18 |
| | 2 | | | 14-21 |
| | 4 | | | 15-21 |
| | | 4 | | 14-23 |
| | | | 6 | 15-23 |
| | 6 | | | 19-21 |
| | | | 6 | 23-25 |
| | | 6 | | 26-27 |

*Non-waterlogged plants started to flower 14-18 weeks after sowing.

unbranched roots, was initiated just below the soil surface. A comparable secondary root system was formed when drained conditions were restored after a long period of continuous waterlogging. After 2 weeks of waterlogging adventitious roots developed on the submerged 14 cm of the stem. On intermittently waterlogged plants adventitious roots remained small (mm); on continuously waterlogged plants they attained a length of 5-10 cm. Primordia of these roots were visible on some non-waterlogged plants as well, but in much smaller numbers.

The specific gravity of all different root types of *C. rubrum* was about 1.00 (± 0.01) g cm⁻³. Microscopic examination of cross-sections revealed some aerenchymatic tissue in the adventitious roots on the stems only. A few plants that did not grow above water level did not produce secondary roots at all. After some weeks these plants died. In both species a stimulation of stem growth was noticed shortly after initiation of adventitious roots.

DISCUSSION

Growth and reproduction of both *R. maritimus* and *C. rubrum* were strongly correlated with waterlogging treatments. The change in the growth pattern of *C. rubrum* was such that the previously developed method for estimating biomass was not suited for waterlogged and non-waterlogged plants together. Results were, however, little influenced by this bias (it resulted in biomasses estimated a little too large for continuously waterlogged plants compared with other treatments and, therefore, reduced effects rather than enhanced them) and thus growth curves remained quite reliable. The two species differed considerably in their responses to waterlogging. Both species showed the response of reverting to a more vertical stature but in *R. maritimus* this response was accompanied by an increase in petiole length (Table 4) until the leaf bases of most rosette leaves reached the water table. This phenomenon has been observed in the field and in our laboratory on other *Rumex* species as well (Voesenek *et al.* 1988).

The role of ethylene in this process as well as in stem elongation is studied at present (e.g. Osborne 1984; Ridge 1987). The effect of plant age will be taken into account in future studies, since young *R. maritimus* plants showed growth stimulation by waterlogging. In *R. maritimus* most rosette leaves were kept above the water table and only a few leaves developed chlorosis and died. In *C. rubrum* no such mechanism was noticed and chlorosis of leaves of waterlogged plants was severe at all times and, therefore, leaf senescence was high as well. The few plants that were waterlogged from 6 weeks onwards did not survive the longest duration of waterlogging. Both in this study and in other studies (Kramer, 1951; Jackson & Campbell 1975), chlorosis was correlated to growth reduction of the above-ground parts and root system. Biomass of above-ground parts of small *C. rubrum* plants was severely reduced in response to waterlogging, whereas biomass of *R. maritimus* plants remained approximately unchanged. Chlorosis of the *C. rubrum* plants that were waterlogged in a later stage was less severe and correspondingly the biomass did not differ significantly from the non-waterlogged plants.

According to Drew (1983), chlorosis and leaf senescence during waterlogging may be caused by: (1) the accumulation of toxins, originating in the soil or in anaerobic roots, (2) mineral nutrient deficiencies caused by a decrease in energy-dependent ion transport in the roots and (3) changes in phytohormone production by the roots. The second possibility is well studied in wheat (Drew & Sisworo 1977; Drew *et al.* 1979; Trought & Drew 1980a,b). These studies support the view that, especially in young plants with limited reserves, nitrogen deficiency is an early consequence of waterlogging and causes premature leaf senescence while mobile nutrients are reallocated from older leaves into younger ones. As a result of oxygen deprivation of the roots, nutrient uptake can only take place passively, by mass flow (Drew & Sisworo 1977; Trought & Drew 1980b). The primary root system of *C. rubrum* degenerated far more than that of *R. maritimus*. After 6 weeks of waterlogging, plants of the former species lost contact with the soil and started floating in the tanks. In *R. maritimus* the root system did not appear to change very much under conditions of intermittent waterlogging. Under conditions of continuous waterlogging new roots without secondary laterals were initiated. *C. rubrum* developed fewer of these new roots and under conditions of intermittent waterlogging only. *R. maritimus* also appeared to be capable of quick and abundant adventitious root formation. Tiny adventitious roots, containing less aerenchyma, were formed by larger *C. rubrum* plants only, and after a longer period of time, compared with *R. maritimus*. Adventitious rooting in *C. rubrum* plants resembles the adventitious rooting pattern of *Epilobium hirsutum* (Etherington 1984).

