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# Flooding regimes and life-history characteristics of short-lived species in river forelands

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## Summary

1. A large-scale outdoor experiment was carried out to study the effect of flooding on growth, survival and reproduction in relation to developmental stage in three short-lived species. Several cohorts of *Chenopodium rubrum*, *Rumex maritimus* and *R. palustris* were raised in accordance with a flooding regime which was based on the average flooding conditions of their natural habitats in river forelands.
2. Survival of submergence in the pre-reproductive phase was high in both species of *Rumex*, but relatively low in *C. rubrum*. Biomass reduction following flooding depended on plant size before flooding and on the mean temperature of the flood-water.
3. Both *Rumex* spp. were less reduced in size during flooding, and better capable of regeneration afterwards, than *C. rubrum*.
4. Later-raised cohorts of the short-day species *C. rubrum* started to flower after a shorter time and at an earlier developmental stage than earlier cohorts. Flooding had little effect on probability of flowering and caused only a slight delay in flowering in this species. In both long-day species of *Rumex*, flowering stems were not initiated until a minimal leaf number was formed. As a result later cohorts remained vegetative, while flooding delayed flowering until later in the season or even until the following year.
5. All flooded plants of *C. rubrum* and most flooded plants in early cohorts of *R. maritimus* attempted to reproduce in the first growing season. Seed number was severely reduced in *C. rubrum* due to both reduction of plant biomass and destruction of flowers during flooding. In flooded plants of *R. maritimus*, seed output was correlated with plant size at the time of bolting. Seed number was maximized at the expense of seed size in *R. maritimus*.
6. These results suggest that there is a trade-off between survival of flooding and early reproduction in these species, and that there are complex interrelationships between highly variable environmental factors and developmental factors which determine the survival and reproductive success of short-lived species in river forelands.

*Key-words:* *Chenopodium rubrum*, flowering, growth, *Rumex maritimus*, *Rumex palustris*, seed production, survival

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## Introduction

Flooded zones along rivers in the Netherlands are bounded by the main dykes at either side of the river. These ribbon-like zones, which are up to several kilometres wide, are referred to as river forelands. Differences in elevation, both natural and man-made, combined with strongly fluctuating water levels resulting from unpredictable changes in river-water discharge, lead to highly dynamic

hydrological regimes in space and in time in these areas (Van de Steeg 1984; Brock, Van der Velde & Van de Steeg 1987; Blom 1990; Blom *et al.* 1990). The occurrence of several *Rumex* species within restricted zones along elevational gradients in these forelands suggests that these species differ in flooding tolerance.

Comparative studies concerning different aspects of flooding tolerance in *Rumex* have revealed a dichotomy between species from high elevations

on the one hand and species from low and intermediate elevations on the other (e.g. Laan *et al.* 1989; Voeselek & Blom 1989; Voeselek, Blom & Pouwels 1989; Laan & Blom 1990; Laan *et al.* 1990). These studies were mostly performed on young vegetative plants grown under controlled conditions where flooding was treated as a stress factor (*sensu* Grime 1979). In the lowest areas of river forelands, flooding will primarily be experienced as a disturbance by short-lived ruderal species (Menges & Waller 1983). Floods may occur at several stages of the life cycle and these stages should all be included in studies of flooding tolerance. For example, *Rumex* species from frequently flooded areas have persistent seed banks, whereas species from higher elevations have transient ones (Voeselek & Blom 1992). A distinction between avoidance strategies, such as survival through periods of adverse conditions by means of persistent seeds, and tolerance strategies, such as metabolic adaptations, is extremely useful in this respect (Crawley 1986).

In order to study the interaction between natural flooding regimes and reproductive behaviour of established plants, three co-occurring species from low, frequently flooded areas of the river forelands were selected. *Chenopodium rubrum* L., *Rumex maritimus* L. and *R. palustris* Sm. are short-lived species with different life histories. Both *Rumex* spp. are annual if they reach a mature vegetative size before a certain photoperiod has passed (Van der Sman, Blom & Van de Steeg 1992). This photoperiod is longer for *R. palustris*, which displays the biennial strategy more often in the river forelands than does *R. maritimus*. In contrast to both *Rumex* spp., the short days of late summer and autumn promote early flowering in the strictly annual *C. rubrum*. In a glasshouse experiment, *R. maritimus* appeared to be much more tolerant towards flooding than *C. rubrum* (Van der Sman, Van Tongeren & Blom 1988), but duration, time and frequency of flooding were all factors that considerably modified growth, the onset of flowering and seed production within one or both species. Plant developmental stage has been shown to play an important role in the rapid under-water elongation response of shoots in *R. maritimus* (Van der Sman *et al.* 1991).

A large-scale outdoor experiment was designed to enable the simultaneous comparison during one growing season of several realistic flooding conditions. Several cohorts of plants of *C. rubrum*, *R. maritimus* and *R. palustris* were raised in accordance with these flooding regimes to study the effect of flooding on growth, survival and reproduction in relation to plant developmental stage. Species differences in flooding tolerance are discussed in relation to differences in life-history characteristics.

## Materials and methods

### SPECIES HABITAT DESCRIPTION AND PLANT MATERIAL

*Chenopodium rubrum* is one of the character-species of the *Chenopodietum glauco-rubri* Lohm. and both *Rumex maritimus* and *R. palustris* are character-species of the *Ranunculo-Rumicetum maritimi* Siss. (Westhoff & Den Held 1975). *C. rubrum* occurs as companion species in the *Ranunculo-Rumicetum* association and, likewise, both *Rumex* spp. occur in the *Chenopodietum*. In the river forelands several plant communities exist which may be interpreted as incomplete stages of these associations or as transitional stages between them (H.M. van de Steeg, unpublished relevés). The *Chenopodietum* may occur on exposed clay soils as well as sandy soils, especially at flood-marks on sandy river beaches, while the *Rumicetum* is more characteristic of wet clay soils. Both *Rumex* spp. also occur in associations of marsh species (*Oenanthion*; Westhoff & Den Held 1975). Germination of plants of *C. rubrum* and both *Rumex* spp. occurs after the subsidence of floods from April onwards and multiple post-flooding cohorts are commonly observed as described for *R. palustris* and *R. crispus* in Voeselek & Blom (1992). Maximum germination in the laboratory is achieved under conditions of light and fluctuating temperatures in all three species. Such patterns appear to be common in wetland species (Thompson & Grime 1983).

The flooding regime used in the outdoor experiment was derived from water-level measurements which were made over the period 1970–87 and analysed in relation to the elevation of three study areas near Nijmegen, the Netherlands. These were a clay-pit, a sandy river beach and a former river bed. These sites provide examples of the habitats in which the above-described plant communities occur in river forelands. The clay-pit area was partly protected by a summer dyke, which contains a sluice that is closed after the subsidence of winter/spring floods to prevent further flooding during the growing season. In unprotected areas, flooding frequency was highly variable between years but in years and sites in which winter floods subsided early (April–May), the mean number of floods was 3–4 per growing season. Mean duration ranged from 10 days of flooding in the highest sites (clay-pit area) to 16 in the lowest (river-bed area). Water depth for the majority of floods was less than 1 m above the soil surface. In the river-bed area, extremely severe floods, i.e. those with a duration of more than 1 month and maximum water levels of several metres above the soil, occurred approximately once every 3 years. Such floods are lethal to established plants in the growing season (Voeselek 1990) and for this reason a moderate regime of four 10-day flooding

periods with a constant depth of 40 cm was chosen for the experiment.

