Flood-induced leaf elongation in *Rumex* species: effects of water depth and water movements

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(Received 13 April 1995; accepted 31 May 1995)

SUMMARY

Several species from the genus *Rumex* are found in Dutch river forelands. Species such as *R. palustris* Sm. from the low, frequently flooded areas are well adapted to wet conditions. *Rumex* species from higher and less frequently flooded sites are poorly adapted and therefore sensitive to flooding. One of the adaptations to flooding is enhanced shoot elongation upon complete submergence, enabling plants to restore leaf-air contact, provided that the water is not too deep. This paper demonstrates the strong variation in the absolute extent of flood-induced leaf elongation among species of the genus *Rumex*. The effects of flooding on shoot dry and fresh weight and internal gas volumes of an elongating and a non-elongating species, *R. palustris* and *R. acetosella* L., were compared. Net water uptake in response to complete submergence was observed in the shoots of both species. Based on results presented here, we conclude that in plants of *R. palustris* water enters the cells and is used for cell expansion leading to petiole elongation, whereas in plants of *R. acetosella* at least part of the water taken up fills the intercellular gas spaces. Elongation of completely submerged *Rumex* plants does not vary with different depths of submergence. This was concluded from the observation that there is little effect of either hydrostatic pressure or irradiance on leaf elongation during complete submergence. However, when *R. palustris* plants were subjected to changing water depth, i.e. alternate periods of complete submergence and waterlogging, they elongated less strongly than under permanent complete submergence. Water movements did not affect leaf elongation induced by submergence.

Key words: Flooding, leaf elongation, *Rumex* species, water depth, water movements.

INTRODUCTION

Terrestrial plants that occur in river forelands have to cope with unpredictable periods of flooding in the growth season (Blom et al., 1994). Long-term survival and reproduction often depend on the ability of plants to regain contact with the atmosphere (Laan & Blom, 1990; van der Sman et al., 1991). In some plants this is accomplished by enhanced shoot elongation (Ridge, 1987), observed in a wide variety of species such as *Ranunculus* species (Musgrave & Walters, 1973; Ridge, 1985; Horton, 1992), *Nymphoides peltata* (Ridge & Amarasinghe, 1984), *Hydrocharis morsus-ranae* (Cookson & Osborne, 1978) and *Oryza sativa* (Métraux & Kende, 1983). The shoot elongation response is induced by large concentrations of the gaseous hormone ethylene within submerged plants (Musgrave & Walters, 1973; Métraux & Kende, 1983). This accumulation is caused by physical entrapment of continuously produced ethylene, as suggested by Musgrave and co-workers in 1972, and recently demonstrated by Voesenek et al. (1993).

The genus *Rumex* provides an excellent model for the ecophysiological study of this adaptation. *Rumex palustris* Sm., *R. crispus* L. and *R. conglomeratus* Murr. can survive long periods of complete submergence and can grow on wet sites in the river forelands, whereas *R. thyrsiflorus* Fingerh. and *R. acetosa* L. are sensitive to flooding and are found on rarely-flooded dikes. *R. acetosella* L. is never flooded under natural conditions (Blom et al., 1994). The flooding-resistant *Rumex* species show a strongly enhanced elongation of young petioles and internodes of flowering stems in response to complete submergence and soil waterlogging (Voesenek & Blom, 1989; Voesenek et al., 1990a; van der Sman et al., 1991). In *R. acetosa* leaf elongation is either inhibited or slightly stimulated in response to flooding (Voesenek & Blom, 1989; Voesenek et al.,
started to develop their fifth leaf, except (1:1 v/v). Plants were grown in a growth chamber filled with a mixture of sand and potting compost. 

In physiological studies dealing with the elongation response, plants were always submerged in water of a restricted depth under stagnant conditions. However, water level measurements gathered over a 17 yr period (1971–1987) show that the natural environment of wetland Rumex species is very dynamic. Their habitat was flooded 0–7 times per growth season, the duration of these floods varied between 0 and 99 d and the water depth ranged from 0–459 cm (van der Sman, 1993). From field observations it is known that Rumex plants growing on the river bank are additionally exposed to short-term fluctuations of the water level. Wave action from passing ships leads to changes of the water level from soil waterlogging to complete submergence of plants or vice versa within a few minutes.

