Germination and emergence of *Rumex* in river flood-plains. I. Timing of germination and seedbank characteristics

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SUMMARY

Field experiments were designed to determine the timing of germination and the character of the seedbank in relation to the field occurrence of three *Rumex* species, which are distributed in a gradient of intensity and predictability of floods in river flood-plains. *Rumex acetosa* is characterized by early autumn germination, a transient type of seedbank, flood-intolerant achenes and a lack of multiple post-flood germination cohorts. These traits fit well into the habitat of *R. acetosa* in river flood-plains: rarely flooded grasslands with a high level of competitive interactions. Both wetland species, *R. crispus* and *R. palustris*, are characterized by late spring germination, a persistent seedbank, flood-tolerant achenes and multiple post-flood germination cohorts. These traits fit into the habitats of both species which are characterized by harsh predictable winter floods and erratic catastrophic summer floods. Timing of germination and seedbank characteristics are important life-history traits, at least partly explaining the distribution of *Rumex* species in flood-dominated river flood-plains.

Key-words: dormancy, flooding, germination timing, *Rumex*, seedbank.

INTRODUCTION

The seedling phase is probably one of the most vulnerable stages in a plant's life cycle (Cavers & Harper 1967; Harper 1977; Marks & Prince 1981; Fenner 1987). The timing of germination and seedling emergence determine, to a great extent, the environmental risks to which a seedling may be exposed (Badger & Ungar 1991). Germination timing will maximize seedling survival and plant reproduction (Venable 1984; Badger & Ungar 1991). In stable environments with relatively high levels of competitive interactions, selection will favour early germination to avoid a subordinate position in a plant size hierarchy (Weaver & Cavers 1979; Van der Toorn & Pons 1988). Competition leads to survival of the largest individuals (Ross & Harper 1972). Environmental harshness and 'catastrophes' will favour both late germination and multiple germination periods. Germination after a harsh period will increase survival probabilities of seedlings, whereas in unpredictable environments multiple cohorts of emerging seedlings prevent total elimination on the population level (Venable 1984; Silvertown, 1987; Zammit & Westoby 1987; Andersson 1990; Badger & Ungar 1991).

Timing of germination is regulated by the dormancy status of seeds and their germination requirements (Karssen 1982; Baskin & Baskin 1985; Washitani & Masuda 1990). Both can be interpreted as delay mechanisms which may prevent germination and stimulate the formation of a buried seedbank (Washitani & Masuda 1990). Differentiation in dormancy levels and germination requirements will lead to either a more temporary or transient seedbank or a more persistent type of seedbank (Thompson & Grime 1979).

Rumex species occur in particular zones of flooding gradients in river flood-plains in The Netherlands. *Rumex acetosa* L. is mainly found on rarely flooded dikes and river levees, whereas *R. palustris* Sm. occurs on frequently flooded mud-flats of former river beds. *Rumex crispus* L. occupies intermediate sites in river flood-plains (Blom *et al.* 1990; Voesenek 1990). Inundations in Dutch river flood-plains during the growing season are erratic and can be classified as 'catastrophes'. Winter floods, however, are more or less predictable in timing and duration. It is hypothesized that *Rumex* species from stable, seldomly-flooded grasslands (e.g. *R. acetosa*) are characterized by early germination (shortly after achene release in the late summer/autumn) and a transient type of seedbank. *Rumex* species from habitats with a harsh winter season (predictable winter floods) and a catastrophical growing season (e.g. *R. palustris* and to a lesser extent *R. crispus*) will be characterized by delay mechanisms resulting in late (spring) and multiple germination flushes as well as a persistent type of seedbank.

This paper describes germination after achene release, viability of achenes during burial in an artifical seedbank and seedling emergence from buried achenes. All experiments in these three *Rumex* species had a reciprocal design and were conducted under field conditions. The objectives were to determine (a) the timing of germination (early vs. late; multiple germination cohorts), (b) the character of the seedbank (transient vs. persistent) and (c) the relation between these life-history traits and the field distribution of the species in a gradient with predictable winter and unpredictable summer floods.