Seeds of *C. rubrum*, *R. maritimus* and *R. palustris* were harvested in 1986 in the clay-pit area inside the summer dyke. The total seed output from five plants per species was mixed and dry-stored in the laboratory.

#### OUTDOOR FLOODING EXPERIMENT

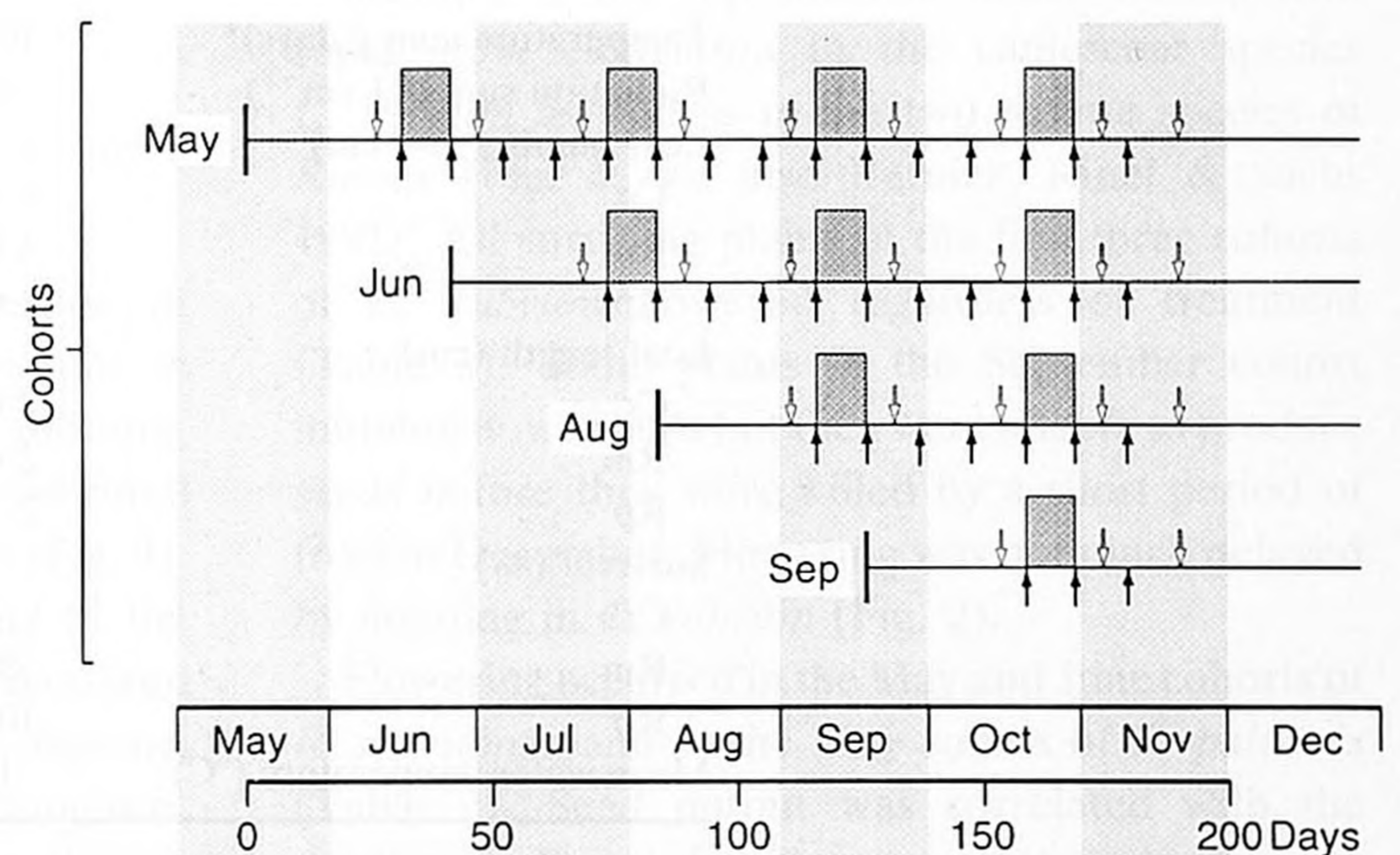
Uniform germination was achieved as described previously (e.g. Van der Sman *et al.* 1991). After 4 days, germinating seeds were transplanted into pots (16 cm in diameter  $\times$  50 cm high) filled with a 1:1 mixture (vol.) of river sand and peat. Seven seedlings were transplanted per pot and thinned to one seedling per pot after 2 weeks. Four cohorts, each of 50 pots species<sup>-1</sup>, were raised in large basins of water (length  $\times$  width  $\times$  depth: 8  $\times$  2  $\times$  1 m). Four basins, of which two were flooded, were divided lengthwise and each cohort was split between two basin-halves with parallel plant arrangements in the one to be drained and the one to be flooded. The first cohort was sown on 14 May 1987, 32 days before the start of the first 10-day flooding period (Fig. 1). The following cohorts were sown at 6-week intervals, immediately after subsequent flooding periods, on 25 June, 6 August and 17 September, respectively. Drained conditions were provided by a water level of 5–10 cm in the basins. To simulate flooding according to the regime shown in Fig. 1, basins were filled with tap-water until the water level reached an overflow approximately 40 cm above the soil level in the pots. At this point the water depth in the basins was 90 cm. After 10 days water was pumped out to restore the water level to that provided by the drained conditions. Filling and emptying the basins both took approximately 8 h.

#### Measurements

Irradiation and temperature were continuously

monitored during the study period. These parameters are presented for each cohort as radiation and temperature sums (with 10°C as base temperature; Van der Sman, Blom & Van de Steeg 1992) over the growth period up to first flooding. During flooding periods, water temperatures were measured twice daily, at approximately 08.00 and 17.00 hours. Before and after each flooding period (Fig. 1) the following parameters were measured for all plants: the cumulative number of leaves on the main shoot that were  $\geq 1$  cm in length (see Van der Sman, Blom & Van de Steeg 1992), the number of dead leaves on the main shoot, the number of axillary shoots, the length, width and petiole length of the largest leaf, and the length of the main stem. Before and after the first flooding period of each cohort, three plants per species and treatment were harvested to determine the dry weight of shoots, the maximum diameter ( $r$ ) of tap roots, and the length ( $h$ ) of this root if it was  $\geq 1$  mm in diameter. The volumes of tap roots were estimated from these parameters as  $0.5\pi r^2 h$ . Of the remaining 20 plants per species, cohort and treatment, five randomly selected plants were measured every 10 or 11 days (Fig. 1) with respect to the above-mentioned non-destructive parameters, as well as the number of living leaves on axillary shoots ( $\geq 1$  cm) and the lengths of axillary stems. Twice a week, the developmental stage of all plants was recorded, distinguishing the following stages: vegetative, bolting (*Rumex* spp.), flower buds visible, flowering, ripe fruits (*R. maritimus*, golden brown; *R. palustris*, dark red brown; *C. rubrum*, black). Ripe seeds (including perianths) were collected in November and weighed after sieving and cleaning several times. This was done for all reproductive plants of both *Rumex* spp. and for a maximum of 10 plants per cohort and treatment of *C. rubrum*. For each species, cohort and treatment, five samples of 100 seeds were taken from each of three plants. After removal of perianths, seeds were counted and weighed to determine mean seed weights. The empty perianths were also weighed

