Adaptations to flooding in plants from river areas

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ABSTRACT


Flooding frequencies and intensities determine both species composition and the behaviour of individual plants along many rivers in the world. In this context, this paper describes the vegetation zonation associated with the fluctuating water levels of the river Rhine in the eastern part of The Netherlands. To obtain insight into the morphological and physiological processes of plants that have been shown to possess contrasting tolerances to flooding, certain species were chosen as being representative of the vegetation types from the river foreland and subsequently used in experimental studies. These species, of the genera Rumex and Chenopodium, were subjected to various flooding regimes in order to study their adaptive responses upon waterlogging of the soil, submergence and related changing environmental factors.

This study has revealed that differential responses towards flooding in plants can be explained, at least partly, by an ability to elongate petioles and stems in order to protrude above the water surface. The hormone ethylene is involved in the regulation of this process. Renewed contact between leaves and the open air after submergence stimulates the formation of a new aerenchymatous root system in the flood-tolerant species. Increased porosity enables the plants to perform longitudinal transport from aerial and photosynthetic oxygen to the rhizosphere. The internal aeration system of flood-intolerant species is not sufficient to sustain an aerobic stale in the root-soil environment. Another mechanism plants use to survive flooding is to change their timing of reproduction. Two strategies are involved: some species delay their flowering and seed production during flooding periods and survive as vegetative plants; others are able to accelerate flowering during short dry periods in order to produce seeds in the short intervals between two successive floods.

The model system in which individual plants serve as indicator species, while additionally representing large groups of co-occurring plants, appears to be a manageable tool in studies on adaptations to flooding.

INTRODUCTION

Flooding is an important environmental factor that influences plant composition and plant growth in many parts of the world. At least two types of flooding can be distinguished: regular floods, which result from the tidal
movements of primarily salt water and are most often found in coastal areas; and irregular floods, which predominantly occur along rivers and are caused by unpredictable changes in the water levels of these rivers. The adaptations observed in plants exposed to regular floods may differ greatly from the responses of plants occurring in areas subjected to more irregular water movements. The behaviour of plants from coastal tidal areas has been extensively reported (e.g. Beeftink, 1975; Barnes, 1977; Jefferies and Davy, 1979; Blom, 1983; Ernst, 1985; Huiskes et al., 1985, 1987; Rozema et al., 1985; Van Diggelen, 1988), while the effects of regular floods on plants have been described by, for example, Etherington (1983), Kozlowski (1984), Crawford (1987), Blom (1990), Davy et al. (1990), Ernst (1990) and Jackson (1990).

This paper reports on vegetation zonation owing to variations in the hydrological characteristics of river areas and on flooding responses with adaptive value in plants occupying low- to high-situated habitats in river areas in The Netherlands. The flood plains in the Dutch river ecosystems consist of river banks, wetlands and former river beds. The flood plains are subjected to inundation at times when the river is carrying large quantities of water. A part of that water originates from melting snow in the mountains of Switzerland. The strongly fluctuating water levels that occur both in winter and during the growing season are, however, mainly a consequence of peak periods in precipitation. The principal river, the Rhine, and its tributaries drain large areas before reaching The Netherlands. The mean discharge of the river Rhine is 2200 m$^3$ s$^{-1}$, but during extremely wet periods very high maxima of 19 500 m$^3$ s$^{-1}$ have been found. The flooding of grasslands during the growing season used to be a very rare phenomenon due to the protection provided by small dikes against high water. In the last few decades, however, extremely high water levels have brought about more frequent flooding of these forelands in spring and summer. These floods probably result from river bed "improvements", an increase in the number and size of hydrotechnical works and the improved drainage of upstream agricultural areas. Consequently, much of the precipitation is discharged, thus causing larger fluctuations in water levels within shorter lapses of time, both in winter and summer. The end result is that large areas of the river forelands are inundated for longer or shorter periods. The time of the year when the floods occur, the height of the water level and the duration and frequency of the floods are unpredictable (van de Steeg, 1984).

The hypothesis on which our studies have been based is that plants growing in those river flood plains must have developed adaptations to survive periods of severe inundation. The severity of the flooding can range from waterlogging of the soil to submergence of the whole plant. While the responses of plants in waterlogged soils may differ from those of plants facing submergence, both conditions greatly influence the physiology, morphology and population biology of the plants (van der Sman et al., 1988; Blom, 1990; Laan,
1990; Voesenek, 1990). As many river forelands are characterized by differences in elevation and thus to the extent to which they are inundated, plant zonation caused by these differences can often be distinguished. At present, we are studying indicator species distributed along the elevation gradients in the river ecosystems. These species represent larger groups of plants — vegetation types or communities — that occur in the same habitats. Species of the genera *Rumex* and *Chenopodium* have been chosen as indicators. We have applied long-term observations in the field to study the variation in species composition and plant behaviour in relation to flooding and related environmental changes, and have conducted experiments to obtain insight into the morphological and physiological responses of the indicator plants.

