Phenology and seed production in Chenopodium rubrum, Rumex maritimus, and Rumex palustris as related to photoperiod in river forelands


Reproductive development in three species from irregularly flooded areas of river forelands was studied in relation to time of emergence. In Chenopodium rubrum, flowering was induced earlier in plants germinated in April–May than in later cohorts. However, the period of vegetative growth diminished and the life cycle was completed in a shorter time in later germinated plants. Seed number was reduced, but seed size as well as reproductive effort per plant increased in later cohorts. Plants of both Rumex species flowered after a certain number of leaves had developed and before a critical photoperiod had passed. In earlier cohorts, the main shoot and several axillary shoots elongated and flowered. Fewer axillary shoots flowered closer to the critical photoperiod, and this resulted in a reduced seed output in later cohorts. The critical photoperiod as well as the time needed for completion of the life cycle was longer in Rumex palustris than in Rumex maritimus. It is argued that in the riparian habitat, plants of both Rumex species are only occasionally able to complete their life cycle in one growing season. Survival of these species on the population level will rely more upon adaptations towards flooding during the established phase than is the case for C. rubrum.

Key words: flowering phenology, photoperiod, seed production, Chenopodium rubrum, Rumex maritimus, Rumex palustris.

Introduction

River forelands, stretching from the riverbank to the main dike, provide one of the most uncertain habitats for plants (Van de Steeg 1984; Brock et al. 1987; Blom 1990; Blom et al. 1990). A striking aspect of flooding in these areas is the variation in the length of the growing season. Elevational differences of a few decimetres can cause the growing season to vary by a month or more. Successive years differ to such an extent that the lowest areas may dry out in April or remain flooded until as late as September. Survival of populations of annual and biennial plants depends upon successful regeneration by seed, and this process involves a number of important life-history traits that are greatly affected by limiting factors such as a short growing season (Grime 1979).

This paper discusses flowering phenology and seed output in the first season of growth for three representative species from the lower elevations in the river forelands. These life-history phenomena are compared for plants that germinated at different times during the growing season. Red goosefoot, Chenopodium rubrum L., and the two dock species Rumex maritimus L. and Rumex palustris Sm. cohabit mud flats of former riverbeds and both clay and sand pits (see Salisbury 1942; Hejny 1960; Van der Sman et al. 1988; Voesenek 1990). Under ruderal conditions, the greatest emergence of C. rubrum is in May–June (Williams 1969; Roberts and Neilson 1980), and that for R. maritimus is in April–May (Roberts and Boddrell 1985). All three species show a maximal germination response under a combination of fluctuating temperatures and light (Cumming 1959; Voesenek 1990; A. J. M. Van der Sman, unpublished data), which is common for wetland species. This response provides a mechanism whereby spring germination is initiated by an increase in irradiance and a falling water table (Thompson and Grime 1983). Because germination is inhibited under strictly anaerobic conditions in all three species (Voesenek 1990; A. J. M. Van der Sman, unpublished data), germination on the river forelands depends upon the subsidence of winter and (or) spring floods. Reproductive development is studied in outdoor experimental
Materials and methods

Seeds of *C. rubrum*, *R. maritimus*, and *R. palustris* were collected from riparian areas near Nijmegen in the year preceding each experiment and then stored dry at room temperature. After removal of perianths (*Rumex* spp.), a mixed seed sample from five different parent plots of each species was imbibed (12 h light: 12 h dark at a temperature of 25-10°C (light:dark); mean photosynthetically active radiation (PAR) (400–700 nm) during the light period was 30 μmol m⁻² s⁻¹). After 4 days, five to seven seedlings were transplanted into individual pots (diameter 16 cm, height 50 cm in outdoor experimental plots; 10-cm pots in photoperiod experiment) with perforated bases. Each pot was filled with a 1:1 (v/v) mixture of river sand and peat soil. Seedlings were thinned to one per pot within 2 weeks.