Fig. 1. Experimental design of the outdoor flooding experiment. Growth periods of four cohorts of *Chenopodium rubrum*, *Rumex maritimus* and *R. palustris* in relation to four 10-day flooding periods (small shaded blocks). Per cohort and species, 20 plants were kept drained and 20 were flooded. Alternate months are indicated by a light tone. Measurement times:  $\downarrow$  all plants;  $\uparrow$  five plants per species and treatment.



and from the mean values of these 15 samples per species, cohort and treatment, the total number of seeds produced was estimated for all plants.

#### Germination characteristics

Seeds were incubated under the following conditions: constant temperatures of 10°C and 20°C, and fluctuating temperatures of 12 h at 20°C and 12 h at 10°C, both in the light ( $15 \mu\text{mol m}^{-2} \text{s}^{-1}$  PAR during the 12-h day) and in the dark. Three samples of 50 seeds each from a mixture of five plants per species, cohort and treatment were incubated in each of the above regimes in Petri dishes on filter paper (Schleicher & Schüll 595) watered with demineralized water. As soon as radicles appeared, germinated seeds were removed. After 3 weeks, ungerminated seeds were placed into the regime with fluctuating temperatures and light, which normally induced near 100% germination (Van der Sman, Blom & Van de Steeg 1992). Ungerminated seeds were stained with tetrazolium chloride (1% weight/vol., Sigma Chemical Co., St Louis, Miss., USA) which colours live tissue red (Moore 1972).

#### Data analysis

All tests were carried out with the SAS statistical package (SAS Institute Inc. 1985). Correlation analysis was performed using the Pearson rank correlation test. The General Linear Models procedure was used for all unbalanced analyses of variance. Significance of differences between means were tested using Student's *t*-test. In *C. rubrum* and *R. maritimus*, between-plant differences in mean

seed size were tested as a nested effect within the effects of cohort and flooding treatment. In *C. rubrum*, the effects of cohort and flooding treatment were not tested separately but as one main treatment effect because too many cells were empty in the case of flooded plants, due to plant death.

## Results

### FLOODING TOLERANCE IN THE PRE-REPRODUCTIVE PHASE

Plant biomass is correlated with the product of the number of living leaves and maximum leaf length in these species (Van der Sman, Van Tongeren & Blom 1988; Voeselek 1990). These parameters were therefore chosen to represent plant growth in relation to radiation and temperature sums up to the first flooding period per cohort (Table 1). Growth rates appeared to depend on temperature during the larger part of the growing season (see also Van der Sman, Blom & Van de Steeg 1992). Radiation was probably only limiting in the last, September cohort (Table 1).

The initiation of leaves stopped during the period of first flooding for all cohorts, whereas leaf senescence on the main shoot was high only in the first three cohorts (Fig. 2). In addition, most axillary shoots died. In both *Rumex* species, the oldest leaves of the main shoot died first. In *C. rubrum*, old as well as young leaves died. In the June and August cohorts, mean above-ground dry weight was reduced immediately after the first flooding period by 90% in *R. palustris*, 95% in *R. maritimus* and 98% in *C. rubrum*, compared to drained plants of the same

**Table 1.** Total number of living leaves and maximum leaf length (mean  $\pm$  SE,  $n = 5$ ) immediately before first submergence in relation to temperature and radiation sums over the first 32 days of growth in *Chenopodium rubrum* (Cr), *Rumex maritimus* (Rm) and *R. palustris* (Rp). Percentage survival ( $n = 20$ ) after the first flooding period is presented in relation to the mean temperature of the flood-water

|   | Cohort        |                |                |               |
|---|---------------|----------------|----------------|---------------|
|   | May           | June           | August         | September     |
| Temperature sum ( $^{\circ}\text{days}$ )*    | 103           | 254            | 238            | 92            |
| Radiation sum ( $\text{kJ cm}^{-2}$ )         | 40            | 52             | 35             | 22            |
| Leaf number ( $\geq 1$ cm)                    |               |                |                |               |
| Cr  | $6.0 \pm 0.0$ | $32.8 \pm 2.5$ | $23.0 \pm 2.4$ | $0.0 \pm 0.0$ |
| Rm  | $4.0 \pm 0.0$ | $21.2 \pm 1.3$ | $21.6 \pm 0.8$ | $2.0 \pm 0.0$ |
| Rp  | $3.8 \pm 0.2$ | $23.6 \pm 1.2$ | $18.4 \pm 0.4$ | $2.0 \pm 0.0$ |
| Leaf length (cm)                              |               |                |                |               |
| Cr  | $2.0 \pm 0.2$ | $9.3 \pm 0.6$  | $5.2 \pm 0.3$  | $0.2 \pm 0.1$ |
| Rm  | $2.4 \pm 0.1$ | $11.6 \pm 0.5$ | $9.8 \pm 0.4$  | $1.1 \pm 0.1$ |
| Rp  | $2.1 \pm 0.2$ | $11.6 \pm 0.4$ | $9.0 \pm 0.2$  | $1.4 \pm 0.2$ |
| Survival (%)                                  |               |                |                |               |
| Cr  | 0             | 65             | 50             | 95            |
| Rm  | 85            | 100            | 100            | 100           |
| Rp  | 100           | 100            | 100            | 100           |
| Mean water temperature ( $^{\circ}\text{C}$ ) | 14.2          | 17.1           | 17.8           | 10.3          |

\* Base temperature 10°C.