This paper describes the hydrology and related zonation of the vegetation types to which the species under study belong. *Rumex* species from high, intermediate and low elevated sites were experimentally subjected to various flooding regimes in order to identify and quantify any relevant adaptive feature and to test whether their distribution might be caused by a differential response to flooding. We also compared the reproductive adaptations of *Rumex* plants with the responses of *Chenopodium* species from over-wet soils. The mechanisms in plants and the adaptive values of the various responses on flooding will be discussed.

VEGETATION ZONATION IN RELATION TO HYDROLOGY

In the river Rhine, extremely high water peaks alternate with periods of low water levels; the pattern and duration of these changes are unpredictable (Fig. 1). This rain-borne pattern almost totally masks the more regular rhythm of relatively low water levels in autumn and winter, and higher levels from April to July, which used to be caused by the huge quantities of melting snow from the higher mountains in the Swiss Alps. This hydrological pattern enables us to distinguish several zones of decreasing elevation that are subjected to flooding at increased frequencies and for longer periods of time. From the ecological point of view, it is the main vegetation period that is of special interest, and in that period four hydrological zones can be distinguished, each characterized by its own vegetation types (Table 1).

The seldomly flooded zone is occupied by vegetation types intolerant to flooding. Under natural conditions, an ecotype consisting of hardwood forest can be expected.

The frequently flooded zone is inhabited by tolerant vegetation types — a *Salix* softwood and representatives of the Phragmitetalia.

In the mainly agricultural river area, we find predominantly grasslands of the Arrhenatherion and Agrostietalia communities. Owing to the long periods of inundation that the over-wet zone is subjected to, only summer annuals are able to occur as pioneer plants.
WATER LEVELS RHINE

Fig. 1. Changes in the water level of the river Rhine near Nijmegen, The Netherlands, in 1986 and 1987. The zonation of *Rumex* species is shown.

<table>
<thead>
<tr>
<th>Hydrological zonation</th>
<th>Ecotypes</th>
<th>Vegetation types</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Natural</td>
</tr>
<tr>
<td>Seldomly flooded</td>
<td>Hardwood forest</td>
<td>Ulmion</td>
</tr>
<tr>
<td>Frequently flooded</td>
<td>Softwood forest Wetland plants Closed to open grassland</td>
<td>Salicion albae Phragmitetea</td>
</tr>
<tr>
<td>Over-wet</td>
<td>Summer annuals</td>
<td>Bidentetea</td>
</tr>
<tr>
<td>Aquatic</td>
<td>Aquatic plants</td>
<td>Potametea</td>
</tr>
</tbody>
</table>

High turbidity during the periods of high water excludes plant growth in large parts of the aquatic zones of the Rhine tributaries. Only in the stagnant waters of the river foreland do such aquatic plants as *Nymphoides peltata* (S.G. Gmel.) O. Kuntze and *Nuphar lutea* (L.) Sm. occur.

Hay fields and grazed grasslands are the most commonly occurring ecosys-
ADAPTATIONS TO FLOODING IN PLANTS FROM RIVER AREAS

Rumex species and their vegetation types in an outdike river foreland and a seepage area protected by dikes. Three transects each were described in the river area near Nijmegen, The Netherlands

<table>
<thead>
<tr>
<th></th>
<th>Outdike foreland</th>
<th>Indike seepage area</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R. acetosa</td>
<td>R. crispus</td>
</tr>
<tr>
<td>Arrhenatheretum</td>
<td>3 1 1</td>
<td>-  -</td>
</tr>
<tr>
<td>Lolio–Cynosuretum</td>
<td>+ 1 1</td>
<td>+  +</td>
</tr>
<tr>
<td>Transition type</td>
<td>-  -</td>
<td>+  2</td>
</tr>
<tr>
<td>Ranunculo–</td>
<td>-  -</td>
<td>+  -</td>
</tr>
<tr>
<td>Alopecuretum</td>
<td>-  -</td>
<td>-  -</td>
</tr>
</tbody>
</table>

\(^1\)Numbers per m\(^2\): + = \leq 0.5; 1 = 0.5–1.5; 2 = 1.5–2.5; 3 = 2.5–3.5, etc.; - = Rumex species absent.