MATERIALS AND METHODS

Plant material and Rumex habitats in river flood-plains

Rumex acetosa is a polycarpic perennial, with a fibrous rooting pattern (Voesenek & Blom 1987), which possesses a limited capacity for vegetative propagation (Grime *et al.* 1988). This species was studied in a meadow with a hay and aftermath management (acetosa-zone). The sward is dominated by *Poa trivialis* L., *Elymus repens* L. and *Alopecurus pratensis* L. This meadow is highly elevated and only occasionally flooded for very short periods.

Rumex crispus is a short-lived polycarpic perennial, with a distinct tap root (Grime *et al.* 1988). It occurs on intermediate sites in the elevational river gradient; inundations are frequent but of limited duration. This *Rumex* species was studied on the bank of a former river bed which was grazed by cattle (crispus-zone). Dominant plant species are *Elymus repens* L., *Agrostis stolonifera* L., *Potentilla reptans* L. and *Phalaris arundinacea* L.

Rumex palustris is a tap-rooted monocarpic annual, biennial or short-lived perennial (Voesenek & Blom 1987). *Rumex palustris* was studied on a mud-flat in a former river bed (palustris-zone). Dominant plant species in this zone are *Gnaphalium uliginosum* L., *Juncus bufonius* L., *Limosella aquatica* L. and *Rumex maritimus* L. The inundations in this area are frequent, deep and prolonged.

For use in all experiments achenes enclosed in perianths were collected in 1986 in the areas under study. The achenes were stored at room temperature in the dark. Achene mixtures of several plants belonging to one river population were used.

Germination after achene release

In a field experiment achenes of the three *Rumex* species were reciprocally sown in gaps (30 × 30 cm) created by the removal of the top-soil layer (2 cm). During the period of natural fruit release, achenes were slightly pushed into the soil surface in a grid pattern (256 achenes per plot; 1 cm distance between achenes). *Rumex acetosa* was sown in all three zones on 21–22 August 1986; *R. crispus* and *R. palustris* on 31 October 1986. A short-term flooding (25 October–10 November) caused a delay in sowing for *R. crispus* and *R. palustris* in the palustris-zone until 12 November 1986.

In *R. acetosa* the achenes are released from the flowering spike shortly after ripening (July/August). In both *R. crispus* and *R. palustris*, however, achene release is delayed until dispersal is enforced by the first autumn storms (October). During achene release, most perianths of *R. acetosa* are separated from the achenes. The opposite is true for *R. crispus* and *R. palustris*: achene drop does not release the achenes from the perianths. Natural germination after achene release was mimicked by sowing the achenes of *R. acetosa* without perianth, whereas the achenes of both other species were sown either with or without perianths. Germination (primary root ≥ 2 mm) was recorded every week; germinated achenes were removed from the plots. The experiments with *R. acetosa* were performed in three, those with *R. crispus* and *R. palustris* in two replicate plots per zone.

The soil-moisture content of the top 5 cm layer was measured in 70 cm^3 soil samples per zone every week.

Viability of achenes in an artificial seedbank

Achenes of all three *Rumex* species were reciprocally buried in the soil in the various zones. Twenty-five achenes were put in nylon bags (5 × 5 cm; mesh size: 0·25 × 0·10 mm) and subsequently buried in plots (1·2 × 1·2 m) at the time of natural achene release (*R. acetosa*: 21–22 August 1986; *R. crispus*: 31 October 1986; *R. palustris*: 23 October 1986). Every plot contained 36 bags with achenes of one species buried in a grid pattern at a depth of 5 cm. Every zone contained three plots, one for each species. Care was taken to minimize soil disturbance. On 5–11 (depending on the flooding regime of a certain zone) subsequent dates within a 2-year period, bags from each location (three replicates per species per zone) were retrieved from the field plots. In the laboratory, the bags were washed out with tap water. Intact achenes were incubated in petri-dishes (diameter: 70 mm) on two layers of moistened Schleicher & Schüll filter paper in a temperature-controlled germination cabinet: day temperature 25°C (12 h) and night temperature 10°C. The photosynthetic photon-flux density (Philips TL 8W/33XE3 tubes) during the light period was 30 µE m^{-2} s^{-1}. Previous experiments resulted in nearly complete germination within 1 week of all *Rumex* achenes under these conditions. Achenes not germinating within 2 weeks were stained with 1 % (w/v) solution of tetrazoliumchloride (Sigma) to test the viability (Moore 1972).