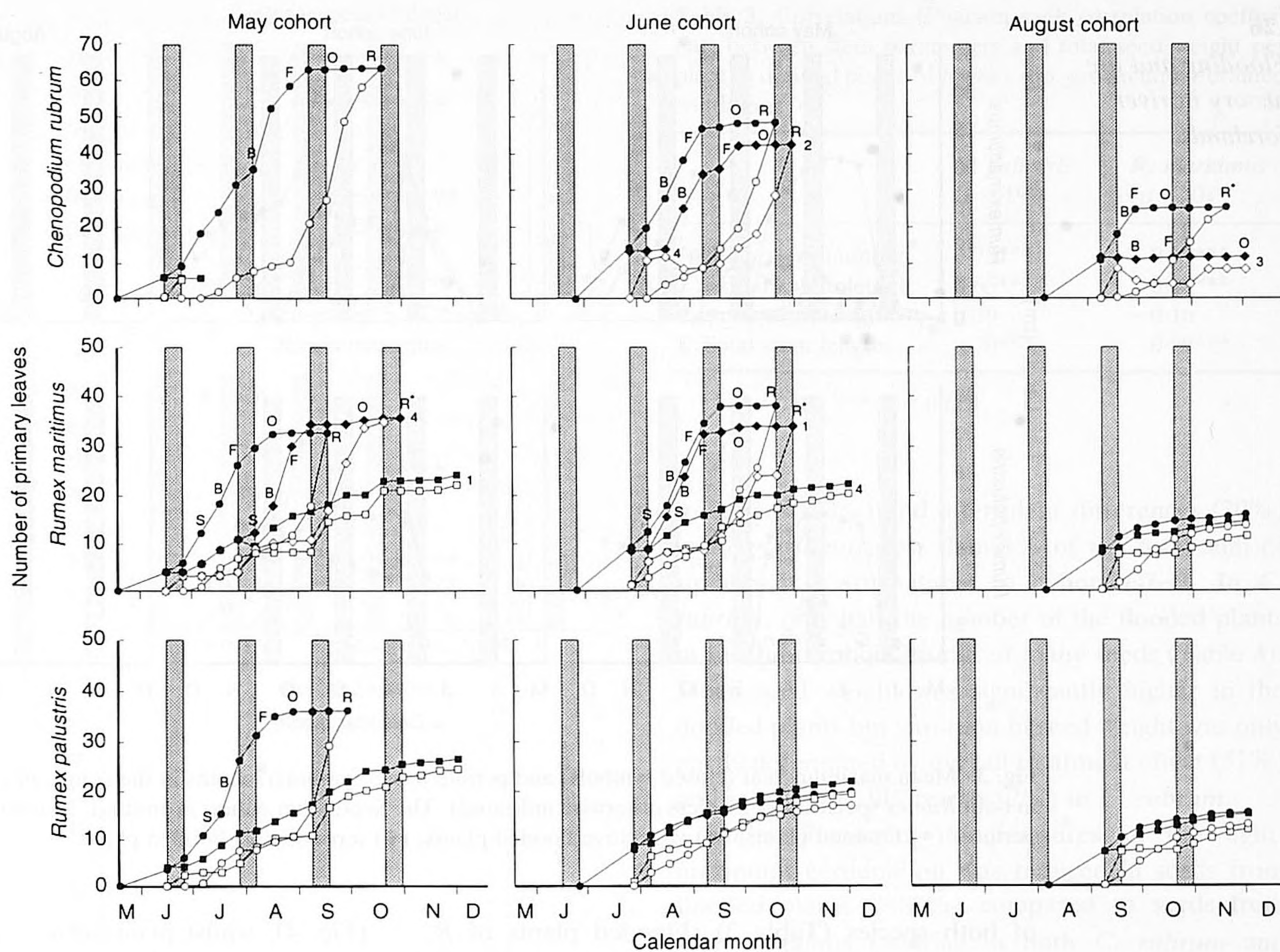


Fig. 2. Mean cumulative initiation (closed symbols) and loss (open symbols) of primary leaves during the course of the outdoor experiment ( $n = 5$  unless otherwise indicated). The September cohort is omitted. Shaded areas indicate flooding periods. (●) Drained plants; (■) vegetative flooded plants; (◆) reproductive flooded plants. Reproductive development of the main shoot is indicated with letters: S = stem elongation (*Rumex* spp.), B = appearance of buds, F = in full flower, O = out of flower, R = ripe fruits (R\* = incompletely ripened).

age. In the May cohort, above-ground biomass of both *Rumex* species was reduced by as much as 99% and *C. rubrum* was killed by flooding. In the September cohort, plants were much less affected in size by flooding and survival was high in all three species (Table 1). Tap roots were only large enough to be measured after flooding in the second and third cohorts; mean estimated volumes were reduced by 86% in *R. palustris*, 91% in *R. maritimus*, and 93% in *C. rubrum* in these cohorts. In accordance with these results, *C. rubrum* showed the highest mortality in all cohorts (Table 1).

#### VEGETATIVE GROWTH IN RELATION TO THE FLOODING REGIME

During submergence periods, the orientation of leaves and branches changed from horizontal to vertical within a day in all three species. In addition, all vegetative plants of both *Rumex* species exhibited fast extension of the petioles of young leaves (Fig. 3). The water surface was not reached by any of the plants. The extended leaves were easily damaged and did not survive for more than a few days or, exceptionally, a few weeks after submergence. After submergence, plants of both *Rumex* spp.

resumed normal growth patterns. Plants of *C. rubrum* recovered from submergence by developing new leaves from the apex and/or a few scattered leaf axils but they exhibited a stunted growth habit, quite different from that of drained plants. Plants of all three species which survived the first flooding period also survived subsequent flooding periods.

#### REPRODUCTIVE DEVELOPMENT IN RELATION TO THE FLOODING REGIME

Transition to the reproductive phase started with rapid stem elongation in the caulescent species *C. rubrum* as well as in the two rosette species of *Rumex* (Fig. 4; see also Bernier, Kinet & Sachs 1981). All surviving plants in the first three cohorts of *C. rubrum* flowered regardless of treatment (Table 2). Some plants in the September cohort initiated flower buds but they were unable to produce seeds before they were killed by a short period of frost in December. Flowering was not much delayed by flooding in *C. rubrum* (Fig. 2).

Flowering occurred in the May and June cohorts of *R. maritimus* and in the May cohort of *R. palustris* (Table 2). Seed output was correlated with the number and size of axillary stems in drained plants