**Phenology in outdoor experimental plots**

To study reproductive development in relation to time of emergence, plants were grown in cohorts for three consecutive years, i.e., 1987–1989, inclusive. Immediately after transplantation of each cohort, the pots were placed 16 cm apart, in outdoor basins of water (length × width × depth: 8 × 2 × 1 m; water level 5 cm). During extremely dry periods, young seedlings were watered by sprinkling to prevent desiccation. The soil moisture content in the pots averaged 31% by weight (about 24% in the upper 10-cm and about 38% in the lower 10-cm soil layer). Daily radiation and temperatures were recorded throughout the course of the study period. The latter are presented as temperature sum, i.e., the number of degree-days over a certain period, with 10°C as base temperature. This base was chosen because none of the species showed significant growth at lower temperatures.

In 1987, four cohorts (each of 20 plants per species) were planted at 2-week intervals, on 18 May, 29 June, 10 August, and 21 September. This was designed to approximate the extremes in length of the growing season. Only the plants of the first cohort of *R. palustris* flowered and those of the first and second cohorts of *R. maritimus*. Both flowering cohorts of *R. maritimus* showed marked differences in flowering characteristics. Therefore, for both *Rumex* species, six cohorts (12 plants per species per cohort) were planted in the following year. Two-week intervals separated each cohort, which commenced on 2 May and ended on 11 July. In the 3rd year seven cohorts (12 plants per species per cohort) of all three species were planted at 1-week intervals, starting from 10 April until 22 May. The latter was designed to study reproductive development with respect to the length of the growing season under the most favourable conditions of spring germination.

**Plant measurements**

Vegetative growth of rosettes in both species of *Rumex* was measured by recording the number of leaves ≥1 cm long, the number of dead leaves, and the length of the longest leaf (including petiole) of the main shoot. The number of axillary shoots and the number of living leaves per shoot were counted approximately every 10 days. The same parameters were measured for plants of *C. rubrum* but including the lengths of the main stem and of branches (longer than 1 cm). The transition to the generative phase was recorded. Several stages were distinguished, i.e., bolting (*Rumex* spp.), appearance of clearly visible flowering buds (*C. rubrum*), duration of flowering, and seed ripening. Dates were recorded per plant for these parameters; 50% values per cohort are presented in the results section. The numbers and final lengths of flowering shoots were measured for both *Rumex* species. Seeds with perianths were harvested from each sample plant and for each of the three species. All seed samples were sieved to remove dead leaves and sand and then weighed to estimate total seed production per plant. The total seed output of five plants per cohort was mixed. From these mixtures, 2 × 4 subsamples of 50 seeds were weighed to estimate individual seed weights. These samples were also used to determine germination response. After the seed harvest, the stems were dried (48 h at 70°C) and weighed. In 1989, seeds were harvested from five plants per cohort. Total aboveground weights (including seeds) were determined and seed weight estimated (from the ratio between seed weight and weight of all other aboveground parts of the first five plants) for the remaining seven plants. In December 1987, four plants per species were harvested from all cohorts to determine dry weights (48 h at 70°C) of vegetative shoots and tap roots.

Statistical analyses were performed with the SAS statistical package (SAS Institute Inc. 1985). To compare the means per cohort of several parameters, Bonferroni t-tests were used after an analysis of variance with the general linear models procedure for unequal cell sizes. Pearson rank correlation tests were used on the data on stem length and seed output per plants of all individual plants of both species of *Rumex*.

**Photoperiod and flowering of Rumex species**

To determine the effects of photoperiod on flowering, plants of both *Rumex* species were grown in either 13-h (short day = SD) or 18-h (long day = LD) photoperiods in similar growth rooms (PAR = 120 μmol m⁻² s⁻¹; 400-W sodium lamps, supplemented with 85-W Sylvania GRO-LUX lamps; 15:25°C, dark:light). Starting February 1989, eight series (12 plants per series per species) were subjected to either 2, 4, 6, or 8 weeks SD or LD and thereafter changed to the other regime. Two additional series remained in either LD or SD to serve as controls. Plant growth was measured in the same way as indicated for the outdoor experiments.