In this paper the following questions will be addressed: (a) To what extent do Rumex species, varying in flooding resistance, enhance their leaf elongation upon partial and complete submergence? (b) Are there differences in water uptake between submerged plants of an elongating and a non-elongating Rumex species? (c) Can completely submerged Rumex plants adjust their leaf elongation response according to water depth by responding to hydrostatic pressure or irradiance? (d) Is shoot elongation of submerged Rumex plants affected by a rapidly fluctuating water level causing periodic emergence of the shoot? (e) Is submergence-induced leaf elongation of Rumex plants influenced by water movements?

Materials and Methods

Plant material

Seeds of Rumex palustris, R. conglomeratus, R. crispus, R. thyrsiflorus and R. acetosa were collected from river areas near Nijmegen, The Netherlands. Rumex acetosella seeds were gathered from plants growing near the Nijmegen Botanical Gardens. Seeds were germinated on moist filter paper in Petri dishes, under a 12 h light/12 h dark regime of 25 °C for 7 d (PPFR of 25 μmol m⁻² s⁻¹ over the waveband 400–700 nm), with the exception of R. acetosella seeds which were kept at 27 °C for 10 d. Seedlings were transferred to 200 ml plastic pots filled with a mixture of sand and potting compost (1:1 v/v). Plants were grown in a growth chamber (16 h/8 h light/dark; 20 °C; 40–70% RH; PPFR 180 μmol m⁻² s⁻¹) for 16–20 d. At this time, rosettes started to develop their fifth leaf, except R. thyrsiflorus plants, which had four leaves. Thus, leaf 5 (or leaf 4) is the youngest leaf. Unless otherwise stated, experiments were performed under the above-mentioned growth conditions and 8–10 replicates were used. In some experiments responses of R. palustris and R. acetosella plants to certain flooding treatments were compared. In this way the flooding responses of a well-adapted species were studied, and distinguished from general phenomena also displayed by flooding-sensitive plants. Where the word ‘submergence’ is used without an adjective, complete submergence is meant.

Effects of flooding on shoot elongation of four Rumex species

Plants of R. palustris, R. acetosa, R. thyrsiflorus and R. acetosella were exposed to four flooding treatments each lasting 7 d. Treatments were: waterlogging, partial submergence (i.e. half of the shoot height was under water at the start of this treatment), complete submergence and a free-draining control. At the start and end of the experiment the total length (petiole + lamina) of all leaves was measured. Shoot height was defined as the length of the longest leaf.

Flood-induced water uptake in two contrasting Rumex species

Twenty plants of either Rumex palustris or R. acetosella were used. At the start of the experiment five plants per species were harvested and the remaining 15 plants were randomly divided over three treatments, i.e. waterlogging, submergence and a free-draining control, and harvested after 6 d. Shoot fresh weight was recorded and the internal gas volume was determined using the modified pycnometer method of Jensen et al. (1969). All gas was removed from shoots by keeping them under distilled water while applying a vacuum of 10⁴ Pa for several minutes. Finally, shoot dry weight was determined. Data on internal gas volumes provide information about the distribution of water that enters the shoot upon submergence between cells and intercellular spaces. The amount of water in plants was calculated by subtracting dry weight from fresh weight.

Effects of hydrostatic pressure on submerged plants

Flooding-resistant R. palustris, R. conglomeratus and R. crispus plants were used. Under natural conditions R. palustris grows in the lowest areas of the river forelands, and is therefore confronted with deeper floods than are the other two species (Blom et al., 1994). R. palustris and R. crispus can survive in extremely turbid water, whereas occurrence of R.
Effects of flooding on leaf elongation in Rumex

Table 1. Underwater light (µmol m⁻² s⁻¹ PPFR) at several locations from river areas near Nijmegen, The Netherlands

<table>
<thead>
<tr>
<th>Location</th>
<th>Water depth (cm)</th>
<th>PPFR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Erlecoms veer</td>
<td>5-30</td>
<td>1</td>
</tr>
<tr>
<td>(running)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kekerdomsewaard</td>
<td>20</td>
<td>66</td>
</tr>
<tr>
<td>(turbid)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Groenlanden</td>
<td>30</td>
<td>152</td>
</tr>
<tr>
<td>(clear)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kekerdomsewaard</td>
<td>30</td>
<td>160</td>
</tr>
<tr>
<td>(clear)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Measurements were conducted on a clouded day (20 June 1991). Above-water irradiance: 1162 µmol m⁻² s⁻¹ PPFR.