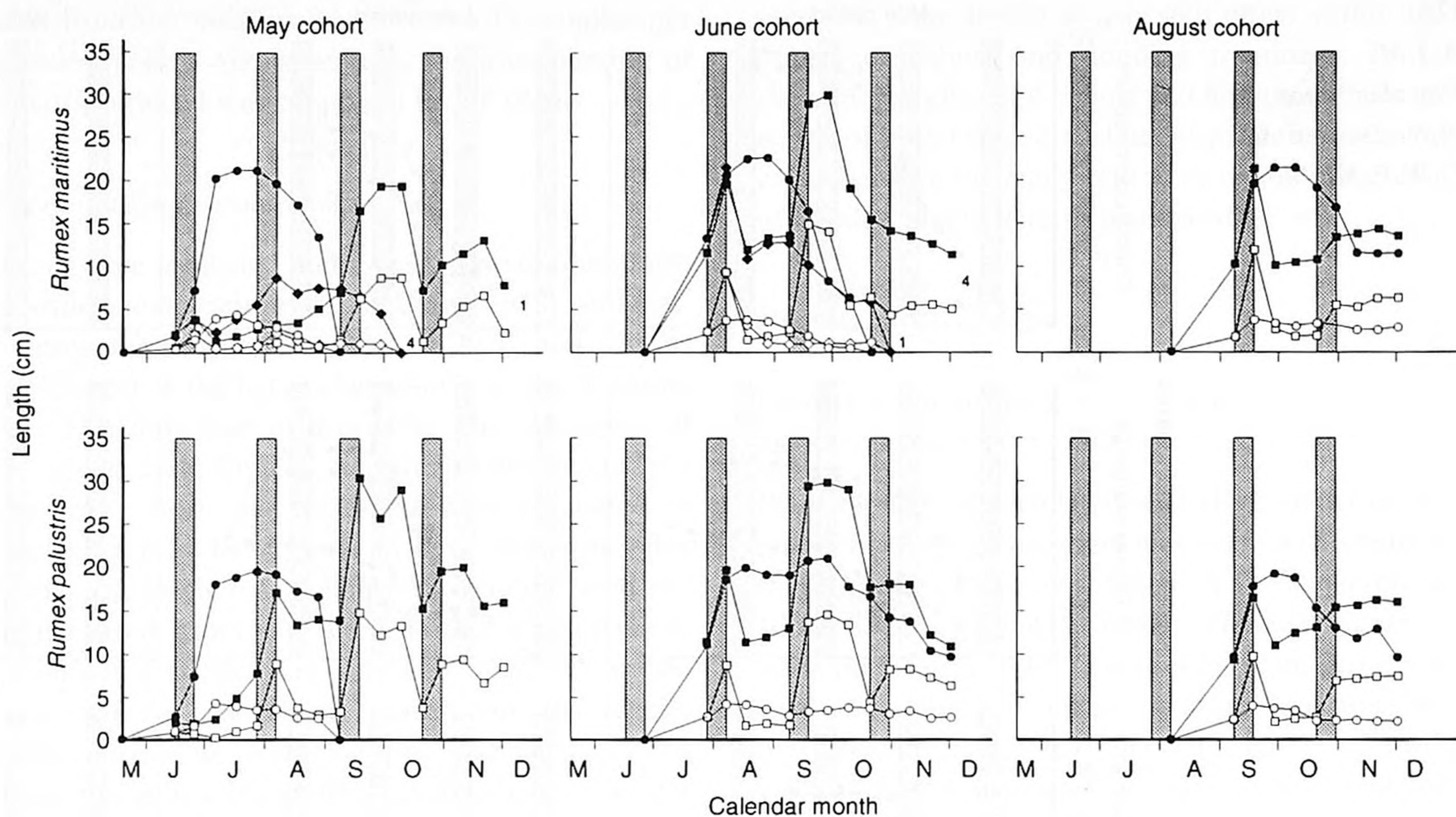


Fig. 3. Mean maximum leaf (closed symbols) and petiole (open symbols) lengths in the course of the outdoor experiment in both *Rumex* species ( $n = 5$  unless otherwise indicated). The September cohort is omitted. Shaded areas indicate flooding periods. (●) Drained plants; (■) vegetative flooded plants; (◆) reproductive flooded plants.

of both species (Table 3). Flooded plants of *R. palustris* all remained vegetative, while percentage of plants flowering was reduced in flooded plants of *R. maritimus* (Table 2). Flowering occurred after approximately 12 primary leaves were initiated in drained as well as flooded plants of *R. maritimus* (see also Van der Sman, Blom & Van de Steeg 1992). At this stage, flooded plants possessed fewer ( $\leq 4$ ) axillary leaves than drained plants ( $c. 45$ ), and they did not produce axillary stems. Plants of both *Rumex* spp. which remained vegetative either reached the 12-leaf stage, at which flowering could commence, too late in the season, or did not reach this stage at all before the onset of the winter (September cohort).

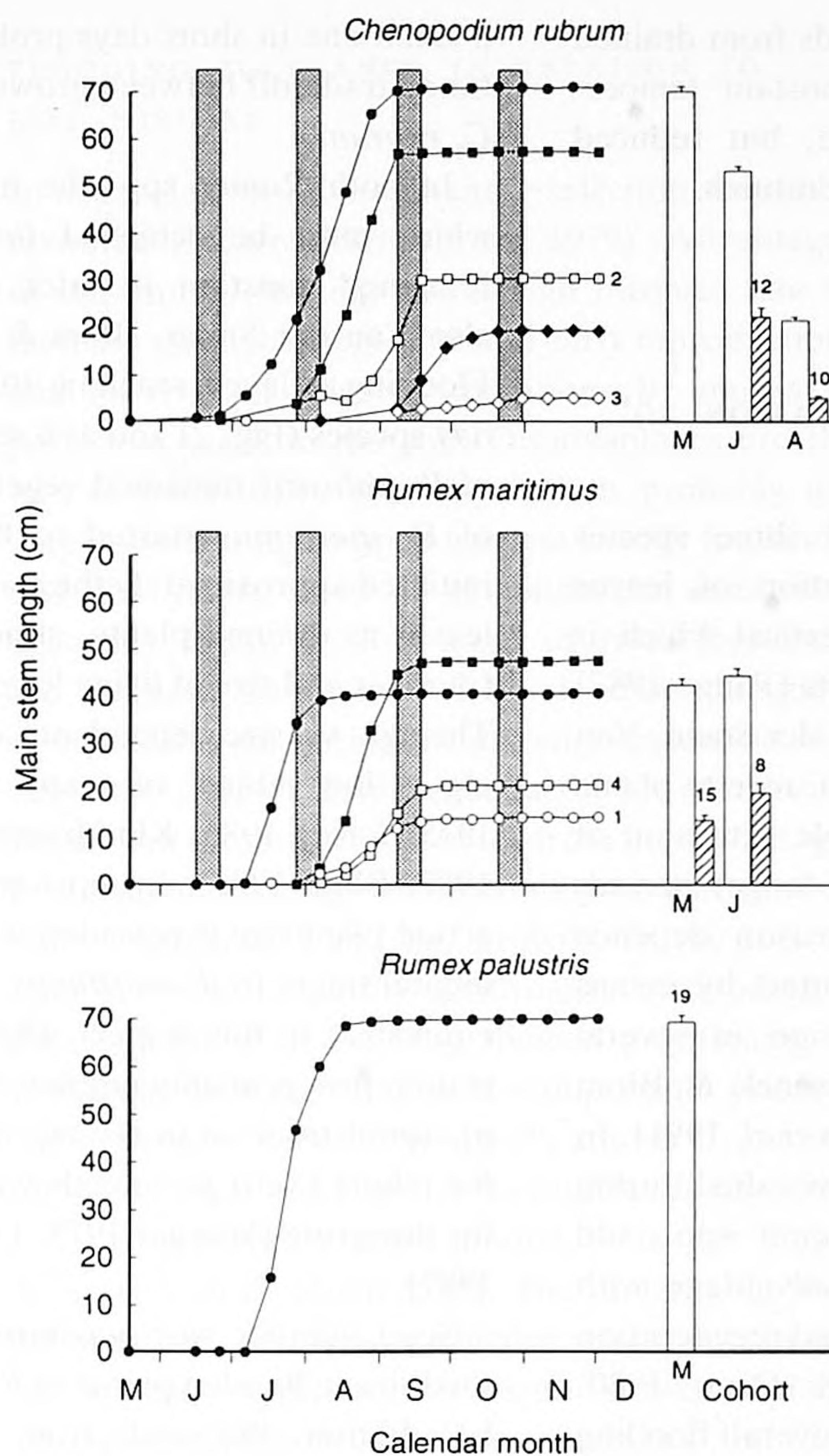
Submergence reduced the final size of reproductive plants compared to drained conditions. Flowering plants of *R. maritimus* produced approximately the same total number of primary leaves under flooded as under drained conditions (Fig. 2), but stems of flooded plants remained significantly smaller

(Fig. 4), whilst plants of *C. rubrum* were reduced in both respects after flooding. In addition, submergence of flowering plants resulted in severe loss of flowers and only a small number of seeds was produced by flooded plants (Table 4). Only two plants of *C. rubrum* in the August cohort, which was in full flower just before the start of the last flooding period, produced a few large seeds. In *R. maritimus*, however, new flowering shoots developed from axillary nodes of stem leaves after flooding. This resulted in a relatively constant seed output which was correlated with plant size (biomass estimated from the product of the number of living leaves and maximum leaf length) at the time of bolting (Pearson rank correlation coefficient 0.78,  $n = 22$ ,  $P < 0.001$ ).

