Flooding tolerance of *Carex* species in relation to field distribution and aerenchyma formation


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**SUMMARY**

The flooding tolerance of *Carex* species was studied in relation to their field distribution and their capacity to form root aerenchyma under controlled conditions. In an alpine meadow, six *Carex* species were selected which were distributed in a clear zonation correlating with water content of the soil. *Carex sempervirens* and *C. ferruginea* were only found on nonflooded soil, the latter species preferring moister conditions. *Carex davalliana* and *C. nigra* were both associated with water-saturated soil, whereas *C. limosa* and *C. rostrata* preferred partially submerged conditions. *Carex davalliana* and *C. limosa* were bound to flooded soils with a relatively high redox potential and horizontally flowing groundwater. *Carex rostrata* and *C. nigra* grew in stagnant soil-flooded conditions with low soil redox potentials. The amount of aerenchyma in the roots of all species increased when grown in oxygen-deficient stagnant agar. This increase in root porosity, combined with increased root diameter, presumably improved internal aeration of the roots. Although all species survived experimental soil flooding, partial submergence was lethal to *C. sempervirens* and, surprisingly, also to the wetland species *C. davalliana*. *Carex ferruginea* showed a reduced growth rate during partial submergence. The three other species, all wetland plants, reached highest biomass production under soil-flooded and partially submerged conditions, with slower growth on free-draining soil. It is concluded that aerenchyma is not constitutive in the *Carex* species under study, and is best developed in *Carex* species from wetlands. Species with less aerenchyma perform poorly when soil-flooded, but conditions of partial submergence could even affect species with a considerable amount of root aerenchyma.

Key words: aerenchyma, *Carex*, field distribution, flooding, roots, soil moisture, waterlogging.

**INTRODUCTION**

Soil flooding results in a variety of stresses for plants (Blom, 1999) of which oxygen deficiency is often the underlying factor (Jackson & Drew, 1984; Drew, 1997). These low oxygen concentrations are caused by slow gas diffusion in water-saturated soil (Jackson, 1985). Low oxygen availability reduces respiration and growth in nonadapted roots (Laan et al., 1990, 1991) and can eventually lead to the death of root meristems. Some microorganisms use electron acceptors other than oxygen for respiration under these conditions (Laanbroek, 1990), resulting in the formation of potentially phytotoxic metal ions such as Fe^{2+} (Ponnampерuma, 1972; Laan et al., 1989b) and Mn^{2+} (Ponnamperuma, 1972; Waldren et al., 1987), and anions like sulphide (Lamers et al., 1998). Potentially harmful gases, such as ethylene, can also accumulate (Visser et al., 1996b) and damage plant organs or at least limit growth (Visser et al., 1997). Finally, nutrient uptake during flooding is usually limited, resulting in lower biomass production (Trought & Drew, 1980).

A typical feature of plant species growing in regularly or permanently flooded soil is the presence of thick, mostly unbranched roots that contain aerenchyma, consisting of an extensive network of air spaces throughout the root cortex (Armstrong, 1979; Jackson & Drew, 1984; Jackson & Armstrong, 1999). Various studies suggest a strong positive relationship between the frequency of flooding of a plant species and the capacity of such a species to develop aerenchyma in its roots. Justin & Armstrong (1987) tested and confirmed this hypothesis on 91 species from habitats contrasting in soil moisture. Even between species of the same genus, such as
and experiments focused on six Carex species. Observations investigated species and study area flooding in the species’ habitat and the flooding tolerance of the species. Moog (1998) found high root porosity in C. extensa, although this species is from well drained soil. This suggests that aerenchyma is constitutively formed in Carex species from flooding-prone and drained habitats, possibly implying that soil flooding is not a strong selective stress factor for the habitat preference of these species, as internal aeration of the roots prevents flooding-induced injury to the plant.

Carex species are numerous in valleys on mountain slopes of the Austrian Alps (Lauber & Wagner, 1996). Alternating steep slopes and level valley floors, combined with a large capture area for rain and snow, create a mosaic of dry, moist and wet soil as well as differences in flow rate of groundwater. Wet sites are often dominated by Carex species, but species from this genus are also found in any other alpine or subalpine habitat.

In this study, six Carex species were selected from habitats differing in degree of soil flooding and situated in the valley of a small brook, the Lausbachtal (Serfau, Austria). We evaluated the hypothesis that soil flooding does not limit the potential, pH and the standing biomass of the selected Carex species were measured.

Description of the vegetation. Two to four plots of 0.5–2 m² (area depending on the homogeneity of the vegetation) were selected along each transect, reflecting the various vegetation types. Further, three plots were selected in vegetation with dominance of C. nigra, C. rostrata and C. sempervirens, respectively. The vegetation in each plot was described according to the method of Braun-Blanquet (1928). Nomenclature of species was adopted from Lauber & Wagner (1996).