**Field observations on Rumex species**

This study was done to determine whether flowering of both *Rumex* species is related to the time of germination under field conditions as well as in outdoor plots. Four longitudinal plots (each 10 m × 50 cm) were set out in August 1988 in the river forelands near Nijmegen. The plots were situated parallel to the river at different elevational levels with different flooding frequencies and durations. One of the plots was located in a clay pit at approximately 9.70 m with respect to mean sea level (Amsterdam Ordnance Datum = NAP). In 1988, this plot was free of flood water from 20 June onwards. Three other plots were placed at different elevational levels (9.25, 9.05, and 8.90 m NAP) on the shore of an old riverbed, where the winter–spring floods started to subside on 24 June, 28 June, and 22 July, respectively. Within-plot elevational differences ranged from 10 cm in the highest plot (clay pit) to 4 cm in the lowest. As a result of these variations, more than 50% of the intermediate plot on the old riverbed shore remained waterlogged until 18 July. Plant locations were recorded by two coordinates, and each plant was followed until November 1988. Once a month the following data were recorded for each plant: survival, number of living leaves, length of longest leaf, phase of development, and stem length.

**Results**

**Phenology in outdoor experimental plots**

*Chenopodium rubrum*

Several developmental features were constant regardless of cohort (Fig. 1). Seedlings possessed an opposite leaf arrangement until the seventh primary leaf became visible. Leaves 10–40, if present on the main shoot, all attained maximum lengths of 10–16 cm. This value was rather constant per plant, but different between plants from the same or different
Fig. 1. Vegetative development in outdoor experimental plots (plants from cohort II of 1987). *Chenopodium rubrum* at the age of (a) 2 weeks, (b) 3 weeks, and (c) 5 weeks; *Rumex maritimus* at the age of (d) 2 weeks, (e) 3 weeks, (f) 4 weeks, and (g) 6 weeks (transition to flowering, i.e., early bolting stage); *Rumex palustris* at the age of (h) 2 weeks, (i) 3 weeks, and (j) 4 weeks. Primary leaves are numbered in the order of their appearance. †, the axillary shoot of dead primary leaves.
coherens. Secondary shoots appeared in the first two leaf axils as soon as the fifth and sixth leaves were observed. In most cases, additional shoots emerged later from the cotyledonary axils. The primary stem remained short during the vegetative stage. In contrast, the first axillary shoots (in leaf axils 1–6) grew large, resulting in a rosette-like appearance (Fig. 1).

After transition to the generative phase, small red flowering buds appeared on the main stem. These were soon followed by flower buds on the large branches. They developed from the top downwards (see Lang 1965). Flowering was accompanied by an acceleration in leaf initiation and primary stem growth. This closely resembled bolting in rosette species of *Rumex*. Leaf form and degree of branching of the inflorescence were rather variable in *C. rubrum* (see also Cumming 1969; Williams 1969).

In contrast with the characters described above, the timing of flowering and the investment in seed production were strongly affected by the timing of germination. Plants of *C. rubrum* grown in April and May showed vigorous vegetative growth before flowering in long days (>15 h). The number of primary leaves initiated before flowering was proportional to the temperature sum up to that time (Table 1).

This relationship is surprisingly strong considering that durations that were presented as 50% values are rather crude and that each normal summer day corresponds to 6–10 degree-days. Plants that started growth after May showed transition to the generative phase correspondingly later in time, but in progressively earlier stages of growth. The duration of flowering correspondingly decreased, as well as leaf increment during flowering. Mean leaf numbers at the onset of bolting as well as mean total leaf numbers were highly significantly different between cohorts I, II, and III of 1987. The duration of the period of seed ripening apparently increased, but many of the immature seeds that fell from the latest flowering plants were readily capable of germination. Smaller plants produced fewer seeds than larger ones, but plants of the latest flowering cohort allocated up to five times more dry matter into seeds per unit aboveground (stem) weight than those of the early flowering cohorts (Table 2). The ratio between the weights of stems and tap roots was constant regardless of cohort (about 3.8 for cohorts I–III of 1987). Mean individual seed weight increased from 0.03 mg for the earliest flowering cohort of 1989 up to 0.09 mg for cohort III of 1987, but mean seed number decreased from over 200,000 to 2000 per plant for these two species, respectively. Seeds of all size categories required fluctuating temperatures for germination; however, the largest seeds showed a diminished requirement for light (70% germination in the dark compared with 5% of small seeds).