Rumex conglomeratus is restricted to clear seepage water (unpublished data). For each species 20 plants received one of the following treatments: submergence in 30 cm deep water, submergence in 100 cm deep water, or drainage. Half of the plants were harvested after 1 wk, the rest were treated for 8 wk. Algae were removed by filtering. None of the plants reached the water surface during the experiment. Before and after the experiment leaf lengths were measured. The experiment was performed in a growth chamber (16 h/8 h light/dark; PPFR 110 µmol m⁻² s⁻¹). Soil was gently washed off the roots before the start of the experiment in order to maintain a constant PPFR. To avoid interference of stress ethylene produced by this procedure, a waiting period of about 5 h was kept before the plants were submerged. Removal of the soil does not change the shoot elongation response provided that plants stay submerged (data not shown). Increases of leaf lengths, leaf blade areas and dry and fresh shoot weights were determined. Because there was only one experimental set-up, it was impossible to impose all treatments simultaneously and the experiment ran for three successive periods of 5 d. Water temperatures were in the range 24–29 °C, but did not differ between treatments.

Effects of light intensity on submerged plants

Underwater light intensities in flooded field sites at several locations around Nijmegen were measured using a Licor® QSM-2500 quantum spectrometer (Table 1). An indoor experiment tested the effects of a similar range of four underwater light treatments (PPFR 1–150 µmol m⁻² s⁻¹) on flooding-resistant R. palustris plants. Increases of leaf lengths and total shoot height, and changes in fresh and dry shoot weights were determined over a period of 5 d. Water temperatures were in the range 24–29 °C, but did not differ between treatments.

Effects of a fluctuating water level

Plants of R. palustris and R. acetosella received one of the following treatments: permanent complete submergence or alternate submergence and waterlogging. The second treatment was realized by fixing pots with plants in a PVC plate that was moved up and down in a 160 l container filled with stagnant water. Every 9 min the position of the plants was changed from submerged to waterlogged or vice versa. The water was filtered and the soil in all pots was covered over with a piece of cotton cloth in order to prevent a decrease of underwater light intensity by dislodged soil particles. Permanently submerged plants were exposed to underwater light of 100 µmol m⁻² s⁻¹ (PPFR). In the apparatus, PPFR varied between 87 µmol m⁻² s⁻¹ (underwater) and 115 µmol m⁻² s⁻¹ (above-water). The experiment ran for 4 d and increases of leaf lengths, leaf blade areas, shoot dry and fresh weights during this period were determined. Leaf blade areas were measured with a Licor portable area metre (model I-3000/I-3050A), and values were expressed as half the total area.

Effects of water movements on submerged plants

Water movements were simulated by the above-mentioned system. Plants stayed submerged and were exposed to a water velocity of 6 cm s⁻¹. One movement consisted of an upward or downward transfer of the plants over a distance of 30 cm. Plants of R. palustris and R. acetosella were subjected to 180, 7-4 and 0 movements per hour for 5 d (16 h/8 h light/dark; PPFR 110 µmol m⁻² s⁻¹). Soil was gently washed off the roots before the start of the experiment in order to maintain a constant PPFR. To avoid interference of stress ethylene produced by this procedure, a waiting period of about 5 h was kept before the plants were submerged. Removal of the soil does not change the shoot elongation response provided that plants stay submerged (data not shown). Increases of leaf lengths, leaf blade areas and dry and fresh shoot weights were determined. Because there was only one experimental set-up, it was impossible to impose all treatments simultaneously and the experiment ran for three successive periods of 5 d. After the whole experiment was completed, only plants that had equal lengths of leaves 3, 4 and 5 at the start of each run were selected from the data bank and used for further calculations. This was to eliminate batch variation between plants subjected to different treatments. The final selection of plants contained 8–10 individuals per species and treatment.

Statistical analysis

All results were tested by one-way ANOVA, followed by a Tukey test. In the fluctuating water level experiment, however, the effects of the two treatments were compared using a t-test. All statistical analyses were made according to Sokal & Rohlff (1981).

RESULTS

Rumex species differed strongly in their shoot elongation response to one week of flooding (Fig. 1). R. palustris plants elongated most upon (complete) submergence, but also under waterlogged conditions flood-induced elongation of leaves 4 and 5 and shoot
height were significant. The youngest leaf showed a smaller length increase upon complete submergence than during partial submergence. Plants of *R. acetosa* and *R. thyrsiflorus* only significantly increased their length upon partial and complete submergence. By contrast, flooded *R. acetosella* plants did not elongate more than drained plants. In all species, younger leaves elongated more than older ones, and the oldest leaves (= leaves 1 and 2; data not shown) did not elongate much.