In *R. maritimus*, mean seed weight was significantly lower in flooded plants than in drained plants (Table 4). Fruits of flooded plants appeared to be incompletely ripened (Fig. 2) and possessed seeds of a lighter colour than drained plants. Variation in seed weight was largely determined by flooding

Table 2. Percentage flowering per cohort and treatment in *Chenopodium rubrum*, *Rumex maritimus* and *R. palustris* ( $n =$  number of plants which survived up to the flowering stage)

| Cohort    | <i>C. rubrum</i> |     |         |     | <i>R. maritimus</i> |     |         |     | <i>R. palustris</i> |     |         |     |
|-----------|------------------|-----|---------|-----|---------------------|-----|---------|-----|---------------------|-----|---------|-----|
|           | drained          |     | flooded |     | drained             |     | flooded |     | drained             |     | flooded |     |
|           | %                | $n$ | %       | $n$ | %                   | $n$ | %       | $n$ | %                   | $n$ | %       | $n$ |
| May       | 100              | 20  | —       | 0   | 100                 | 20  | 88      | 17  | 95                  | 20  | 0       | 20  |
| June      | 100              | 20  | 100     | 13  | 100                 | 20  | 35      | 20  | 0                   | 20  | 0       | 20  |
| August    | 100              | 20  | 100     | 10  | 0                   | 20  | 0       | 20  | 0                   | 20  | 0       | 20  |
| September | 45               | 20  | 21      | 19  | 0                   | 20  | 0       | 20  | 0                   | 20  | 0       | 20  |



**Fig. 4.** Mean length of the main stem ( $n = 5$  unless otherwise indicated) per species, cohort ( $\bullet$  May,  $\blacksquare$  June;  $\blacklozenge$  August) and treatment (closed symbols: drained; open symbols: flooded). Mean ( $\pm$ SE,  $n = 20$  or indicated if less) final heights of all flowering plants are presented as bars (open: drained; shaded: flooded; cohorts: M = May; J = June; A = August).

**Table 4.** Mean ( $\pm$ SE) estimated seed number per plant and individual seed weight per cohort and treatment of *Chenopodium rubrum*, *Rumex maritimus* and *R. palustris*. The nested model explained 54% of the variation in seed weight in *C. rubrum* and 93% in *R. maritimus* (see text). Values followed by the same superscript letter are not significantly different

| Cohort              | Treatment | $n$ | Estimated seed number | Individual seed weight ( $\mu\text{g}$ ) |
|---------------------|-----------|-----|-----------------------|--|
| <i>C. rubrum</i>    |           |     |                       |  |
| May                 | drained   | 10  | $53\,000 \pm 2000^a$  | $61 \pm 3^b$                             |
|                     | flooded   | 0   | —                     | —  |
| June                | drained   | 10  | $44\,000 \pm 1000^b$  | $65 \pm 2^b$                             |
|                     | flooded   | 6*  | $990 \pm 200^d$       | $85 \pm 4^a$                             |
| August              | drained   | 10  | $27\,000 \pm 3000^c$  | $92 \pm 4^a$                             |
|                     | flooded   | 2†  | $\leq 10$             | —  |
| <i>R. maritimus</i> |           |     |                       |  |
| May                 | drained   | 20  | $23\,000 \pm 2000^a$  | $217 \pm 7^a$                            |
|                     | flooded   | 15  | $850 \pm 160^c$       | $120 \pm 5^b$                            |
| June                | drained   | 20  | $13\,000 \pm 2000^b$  | $211 \pm 7^a$                            |
|                     | flooded   | 7   | $950 \pm 240^c$       | $108 \pm 10^c$                           |
| <i>R. palustris</i> |           |     |                       |  |
| May                 | drained   | 19  | $8\,200 \pm 400$      | $593 \pm 5$                              |

\* The remaining seven flowering plants produced  $\leq 10$  seeds.

† The remaining eight flowering plants did not produce seeds.

**Table 3.** Correlations (Pearson rank correlation coefficient) between stem parameters and total seed weight per plant in drained plants of *Rumex* spp. grown under drained conditions

|                               | <i>R. palustris</i><br>( $n = 19$ ) | <i>R. maritimus</i><br>( $n = 40$ ) |
|-------------------------------|-------------------------------------|-------------------------------------|
| Axillary stem number          | 0.73***                             | 0.81***                             |
| $\Sigma$ Axillary stem length | 0.65**                              | 0.88***                             |
| Primary stem length           | 0.39                                | -0.16                               |
| $\Sigma$ Total stem length    | 0.70***                             | 0.89***                             |

\*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

treatment (73%) and inter-plant differences (20%) in *R. maritimus*; less than 1% of the total sum of squares was attributable to cohort effect. In *C. rubrum*, only half the number of the flooded plants in the June cohort produced many seeds (Table 4). Mean seed weight was significantly higher in the flooded plants but variation in seed weight was only partly determined by overall treatment effect (51%) and inter-plant differences (2%) in *C. rubrum*.

Under fluctuating temperatures in the light, maximum germination was reduced in seeds from flooded plants ( $\geq 80\%$ ) compared to seeds from drained plants ( $\geq 98\%$ ) in both *C. rubrum* and *R. maritimus*. Ungerminated seeds appeared to be dead. Under all other conditions, seeds from flooded plants showed higher germination percentages than those of drained plants. At constant temperatures in the light, seeds from flooded plants showed 10–30% germination and from drained plants 0–10%. In the dark, seeds from flooded plants showed approximately the same germination percentages as in the light under all temperature



conditions, whereas in darkness seeds from drained plants hardly germinated under constant temperatures and showed highly variable, but reduced germination under fluctuating temperatures.