Soil water content, redox potential and pH. Water content of the soil was measured (n = 3) with time-domain reflectometry at regular distances (0.5–1.0 m) along the transects and in the four corners of each plot, using a TRIME-FM Field Measurement Device (IMKO Micromodultechnik GmbH, Ettlingen, Germany) with a P2-probe of 110 mm. The redox potential of the soil was measured (n = 3) at a depth of 0.10 m in each plot with three platinum electrodes, a double junction Ag/AgCl-reference electrode, and a Consort D914 pH/mV-meter (Consort, Turnhout, Belgium). Stable readings were generally obtained after 60–120 min. The pH in the soil was measured (n = 3) at a depth of 0.05–0.10 m, with a Hannah pH Wand combined meter and electrode (Cole Parmer, Vernon Hills, IL, USA).

Biomass. Aboveground biomass was cut along each transect from 5–6 plots of 0.20 × 0.20 m, situated 1–3 m apart. Plant material of the Carex species under investigation was separated, and fresh weights of the various fractions determined. The material was dried in paper bags at 35°C for 2 d before transport to the laboratory, then dried at 80°C for 2 d and reweighed to determine dry weight.

Glasshouse experiment

Growth of plants. Approximately thirty ramets (each of a different clone) of each species were collected from the field sites and brought in plastic bags to the glasshouse at the Botanical Garden, University of Nijmegen, the Netherlands. Ramets were planted in 2-l pots (diam. 14 cm) containing a 1 : 1 mixture of valley of the Lausbach (Serfau, Austria). Carex davalliana Sm., C. ferruginea Skop., C. limosa L., C. nigra L., C. rostrata Stokes and C. sempervirens Vill. were found to occur in a clear zonation in these transects, each species dominating a specific vegetation type, and at least two species present in each transect.

The relative altitude within each transect was determined at intervals of 0.25 m. Relevés were taken of the various vegetation types along the transects (see Vegetation analysis section), and soil moisture, redox potential, pH and the standing biomass of the selected Carex species were measured.

Materials and methods

Field experiments

Investigated species and study area. Observations and experiments focused on six Carex species occurring in five transects (Table 1) set out July 1997 at the Komperdell Alm (2000–2100 m asl) in the

Rumex (Laan et al., 1989a; Visser et al., 1996a) and Ranunculus (He et al., 1999), there is a positive correlation between root aerenchyma content and frequency of flooding in the species’ habitat.
sand and clay. Each species was kept in moisture conditions similar to those in the field (i.e. soil flooding for *C. davalliana*, *C. nigra*, *C. limosa* and *C. rostrata*, and moist soil for *C. ferruginea* and *C. sempervirens*) for 5 months. Light intensity was at least 200 µmol m⁻² s⁻¹ PPFD, maximum 1200 µmol m⁻² s⁻¹ PPFD, for 16 h, and temperatures 20–28°C.

**Leaf and root anatomy.** After 5 months of growth, root segments 5–10 cm from the apex were taken from each *Carex* species in order to prepare fresh cross sections for light microscopy and samples for SEM. Root samples were taken from the bottom of the pots, where the soil was saturated with water. Leaf samples were prepared for investigation by light microscopy. Fresh segments were infiltrated with water under vacuum to remove air from the tissues, then cross sections were made with a razor blade and inspected with an Olympus BX-40 microscope (Olympus Optical Co., Ltd., Tokyo, Japan). For SEM, fresh segments were fixed overnight in a phosphate buffer (0.15 M KH₂PO₄ and 0.08 M Na₂HPO₄) containing 3% glutaraldehyde. The tissue was subsequently washed twice with buffer without fixative and twice with water, each step lasting 10 min. Water in the tissue was gradually replaced by placing the tissue in increasing ethanol concentrations (30, 50, 70 and 90%, then three times in 100%; each step lasting 15 min). Segments were cut to a final length of 2 mm after the 70% ethanol stage. Critical-point drying with CO₂ allowed removal of ethanol without distortion of the tissue. Finally, the segments were fixed on an aluminium disk with carbon glue, sputtered with a 4-nm-thick layer of gold and inspected with a JSM-T300 scanning electron microscope (Jeol Ltd, Tokyo, Japan).

**Treatments and harvest.** After 5 months, all species had formed new tillers, which were cut and selected for homogeneity. Thirty young tillers per species were placed in a container with fresh water for 1 wk to allow new root formation, then weighed, planted in 14-cm pots of fresh sand-clay mixture and grown in the glasshouse in the light and temperature conditions previously described. Of each species, 10 plants were placed in free-draining, and 10 in soil-flooded conditions (water level at the soil surface) and 10 were partly submerged (water level 5 cm above soil surface).