All plants from cohort IV (1987) died in December after a short period of frost. These plants had six or less primary leaves, all of which were smaller than 1 cm in length. Where seeds had been germinated 2 weeks earlier, the resulting plants produced only a few, large seeds in November (A. J. M. Van der Sman, unpublished data).

**Rumex species**

Seedlings of *R. maritimus* and *R. palustris* developed in a similar manner (Fig. 1). Primary leaves emerged successively from a leaf sheath that became fragmented and disintegrated after rainfall. The first five leaves could be recognized easily afterwards by their specific growth habit. At first, seedlings of *R. palustris*, which had originated from larger seeds, were slightly larger than those of *R. maritimus*, but the situation was reversed after the seven-leaf stage. Leaves 7–12 of both species attained a maximum length of 20–25 cm. As in *C. rubrum*, variation occurred between individual plants from the same cohort and from different cohorts. *Rumex maritimus* possessed relatively longer and narrower leaves than *R. palustris* (Fig. 1), but these differences were not statistically significant. In both species, axillary shoots developed three nodes below newly emerging leaves. The maximum photosynthetic leaf area was usually reached after the 12-leaf stage. At this stage transition to the reproductive phase became apparent with the bolting of the main shoot (Fig. 1g). Bolting was accompanied by an increase in the initiation of leaves, which is shown for primary shoots in Fig. 2a. Flowers appeared approximately 21 days after the onset of bolting. Flowers developed on the upper part of the stem, and also downwards on older stem nodes.

Rosettes that remained vegetative deteriorated from the time that the rosette size was maximum onwards (Fig. 2b). Leaf birthrate decreased, whereas death rate increased, until after several weeks a constant number of vital leaves remained (about 2 primary and 11 axillary leaves). Apart from this phenomenon, later developing leaves were progressively shorter in length.

In sharp contrast with that in *C. rubrum*, plants of both *Rumex species* flowered at the same phenological stage regardless of treatment, i.e., at the time of maximum leaf area (12 primary leaves). This was reached after a relatively constant temperature sum (Table 1). All cohorts of *R. maritimus* that reached this stage before 11 August (photoperiod 15 h) and those of *R. palustris* that did so before 27 July (photoperiod 16 h) bolted and flowered. Differences in growth parameters of the main flowering shoot were small between species of *Rumex* (see Van der Sman et al. 1991). Mean primary stem length in plants of *R. maritimus* was 50 cm, and those of *R. palustris* reached 74 cm. Only plants from the latest flowering cohorts, which flowered with only one main stem, had in some cases significantly shorter stems (e.g., the flowering plants of *R. maritimus* from cohort V of 1988). Large differences occurred, however, with respect to the number and size of secondary stems, which elongated from rosette leaf axils in the order of axil appearance. Later flowering cohorts produced fewer, shorter secondary stems and consequently fewer seeds than earlier cohorts. Total seed weight per plant was highly correlated with total stem length (summed heights of primary and secondary stems) throughout all cohorts (Fig. 3). This was in sharp contrast with that found in *C. rubrum* and indicated a constant mean seed weight to aboveground weight ratio.

Mean individual seed weight per cohort of *R. maritimus* varied between 0.18 and 0.27 mg, and that for *R. palustris* varied between 0.50 and 0.60 mg. The lowest weights were found for cohorts I–III of 1989, which also produced the largest total seed weights and seed numbers of approximately 80,000 (*R. maritimus*) and 30,000 (*R. palustris*) per plant. Statistical analysis of the limited data on individual seed weight was not attempted. No differences in germination characteristics were found between small and large seeds of both species, but large seeds showed a higher percentage of emergence from up to a 2.5 cm sowing depth (data not shown).