In the higher lying zones. In the Rhine region of the eastern part of The Netherlands, we have compared the floral composition of such grasslands situated between the main dikes and the river with the vegetation of the inland seepage area behind the dikes. In both areas, we distinguished four grassland types; within each type various species of Rumex can be found (Table 2). Also within each type certain groups of plants reach an upper limit, which is probably determined by the competitive ability of the species; the lower limits are determined by the degree of tolerance to flooding. The highest lying grassland is the hay field community Arrhenatheretum elatioris, which consists of species such as Arrhenatherum elatius (L.) J. & C. Presl, Trisetum flavescens (L.) Beav., Anthriscus sylvestris (L.) Hoffm. and Heracleum sphondylium L. The second grassland type at a lower elevation can be classified as Lolio–Cynosuretum. The main species here are Lolium perenne L., Plantago lanceolata L. and Ranunculus acris L.. Species of both communities are intolerant to flooding. An intermediate grassland type, here indicated as a transition (Table 2), consists mainly of Alopecurus pratensis L., Cirsium arvense (L.) Scop. and Elymus repens (L.) Gould. At the lower elevations a group of species, often with aerial stolons, becomes competitive and forms the flooding-tolerant community of the Ranunculo–Alopecuretum geniculatis. Characteristic species are Agrostis stolonifera L., Alopecurus geniculatus L., Ranunculus repens L. and Lysimachia nummularia L.

RUMEX ZONATION IN RELATION TO FLOODING

Rumex species belong to a cosmopolitan genus that is one of the few genera with species clearly zoned along the flooding gradient in the river foreland (Fig. 2). Rumex acetosa L. and Rumex thyrsiflorus Fingerh. are polycarpic perennials that mainly flower in the second growing season. They are re-
restricted to the higher lying zones that are only seldom flooded in summer, and then only for very short periods. *Rumex thyrsiflorus* grows in sandy soils, *R. acetosa* in more clayish substrates. The former occurs mainly in hay fields, the latter mainly in grazed areas. *Rumex obtusifolius* L., *Rumex crispus* L. and *Rumex conglomeratus* Murr. are relatively short-lived polycarpic perennials. *Rumex obtusifolius* mainly occurs in the transitional, infrequently flooded zone between the *R. acetosa* habitat and the frequently flooded zone of *R. crispus* and *R. conglomeratus*. These three perennial species are mainly found in cattle-grazed grasslands. *Rumex palustris* Sm. and *Rumex maritimus* L. are monocarpic annuals, biennials or short-lived perennials inhabiting the over-wet zones. The length of their life cycle depends on the environmental conditions; flowering may occur if the seeds germinate before June. These species occur on river banks and along former river beds, characterized by frequent, deep and prolonged floodings. These mud flats are only exposed to the open air during a part of the summer season and possess a badly aerated clayish soil. *Chenopodium rubrum* L., on the other hand, is more characteristic of the well-aerated sandy soil of river banks.

The zonation of *Rumex* species in flooding gradients is clearly demonstrated in Tables 2 and 3. In the higher river foreland, *R. acetosa* is restricted to the Arrhenatheretum and Lolio–Cynosuretum, both communities of the flood-sensitive Arrhenatherion alliance. *Rumex crispus* and *R. conglomeratus* attain their optimum conditions in the flood-tolerant Ranunculo–Alopecuru-retum geniculatis community. In the low dynamic indike seepage area with more restricted flooding depths, *R. acetosa* is also able to inhabit the transitional zone. *Rumex palustris* and *R. maritimus* are characteristic species of the Rumicetum maritimi community of the over-wet areas.
TABLE 3

Zonation of *Rumex* species on an intact and eroded slope along a clay pit in the river area

<table>
<thead>
<tr>
<th>Intact slope</th>
<th>Eroded slope</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ace.</td>
</tr>
<tr>
<td>Lolio–Cynosuretum</td>
<td>1'</td>
</tr>
<tr>
<td>Juncetum compressi</td>
<td>1</td>
</tr>
<tr>
<td>Rumicetum maritimi</td>
<td>2</td>
</tr>
</tbody>
</table>

1' Numbers per m², see Table 2.