The more rapid decay of the primary roots of *C. rubrum* in comparison with *R. maritimus*, as well as the lack of aerenchyma in the less abundant adventitious roots, may thus be the cause of heavier chlorosis and faster leaf senescence in this species, acting by means of both toxicity and nutrient deficiency. The latter mechanism may also account for the heavier chlorosis of younger *C. rubrum* plants, which possess less nutrient reserves than older ones.

R. maritimus appears to be a species that is able to continue aerobic metabolism quite well under waterlogged conditions (P. Laan, personal communication), probably by means of oxygen diffusion from above-ground parts into the root-system (Armstrong 1978). Adventitious root formation, the development of aerenchyma in these roots, and related physiological processes are now under study in our laboratory.

In our experiment, as soon as adventitious roots became visible, an acceleration in stem growth was measured on plants from both species, which demonstrates the importance of

these roots (Kramer 1951; Etherington 1984). The importance of adventitious roots can also be inferred from the more damaging effects of intermittent waterlogging that prevented the survival of these roots in both the species, and also the death of *C. rubrum* plants that were unable to produce them at all.

Reproduction appeared to be even more distinctly influenced than biomass by waterlogging. Flowering of *C. rubrum* was delayed up to several months due to continuous waterlogging treatments. Seed production of this species was reduced because of waterlogging treatments, whereas seed production of *R. maritimus* was decreased as a result of early intermittent waterlogging treatments only. All differences in seed production could be ascribed to differences in seed numbers.

In conclusion, *R. maritimus* appeared to be well adapted to partial waterlogging which is in accordance with its occurrence on former river-bed soils with a low oxygen status. In contrast, *C. rubrum* seemed to be damaged easily by waterlogging, which may be one of the factors that determine the lack of abundant and tall specimens of this species in those sites.

However, the responses of both species were modified greatly by the applied treatments. Waterlogging in the early stages had the most remarkable stimulating effect on stem and leaf growth and resulted in the largest seed output in *R. maritimus*. On the other hand, early waterlogging appeared to be particularly harmful for *C. rubrum* plants. A large fluctuation in the water level appears to be relatively damaging for both species.

Therefore, the number of days of flooding per season is not the only factor that needs to be registered in the field. Equally important factors are time (with respect to the life-stages of plant species) and the frequency of flooding during the growing season. Another, and equally important factor, will be the occurrence of periods of complete plant submergence, including winter inundations.

Future investigations will include field studies as well as experiments on the physiological mechanisms that are involved in the adaptive processes in relation to waterlogging and submergence.

ACKNOWLEDGEMENTS

We would like to thank Dr R. Gulati for correcting an earlier version of the English text and T. van der Mast for her valuable help with the experiments. The investigations were supported by the Foundation for Fundamental Research (BION), which is subsidized by The Netherlands organization for scientific research (NWO).

REFERENCES

- Armstrong, W. (1975): Waterlogged soils. In: Etherington, J.R. (ed.): *Environment and Plant Ecology*. Wiley and Sons, London.
- (1978): Root aeration in the wetland condition. In: Hook, D.D. and Crawford, R.M.M. (eds): *Plant Life in Anaerobic Environments*. Ann Arbor, Michigan.
- Bernier, G., Kinet, J.M. & Sachs, R.M. (1981): *The Physiology of Flowering, 1. The Initiation of Flowers*. CRC Press Inc, Florida.
- Brock, Th.C.M., Van der Velde, G. & Van de Steeg, H.M. (1987): The effects of extreme water level fluctuations on the wetland vegetation of a nymphaeid-dominated oxbow lake in the Netherlands. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 27: 57–73.
- Cumming, B.G. (1969): *Chenopodium* L. and related species. In: Evans, L.T. (ed.): *The Induction of Flowering*. 156–186. Macmillan, Melbourne.
- Drew, M.C. (1983): Plant injury and adaptation to oxygen deficiency in the root environment: A review. *Plant Soil.* 75: 179–199.
- & Sisworo, E.J. (1977): Early effects of flooding on nitrogen deficiency and leaf chlorosis in barley. *New Phytol.* 79: 567–571.
- Sisworo, E.J. & Saker, S.R. (1979): Alleviation of waterlogging damage to young barley plants by application of nitrate and a synthetic cytokinin and