Emergence of seedlings from buried achenes

Achenes of the three *Rumex* species were buried in a reciprocal design. In every *Rumex* zone, 15 experimental plots were created; five replicate plots per species. In both the acetosa-zone and the crispus-zone the top-soil layer (approximately 2 cm) was removed

before sowing, to create a gap. This procedure was not necessary in the palustris-zone as long-lasting floods in winter and spring resulted in the mortality of nearly all established plants. In each plot ($1\cdot3 \times 0\cdot8$ m) achenes of one species were sown in five rows. Each row contained 10 sites spaced at 10 cm. At each site, two achenes were sown at a depth of 1 cm (100 achenes per plot). Achenes were sown at the onset of the growing season (acetosa-zone: 3 April 1987; crispus-zone: 24 April 1987; palustris-zone: 2 August 1988) and not at the time of seed release to avoid interference of sedimentation and erosion due to the winter floods. Emergence of seedlings was recorded every 3 days during the early weeks of the experiment, and then once in every 4 weeks towards the end of the growing season. Grazing in the acetosa- and crispus-zones was mimicked by clipping the surrounding vegetation.

RESULTS

Surface germination

Germination of *R. acetosa* achenes occurred in all *Rumex* zones (Fig. 1). The maximum percentage of germination was highest in the palustris-zone, intermediate in the crispus-zone and lowest in the acetosa-zone, which was positively correlated with the soil-moisture content of the top 5-cm layer of these zones (Fig. 2). Flooding of both the crispus- and palustris-zones during the last days of October probably caused a secondary dispersal of the remaining ungerminated achenes of *R. acetosa* and burial in the seedbank via cracks in the clay soil.

Both *R. crispus* and *R. palustris* showed higher maximum germination in the crispus-zone compared to the acetosa-zone. This difference was also positively correlated with the soil-moisture content (Fig. 2). In these two species the germination of achenes with a perianth was much reduced compared to achenes without a perianth (perianth-imposed inhibition). Furthermore, in *R. palustris* germination was limited at all times compared with *R. crispus*. In the case of these species, flooding also caused secondary dispersal and burial in the seedbank. Germination of *R. crispus* and *R. palustris* in the autumn in the palustris-zone was almost completely prevented due to the flooding regime.

Viability of achenes in an artificial seedbank

The number of viable achenes or the potential seedling recruitment in the artificial seedbank may decrease by predation, germination and death of achenes (Weaver & Cavers 1979). A depletion of viable achenes caused by fauna predation was negligible due to the fine-mesh size of the nylon bags. Germination and achene mortality can be distinguished; remnants of primary roots and achene coats were often found in the bags after germination. Death of achenes was characterized by a 'swollen' morphology and the inability to stain with tetrazoliumchloride.