ROOT RESPONSES

As the first effects of flooding appear in the soil, special attention has been given to changes in the morphology of root systems. A direct effect of flooding is a major decrease in the gas exchange between the atmosphere and the soil (Armstrong, 1979; Kozlowski, 1984). Waterlogged roots must function in almost anaerobic soils as any oxygen remaining in the soil after flooding is very soon exhausted by respiration of the roots and soil micro-organisms (Ponnampeteruma, 1984). Only a small zone near the water surface may remain oxygenated (Drew, 1983). In *Rumex*, there are at least three morphological changes that the root can perform in response to anaerobiosis (Laan et al., 1989b; Voesenek et al., 1989): (1) an increase in root branching; (2) the development of new adventitious roots; (3) an altered vertical distribution of the laterals, with more roots concentrated in the upper layers of the soil. Concomitant with the alterations in root morphology are changes in root anatomy. A high porosity due to expansion of the intercellular spaces is one of the most obvious adaptive responses. The formation of large channels in the root cortex enhances the diffusion of atmospheric or photosynthetic oxygen from the shoot to the roots so that aerobic respiration and growth can be maintained (Justin and Armstrong, 1987; Laan et al., 1989a, b, 1990).

In an experiment in which three *Rumex* species were grown under aerobic and anaerobic conditions, clear-cut differences in gas space development of the newly formed laterals were found. Under anaerobic conditions, the flood-intolerant species *R. thyrsiflorus* appeared to be unable to form aerenchyma in the cortex of the primary roots; the cross-sectional area occupied by the intercellular spaces was ~ 7%. A small increase to 11% was found in the newly formed roots that developed under anaerobic conditions. In *R. crispus*, the primary roots formed under aerobic conditions have only a low porosity. However, as a result of aerenchyma formation a four-fold increase to 28% was recorded in new roots developed under anaerobic conditions. In the flood-tolerant *R. maritimus*, aerenchyma was formed in both primary and newly
formed roots; this was reflected in a high cross-sectional area of intercellular spaces in the primary laterals (14%), which increased to ~36% in the new roots (Laan et al., 1989b). Experiments investigating root architecture and anatomy clearly showed that aerenchyma formation is closely connected with an increase in root length upon flooding. A primary beneficial effect of the change in root morphology is that a high root porosity or the development of aerenchyma enables longitudinal internal oxygen transport in the plant. To a large extent, this process determines flood tolerance, as under waterlogged and even under drained conditions a large portion of the total root oxygen demand is supplied by aerial oxygen (Laan et al., 1990). Moreover, under conditions of total submergence of the shoot, photosynthetic oxygen can also be used for root respiration (Table 4). By this phenomenon, a state of aerobiosis can be maintained by the flood-tolerant species under situations of low oxygen concentration in the root environment. Although flood-intolerant *Rumex* species showed some internal aeration, this appeared to be insufficient for sustaining an aerobic state in the root system.

A second advantage of the formation of aerenchyma in new roots is that the plant oxidizes a certain part of the soil, including the rhizosphere. In this way, the uptake of essential macro-nutrients can be improved and the uptake of potential phytotoxins prevented (Laan et al., 1989a; Laanbroek, 1990). We may therefore conclude that the size of the root system, the distribution of the laterals over the tap root, the ability to form new aerenchymatous roots

| TABLE 4 |

| Contribution of longitudinal internal oxygen transport to respiration in *Rumex* species from dry to wet environments (in percentages ± SE of total root respiration at COPR = ~55 μM O₂) |

(a) A comparison of three species under aerobic and anaerobic conditions. Age of plants = 5–7 weeks

<table>
<thead>
<tr>
<th></th>
<th><em>R. thyrsiflorus</em></th>
<th><em>R. crispus</em></th>
<th><em>R. maritimus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Aerobic</td>
<td>&lt;2</td>
<td>22±4</td>
<td>29±5</td>
</tr>
<tr>
<td>Anaerobic</td>
<td>&lt;5</td>
<td>39±2</td>
<td>54±8</td>
</tr>
</tbody>
</table>

(b) *R. maritimus* subjected to different submergence levels of the shoots (data after Laan and Blom, 1990)

<table>
<thead>
<tr>
<th>Shoot submergence (%)</th>
<th>25</th>
<th>50</th>
<th>75</th>
<th>100</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>38±10</td>
<td>26±5</td>
<td>15±3</td>
<td>&lt;5</td>
</tr>
</tbody>
</table>

1COPR means critical oxygen pressure for respiration, i.e. the oxygen concentration of the solution below which respiration depends on oxygen concentration (see Laan et al., 1990).
and the degree of internal aeration due to differences in porosity at least partly explain the differential responses towards flooding in *Rumex* species.