The effects of various flooding treatments on shoot dry weight were similar in *R. acetosella* and *R. palustris*, although plants of the latter species were generally much larger (Table 2). However, the two species did differ when other parameters were compared; submerged *R. palustris* plants showed larger increases of shoot fresh weight and internal gas volume than did submerged *R. acetosella* plants. In the latter plants a decline in gas volume was observed. In neither species were fresh or dry weights or internal gas volume affected by soil waterlogging.

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**Table 2.** Means (± SE) of shoot fresh and dry weight (mg) and shoot internal gas volume (µl) of *Rumex palustris* and *Rumex acetosella* before and after 6 d of drainage, waterlogging or complete submergence (n = 5)

<table>
<thead>
<tr>
<th>Species</th>
<th>Day 0 Drained</th>
<th>Day 6 Drained</th>
<th>Day 6 Waterlogged</th>
<th>Day 6 Submerged</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>R. palustris</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F. wt</td>
<td>989 ± 23</td>
<td>1900 ± 106</td>
<td>2129 ± 150</td>
<td>1838 ± 184</td>
</tr>
<tr>
<td>D. wt</td>
<td>74 ± 3</td>
<td>164 ± 6 a</td>
<td>163 ± 15 a</td>
<td>78 ± 7 b</td>
</tr>
<tr>
<td>Int. vol.</td>
<td>237 ± 13</td>
<td>445 ± 29</td>
<td>566 ± 82</td>
<td>543 ± 115</td>
</tr>
<tr>
<td><em>R. acetosella</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F. wt</td>
<td>418 ± 49</td>
<td>875 ± 48 a</td>
<td>899 ± 46 a</td>
<td>526 ± 63 b</td>
</tr>
<tr>
<td>D. wt</td>
<td>29 ± 4</td>
<td>70 ± 7 a</td>
<td>71 ± 7 a</td>
<td>27 ± 3 b</td>
</tr>
<tr>
<td>Int. vol.</td>
<td>90 ± 13</td>
<td>174 ± 9 a</td>
<td>163 ± 10 a</td>
<td>50 ± 6 b</td>
</tr>
</tbody>
</table>

Different letters indicate significant differences (P ≤ 0.05) between treatments and within species and parameters on day 6.

Int. vol. = Internal gas space.
Effects of flooding on leaf elongation in Rumex

Table 3. Mean (±SE) increase of leaf lengths and shoot height (mm) of Rumex plants during one or two weeks of complete submergence at two water depths (hydrostatic pressures) compared with drained controls (n = 10)