Achenes of *R. acetosa*, buried in nylon bags in the different *Rumex*-zones, showed a clear decline in the percentage of viable achenes to approximately 20% after 2 years (Fig. 3). In all zones, 35–40% of the achenes germinated within 2 weeks after burial, resulting in a sharp decrease of the number of remaining viable achenes. The decline in the number of viable *R. acetosa* achenes in the acetosa-zone and the crispus-zone during the summer and spring of 1987 respectively was also caused by germination. The decreasing number of viable achenes of *R. acetosa* in the palustris-zone, however, was related to achene mortality. Achenes of this species obviously could not resist frequent and
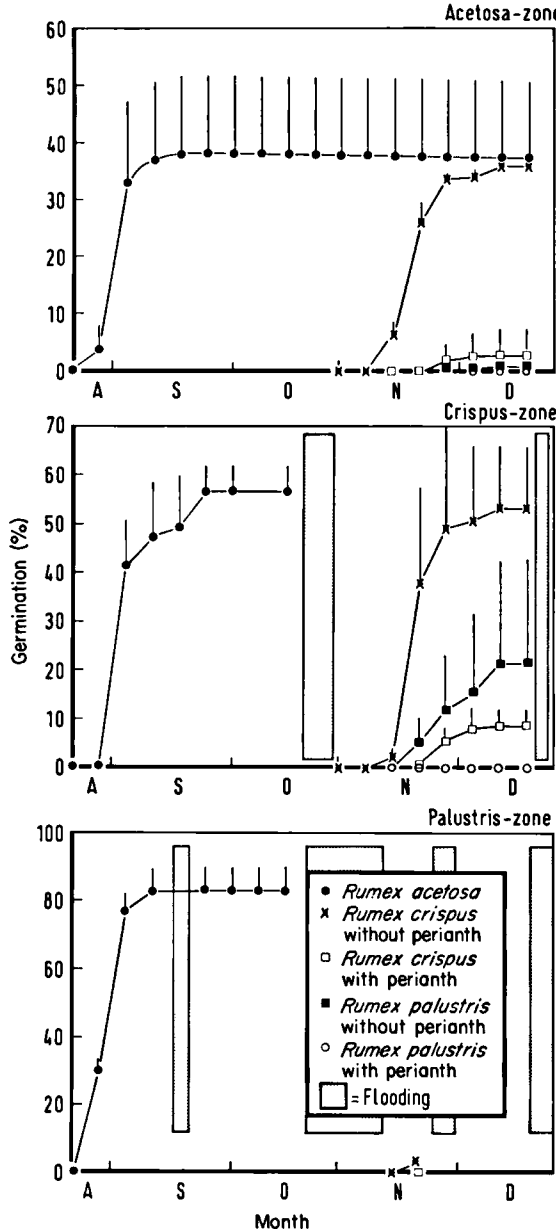
Fig. 1. Cumulative germination (%, mean + SD); *n* = 3 (*R. acetosa*) or 2 (*R. crispus* and *R. palustris*) of surface-sown achenes of three *Rumex* species in three *Rumex*-habitats. The zone with *R. acetosa* is only very occasionally flooded, whereas the zone with *R. palustris* is characterized by frequently occurring and prolonged floods. *R. crispus* occupies an intermediate position in this flooding gradient. Achenes were sown shortly after natural achene release.

prolonged floods. This is confirmed by laboratory experiments in which a low hypoxia tolerance of achenes of *R. acetosa* was observed (see Voesenek *et al.* 1992).

In all three zones, most achenes of *R. crispus* were still viable after 2 years of burial
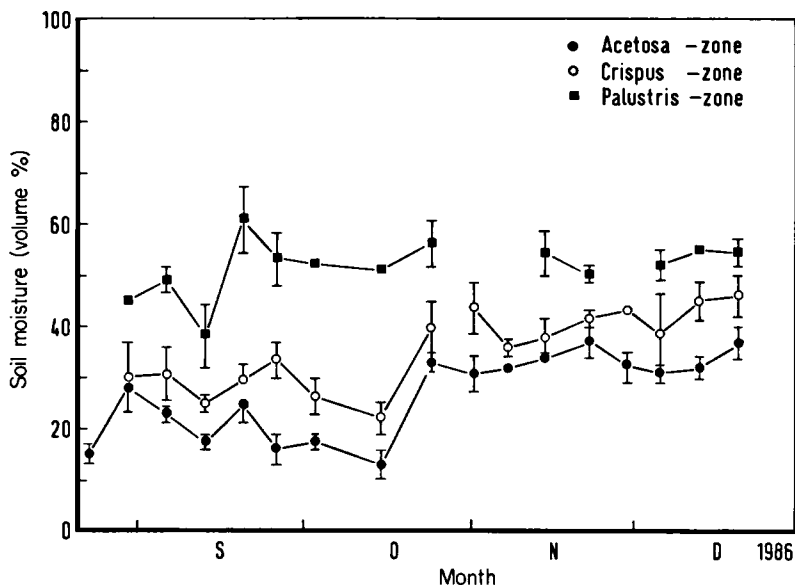
Fig. 2. The mean soil-moisture content by volume ($\pm$ 1 SD; $n = 3$) of the top 5 cm layer of the three *Rumex*-zones in a river area during the autumn of 1986.

(Fig. 3). Nevertheless, differences in seedbank behaviour still existed between the three zones. A viability of more than 80% of *R. crispus* achenes, buried for 2 years in the acetosa-zone, was observed. In the crispus-zone, with frequent but short-lasting floods, more germination occurred during the growing seasons of 1987 and 1988 resulting in a clear decline in the number of viable achenes in the seedbank. *Rumex crispus* achenes buried in the palustris-zone showed no decline in the number of viable achenes. Long-term floods, even in the growing season, did not affect the achene viability of this species.