**SHOOT RESPONSES**

Species of the more elevated areas, *R. acetosa* and *R. thyrsiflorus*, succumb to flooding. Species of the intermediate and lower areas, *R. obtusifolius*, *R. crispus*, *R. conglomeratus*, *R. palustris* and *R. maritimus*, generally survive prolonged and deep floods if one or more of their leaves protrude above the water surface. This is functionally related to an increase in photosynthetic area and the diffusion of air to the oxygen-deficient roots (Laan and Blom, 1990).

Experiments indicate that shoot responses such as petiole and stem elongation are regulated by the gaseous growth substance ethylene (Voosenek and Blom, 1989; Voosenek et al., 1990). The effects of ethylene vary significantly between the *Rumex* species and depend on the interaction between a plant’s sensitivity towards ethylene and the active endogenous concentrations.

Osborne (1985) distinguished three types of target cells in plants, based on their growth responses to ethylene and other growth substances such as auxin or gibberellin. Type 1 cells elongate in response to auxin, but lateral expansion is slightly inhibited by ethylene. Cells in abscission zones, classified as Type 2 cells, are stimulated to elongate in response to ethylene, but not in response to auxin. Type 3 cells, often found in aquatic and semi-aquatic plants, expand in response to both auxin and ethylene. When the two hormones are supplied simultaneously, the effects are additive, resulting in “supergrowth” (Stange and Osborne, 1988). The sensitivity of petioles of *R. acetosa*, *R. crispus* and *R. palustris* to ethylene was studied in experiments in which ethylene and other growth substances were applied exogenously. Intact plants as well as excised petioles were used in these experiments. In *R. acetosa*, the application of ethylene (1–20 p.p.m.) resulted in equal or slightly inhibited growth during a 4-day period (Voosenek and Blom, 1989). The inhibited extension of petioles in this species resulted from reduced cell expansion (Voosenek et al., 1990). Both other species, however, showed a marked stimulation of cell expansion that resulted in elongated petioles (up to 200% of control). Completely submerged *Rumex* plants showed very similar growth responses. Preliminary results have indicated that the simultaneous application of a gibberellin (GA₃; 10 μM) and ethylene (5 p.p.m.) increases the length of petioles of *R. crispus* and *R. palustris* even more. This additive effect must be interpreted as “supergrowth”. In summary, from these results it is obvious that petioles of *R. acetosa* mainly contain target cells belonging to Type 1, whilst *R. crispus* and *R. palustris* possess predominantly Type 3 cells.

Plants regulate their internal ethylene concentrations through diffusion to the atmosphere and the activity of enzymes that control the production rate
(Osborne, 1984). Enzyme activity can be influenced by environmental stress and by ethylene itself. To study the endogenous ethylene concentration and ethylene production, we have to consider two fundamentally different flooding regimes: complete and partial submergence. Complete submergence results in the entrapment of ethylene in the plant, a consequence of the 10 000-fold lower ethylene diffusion coefficient in water (Jackson, 1985). Regulation of the endogenous ethylene concentration by diffusion to the atmosphere is therefore strongly hampered. All *Rumex* species under study showed a nearly three-fold increase in the internal ethylene concentration within 12 h after the onset of submergence (Table 5). These enhanced ethylene levels are related to inhibited petiole growth in *R. acetosa* and the stimulation of growth in both other species. Enhanced growth can restore leaf–atmosphere contact if the distance to the water surface can be bridged (Voesenek and Blom, 1989). Long-term survival of *R. crispus* and *R. palustris* under flooded conditions can only be guaranteed if the shoot reaches above the water surface. This is not so in *R. acetosa*; plants of this species die despite the fact that the leaf tips protrude above the water surface (Table 6). This is probably related to limited or hampered oxygen diffusion through the leaves and petioles to the roots.

Ethylene production in response to partial submergence or waterlogging has been monitored with a recently developed and very sensitive laser-driven intracavity photoacoustic detection system (Harren et al., 1990). The production of ethylene increased two-fold in *R. acetosa* during waterlogging, whereas in both *R. crispus* and *R. palustris* there was a nearly 20-fold increase in production. Petiole growth was not influenced in *R. acetosa*, while growth stimulation was observed in both other species (Voesenek, 1990).

In summary, the results with respect to ethylene economy indicate that *Rumex* species have a finely tuned balance between ethylene production, concentration and sensitivity (type of target cell). However, complete submergence interferes with this balance between concentration and sensitivity due to the inhibited ethylene diffusion to the atmosphere. In *R. acetosa*, this may lead directly to inhibited growth and so contributes to the low flooding resistance of this species.