<table>
<thead>
<tr>
<th>Species</th>
<th>Leaf 3</th>
<th>Leaf 4</th>
<th>Leaf 5</th>
<th>Shoot height</th>
</tr>
</thead>
<tbody>
<tr>
<td>R. palustris</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 wk drained</td>
<td>13 ± 1 b</td>
<td>34 ± 2 b</td>
<td>60 ± 3 c</td>
<td>25 ± 2 c</td>
</tr>
<tr>
<td>1 wk 30 cm</td>
<td>21 ± 1 a</td>
<td>57 ± 2 a</td>
<td>85 ± 4 b</td>
<td>52 ± 2 b</td>
</tr>
<tr>
<td>1 wk 100 cm</td>
<td>21 ± 1 a</td>
<td>58 ± 4 a</td>
<td>102 ± 4 a</td>
<td>67 ± 3 a</td>
</tr>
<tr>
<td>2 wk drained</td>
<td>10 ± 2 b</td>
<td>32 ± 4 b</td>
<td>64 ± 4 b</td>
<td>64 ± 4 b</td>
</tr>
<tr>
<td>2 wk 30 cm</td>
<td>22 ± 1 a</td>
<td>64 ± 4 a</td>
<td>135 ± 5 a</td>
<td>94 ± 5 a</td>
</tr>
<tr>
<td>3 wk 100 cm</td>
<td>24 ± 1 a</td>
<td>60 ± 2 a</td>
<td>146 ± 2 a</td>
<td>105 ± 2 a</td>
</tr>
<tr>
<td>R. conglomeratus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 wk drained</td>
<td>8 ± 2 b</td>
<td>28 ± 4 c</td>
<td>48 ± 5 b</td>
<td>16 ± 4 b</td>
</tr>
<tr>
<td>1 wk 30 cm</td>
<td>27 ± 2 a</td>
<td>65 ± 4 b</td>
<td>81 ± 8 a</td>
<td>60 ± 4 a</td>
</tr>
<tr>
<td>1 wk 100 cm</td>
<td>33 ± 2 a</td>
<td>82 ± 4 a</td>
<td>71 ± 8 ab</td>
<td>71 ± 4 a</td>
</tr>
<tr>
<td>2 wk drained</td>
<td>6 ± 2 b</td>
<td>28 ± 5 b</td>
<td>71 ± 6 b</td>
<td>25 ± 7 b</td>
</tr>
<tr>
<td>2 wk 30 cm</td>
<td>33 ± 4 a</td>
<td>80 ± 4 a</td>
<td>145 ± 11 a</td>
<td>108 ± 5 a</td>
</tr>
<tr>
<td>2 wk 100 cm</td>
<td>31 ± 1 a</td>
<td>78 ± 3 a</td>
<td>138 ± 9 a</td>
<td>89 ± 9 a</td>
</tr>
<tr>
<td>R. crispus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 wk drained</td>
<td>8 ± 1 b</td>
<td>22 ± 3 b</td>
<td>53 ± 4 b</td>
<td>11 ± 2 b</td>
</tr>
<tr>
<td>1 wk 30 cm</td>
<td>26 ± 2 a</td>
<td>57 ± 4 a</td>
<td>81 ± 8 a</td>
<td>47 ± 4 a</td>
</tr>
<tr>
<td>1 wk 100 cm</td>
<td>29 ± 2 a</td>
<td>60 ± 4 a</td>
<td>83 ± 7 a</td>
<td>54 ± 3 a</td>
</tr>
<tr>
<td>2 wk drained</td>
<td>3 ± 2 b</td>
<td>17 ± 3 b</td>
<td>45 ± 5 b</td>
<td>8 ± 2 b</td>
</tr>
<tr>
<td>2 wk 30 cm</td>
<td>26 ± 2 a</td>
<td>60 ± 5 a</td>
<td>119 ± 9 a</td>
<td>71 ± 6 a</td>
</tr>
<tr>
<td>2 wk 100 cm</td>
<td>28 ± 2 a</td>
<td>64 ± 7 a</td>
<td>98 ± 10 a</td>
<td>57 ± 6 a</td>
</tr>
</tbody>
</table>

Different letters indicate significant differences (P ≤ 0.05) between treatments and within species, elongation parameters and duration.

Table 4. Mean (±SE) shoot elongation responses (mm) and increases of shoot fresh and dry weight (mg) of Rumex palustris during 5 d of complete submergence under various light regimes (µmol m⁻² s⁻¹ PPFR) (n = 10)

<table>
<thead>
<tr>
<th>Irradiance</th>
<th>Leaf 3</th>
<th>Leaf 4</th>
<th>Leaf 5</th>
<th>Shoot height</th>
<th>F. wt</th>
<th>D. wt</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>11 ± 1</td>
<td>32 ± 2</td>
<td>6 ± 1 c</td>
<td>12 ± 1 bc</td>
<td>167 ± 30</td>
<td>−1 ± 1 b</td>
</tr>
<tr>
<td>35</td>
<td>11 ± 0</td>
<td>30 ± 2</td>
<td>31 ± 3 ab</td>
<td>13 ± 1 b</td>
<td>267 ± 45</td>
<td>7 ± 2 a</td>
</tr>
<tr>
<td>75</td>
<td>11 ± 1</td>
<td>30 ± 2</td>
<td>39 ± 3 a</td>
<td>17 ± 1 a</td>
<td>286 ± 55</td>
<td>5 ± 2 a</td>
</tr>
<tr>
<td>150</td>
<td>10 ± 1</td>
<td>32 ± 2</td>
<td>28 ± 3 b</td>
<td>16 ± 1 ab</td>
<td>228 ± 33</td>
<td>3 ± 1 ab</td>
</tr>
</tbody>
</table>

Different letters indicate significant differences (P ≤ 0.05) between treatments within parameters.

When three flooding-resistant Rumex species were submerged, they all had significant shoot elongation responses (Table 3). Leaves 3 and 4 mainly grew during the first week, but leaf 5 and shoot height also increased substantially in the second week. Hydrostatic pressure had little effect on this response, although there was a tendency for deeper submerged plants to elongate more in the first week and less in the second week compared with plants submerged in shallower water.