Cohorts emerging over the course of the season showed
Table 1. Reproductive development of cohorts of *Chenopodium rubrum*, *Ranunculus maritimus*, and *R. palustris* in outdoor experimental plots

<table>
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<tr>
<th>Cohort</th>
<th>Period of vegetative growth</th>
<th>Weather</th>
<th>% flowering</th>
<th>Duration</th>
<th>Leaf n^4</th>
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Note: There were 20 plants per species per cohort in 1987 and 12 in each of 1988 and 1989. nd, not determined.

1From the time of germination until 50% of the plants had flowering buds (*C. rubrum*) or bolted (*Ranunculus* spp.).
2Temperature sum (T) in degree-days (10°C base temp.) and radiation sum (R) as 10^3 J cm^{-2} during the period of vegetative growth.
3Period of flowering (Veg.), flowering (Fl.), the time until 50% of the plants were out of flower, and seed ripening (Rip.), the time until 50% of the plants were ripe.
4Veg., number of primary leaves (>1 cm in length) initiated during the period of vegetative growth. Tot., total number of leaves (median values per cohort).
5Plants died in December (see text).
6Plants remained vegetative in the year of germination.
Table 2. Sizes and total seed weight of plants of C. rubrum in outdoor experimental plots

<table>
<thead>
<tr>
<th>Cohort</th>
<th>Date planted</th>
<th>Plant height (cm)</th>
<th>Seed wt. per plant (g)</th>
<th>Seed wt. to stem wt.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1987</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>10 Apr.</td>
<td>85.0 ± 3.4ab</td>
<td>14.5 ± 1.9ab</td>
<td>0.79 ± 0.07b</td>
</tr>
<tr>
<td>II</td>
<td>17 Apr.</td>
<td>81.7 ± 6.1abc</td>
<td>13.3 ± 2.5ab</td>
<td>0.63 ± 0.11b</td>
</tr>
<tr>
<td>III</td>
<td>24 Apr.</td>
<td>88.7 ± 2.6ab</td>
<td>17.8 ± 1.6a</td>
<td>0.62 ± 0.03b</td>
</tr>
<tr>
<td>IV</td>
<td>1 May</td>
<td>94.0 ± 2.0a</td>
<td>16.0 ± 1.0a</td>
<td>0.72 ± 0.04b</td>
</tr>
<tr>
<td>V</td>
<td>8 May</td>
<td>85.9 ± 2.7ab</td>
<td>18.6 ± 1.6a</td>
<td>0.73 ± 0.02b</td>
</tr>
<tr>
<td>VI</td>
<td>15 May</td>
<td>78.3 ± 3.9bc</td>
<td>14.3 ± 2.1ab</td>
<td>0.86 ± 0.03b</td>
</tr>
<tr>
<td>VII</td>
<td>22 May</td>
<td>76.3 ± 2.4bc</td>
<td>15.6 ± 1.0a</td>
<td>0.85 ± 0.02b</td>
</tr>
</tbody>
</table>

Fig. 3. Total seed production in relation to total stem length (summed heights of primary and secondary stems) in all plants of R. maritimus (n = 175) and R. palustris (n = 149) from the outdoor experimental plots. ○, 1987; ▲, 1988; ■, 1989.

progressively slower vegetative development, indicated by an increased temperature sum before reaching the 12-leaf stage, and a slower reproductive development, especially seed ripening (Table 1). Within-cohort variation increased as well, and several plants of R. palustris from the last cohorts to flower were unable to produce ripe seeds on all secondary stems. Generative development was also delayed in cohorts I and II of 1989 for plants of R. palustris that had experienced low temperatures during early vegetative development (Table 1). Occasionally, one plant per cohort of R. palustris bolted (approx. 10 cm) without flowering. This occurred in both flowering and nonflowering cohorts.