After 150 d, plants were harvested, and fresh weights of shoots, roots and rhizomes, and length of the longest leaf were determined. Dry weights were determined after drying the plant material at 105°C for 2 d. Plants with brown or no leaves and no viable roots were considered dead.

**Hydroponic experiments.**

**Growth of plants.** Ramets of each species were taken from the plants in the glasshouse and placed in rafts floating in containers of well aerated nutrient solution as described in Visser *et al.* (1996c). After the development of a new root system, five to eight plants per species were transferred to a stagnant, oxygen-deficient nutrient solution containing 0.1% agar (Visser *et al.*, 1996c). Root growth continued in these conditions in all species except *C. nigra*.

**Root diameter and porosity.** Cross sections of roots of hydroponically grown plants grown for at least 3 wk in either aerated or stagnant, oxygen-deficient medium were prepared for light microscopy as already described. Sections were taken 50 µm behind the root apex and photographed. The areas on the photographs occupied by air spaces were traced with ink onto a transparent plastic sheet. The total area and diameter of each cross section and the area of air spaces were calculated using ImagePro image analysis software.
Statistical analyses

Experimental data and field measurements were analysed with one-way ANOVA to evaluate possible differences between sites and treatments. Tukey post-hoc tests were applied to differentiate between significantly different groups \((P < 0.05)\). Data that were not normally distributed or differed largely in variance were analysed with Kruskal–Wallis ANOVA or Ranks and Dunn post-hoc test. Correlations were analysed with Spearman’s Rank Order Correlation.

RESULTS

Field measurements

Species composition. The number of higher plant species in each relevé differed considerably, from up to 37 species in communities with \(C. \text{ sempervirens}\), to no more than seven in \(C. \text{ limosa}\) vegetation (Table 2). Moreover, species composition differed greatly between plots. When species occupying more than 5\% of a relevé were compared, \(C. \text{ sempervirens}\) was mainly found with \(Sesleria caerulea\), \(Helianthemum nummularia\) ssp. grandiflorum, \(Festuca violacea\), \(Pimpinella major\), \(Lotus corniculatus\) and \(Rhinanthus glacialis\), whereas \(C. \text{ ferruginea}\) occurred with taller-growing herbaceous species such as \(Geranium sylvaticum\), \(Deschampsia caespitosa\), \(Knapia dipsacifolia\), \(Polygonum bistorta\), and also with \(Ligusticum\) \(multellina\), \(Calyccorpus stipitatus\), \(Nardus stricta\) and \(Molinia caerulea\). \(Carex davalliana\) was accompanied by \(M. \text{ caerulea}\), \(Aster bellidiastrum\) and \(Carex panica\), whereas \(C. \text{ nigra}\) vegetation was rather poor in other species of high abundance, except occasionally for \(C. \text{ rostrata}\), \(Trollius europaeus\), \(Potentilla erecta\) and \(P. \text{ bistorta}\). Finally, \(C. \text{ rostrata}\) stands were accompanied by either \(C. \text{ nigra}\) or no other abundant species, whereas \(C. \text{ limosa}\) was found on organic sludge with few higher plants and a well developed moss layer.

The percentage of wetland species was negatively correlated with number of species (Table 2; \(n = 16; r_s = -0.74; P < 0.001\)). This was also the case for water content of the soil and the number of higher plant species in the relevés (Fig. 1). Plant communities on flooded soil never consisted of more than 15 different higher plant species.

Biomass. Only one \(Carex\) species was present at both the lowest and the highest end of a transect (Fig. 2). Between these extremes, the two \(Carex\) species coexisted or were replaced by a third, intermediate species. At the low end of the transects, particularly, most of the standing biomass was formed by \(Carex\) species.

Soil parameters. A gradient in soil-water content was found along each transect (Fig. 3). Soil water content in the DFS, DF and LRN transects decreased with distance from the low end of the transects. The soil at the low end of each of these transects was observed to be water-saturated. In the FS transect the gradient in water content was less clear, with highest moisture levels at the bottom of the shallow gully. The soil water content at the lower part of the RN transect appeared lower than in the middle section, although at both locations the soil was observed to be flooded, with water running at the surface. Here, changes in the content of organic soil matter along the transect might explain the difference in soil water content.