### TABLE 5

The endogenous ethylene concentration (p.p.m. ± 1 SE) in submerged (~ 12 h) and non-submerged shoot tissue of *R. acetosa*, *R. crispus* and *R. palustris*

<table>
<thead>
<tr>
<th></th>
<th>Control</th>
<th>Submerged</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>R. acetosa</em></td>
<td>0.28 ± 0.07</td>
<td>0.76 ± 0.17</td>
</tr>
<tr>
<td><em>R. crispus</em></td>
<td>0.34 ± 0.05</td>
<td>0.83 ± 0.16</td>
</tr>
<tr>
<td><em>R. palustris</em></td>
<td>0.26 ± 0.02</td>
<td>0.64 ± 0.07</td>
</tr>
</tbody>
</table>
TABLE 6
Survival (%; n = 8) of Rumex species after 3, 6 and 9 weeks of partial and complete submergence (a greenhouse experiment; data according to Voesenek, 1990)

<table>
<thead>
<tr>
<th>Duration (weeks)</th>
<th>3</th>
<th>6</th>
<th>9</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>R. acetosa</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf tips above water surface</td>
<td>88</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Completely submerged</td>
<td>38</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>R. crispus</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf tips above water surface</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Completely submerged</td>
<td>100</td>
<td>38</td>
<td>13</td>
</tr>
<tr>
<td><strong>R. palustris</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf tips above water surface</td>
<td>100</td>
<td>100</td>
<td>88</td>
</tr>
<tr>
<td>Completely submerged</td>
<td>100</td>
<td>50</td>
<td>0</td>
</tr>
</tbody>
</table>

REPRODUCTIVE STRATEGIES

Rumex maritimus and Chenopodium rubrum were chosen as experimental material for our studies on flowering and seed production in response to flooding and related environmental factors.

While both species occur on the same low-lying river banks that are frequently flooded for long periods of time, they seem to have adopted different strategies for surviving this extreme habitat. Throughout the growing season, whenever the floods have subsided, varying numbers of C. rubrum plants can be found — both larger individuals and sometimes quite large numbers of very small ones. All plants flower and then die at the end of the growing season. Rumex maritimus can be found abundantly in one year and only sparsely in the next, depending on the prevailing conditions. Flowering may occur during the first year of growth, but in some years large numbers of vegetative individuals still remain at the end of the growing season. Figure 3 presents the results of greenhouse experiments in which the effects of different waterlogging regimes on the growth of both species were studied. Chenopodium rubrum plants suffered from waterlogging; the number of leaves and biomass decreased significantly. In R. maritimus, a small decrease in leaf number, but a significant increase in stem length, was found under flooded conditions. Reproductive responses (Fig. 4) showed remarkable differences between the two species. Both species were strongly affected by waterlogging applied at various stages of the life cycle (van der Sman et al., 1988). In C. rubrum, there was a tendency towards reduction of seed output, while in R. maritimus there was an increase in seed output compared with non-waterlogged plants.
Fig. 3. Effects of flooding on the growth parameters of *C. rubrum* and *R. maritimus* (*n* = 5; ± SE). Experiments were carried out in a greenhouse where 6-week-old plants were partially submerged for 6 weeks (biomass in g dry weight).

Fig. 4. Effects of flooding on the reproductive parameters of *C. rubrum* and *R. maritimus*. Experiments were carried out in a greenhouse. Plants were subjected to partial submergence for 0, 2 and 6 weeks at an earlier and later stage of the life cycle.
To bridge the gap between these entirely conditioned circumstances and the natural situation, large-scale experiments were performed in an experimental garden which mimicked the flooding situation in the river habitats. In these garden plots, plants were kept under submerged conditions for varying periods of time. Germination was also varied according to the applied flooding regimes, as germination of these species can only take place after the floods have subsided.

These experiments have shown that *C. rubrum* can barely survive a prolonged period of submergence. Floods lasting 4 weeks always resulted in the death of all plants of this species. Ten-day-long floods showed survival of some plants, depending on the developmental stage at the start of the flooding period. Small plants were less capable of surviving floods than larger ones — although seedlings appeared to be rather insensitive — but individual plants that were already flowering when flooded would, in most cases, not produce mature seeds afterwards. *Rumex maritimus* plants could survive as much as 4 weeks of submergence and had a 100% survival rate when subjected to 10 days of flooding. The flooding apparently reduces the chance of flowering in this species; a number of the submerged plants remained vegetative, whereas non-submerged controls flowered. Flooding of flowering *R. maritimus* plants resulted in the abortion of flowers, as was the case with *C. rubrum*, but afterwards axillary shoots resumed flowering in several cases, which never happened in *C. rubrum*. The adaptive flooding responses of *R. maritimus* were petiole elongation, stem elongation and, after plants managed to reach the water surface, adventitious root formation.