Most plants from the later flowering cohorts survived after flowering with vegetative axillary shoots in the rosette leaves. By the end of December 1987, mean dry weights of tap roots from flowering plants ranged from less than 1 g for plants without vegetative shoots remaining to 3 g (R. maritimus) and 5 g (R. palustris) for plants with three vegetative axillary shoots. By this time, vegetative plants possessed tap roots up to 5 g (R. maritimus, cohort III) and 7 g (R. palustris, cohort II). Plants from cohort IV of 1987 were unable to reach the maximum rosette size. In November, after 120 degree-days, plants from this cohort possessed up to five primary leaves with a maximum length of 3–4 cm, and in December dry weights of tap roots were only 10–15 mg for R. maritimus and 30 mg for R. palustris. However, most of these very small plants survived 4 months submergence during the winter. In the following growing season these small plants flowered and set seed, just as all the other vegetative plants and the remaining vegetative shoots of flowering plants.
Photoperiod and flowering of Rumex species

Plants of *R. palustris* did not flower in this study. Plants of *R. maritimus* all flowered if they received 6 or more weeks LD (Table 3), irrespective of SD given afterwards. The main shoot bolted after 10 primary leaves had been formed. At this stage plants possessed five axillary shoots with a total of 11 secondary leaves. The series that had been placed in SD after 4 weeks LD subsequently showed a progressive delay in bolting and incomplete flowering (Table 3). In all series, however, bolting occurred after approximately 10 leaves had been initiated in LD. Duration of flowering increased with the period spent in SD before or after LD. The latter started to bolt at the same time as the normally developing plants, but flowering was delayed by a month. A short flowering stem (8.5 cm) was formed, with many small leaves and fewer flowers than other plants. Eventually seeds (0.34 g) were produced, but ripening was delayed and incomplete.

Plants that were grown in various SD periods and then placed in LD subsequently showed a progressive delay in bolting and flowering (Table 3). In all series, however, bolting occurred after approximately 10 leaves had been initiated in LD. Duration of flowering increased with the time spent in SD before LD, as did total leaf number, plant height, and seed weight per plant, with the exception of series 8SD/LD (Table 3). This last series produced a relatively low total seed weight and a low ratio between seed weight and aboveground (stem) weight. This ratio increased with the period of SD before or after LD in all series up to series 6SD/LD and 8SD/LD. By the time these series had flowered, plants had grown for over three-quarters of a year on the limited substrate in the small pots, and a shortage of nutrients may well have occurred.

Field observations on Rumex species

The largest plants of both *Rumex* species were found in the highest of the three plots on the riverbed shore (approx. five leaves per plant in August; length of longest leaf 20 cm), followed by the plot in the clay pit (four leaves, leaf length 7 cm). Within-plot variation was much larger in the clay pit than on the relatively flat riverbed shore. The two lower pots on the riverbed shore did not differ significantly from each other with respect to plant size (three leaves, leaf length 3 cm). In the lowest plot, newly germinated seedlings were found during the second observation in September.

Flowering occurred only in plants growing in sites where flood water had subsided before the end of June. Flowering of plants of *R. maritimus* in the intermediate plot on the riverbed shore occurred only in the higher parts. In all plots more large plants flowered than small ones. A significantly higher percentage of plants of *R. maritimus* flowered compared with those of *R. palustris* (Table 4). All flowering plants had

### Table 4. Percent flowering plants in September 1988 of *R. maritimus* and *R. palustris* in four plots (each 10 m × 50 cm) at different elevations in two sites of the river forelands near Nijmegen, The Netherlands

<table>
<thead>
<tr>
<th>Site</th>
<th>Plot</th>
<th>NAP*</th>
<th>Start of the season 1</th>
<th><em>R. maritimus</em> 2</th>
<th><em>R. palustris</em> 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clay pit</td>
<td>1</td>
<td>9.70</td>
<td>20 June</td>
<td>63 (30)</td>
<td>17 (63)</td>
</tr>
<tr>
<td>Riverbed</td>
<td>2</td>
<td>9.25</td>
<td>24 June</td>
<td>58 (36)</td>
<td>25 (16)</td>
</tr>
<tr>
<td>Riverbed</td>
<td>3</td>
<td>9.05</td>
<td>28 June – 18 July</td>
<td>6 (31)</td>
<td>0 (75)</td>
</tr>
<tr>
<td>Riverbed</td>
<td>4</td>
<td>8.90</td>
<td>22 July</td>
<td>0 (15)</td>
<td>0 (28)</td>
</tr>
</tbody>
</table>