The abundance of the six \(Carex\) species was clearly segregated along a soil water gradient (Table 1). No. of higher plant species

**Table 2. Number of plant species and vegetation cover in relevés taken in vegetation types dominated by selected Carex species**

<table>
<thead>
<tr>
<th>Dominant Carex species</th>
<th>Number of relevés</th>
<th>Number of higher plant species (percentage wetland indicators)</th>
<th>Vegetation cover</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Higher plants</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Moss layer</td>
</tr>
<tr>
<td>(C. \text{ sempervirens})</td>
<td>3</td>
<td>37 (0%)</td>
<td>97%</td>
</tr>
<tr>
<td>(C. \text{ ferruginea})</td>
<td>4</td>
<td>21 (5%)</td>
<td>96%</td>
</tr>
<tr>
<td>(C. \text{ davalliana})</td>
<td>3</td>
<td>14 (14%)</td>
<td>77%</td>
</tr>
<tr>
<td>(C. \text{ nigra})</td>
<td>3</td>
<td>13 (31%)</td>
<td>93%</td>
</tr>
<tr>
<td>(C. \text{ rostrata})</td>
<td>3</td>
<td>3 (67%)</td>
<td>0–20%</td>
</tr>
<tr>
<td>(C. \text{ limosa})</td>
<td>1</td>
<td>7 (86%)</td>
<td>10%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>80%</td>
</tr>
</tbody>
</table>

\(^1\)Wetland indicators defined as described by Lauber & Wagner (1996).
Flooding tolerance of Carex species

3). *Carex sempervirens* was found on moderately moist soil, whereas *C. ferruginea* was located in somewhat higher soil moisture. The other species, however, were found on wet to permanently flooded soil. Shoots of *C. rostrata* (RN transect) and *C. limosa* (LRN transect) and occasionally *C. nigra* (middle of RN transect) were even observed to be partially submerged in 1–15-cm deep water.

The soil redox potentials measured in each plot (Table 3) showed that root systems of *C. sempervirens* and *C. ferruginea* grew under more or less aerated conditions (i.e. redox potential >330 mV), whereas the other species experienced conditions of reduced soil. Redox potentials were particularly low in *C. nigra* and *C. rostrata* vegetation, and considerably higher in the wet *C. limosa* and *C. davalliana* stands.

Usually, flooded soil with high organic matter content tends to develop a lower redox potential than flooded mineral soil. In this case, as shown in Table 3, low redox potentials coincided with either soil with high organic matter content (*C. nigra* stand) or almost entirely mineral soil (*C. rostrata* stand), whereas the highly organic soil on which *C. limosa* grew, showed only slight reduction of redox potential.

Soil pH was about 7 in most transects (data not shown), and did not differ much along each transect or between transects. Maximum pH was 7.5, found in the *C. ferruginea* vegetation of the DF transect, whereas the lowest pH was 6.1, at the high end of the *C. ferruginea* community in the DFS transect.

Glasshouse experiments

Leaf and root anatomy. Leaves of all species contained large air spaces, which appeared similar between species (data not shown). Roots of each species taken from the bottom of the pots had been growing in the water-saturated lower portion of the soil column. They therefore supposedly reflect the ability of root anatomy to adapt to oxygen-deficient conditions. The structure of the root cortex was comparable between species, showing lysigenous aerenchyma formation (Fig. 4), although the relative diameter of the air spaces differed to some extent. Lysis of cortex cells in roots of *C. sempervirens*, C.
Table 3. Soil parameters in vegetation dominated by selected Carex species \( \pm SE \); \( n = 3 - 12 \) for water content and redox potential \( n = 3 \) for organic content

<table>
<thead>
<tr>
<th>Dominant Carex species</th>
<th>Water content (%( v/v ))</th>
<th>Redox potential (mV)</th>
<th>Organic matter content (%( w/w ))</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. sempervirens</em></td>
<td>44 ± 2(^a)</td>
<td>454 ± 61(^c)</td>
<td>21 ± 2(^a)</td>
</tr>
<tr>
<td><em>C. ferruginea</em></td>
<td>54 ± 3(^b)</td>
<td>419 ± 46(^e)</td>
<td>18 ± 1(^b)</td>
</tr>
<tr>
<td><em>C. davalliana</em></td>
<td>74 ± 2(^d)</td>
<td>164 ± 21(^e)</td>
<td>29 ± 2(^c)</td>
</tr>
<tr>
<td><em>C. nigra</em></td>
<td>67 ± 2(^e)</td>
<td>-166 ± 69(^f)</td>
<td>76 ± 3(^i)</td>
</tr>
<tr>
<td><em>C. rostrata</em></td>
<td>80 ± 3(^g)</td>
<td>-241 ± 74(^f)</td>
<td>7 ± 1(^j)</td>
</tr>
<tr>
<td><em>C. limosa</em></td>
<td>86 ± 1(^j)</td>
<td>293 ± 67(^f)</td>
<td>71 ± 0(^j)</td>
</tr>
</tbody>
</table>

Different letters within a column indicate significant difference at \( P < 0.05 \).