Most *R. palustris* achenes remained viable (approximately 90%) after 2 years of burial in the various *Rumex*-zones (Fig. 3).

The results of artifical seedbank experiment indicate that the seedbanks of *R. crispus* and *R. palustris* were rather persistent compared to *R. acetosa*. Transplantation of achenes into soils of other zones hardly influenced their seedbank character, indicating that achene properties overrule the habitat differences among the various zones.

Emergence of seedlings from buried achenes

In all zones, *R. acetosa* seedlings emerged within the first 40 days after sowing to a maximum of 40–50% (Fig. 4). Very few seedlings emerged during the remaining growing season. No emergence at all occurred during and after inundation periods in the summer (crispus-zone) and the autumn (palustris-zone).

Limited seedling emergence of *R. crispus* occurred in the acetosa-zone (maximum approximately 30%), whereas a high germination percentage was observed in the palustris-zone. Intermediate germination percentages were observed in the natural habitat of *R. crispus* (Fig. 4). Emergence percentages appeared to be positively correlated with the soil-moisture content of the respective zones (Fig. 2). New seedlings emerged in
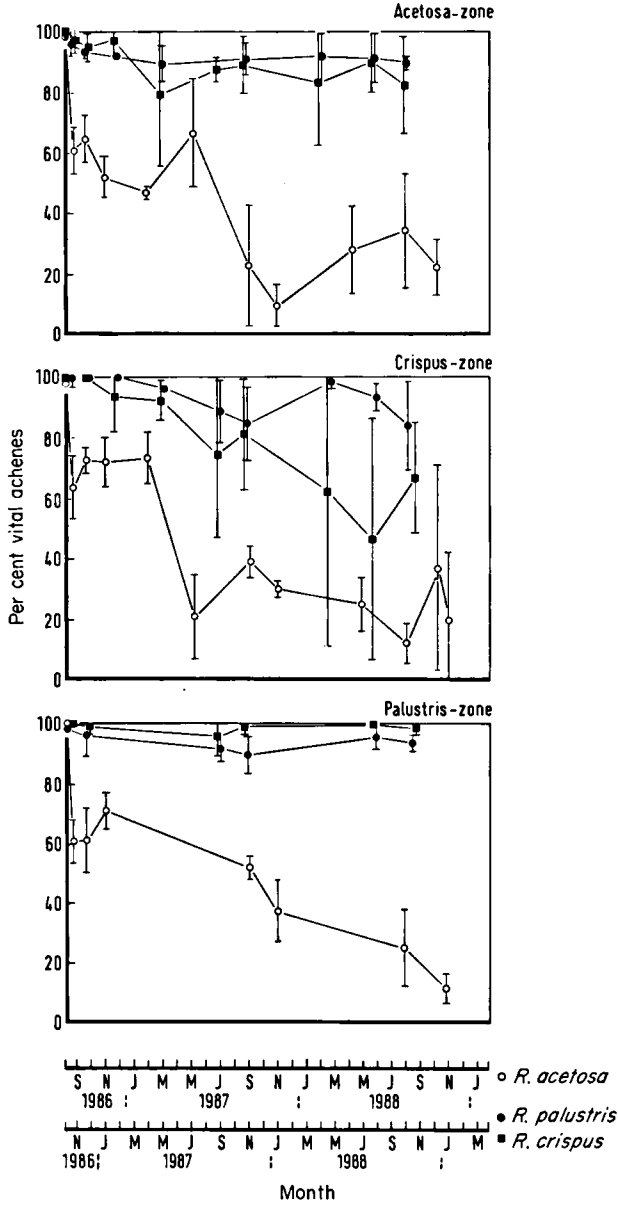
Fig. 3. The percentage of viable achenes ($\pm$ 1 SD; $n = 3$) of *Rumex acetosa, R. crispus* and *R. palustris* buried at a depth of 5 cm in three *Rumex*-zones. Achenes were buried at the moment of natural release.

the crispus-zone shortly after a summer flood. A second emergence flush was absent after the autumn flood in the palustris-zone (Fig. 4).