- **Note**: Differences in percent flowering species are highly significant. Differences between plots 1 and 2 are not significant. Differences between plots 1 and 2 on one hand and plot 3 on the other are highly significant for *R. maritimus* (χ²; *p* < 0.001).
- **1** Mean height (m) above sea level (Amsterdam Ordnance Datum).
- **2** Subsidence of winter–spring floods.
- **3** Total number of plants per plot given in parentheses.
already bolted on 10 August, with the exception of five plants of *R. maritinuis* from the clay pit. In October, seeds on all generative plants of *R. palustris* and several plants of *R. maritinuis* in the clay pit were ripening. The remaining plants of *R. maritinimus* were in full flower. The last field observations in the other plots were made in September because the riverbed was flooded for several weeks in October, and this resulted in the death of all reproductive plants. At that time most plants of *R. maritinimus* had just flowered, and those of *R. palustris* were still in bud. All flowering plants had only one main stem. Only those of *R. maritinimus* from the highest plot on the riverbed shore attained a mean stem length that was comparable to the plants in the outdoor plots (46 cm). Plants in the clay pit remained much smaller than in the outdoor plots (*R. maritinimus* 18 cm; *R. palustris* 33 cm). More than 80% of the flowering plants in this plot survived until seed ripening. Loss of plants was primarily caused by predation of the chrysomelid beetle *Gastrophysa viridula*.

**Discussion**

The controls of flowering and seed production are quite different for *C. rubrum* on one hand and for *R. maritinimus* and *R. palustris* on the other. They have contrasting photoperiodic responses. In the short-day plant *C. rubrum*, flowering occurred as a response to daylength and appeared relatively independent of the amount of vegetative growth. In the two long-day species of *Rumex*, stem elongation and subsequent flowering always occurred after a rather constant number of leaves had formed. All three species fit into the life-history classification that Klinkhamer et al. (1987) suggested for short-lived species based on the control of flowering. In riparian habitats both control types of flowering can result in the production of large numbers of seeds should floods recede early enough in the growing season.

According to Cook (1976), three factors determine potential seed number in *C. rubrum*. These are (i) the total number of axillary bud primordia on the plant at the start of flower induction, (ii) the increased rate of organ initiation during the process of induction, and (iii) the duration of this higher rate of organ initiation. Cook demonstrated that the last two factors are affected by the induction photoperiod. The early rate of organ initiation was higher in a longer photoperiod than in a shorter one, and the rate of differentiation, which determines the duration of this higher rate of organ initiation, was lower. Our findings agree with those of Cook, e.g., in outdoor plots both the duration of flowering and leaf increment during flowering decreased in late-induced plants of *C. rubrum* (Table 1). Under natural conditions the first factor is also related to photoperiod; long days favour vegetative growth in *C. rubrum* (Cumming 1961). Our results show that large, early-germinated plants also started to flower earlier than late-germinated plants in a longer photoperiod. Thus, photoperiod clearly determines the potential seed output of this species, resulting in very large differences between plants grown at the extremes of the growing season.

Seed size is determined by seed number that in turn is governed by the photoperiod during flower induction, and natural induction tends to minimize seed size and maximize seed number in *C. rubrum* (Cook 1975). There is probably little need for competitive advantage of large seedlings that result from large seeds in these open habitats. However, high capacity for germination in the dark together with their size may give larger seeds a better chance to emerge from deeper soil layers on sandy river beaches or from cracks in the clay of old riverbeds (see Harper et al. 1970). We not only found larger seeds on plants flowering in short days but also up to a five times larger seed output with respect to other plant parts (stem and tap root) in comparison to plants flowering in long days. The latter showed a partitioning of biomass comparable to that described by Williams (1969) for this species. This indicated an increasing reproductive effort in plants of *C. rubrum* nearer the physiologically optimal photoperiod for flowering.