## Discussion

### GROWTH AND SURVIVAL IN RELATION TO FLOODING

Upon submergence, plants of all three species showed the response of reorientation of leaves and branches from prostrate to vertical which is commonly observed in aquatic plants (Ridge 1987) and important in shallow water (Van der Sman, Van Tongeren & Blom 1988). In addition, rosette plants of both *Rumex* spp. exhibited petiole extension of younger leaves (Fig. 3). Survival of longer periods of submergence in the growing season depends on the restoration of shoot-air contact by means of rapid under-water shoot extension in several flooding-tolerant *Rumex* spp. (Voeselek & Blom 1989; Laan *et al.* 1990; Van der Sman *et al.* 1991). In *C. rubrum*, young as well as old leaves died during submergence, whereas in both *Rumex* spp., old leaves died first. The latter is of advantage with respect to growth of younger leaves and regeneration of shoots afterwards (Throught & Drew 1980; Jackson & Drew 1984). The higher overall flooding tolerance in *R. palustris* may result from a more efficient use of stored assimilates and/or a relatively high rate of alcoholic fermentation compared to *R. maritimus* (Laan & Blom 1990; Voeselek 1990). The flooding tolerance of plants of both *Rumex* spp. and *C. rubrum* was highest in the September cohort (Table 1). The mean temperature of the flood-water was near the base temperature for growth of these species during the last flooding period (Van der Sman, Blom & Van de Steeg 1992) and this illustrates the important role of metabolic rates in the survival of submergence.

### REPRODUCTION IN RELATION TO FLOODING

Plants of *C. rubrum* started to flower at an earlier stage and completed their life cycle in a shorter time in later cohorts (Fig. 2; see also Van der Sman, Blom & Van de Steeg 1992). The inability of plants of *C. rubrum* in the September cohort to produce seeds was probably due to low irradiance and/or insufficient photosynthesis (Kinet, Sachs & Bernier 1985). Flooding hardly reduced the probability of flowering in *C. rubrum* (Table 2). The onset of flowering, however, was not completely independent of size because large plants of *C. rubrum* flowered earlier than small ones (Fig. 2; see also Cumming 1969; Cumming & Seabrook 1985). A large size-requirement in long days, gradually changing to

a small one in short days probably results in a fine-tuned trade-off between growth and reproduction in *C. rubrum*.

In both *Rumex* spp. the minimum leaf number which must be achieved for flowering to occur remained constant in later cohorts (Fig. 2, see also Van der Sman, Blom & Van de Steeg 1992). Flooding delayed reaching this stage in both long-day species (Fig. 2) and as a result all flooded plants of *R. palustris* remained vegetative. Flooded plants of *R. maritimus* started to flower after they had initiated approximately the same number of primary leaves as drained plants, although their actual size (number and size of living leaves) was much smaller. The age- vs. size-dependency of the onset of flowering is the subject of many studies (e.g. Werner 1975; Lacey 1986; Klinkhamer, De Jong & Meelis 1987; Blom 1988). In most cases some measure of actual plant size is considered to represent developmental stage. In *R. maritimus*, stage and size are not equivalent in this respect. Flowering in this species is therefore probably not determined by the amount of stored reserves in the tap root, as was suggested for (short-lived) perennials with a size requirement for flowering (Werner 1975; Lacey 1986; Silvertown 1987).

Seed number was maximized at the expense of seed size in flooded plants of *R. maritimus* (Table 4). In addition, the seeds from flooded plants of *R. maritimus* had a lighter colour and were less dormant than seeds from drained plants. This suggests that they lack a hard seed coat, which may be the result of both immaturity and development under wet conditions (Silvertown 1984). This appears to be disadvantageous as it may result in the generation of small seedlings under adverse conditions for germination and establishment. Flooded plants of *C. rubrum* hardly managed to produce seeds, but in contrast to *R. maritimus*, those which did possess relatively large seeds compared to drained plants (Table 4). Potential seed number is determined early in *C. rubrum* (Cook 1976) and depends, together with seed size, on photoperiod during flower induction (Cook 1975). If the number of flowers is reduced afterwards, overfilling of the seeds is likely to occur (Harper, Lovell & Moore 1970). In *C. rubrum*, the larger seeds from flooded plants as well as from later cohorts of drained plants were less dormant than small seeds (see also Van der Sman, Blom & Van de Steeg 1992; Cumming 1969). Decreased dormancy of the larger seeds which are produced on plants grown in short days is also found in *C. album* and in this species is caused by thinner seed coats (Karssen 1970). A large part of the seed-size variation in *C. rubrum* was not explained by treatment effects (Table 4) and must be ascribed to within-plant seed size variation or seed polymorphism (Harper, Lovell & Moore 1970).

In unpredictable environments *r*-selection should be favoured (Stearns 1976; Grime 1979). Advantages of the annual strategy are a high intrinsic rate of increase through fast growth and early reproduction, and survival of adverse conditions by means of persistent seeds in the soil. Disadvantages are the loss of competitive ability, which is probably not very important in the open habitats in river forelands, and the yearly need of establishment microsites (Crawley 1986). In low areas of river forelands, the frequent occurrence of floods allows frequent re-establishment during the growing season but also acts as a stress or disturbance factor for established plants. All three species profited from the advantages of the annual strategy under conditions that allowed early germination and fast growth. In the case of later germination and/or disturbance by flooding in the established phase they showed partitioning of resources to different fitness components (Harper 1977; Venable 1984). The strictly annual *C. rubrum* allocated even more resources into seeds than into other structures in later cohorts (Van der Sman, Blom & Van de Steeg 1992). The remarkable plasticity with respect to reproductive parameters in this species was typically expressed between plants (Bradshaw 1965). Seed polymorphism in *C. rubrum*, however, was only partly regulated by environmental control (Table 4). Within-plant seed size variation may act as a kind of bet-hedging against unpredictable conditions in the habitat (Harper, Lovell & Moore 1970). For example, in *Atriplex triangularis*, small seeds are incorporated into a persistent seed bank and thus ensure long-term population survival, whereas large seeds germinate early and have a better chance of surviving until the reproductive stage (Khan & Ungar 1986). Both *Rumex* spp. allocated more resources into vegetative growth in later cohorts and instead of plasticity in reproductive parameters they showed within-plant plasticity with respect to traits promoting survival, such as the ability to produce different leaf types under flooded and drained conditions. *R. maritimus* flowered more rapidly and was more susceptible to flooding than *R. palustris*. The three species appear to have features corresponding to the opposing strategies of stress tolerators and ruderals which may be found in the most frequently flooded parts of river floodplains (Menges & Waller 1983). *R. palustris* is best capable of maintaining occupation of sites which probably explains its occurrence in associations of marsh species. This species may be described as a stress-tolerant ruderal (*sensu* Grime 1979), while *R. maritimus* and *C. rubrum* possess increasingly ruderal characteristics.