Table 4. Survival of Carex species after being grown in the glasshouse at different soil water tables for 150 d (\( n = 10 \))

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Drained (%)</th>
<th>Soil-flooded (%)</th>
<th>Partially submerged (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. sempervirens</em></td>
<td>90</td>
<td>80</td>
<td>0</td>
</tr>
<tr>
<td><em>C. ferruginea</em></td>
<td>100</td>
<td>100</td>
<td>90</td>
</tr>
<tr>
<td><em>C. davalliana</em></td>
<td>100</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td><em>C. nigra</em></td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td><em>C. rostrata</em></td>
<td>100</td>
<td>90</td>
<td>100</td>
</tr>
<tr>
<td><em>C. limosa</em></td>
<td>90</td>
<td>80</td>
<td>100</td>
</tr>
</tbody>
</table>

were interrupted by lamellas of cell-wall remnants (Fig. 4b). In all species the exodermis was intact, consisting of 2–7 layers of small cells with thick walls, and had no part into aerenchyma formation.

**Survival.** Within three months of partial submergence, most *C. davalliana* plants apparently died, as virtually no standing biomass remained. Moreover, performance of *C. sempervirens* was poor under these circumstances. After five months, at the end of the experiment, none of the *C. davalliana* and *C. sempervirens* plants had survived partial submergence (Table 4). By contrast, only low, if any, mortality was found in the other treatments and species.

**Growth parameters.** Neither drained nor soil-flooded conditions affected dry weight in *C. sempervirens*, *C. ferruginea* and *C. davalliana* plants (Table 5). However, partial submergence led either to death (*C. sempervirens* and *C. davalliana*; Table 4) or to a severe decrease in biomass (*C. ferruginea*). In *C. nigra*, root systems grew faster in soil-flooding than drained conditions. Partial submergence had no negative effect on growth of this species. In *C. limosa*, dry weights under soil-flooded and partially submerged conditions tended to be greater than on free-draining soil, but the heterogeneity of the plants was too large to allow determination of the significance of this pattern. *C. rostrata* was the only species with the greatest dry weight of both root and shoot under partially submerged conditions. Calculation of RGR per individual plant on a fresh-weight basis...
confirmed the results shown in Table 5 (data not shown).

The distribution of biomass during soil flooding and partial submergence changed in most species in favour of the belowground plant parts (i.e. rhizome and roots, Table 5). Only in *C. sempervirens* and in *C. limosa* were no changes observed.

Shoot length was negatively affected by soil flooding in *C. davalliana* and *C. ferruginea*, and not affected in *C. sempervirens*, *C. nigra* and *C. rostrata* (Fig. 5). Shoots of *C. limosa* grown in partly submerged conditions were significantly longer than those grown in drained conditions. The opposite was found for *C. ferruginea*.

**Hydroponic experiments**

*Root diameter and porosity.* Roots of *C. ferruginea*, *C. davalliana* and *C. rostrata* formed in stagnant agar were of greater diameter, whereas the diameters of roots of *C. sempervirens* and *C. limosa* did not respond to oxygen deficiency (Fig. 6). *C. nigra* and

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**Table 5. Biomass (g d.wt) of the various plant compartments and below- to aboveground biomass ratio of Carex species after being grown in the glasshouse at different soil water tables for 150 d (± SE; n = 8–10)**