The emergence of *R. palustris* seedlings was characterized by low overall percentages (Fig. 4). Most seedlings were found in cracks caused by drying of the clay soil. The various zones showed no differences in seedling emergence and like both of the other species no seedling emergence occurred during floods. But, as with *R. crispus*, new seedlings emerged
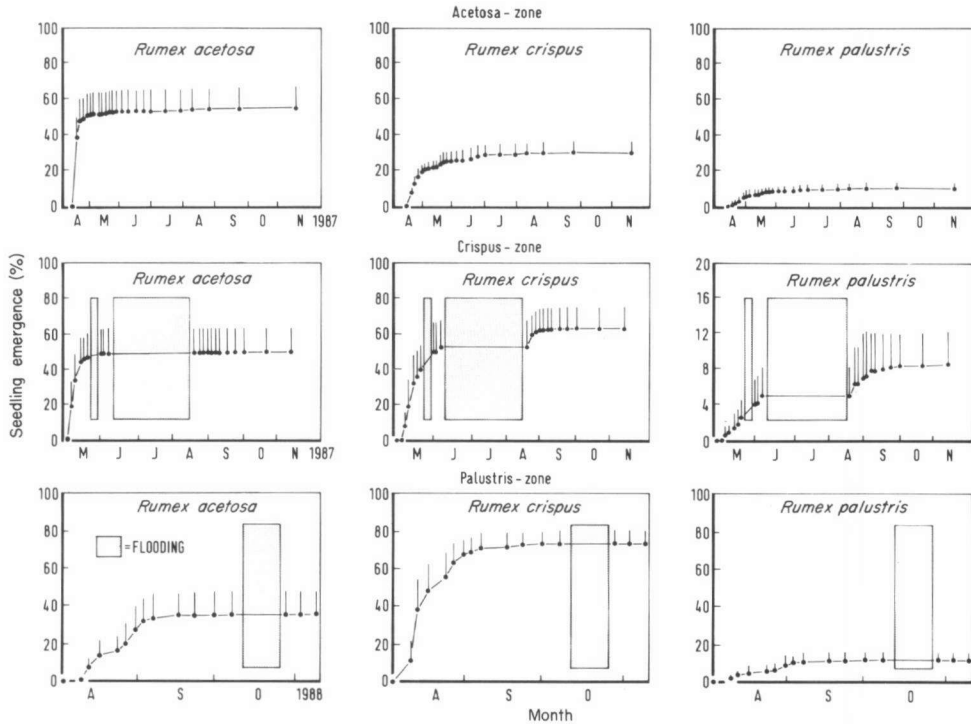
Fig. 4. Cumulative seedling emergence (%, mean + SD) of *Rumex acetosa*, *R. crispus* and *R. palustris*; achenes buried at a depth of 1 cm in various *Rumex*-habitats of the river area. Experiments started at the onset of the growing season (acetosa-zone) or after the subsidence of winter/spring floods (crispus/palustris-zone).

shortly after subsidence of the summer flood in the crispus-zone. No extra emergence occurred in its natural zone after an autumn high water (Fig. 4).

DISCUSSION

In *R. acetosa*, early achene release, easy separation of perianth and achene and therefore lack of perianth-imposed inhibition of germination, all facilitate early (i.e. autumn) germination of this species. The relatively open character of the grassland with *R. acetosa* due to summer mowing favours seedling establishment in autumn. Additional gaps are created in this period by the trampling of cattle and the activity of moles. Early germination before the initiation of growth of grasses is an important strategy which is also observed in other grassland species; this trait will contribute to a higher competitive performance (During *et al.* 1985; Van der Toorn & Pons 1988) and will not decrease survival probabilities of seedlings as harsh conditions (e.g. predictable winter flooding) are lacking in this highly elevated grassland. The timing of germination of *R. acetosa* in river flood-plains is in agreement with observations of Putwain & Harper (1970) and Roberts & Boddrell (1985). Due to early germination (Fig. 1) only a limited number of achenes of *R. acetosa* remain ungerminated and will eventually enter the seedbank. The number of achenes entering the seedbank will vary from year to year due to annual variations in surface germination related to the moisture content of the top-soil layer. This

is in agreement with Oomes & Elberse (1976) who showed that *R. acetosa*, compared with other species, germinated less uniformly and at a lower rate in micro-sites with low soil moisture.