- comparison between the effects of waterlogging, nitrogen deficiency and root excision. *New Phytol.* **82**: 315–329.
- Etherington, J.R. (1984): Comparative studies of plant growth and distribution in relation to waterlogging X. Differential formation of adventitious roots and their experimental excision in *Epilobium hirsutum* and *Chamaenerion angustifolium*. *J. Ecol.* **72**: 389–404.
- Hejny, S. (1960): *Oekologische Charakteristik der Wasser- und Sumpfpflanzen in den Slowakischen Tiefebene (Donau- und Theissgebiet)*. Verlag Slowakische Akademie Wissenschaften, Bratislava.
- Iversen, Joh. S. (1949): Determination of the specific gravity of the roots of swamp, meadow and dry-soil plants. *Oikos* **1**: 1–5.
- Jackson, W.T. (1955): The role of adventitious roots in recovery of shoots following flooding of the original root system. *Am. J. Bot.* **42**: 816–819.
- Jackson, M.B. & Campbell, D.J. (1975): Movement of ethylene from roots to shoots, a factor in the responses of tomato plants to waterlogged soil conditions. *New Phytol.* **74**: 397–406.
- & Campbell, D.J. (1976): Waterlogging and petiole epinasty in tomato; the role of ethylene and low oxygen. *New Phytol.* **76**: 21–29.
- Jones, R. & Etherington, J.R. (1971): Comparative studies of plant growth and distribution in relation to waterlogging IV. The growth of dune and dune slack plants. *J. Ecol.* **59**: 793–801.
- Kramer, P.J. (1951): Causes of injury to plants resulting from flooding of the soil. *Plant Physiol.* **26**: 722–736.
- Osborne, D.J. (1984): Ethylene and plants of aquatic and semi-aquatic environments: A review. *Plant Growth Reg.* **2**: 167–185.
- Ridge, I. (1987): Ethylene and growth control in amphibious plants. In: Crawford, R.M.M. (ed.): *Plant Life in Aquatic and Amphibious Habitats*. 53–76. Blackwell Scientific Publications, Oxford.
- Salisbury, E.J. (1942): *The Reproductive Capacity of Plants, Studies in Quantitative Biology*. G. Bell and Sons Ltd, London.
- SAS Institute Inc. (1985): *SAS Users Guide: Statistics*, Version 5 edition. SAS Institute Inc., Cary, NC.
- Schat, H. (1984): A comparative ecophysiological study on the effects of waterlogging and submergence on dune slack plants: growth, survival and mineral nutrition in sand culture experiments. *Oecologia* **62**: 279–286.
- Trought, M.C.T. & Drew, M.C. (1980a): The development of waterlogging damage in wheat seedlings (*Triticum aestivum* L.) II. Accumulation and redistribution of nutrients by the shoot. *Plant Soil* **56**: 187–199.
- & Drew, M.C. (1980b): The development of waterlogging damage in young wheat plants in anaerobic solution cultures. *J. Exp. Bot.* **31**: 1573–1585.
- Tüxen, R. (1979): *Die Pflanzengesellschaften Nordwestdeutschlands*. AR Gartner Verlag KG, Vaduz.
- Van de Steeg, H.M. (1984): Effects of summer waterlogging on flora and vegetation of river foreland in the Rhine area. *Acta Bot. Neerl.* **33**: 365–366.
- Voesenek, L.A.C.J. & Blom, C.W.P.M. (1987): Rooting patterns of *Rumex* species under drained conditions. *Can. J. Bot.* **65**: 1638–1642.
- Voesenek, L.A.C.J., Blom, C.W.P.M. & Pouwels, R.H.W. (1988): Root and shoot development of *Rumex* species under waterlogged conditions. *Can. J. Bot.* (in press).