Extremely low light (1 µmol m⁻² s⁻¹ PPFR) had negative effects on development of leaf 5 and to a lesser extent on shoot height and biomass production of submerged R. palustris plants (Table 4). Elongation of R. palustris leaves was reduced by exposure to a fluctuating water level compared with permanent submergence. In R. acetosella plants, length increase of the leaves was similar under the two treatments (Fig. 2a, b). The expansion of the leaf blade area was hardly affected. In both species, the youngest leaf had a greater leaf blade area under the fluctuating water level regime (Fig. 2c). Although there were no effects on fresh weight (data not shown), shoot biomass production was stimulated in R. palustris plants under the fluctuating water level regime (Fig. 2d).

Water movements did not affect leaf elongation, leaf blade area and shoot dry and fresh weights of submerged R. palustris and R. acetosella plants significantly (data not shown).
plants it doubled. In general, no differences were observed shoot elongation response of (frequency, duration and depth) in the natural habitat. Therefore, the development of new leaves under these conditions. Although *R. acetosa* and *R. thyriflorus* grow at higher, rarely flooded sites in the river area, their shoots also elongated upon (partial) submergence. *R. acetosella* was the only species that did not display this adaptation. Plants of this species are never flooded in their natural habitat. Therefore, the observed shoot elongation response of *Rumex* species is positively correlated to the flooding intensity (frequency, duration and depth) in the natural habitat.

Remarkably, shoot biomass production upon drainage, waterlogging and submergence showed the same pattern in the two contrasting *Rumex* species, despite the overall higher values in *R. palustris* (Table 2). Shoot dry weight did not change during 6 d of submergence, but in waterlogged and drained plants it doubled. In general, no differences were found between waterlogged and drained plants. For *R. acetosella* this is an unexpected result, considering that plants of this species are never flooded in their natural habitat. Nevertheless, the two species varied in their reactions to submergence. The water uptake into the shoots of submerged plants differed between species. During 6 d of submergence a mean net water uptake of 854 µl (93% of the initial amount of water) was observed in *R. palustris* shoots. This was accompanied by a mean net enlargement of the internal gas volume by 300 µl. However, in submerged *R. acetosella* shoots a mean net water uptake of 113 µl (29%) and a mean net reduction of the internal gas spaces by 40 µl were found. From these data it is clear that during submergence *R. acetosella* shoots display a lower water uptake than do the elongating shoots of *R. palustris* plants. Moreover, we conclude that in *R. acetosella* at least part of the water entering fills gas spaces and is not taken up into cells; this can be seen as a dark green colouring of large parts of the shoot. In submerged *R. palustris* plants this dark green colour is only observed in small parts of old leaves. Since petiole elongation in this species is caused by cell expansion (Voesenek et al., 1990b), we conclude that the water entering the shoot of *R. palustris* during submergence is mainly used for cell expansion leading to enhanced petiole elongation.
Shoot elongation seems advantageous only if there is a reasonable chance of reaching the water surface. Therefore, under changing conditions it might be beneficial to submerged plants to register water depth and to regulate shoot elongation accordingly. Since hydrostatic pressure increases and light intensity decreases with water depth (Gessner, 1952; Dale, 1984), we investigated the influence of these two factors on underwater shoot elongation.

The effects of hydrostatic pressure were studied by submerging plants of *R. palustris*, *R. crispus* and *R. conglomeratus* for 2 wk at two different water depths. Although in all three *Rumex* species leaves 3, 4 and 5 showed a significant shoot elongation response upon submergence, there was little effect of hydrostatic pressure. Plants tended to elongate more in deeper water during the first week, but this was usually non-significant (Table 3). Until now, studies on the effects of hydrostatic pressure on plant growth (Gessner, 1952; Ferling, 1957; Dale, 1981, 1984) have mostly been made using aquatic species, and were aimed at explaining the depth distribution of these species in the field by investigating their tolerance to very high hydrostatic pressures, with effects found only at pressures similar to water depths of 5 m or more, which exceed the maximum depths naturally occupied by the plants under study.