<table>
<thead>
<tr>
<th>Species</th>
<th>Treatment</th>
<th>Shoot</th>
<th>Root</th>
<th>Rhizome</th>
<th>Below-to aboveground ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. sempervirens</em></td>
<td>Drained</td>
<td>0.55 ± 0.07</td>
<td>0.23 ± 0.02</td>
<td>0.02 ± 0.01</td>
<td>0.48 ± 0.05</td>
</tr>
<tr>
<td></td>
<td>Soil-flooded</td>
<td>0.54 ± 0.12</td>
<td>0.17 ± 0.04</td>
<td>0.04 ± 0.01</td>
<td>0.48 ± 0.10</td>
</tr>
<tr>
<td></td>
<td>Partially submerged</td>
<td>†</td>
<td>†</td>
<td>†</td>
<td>†</td>
</tr>
<tr>
<td><em>C. ferruginea</em></td>
<td>Drained</td>
<td>1.47 ± 0.16</td>
<td>0.47 ± 0.07</td>
<td>0.19 ± 0.02</td>
<td>0.45 ± 0.03</td>
</tr>
<tr>
<td></td>
<td>Soil-flooded</td>
<td>1.10 ± 0.09</td>
<td>0.56 ± 0.08</td>
<td>0.26 ± 0.04</td>
<td>0.74 ± 0.06</td>
</tr>
<tr>
<td></td>
<td>Partially submerged</td>
<td>0.46 ± 0.10</td>
<td>0.31 ± 0.07</td>
<td>0.21 ± 0.05</td>
<td>1.37 ± 0.20</td>
</tr>
<tr>
<td><em>C. davalliana</em></td>
<td>Drained</td>
<td>2.21 ± 0.24</td>
<td>0.74 ± 0.10</td>
<td>*</td>
<td>0.33 ± 0.02</td>
</tr>
<tr>
<td></td>
<td>Soil-flooded</td>
<td>2.25 ± 0.21</td>
<td>1.01 ± 0.12</td>
<td>*</td>
<td>0.45 ± 0.03</td>
</tr>
<tr>
<td></td>
<td>Partially submerged</td>
<td>†</td>
<td>†</td>
<td>*</td>
<td>†</td>
</tr>
<tr>
<td><em>C. nigra</em></td>
<td>Drained</td>
<td>0.82 ± 0.11</td>
<td>0.55 ± 0.12</td>
<td>0.12 ± 0.01</td>
<td>0.95 ± 0.20</td>
</tr>
<tr>
<td></td>
<td>Soil-flooded</td>
<td>0.96 ± 0.07</td>
<td>1.09 ± 0.12</td>
<td>0.08 ± 0.02</td>
<td>1.21 ± 0.08</td>
</tr>
<tr>
<td></td>
<td>Partially submerged</td>
<td>0.91 ± 0.11</td>
<td>0.81 ± 0.09</td>
<td>0.11 ± 0.02</td>
<td>1.16 ± 0.20</td>
</tr>
<tr>
<td><em>C. rostrata</em></td>
<td>Drained</td>
<td>0.64 ± 0.07</td>
<td>0.15 ± 0.02</td>
<td>0.13 ± 0.03</td>
<td>0.45 ± 0.05</td>
</tr>
<tr>
<td></td>
<td>Soil-flooded</td>
<td>0.98 ± 0.13</td>
<td>0.47 ± 0.10</td>
<td>0.19 ± 0.05</td>
<td>0.67 ± 0.08</td>
</tr>
<tr>
<td></td>
<td>Partially submerged</td>
<td>1.31 ± 0.10</td>
<td>0.66 ± 0.09</td>
<td>0.18 ± 0.03</td>
<td>0.63 ± 0.06</td>
</tr>
<tr>
<td><em>C. limosa</em></td>
<td>Drained</td>
<td>0.15 ± 0.03</td>
<td>0.07 ± 0.03</td>
<td>0.04 ± 0.01</td>
<td>0.79 ± 0.19</td>
</tr>
<tr>
<td></td>
<td>Soil-flooded</td>
<td>0.26 ± 0.08</td>
<td>0.11 ± 0.04</td>
<td>0.04 ± 0.01</td>
<td>0.69 ± 0.19</td>
</tr>
<tr>
<td></td>
<td>Partially submerged</td>
<td>0.25 ± 0.06</td>
<td>0.12 ± 0.03</td>
<td>0.04 ± 0.01</td>
<td>0.78 ± 0.18</td>
</tr>
</tbody>
</table>

Different letters within a column and for a given species indicate a significant difference between treatments at \( P < 0.05 \); †, no surviving plants; *, not measurable.

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**Fig. 5.** Shoot length of *Carex* species grown in a glasshouse at different soil water tables (open bars, drained; light grey bars, waterlogged; dark grey bars, partially submerged) for 150 d (± SE; n = 8–10; different letters indicate a significant difference between treatments at \( P < 0.05 \). †, no surviving plants).

**Fig. 6.** Average root diameter of hydroponically grown *Carex* species subjected to aerated conditions (light grey bars) or to stagnant, oxygen-deficient conditions (dark grey bars) in the nutrient solution for at least 3 wk (± SE; n = 4; *, \( P < 0.05 \); **, \( P < 0.01 \); ***, \( P < 0.001 \); nd, not determined).
C. rostrata, in particular, developed rather thick roots when subjected to stagnant agar (diam. > 2.5 mm), whereas roots of C. sempervirens and C. davalliana were much thinner (diam. < 1.5 mm). Diameters of roots from C. limosa and C. ferruginea plants grown on stagnant agar were between these extremes.

The porosity of the roots at 50 mm below the apex increased in all species when treated with oxygen-deficient agar (Fig. 7). Although root porosity differed considerably between the species when grown in aerated conditions (e.g. < 4% for C. sempervirens and c. 23% for C. rostrata), this variation was much smaller under oxygen-deficient conditions. Most species developed aerenchyma, to occupy 20–30% of the cross-sectional area. Roots of C. rostrata even reached a porosity of nearly 40%.