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## References

- Bernier, G., Kinet, J.-M. & Sachs, R.M. (1981) *The Physiology of Flowering. II. Transition to Reproductive Growth*. CRC Press, Orlando, Fla.
- Blom, C.W.P.M. (1988) The realism of models in plant demography. *Acta Botanica Neerlandica*, **37**, 421–438.
- Blom, C.W.P.M. (1990) Responses to flooding in weeds from river areas. *Biological Approaches and Evolutionary Trends in Plants* (ed. S. Kawano), pp. 81–94. Academic Press, London.
- Blom, C.W.P.M., Bögemann, G.M., Laan, P., Van der Sman, A.J.M., Van de Steeg, H.M. & Voeselek, L.A.C.J. (1990) Adaptations to flooding in plants from river areas. *Aquatic Botany*, **38**, 29–47.
- Bradshaw, A.D. (1965) Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics*, **13**, 115–155.
- 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 nymphacid-dominated oxbow lake in The Netherlands. *Archiv für Hydrobiologie. Beiheft Ergebnisse der Limnologie*, **27**, 57–73.
- Cook, R.E. (1975) The photoinductive control of seed weight in *Chenopodium rubrum* L. *American Journal of Botany*, **62**, 427–431.
- Cook, R.E. (1976) Photoperiod and the determination of potential seed number in *Chenopodium rubrum* L. *Annals of Botany*, **40**, 1085–1099.
- Crawley, M.J. (1986) *Plant Ecology*. Blackwell Scientific Publications, Oxford.
- Cumming, B.G. (1969) *Chenopodium* L. and related species. *The Induction of Flowering* (ed. L.T. Evans), pp. 156–186. Macmillan of Australia, Melbourne.
- Cumming, B.G. & Seabrook, J.E.A. (1985) *Chenopodium. Handbook of Flowering II* (ed. A.H. Halevy), pp. 196–228. CRC Press, Orlando, Fla.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley and Sons, New York.
- Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London.
- Harper, J.L., Lovell, P.H. & Moore, K.G. (1970) The shapes and sizes of seeds. *Annual Review of Ecology and Systematics*, **1**, 327–356.
- Jackson, M.B. & Drew, M.C. (1984) Effects of flooding on growth and metabolism of herbaceous plants. *Flooding and Plant Growth* (ed. T.T. Kozlowski), pp. 47–128. Academic Press, Orlando, Fla.
- Karssen, C.M. (1970) The light promoted germination of the seeds of *Chenopodium album* L. III. The effect of the photoperiod during growth and development of the plants on the dormancy of the produced seeds. *Acta Botanica Neerlandica*, **19**, 81–94.

- Khan, M.A. & Ungar, I.A. (1986) Life history and population dynamics of *Atriplex triangularis*. *Vegetatio*, **66**, 17–25.
- Kinet, J.-M., Sachs, R.M. & Bernier, G. (1985) *The Physiology of Flowering. III. The Development of Flowers*. CRC Press, Orlando, Fla.
- Klinkhamer, P.G.L., De Jong, T.J. & Meelis, E. (1987) Life-history variation and the control of flowering in short-lived monocarps. *Oikos*, **59**, 309–314.
- Laan, P., Berrevoets, M.J., Lythe, S., Armstrong, W. & Blom, C.W.P.M. (1989) Root morphology and aerenchyma formation as indicators of the flood-tolerance of *Rumex* species. *Journal of Ecology*, **77**, 693–703.
- Laan, P. & Blom, C.W.P.M. (1990) Growth and survival responses of *Rumex* species to flooded and submerged conditions: the importance of shoot elongation, under water photosynthesis and reserve carbohydrates. *Journal of Experimental Botany*, **41**, 775–783.
- Laan, P., Tossierams, M., Blom, C.W.P.M. & Veen, B.W. (1990) Internal oxygen transport in *Rumex* species and its significance for respiration under hypoxic conditions. *Plant and Soil*, **122**, 39–46.
- Lacey, E.P. (1986) Onset of reproduction in plants: size-versus age-dependency. *Trends in Ecology and Evolution*, **1**, 72–77.
- Menges, E.S. & Waller, D.M. (1983) Plant strategies in relation to elevation and light in floodplain herbs. *American Naturalist*, **122**, 454–473.
- Moore, R.P. (1972) Tetrazolium staining for assessing seed quality. *Seed Ecology* (ed. W. Heydecker), pp. 347–366. Butterworths, London.
- Ridge, I. (1987) Ethylene and growth control in amphibious plants. *Plant Life in Aquatic and Amphibious Habitats* (ed. R.M.M. Crawford), pp. 53–76. Blackwell Scientific Publications, Oxford.
- SAS Institute Inc. (1985) *SAS Users Guide: Statistics 5 edn*. SAS Institute Inc., Cary, N.C.
- Silvertown, J.W. (1984) Phenotypic variety in seed germination behavior: the ontogeny and evolution of somatic polymorphism in seeds. *American Naturalist*, **124**, 1–16.
- Silvertown, J.W. (1987) *Introduction to Plant Population Ecology*. Longman, New York.
- Stearns, S.C. (1976) Life-history tactics: a review of the ideas. *Quarterly Review of Biology*, **51**, 3–47.
- Thompson, K. & Grime, J.P. (1983) A comparative study of germination responses to diurnally fluctuating temperatures. *Journal of Applied Ecology*, **20**, 141–156.
- Trought, M.C.T. & Drew, M.C. (1980) The development of waterlogging damage in wheat seedlings (*Triticum aestivum* L.). II. Accumulation and redistribution of nutrients by the shoot. *Plant and Soil*, **56**, 187–199.
- Van der Sman, A.J.M., Blom, C.W.P.M. & Van de Steeg, H.M. (1992) Phenology and seed production in *Chenopodium rubrum*, *Rumex maritimus* and *Rumex palustris* as related to photoperiod in river flood plains. *Canadian Journal of Botany*, **70**, 392–400.
- Van der Sman, A.J.M., Van Tongeren, O.F.R. & Blom, C.W.P.M. (1988) Growth and reproduction of *Rumex maritimus* and *Chenopodium rubrum* under different waterlogging regimes. *Acta Botanica Neerlandica*, **37**, 439–450.
- Van der Sman, A.J.M., Voeseck, L.A.C.J., Blom, C.W.P.M., Harren, F.J.M. & Reuss, J. (1991) The role of ethylene in shoot elongation with respect to survival and seed output of flooded *Rumex maritimus* L. plants. *Functional Ecology*, **5**, 304–313.
- Van de Steeg, H.M. (1984) Effects of summer inundation on flora and vegetation of river foreland in the Rhine area. *Acta Botanica Neerlandica*, **33**, 365–366.
- Venable, D.L. (1984) Using intraspecific variation to study the ecological significance and evolution of plant life-histories. *Perspectives on Plant Population Ecology* (eds R. Dirzo & J. Sarukhan), pp. 166–187. Sinauer Association, Sunderland, Mass.
- Voeseck, L.A.C.J. (1990) *Adaptations of Rumex in flooding gradients*. PhD thesis, Nijmegen, the Netherlands.
- Voeseck, L.A.C.J. & Blom, C.W.P.M. (1989) Growth responses of *Rumex* species in relation to submergence and ethylene. *Plant, Cell and Environment*, **12**, 433–439.
- Voeseck, L.A.C.J. & Blom, C.W.P.M. (1992) Germination and emergence of *Rumex* in river flood-plains. I. Timing of germination and seedbank characteristics. *Acta Botanica Neerlandica*, **41**, 319–329.
- Voeseck, L.A.C.J., Blom, C.W.P.M. & Pouwels, R.H.W. (1989) Root and shoot development of *Rumex* species under waterlogged conditions. *Canadian Journal of Botany*, **67**, 1865–1869.
- Werner, P.A. (1975) Predictions of fate from rosette size in teasel (*Dipsacus fullonum* L.). *Oecologia (Berlin)*, **20**, 197–201.
- Westhoff, V. & Den Held, A.J. (1975) *Plantengemeenschappen in Nederland*. Thieme & Cie, Zutphen, The Netherlands.

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