Flowering in both species of *Rumex* occurred during and after long days, after a minimal number of leaves had been formed (see Lang 1965; Vince-Prue 1975; Bernier et al. 1981). These species are probably sensitive to flower induction shortly after germination, since short days during early development delayed flowering in *R. maritinimus* and resulted in an increase in the number of leaves before bolting occurred. The development of stems, flowers, and seeds was not influenced by short days. Between-cohort differences in the rate of development in outdoor plots were therefore probably mainly caused by temperature. The minimal number of leaves initiated before flowering (especially the number of secondary leaves) is reduced in small pots and under poor nutrient conditions (A. J. M. Van der Sman, unpublished data). By this means these species maintain approximately the same flowering time under greenhouse conditions, which is advantageous when considering the time required for reproductive development (see Bradshaw 1965). In the field study, plants were smaller and much more variable in the clay pit than on the riverbed shore, but reproductive development was not delayed. This may be caused partly by a lower nutrient availability in the clay pit than on the riverbed shore. Another cause may have been the larger elevational differences in the clay pit; at least part of the plants had probably germinated later than 20 June.

The diminished seed output shown by June plants of *Rumex* spp. mainly resulted from the smaller number and size of secondary stems when compared with earlier germinated plants. In the indoor study, secondary shoots of *R. maritinimus* remained very small and did not flower. In outdoor plots, the oldest (largest) shoot elongated first. Therefore, bolting and flowering of secondary shoots is probably not determined by the main shoot but simply dependent upon their size (leaf number) with respect to photoperiod (see also Lang 1965).

After a certain critical photoperiod, no flowering of *Rumex* occurred at all. Plants of *R. palustris* shifted to the (partly) vegetative strategy earlier in the season in outdoor experiments, and in the field plots fewer plants of *R. palustris* flowered than of *R. maritinimus*. The longer critical photoperiod for flowering in *R. palustris* was related to the time needed for reproductive development, compared with *R. maritinimus*, which was longer and also more susceptible to temperature (see also Hejny 1960). Flowering of *R. palustris* was not simply induced by LD in this study or in other experiments under the conditions provided (≥16 h photoperiod; dark temperature 17°C). High temperatures during the dark period inhibit flowering in several long-day species (Lang 1965; Vince-Prue 1975). This factor may be crucial for *R. palustris*, illustrated by the observation of 100% flowering in an unheated greenhouse with a dark temperature of 10°C (A. J. M. Van der Sman, unpublished data). Adult plants have a cold requirement before flowering occurs in the greenhouse.
in LD. The relationship between induction by LD and vernalization may be extremely complex in species that are sensitive to both (Bernier et al. 1981).

Plants of both *Rumex* species that remained vegetative in short days exhibited a marked reduction in aboveground growth from the time of maximum leaf area onwards. This may be important for their cold hardening, as has been suggested for certain grasses (Hay 1990). This reduction in growth was apparently related to investment in tap roots. We suggest that in the river flood plains, with frequently occurring prolonged winter and spring floods, *R. palustris*, and to a lesser extent *R. maritimus*, will show a tendency towards longer life histories involving more than one growing season. In contrast, the strictly annual *C. rubrum* will complete its life cycle in a shorter time, if germinated later in the growing season (until as late as September). Therefore, survival of *Rumex* populations will probably depend more upon their relative flooding resistance in the established phase than that of populations of *C. rubrum*. This will be the subject of future papers.

**Acknowledgements**

This study was performed with the help of Nina Joosten, Mariette Mans, Rob Vergrouwe, and Helma Pannekoek. We thank Dr. Ir. G. W. M. Barendse and Dr. P. G. L. Klinkhamer for helpful comments on the manuscript. Financial support was given by the Foundation for Fundamental Research (BION), which is subsidized by the Netherlands Organisation for Scientific Research (NWO).