**DISCUSSION**

The composition of plant species in alpine meadows varies considerably between sites of different soil-moisture characteristics. Generally, well drained habitats are occupied by a great number of species, whereas in wetland conditions the variety of higher plant species is less (Fig. 1). On these wet sites, much of the standing biomass consists of Carex species (Fig. 2).

The six Carex species that were investigated in this study showed distinct differences in habitat. There were roughly, three different degrees of soil flooding (Fig. 3, Table 3): (1) none in the C. sempervirens and C. ferruginea communities; (2) water-saturated soil but no water above the soil surface in C. nigra and C. davalliana vegetation; and (3) soil flooding with water levels above the soil surface in communities dominated by C. rostrata and C. limosa. In addition, the organic matter content of the soil separated species into two groups; C. limosa and C. nigra were found in soil with high organic matter content, the remaining species on more or less mineral soil (Table 3).

Ellenberg & Strutt (1988) describe a distinct difference in moisture preference between C. sempervirens and C. ferruginea, the first species indicating habitats with fine, shallow soil on dry, steep slopes which are clear of snow early, the latter growing on soils with good water and nutrient supplies, which never dry out and remain snow-covered until late in spring. This is consistent with the presence of C. ferruginea in shallow gullies (e.g. in the FS transect), where soil moisture is likely to be more stable throughout the year than on the more exposed sites occupied by C. sempervirens (Table 3, Fig. 3).

C. limosa is a species typical of quaking bogs (Ellenberg & Strutt, 1988) and very wet blanket- or valley-bogs (Jermy & Tutin, 1968), which is in accord with the habitat in which the species was found in the valley of the Lausbach. Carex nigra, the second species from organic substrate, is supposed to have a much wider amplitude (Jermy & Tutin, 1968), but in the Alpine region it is, as demonstrated by the high organic matter content of the soil (Table 3), the most important peat former in a stable community on flooded soils (Ellenberg & Strutt, 1988).

Carex davalliana is mainly bound to calcareous spring fens (Ellenberg & Strutt, 1988). The highest biomass in the transects was indeed reached where a small brooklet crossed the DF transect, indicating the preference for soil flooding. Carex rostrata biomass was also particularly high in flowing, but deeper, water (RN transect in Fig. 3). This agrees with Ellenberg & Strutt (1988), who place the species on soil likely to be flooded (Jermy & Tutin, 1968).

The majority of Carex-dominated sites were flooded. In organic substrates, this usually leads to low redox potentials (Mitsch & Gosselink, 1986), caused by a fast depletion of oxygen and subsequent use of alternative electron receptors by micro-organisms (Ponnamperuma, 1972). The soil redox potential, however, was not particularly low in the C. limosa vegetation, although the organic matter content of the soil was high (Table 3). Presumably, strong soil reduction is prevented locally by horizontally flowing base-rich water from the hillside close to this bog, a situation comparable to that in the C. davalliana community. On the other hand, it is not clear why the redox potential was particularly low in the mineral soil of the C. rostrata stand from the RN transect (Table 3). On this site, superficial water flowed down a gentle slope, and organic matter content was low. The fine grain size of the substrate at this site might have impeded flow rates at greater
soil depths, and thus have caused a stagnant situation. In conclusion, based on redox potential the Carex species can be divided into those from: (1) aerated soil, (C. sempervirens and C. ferruginea, characteristic for absence of flooding); (2) moderately reduced soils (C. limosa and C. davalliana, characteristic for flooded soils with horizontally moving groundwater); (3) strongly reduced soils (C. nigra and C. rostrata, on sites with stagnant water).

Although the field distribution of Carex species appears to correspond with differences in soil water level, this does not necessarily imply a causal relationship. Further experiments might supply further evidence of this. Furthermore, it is important to identify the adaptive traits that enable plants to grow in flooded conditions. The presence or absence of such traits should be reflected in the survival and performance of a species during flooding in an experimental set-up and in the field.

Roots of wetland plants can display various acclimations to flooding stress (Jackson & Drew, 1984). The principal characteristic of roots of most wetland plants is the presence of aerenchyma (Armstrong, 1979; Konings & Lambers, 1991). This type of cortical tissue connects the root tips to the aboveground plant parts by means of longitudinal air channels, thereby effectively ventilating the respiring tissues in the flooded root. The roots of Carex species display aerenchyma formation (e.g. C. curta, Smirnoff & Crawford, 1983; C. diruha, C. hirta, C. nigra and C. otrubae, Justin & Armstrong, 1987; C. extensa and C. remotia, Moog & Janiesch, 1990; C. lacustris, Bedford et al., 1991), and are apparently well equipped to withstand the low soil oxygen concentrations that often accompany flooding. All species in our study were capable of developing aerenchyma in the roots (examples given in Fig. 4) when these were growing in water-saturated soil. The structure of the aerenchyma shown in Fig. 4b has been described as ‘spiderweb’ or cyperaceous (Justin & Armstrong, 1987) aerenchyma, and consists of radial files of cells, initially interconnected by remnants of tangential cell walls. This type can be found in most Carex species (Smirnoff & Crawford, 1983; Moog & Janiesch, 1990; Fagerstedt, 1992; Moog, 1998) and other Cyperaceae, such as Eriophorum species (Gaynard & Armstrong, 1987).