These results from the greenhouse and experimental garden plots reveal the existence of different strategies in the two species. *Rumex maritimus* is capable of surviving several flooding regimes and even of thriving under waterlogged conditions. The strategy of this species appears to be maintenance by surviving as a vegetative plant or, when unavoidable, as a generative plant. In the last situation, seed output will probably be reduced under conditions of submergence, but not in the case of waterlogging. The strategy of *C. rubrum* is to flower and thus attempt to produce seeds during the short intervals between two successive flooding periods. Early germinating plants may produce large amounts of seed if the habitat is not flooded during the growing season. Late germinating plants produce small amounts of seed, but within a very short period of time. There seems to be no other adaptive feature for surviving floods in any stage of the life cycle. Even waterlogging is a possible threat for this species.

Parallel with the experimental garden experiments, reciprocal experiments were conducted in the river habitats. During these experiments, it was found that *C. rubrum* was selectively eaten by rabbits. During the growing season, ~ 50% of the plants on the sandy river beaches somehow became damaged. In the typical *R. maritimus* habitat, the wet mud edges of former river beds,
only up to ~10% of the *C. rubrum* plants were eaten. In the field we were not able to state the damage caused by grazing alone. Consequently, a greenhouse experiment was designed to isolate this component and to determine the effect of grazing on growth and reproduction of this species. Rabbit grazing was simulated by clipping the plants. There were two variations: (1) early or late, i.e. before flowering (with a mean of 10 leaves per plant) or after at least 50% of the plants had flowered; (2) high or low, i.e. clipped above the fourth primary leaf or above the cotyledons. This resulted in four series, with a fifth series kept as an unclipped control. Both growth and the onset of flowering of these plants were followed, after which the seeds were collected. The results are presented in Fig. 5 as an example of vegetative growth and in Table 7, which gives the dry weights of stems and seeds. *Chenopodium rubrum* was found to possess a remarkable power for recovering from mechanical damage, which is in contrast to its poor ability to recover from flooding damage. Secondary shoots emerged in the cotyledonary or upper leaf axils after clipping and, compared with the control treatment, total shoot length became even longer after two of the treatments. Results for leaf numbers were much the same and are therefore not presented. Dry weight of stems and seed weight were always slightly reduced, depending on the clipping treatment (Table 7). The best recovery occurred after the less severe treatments as the shoots did
Simulated grazing of *C. rubrum*. Dry weight of stems and seeds at the end of the clipping experiment as well as seed percentage, presented as percentage of above-ground dry weight; means ± SE of 12 plants per series. Means with the same letter are not significantly different. See the text for exact clipping times and heights.

<table>
<thead>
<tr>
<th>Series</th>
<th>Stem weight (g)</th>
<th>Seed weight (g)</th>
<th>Seed percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>0.253 ± 0.021a</td>
<td>0.209 ± 0.023a</td>
<td>44.7 ± 1.8bc</td>
</tr>
<tr>
<td>Early/high</td>
<td>0.234 ± 0.018a</td>
<td>0.160 ± 0.020b</td>
<td>40.1 ± 1.6c</td>
</tr>
<tr>
<td>Late/high</td>
<td>0.146 ± 0.013b</td>
<td>0.138 ± 0.014bc</td>
<td>48.5 ± 2.1ab</td>
</tr>
<tr>
<td>Early/low</td>
<td>0.128 ± 0.020b</td>
<td>0.097 ± 0.011c</td>
<td>44.0 ± 2.8bc</td>
</tr>
<tr>
<td>Late/low</td>
<td>0.099 ± 0.007b</td>
<td>0.104 ± 0.009c</td>
<td>51.2 ± 1.6a</td>
</tr>
</tbody>
</table>

not always appear from both cotyledonary leaf axils, but always from higher leaf axils. The difference between early and late clipping was also quite remarkable; there appeared to be a tendency towards a higher seed yield (as a percentage of above-ground weight) in the late-clipped plants compared with unclipped plants; the opposite was true for the early clipped plants. In addition, plants clipped low had higher seed percentages than plants clipped high. This may be related to the root/shoot ratio being in favour of the roots in the plants clipped late and/or low. Hormone balances may also be changed just after flowering, causing late-clipped plants to invest more of their resources in reproductive tissue. These results indicate that under certain conditions grazing may have a positive effect on plant growth and reproduction. McNaughton (1983) suggests that in a few species moderate levels of herbivory may lead to overcompensation and thus to beneficial effects. Up to now, the physiological background of the phenomenon “overcompensation” has not been made clear (Verkaar, 1988). Paige and Whitham (1987) found an increased seed production in *Ipomopsis aggregata* (Pursh) V. Grant after grazing. However, to understand the effects of grazing on the population level, the impact of herbivory on plant numbers at all stages of the life cycle must be studied. Prins (1990) and Prins and Nell (1990) found a considerable delay in flowering in *Senecio jacobaea* L. and *Cynoglossum officinale* L., and this delay has important effects on their life histories and on their population dynamics.