The hypothesis of a transient seedbank in *R. acetosa* is confirmed by the data of the artificial seedbank experiment (Fig. 3). Nearly all ungerminated achenes entering the seedbank in the autumn (20–60% of the total achene release) will germinate in the next spring or summer. If germination is prevented by prolonged floods (palustris-zone), achenes show a high mortality rate, indicating a lack of resistance towards flooding.

Germination of *R. crispus* and *R. palustris* immediately after achene drop (all achenes being enclosed in perianths) is limited; both species are characterized by late germination in the following spring or summer. Delay mechanisms which inhibit germination in these species are the long attachment of achenes to the mother plant, the low temperatures of the late autumn when the achenes finally drop and the perianth-imposed germination inhibition. Inhibition of germination due to the presence of the perianth has been described for *R. obtusifolius* and *R. crispus* (Cavers & Harper 1966). The field sites of *R. crispus* and *R. palustris* in river flood-plains are characterized by predictable and extremely long winter floods, respectively. Germination and establishment shortly before the winter would probably result in a very high seedling mortality and thus in a decreased fitness.

Many studies show a life-history trade-off between survival and reproduction in relation to the timing of germination. Early germination will favour reproduction, whereas late germination favours survival (Baskin & Baskin 1972; Arthur *et al.* 1973; Marks & Prince 1981; Venable 1984). Late germination of *R. palustris* indeed results in fewer, shorter, secondary flowering stems, and consequently, fewer achenes than in earlier germinated cohorts (Van der Sman *et al.* 1992). Germination later than June even results in the delay of flowering to the following growing season. *Rumex palustris* needs a certain number of leaves before a 'critical' photoperiod has passed, to induce flowering. The delay in reproduction, which often occurs in *R. palustris* when growing in its natural habitat, may be interpreted as a strategy which combines high survival rates with high levels of reproduction (see also Van der Sman *et al.* 1991).

The extra flushes of seedling emergence observed in both wetland species (*R. palustris* and *R. crispus*) after a summer flood of more than 2 months (Fig. 4) can be interpreted as a trait which acts as a buffer towards population elimination due to 'catastrophes'. Intraspecific variation in dormancy levels, probably related to the achene polymorphism which is described for *R. obtusifolius* and *R. crispus* (Cavers & Harper 1966), and altered environmental conditions due to flooding-induced disturbances probably determine the occurrence of multiple germination cohorts.

More than 90% of the achenes released by *R. crispus* and *R. palustris* will either enter the seedbank before or during the winter flooding or float on the water surface to other riparian habitats. In contrast to *R. acetosa*, both *R. palustris* and, to a lesser extent, *R. crispus* will float for several months under laboratory conditions (data not shown).

Variable environmental conditions, 'catastrophes' and disturbances (*sensu* Grime 1979) are often associated with persistent types of seedbanks (Thompson 1978; Thompson & Grime 1979; Westoby 1981; Smits *et al.* 1990). Both *R. palustris* and to a lesser extent *R. crispus* form a persistent type of seedbank (Fig. 3).

In summary, early germination, a transient type of seedbank, flood-intolerant achenes and a lack of post-flood germination flushes are traits which restrict seedling establishment and survival of *R. acetosa* to sites in river flood-plains which have no seasonal harshness (floods).

Late germination, a persistent seedbank, flood-tolerant achenes and multiple post-flood germination flushes are life-history traits associated with a predictable harsh season and unpredictable 'catastrophes'. These traits fit well into the flooding regime of the lower sites of river flood-plains. The differentiation between the crispus-zone and the palustris-zone lies mainly in duration and depth of floods, being much longer and deeper in the palustris-zone. This might explain the more persistent character of the *R. palustris* seedbank and the overall lower percentages of germination when compared to *R. crispus*. Late germination enables seedling establishment of both *R. crispus* and *R. palustris* in stable, undisturbed grassland, due to a subordinate competitive position among early germinators and growing grasses.

In conclusion, timing of germination and seedbank characteristics are important life-history traits, at least partly explaining the field location of *Rumex* species in river flood-plains. The predictability of a harsh season (winter floods) determines the timing of germination. The type of seedbank is closely related to the intensity of 'catastrophes' and disturbances.

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