Hydroponically grown plants of C. davalliana and, especially, C. rostrata developed aerenchyma even in aerated conditions (Fig. 7). When soil flooding was simulated by transferring hydroponically grown plants to an oxygen-deficient, stagnant agar solution, aerenchyma development was enhanced in all species. Additionally, roots often attained a greater diameter when grown in stagnant agar (Fig. 6), further increasing the cross-sectional area of air space.

Although all species formed root aerenchyma to some extent, the performance of the species in flooded conditions varied greatly. Partial submergence led to 100% mortality in C. sempervirens, the roots of which were of the lowest porosity (Fig. 7) and a small diameter (Fig. 6), but also in C. davalliana (Table 4), which is capable of forming aerenchyma and thus attaining high root porosity (Fig. 7). Although all Carex species survived flooding where water levels did not exceed ground level, and four species showed no mortality in partially submerged conditions (Table 4), final biomass differed considerably between treatments and species (Table 5). Two types of response can be distinguished. First, C. sempervirens, C. ferruginea and C. davalliana were not greatly affected by soil flooding, but partial submergence led to decrease in growth or even death of the plant. Second, C. nigra and C. rostrata, displayed reduced growth under free-draining conditions and a high tolerance of soil flooding and partial submergence. Moreover, in C. limosa biomass tended to be lower when not flooded, and shoots grew longer when flooded (Fig. 5). The results are very similar to the responses that Ewing (1996) observed when subjecting C. rostrata and C. stipata to alternating dry and soil-flooded conditions. Leaf elongation rates in these species decreased in drained conditions and recovered during soil flooding or partial submergence. On the other hand, submergence deeper than 50 cm above soil level might even destroy C. rostrata stands (Sjöberg & Danell, 1983).

At first, it might be surprising that C. sempervirens appeared tolerant of soil flooding; however, similar results have been found for another species from calcareous, well drained soil, Sesleria albicans, which survived soil flooding for >2 yr (Dixon, 1996). The low transpiration rate, resulting from the xeromorphic adaptations of plants like S. albicans and C. sempervirens, possibly prevents excessive uptake of phytotoxins produced during soil flooding. Another possibility (Dixon, 1996) is that species originating from wetland ancestors like marsh plants could develop aerenchyma similar to those of their wetland relatives.

Perhaps the most striking result of this study, and one which is difficult to explain, is the vulnerability of C. davalliana to partial submergence. Apparently, internal aeration failed at this high water table, where soil flooding alone had, by contrast, no consequences for survival. The reason might be hampering of gas diffusion between the upper two thirds of the leaves, which were above the water surface, and the submerged parts. However, anatomical studies did not reveal much difference in gas space along the length of leaves of C. davalliana (data not shown). In Eriophorum angustifolium, Gaynard & Armstrong (1987) showed that stomatal density was particularly high >10 cm above the leaf base. Radial oxygen loss from the roots of C. davalliana, an indication of internal oxygen concentration, fell
rapidly when flood water rose to >10 cm above the leaf base, possibly because partial submergence substantially blocked oxygen intake by the stomata of the leaves. A water column above the soil might also have negatively affected the aerated status of the uppermost layers of the soil, with consequences for root growth during soil flooding if the species is shallow-rooted. Iron toxicity might also have played a role under these circumstances, considering the vulnerability of some Carex species to Fe\textsuperscript{3+} (Snowden & Wheeler, 1993). However, Laan et al. (1989b), using the same soil type as in the present study, did not find particularly high free-iron levels in flooded soil.

The data presented in this study lead to the conclusion that partial submergence is a selective stress factor that prevents some Carex species (C. sempervirens, C. ferruginea and C. davalliana) from invading habitats with permanently high water tables. On the other hand, flooding of roots alone is well tolerated by all investigated Carex species, and three species (C. nigra, C. rostrata and C. limosa) even preferred these conditions to free-draining soil. This tolerance is supported by aerenchyma in the roots, which is not constitutive in all species, but always present during soil flooding, natural or simulated. Performance during partial submergence is however not causally linked to aerenchyma content, since some species with aerenchyma might not survive these conditions.

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