Interesting differences with respect to the reproductive strategy of *C. rubrum* have been found for the onset of flowering. Comparing the times when 50% of the plants were flowering, we obtained a delay of 5 and 9 weeks for the severely clipped series (early and late, respectively), and 2 and 5 weeks for the higher clipped series (also early and late, respectively). It may be concluded that this species does not lose much of its capacity for producing seeds after suffering from grazing, but a considerable postponing of flowering may be hazardous as *C. rubrum* appears to have a strategy largely dependent on the rapid completion of its life cycle between two successive floods. Again we
find, as was the case in the flooding experiments in the greenhouse and in the experimental plots, that damage from grazing greatly depends on the grazing regime. It is absolutely necessary, therefore, to study the effects from grazing as well as flooding in the field, however difficult, in order to properly evaluate its ecological significance.

CONCLUSIONS

(1) Hydrological patterns consisting of strongly fluctuating water levels, which are unpredictable both in time and duration, determine to a large extent the zonation of the vegetation in river areas. The lower situated vegetation types are exclusively determined by the flooding resistance of the occurring species; the higher lying types are influenced by the balance of competitive abilities among adjacently growing plants.

(2) An increased understanding of the adaptations and mechanisms of Rumex plants is valuable in explaining the behaviour of co-occurring species. Obviously, the flooding-related characteristics of Rumex mainly resemble the behaviour of other genera distributed along wet to dry environments (e.g. Armstrong, 1979; Drew, 1983; Etherington, 1983; Kozlowski, 1984; Crawford, 1987, 1989; Fagerstedt and Crawford, 1987; Justin and Armstrong, 1987; Waters et al., 1989). Thus the use of indicator species in order to study the mechanisms used to survive different flooding regimes clearly reveals fundamental strategies of adaptation to flooding.

(3) Flood-tolerant Rumex species develop new aerenchymatous roots in the upper soil layers in response to soil waterlogging and submergence, whereas flooding-intolerant species hardly show any similar response under these conditions. The growth of the species under flooded conditions is positively correlated with the development of new flooding-resistant laterals. The increased growth can be attributed to an improved uptake of macro-nutrients and to a prevention of the uptake of phytotoxins. This is caused by the formation of aerenchyma in the shoots and new roots, resulting in radial oxygen loss.

(4) Submergence of flood-tolerant Rumex plants stimulates the growth of petioles, often resulting in the leaves protruding above the surface of the water. Petiole growth in intolerant species is not enhanced and may even be inhibited during total submergence.

(5) The elongation of existing and newly formed petioles is regulated by an increase in ethylene concentration. Differences in the growth of submerged petioles between flooding-intolerant and flooding-tolerant species are attributed more to differences in their sensitivity to enhanced ethylene concentrations in the plant tissue and less to differences in endogenous ethylene levels.

(6) Plants from different populations or species growing in the same habitat and exposed to severe environmental stress factors, such as flooding, may possess different life-history strategies to ensure survival. Some plants behave
as biennials or perennials and survive mainly in their vegetative phases. Others are able to germinate and produce seeds in the short intervals between two successive floods.

(7) The effects of environmental factors on the behaviour of plants strongly depend on the stage of the life cycle (Blom, 1987, 1988). Flood-tolerant species are mainly characterized by a large persistent seed bank, whereas intolerant plants possess a more transient seed bank (Voesenek, 1990). Seedlings of tolerant species have a higher resistance to submergence than intolerant ones. Moreover, the tolerant seedlings release oxygen from their roots (Laan, 1990; Voesenek, 1990). Plants from tolerant species retain high porosities throughout their life cycle, assuring internal oxygen transport. Some tolerant Rumex species develop woody tap roots, which form an increasingly larger physical barrier to oxygen transport and thus to radial oxygen diffusion. However, the tap roots of these plants supply the sugar with which plants survive long-lasting floods (Laan, 1990). Flowering has been proven to be delayed in response to flooding (van der Sman et al., 1988), which often results in reduced seed production. In general, flood-tolerant species secure their reproduction in spite of the unfavourable environmental conditions caused by flooding.

REFERENCES