The data from field measurements of underwater light intensities indicate a strong reduction of light availability even in shallow water (Table 1). This is brought about by light attenuation through water itself, but the presence of soluble material, suspended inorganic particles, phytoplankton and other suspended material causes most of the reduction (Holmes & Klein, 1987). Nevertheless, in submerged *R. palustris* plants, light intensity did not have much effect on elongation of leaves 3 and 4 (Table 4). The development of the youngest leaf (= leaf 5) was retarded and shoot dry weight decreased under the darkest conditions (1 µmol m⁻² s⁻¹ PPFR). This might be expected, since this PPFR is even lower than the light compensation point for well-adapted aquatic angiosperms (7 µmol m⁻² s⁻¹ PPFR at 7 °C (Sand-Jensen & Madsen, 1991). In *Ranunculus pseudofelater* submergence-induced petiole elongation was also the same under light (125 µmol m⁻² s⁻¹ PPFR) or dark conditions (Samarakoon & Horton, 1983).

From the experiments on hydrostatic pressure and light intensity we may conclude that submerged wetland *Rumex* species do not adjust their leaf elongation response to the depth of submergence. Although light quality and temperature can also change with water depth, these aspects were not investigated here because they do not seem very reliable as indices of water depth.

In submerged *R. palustris* plants shoot dry weight increased more if the shoot was regularly desubmerged in a fluctuating water level (Fig. 2d). This is in agreement with the biomass data of waterlogged and submerged plants in Table 2. In *R. palustris* petiole elongation is caused by large concentrations of ethylene (Voesenek & Blom, 1989). When the shoot emerges, most of the accumulated ethylene is released within 1 min (Voesenek *et al.*, 1993). Since both phases of the fluctuating water level treatment (submergence and waterlogging) lasted about 9 min, all ethylene must have been released into the air during waterlogging, and calculations (based on unpublished data) indicate that there was not enough time for ethylene to accumulate to the concentration needed for maximal petiole elongation during submergence. Indeed, under a fluctuating water level *R. palustris* plants showed a reduced elongation response compared with permanently submerged plants (Fig. 2a). *R. acetosella* plants, which had no enhanced shoot elongation upon submergence (Fig. 1d), did not show differences in leaf lengths or shoot dry weight between the two treatments (Fig. 2b, d). This species might not have an increased ethylene concentration under water or might be insensitive to this hormone. The second theory seems more likely, knowing that the differences in petiole elongation between *R. acetosa* and *R. palustris* can also be explained by differences in sensitivity towards ethylene and not by differences in ethylene accumulation during submergence (Voesenek *et al.*, 1993). Under the fluctuating water level regime both *R. palustris* and *R. acetosella* plants showed a faster development of new leaves than when permanently submerged. This is concluded from the greater increase of the area of the youngest leaf in both species (Fig. 2c) and from the slightly greater length of this leaf in *R. acetosella* plants in response to this treatment.

It was expected that submergence-induced leaf elongation would be inhibited in moving water, because turbulence reduces the thickness of the unstirred boundary layer around submerged shoots. It facilitates gas exchange between the plants and their environment (Black, Maberley & Spence, 1981), and ethylene diffusion out of the plant will be enhanced (Ridge, 1987). However, no effect of water movements on leaf elongation was observed here. An explanation might be that although ethylene concentrations in plants are reduced by moving water, they are still large enough for maximal elongation. It is also possible that plants can compensate for this loss of ethylene by increasing the production rate of the hormone. Further investigations will elucidate this mechanism.

This paper demonstrates the large variation in flood-induced shoot elongation present among species of the genus *Rumex*. Comparison of elongating and non-elongating *Rumex* species provided information about the mechanism behind this adaptation. In *R. palustris* water taken up during submergence is used for cell expansion leading to
petiole elongation, whereas submerged R. acetosella plants take up less water and at least part of it fills the intercellular gas spaces. Furthermore, it was shown that water depth influences leaf elongation in wetland Rumex plants only if they are partly submerged. In response to complete submergence these plants always show stimulated elongation, independent of external physical factors such as hydrostatic pressure, light intensity or water movements.

ACKNOWLEDGEMENTS

We thank G. A. M. Broekhuysen and G. M. Bögemann for developing the apparatus used in the fluctuating water level and the water movements experiments, and V. G. E. M. van Geffen, M. D. E. T. van de Mortel, B. Philipsen, C. Schoormans and P. Veenvliet for technical assistance. We are also grateful to J. E. Summers for correcting the English of an early draft of the manuscript and H. M. van de Steeg for fruitful discussions and assistance during light measurements in the field.

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