Water temperature instead of acclimation stage and oxygen concentration determines responses to winter floods

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Abstract

Field observations suggest that flooding events in the growing season are more detrimental than in winter. To clarify mechanisms producing these seasonal differences we analysed the role of plant acclimation, water temperature and oxygen concentration. We first tested the relative effects of seasonal acclimation and water temperature with three grassland species that differed in tolerance to summer floods (i.e. *Rumex crispus*, *Rumex acetosa* and *Daucus carota*). Our second experiment addressed the role of oxygen level relative to water temperature on biomass decay rate on a moderately intolerant species (i.e. *R. acetosa*).

Irrespective of acclimation, biomass loss in warm water was considerably faster than in cold water. Given the concomitant decline in total non-structural carbohydrates, this was ascribed to the impact of water temperature on respiration rate. However, we only found a significant decline in carbohydrates for *R. crispus* and *R. acetosa*. *D. carota* seemed unable to access stored carbohydrates, which may explain its sensitivity for winter- and summer floods. Our second experiment provided no indication that the higher oxygen concentration may mitigate effects of flooding in cold water since a lower oxygen level of the water did not accelerate the rate of biomass loss.

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These findings indicate that temperature-driven respiration of carbohydrate reserves determines a species' response to winter flooding, whereas oxygen level or plant acclimation are unimportant.

1. Introduction

Flooding gradients are characterised by distinct zonation patterns of terrestrial plant species (Keddy, 1984; Brock et al., 1987; Sykora et al., 1988; Van de Steeg and Blom, 1998; Silvertown et al., 1999; Van Eck et al., 2004). The range of each species along the flooding gradient is strongly related to its tolerance to flooding (Carter and Grace, 1990; Squires and Van der Valk, 1992; Sand-Jensen and Frost-Christensen, 1999; He et al., 1999; Vervuren et al., 2003). However, a species' flooding tolerance may vary with different aspects of the floodwater such as sediment load and temperature (Klimesova, 1994; Siebel, 1998; Nabben et al., 1999; Vervuren et al., 2003). This may complicate predictions of species responses to natural water level fluctuations or to changes as a consequence of global warming or human interference in natural water bodies (Maltby, 1991; Nilsson et al., 1991; Knox, 2000; Crawford et al., 2003). In this paper, we will focus on the role of seasonal timing of flooding events on species distribution along flooding gradients.

In temperate wetlands, most floods occur during winter and early spring, with an excess of rain and snowmelt (Breen et al., 1988; Day et al., 1988; Nilsson et al., 1991; Vervuren et al., 2003). In spite of the more frequent occurrence and longer duration of winter floods, available studies do not suggest a role of these floods in producing plant zonation (Klimesova, 1994; Siebel, 1998). In contrast, summer floods may have a dramatic impact on species zonation in river floodplains (Sykora et al., 1988; Van de Steeg and Blom, 1998; Van Eck et al., 2004).

These field observations suggest that floods outside the growing season are not very harmful to plants. This may be due to either the seasonal status of the plants or to characteristics of the flood water (Yoshie, 1995; Lambers et al., 1998; Crawford, 2003). With regard to seasonal status, it has been suggested that cold-acclimation reduces metabolism (Pollock, 1990). However, during winter plants may also be less susceptible due to increased allocation to below ground plant parts (Yoshie, 1995) that may result in lower maintenance respiration (Amthor, 1984) and thus provide an advantage when floods impose oxygen limitation on plants. On the other hand, the high amount of stored carbohydrates in winter plants may extend maintenance of respiration and thus prolong survival (Crawford, 1992, 2003; Lynn and Waldren, 2002).

The water temperature itself may also reduce respiratory costs, since both the rates of anaerobic and aerobic metabolism may be reduced at lower ambient temperatures (Lambers et al., 1998). An indirect effect of lower water temperature is the higher solubility of oxygen in cold water compared to warm water. This may enhance species' internal oxygen concentration and thus avoid damage due to tissue anoxia (Pedersen et al., 1998).

This paper aims to unravel the relative effects of plant acclimation, water temperature and oxygen concentration for species responses to summer and winter floods. First we investigated the effect of acclimation status and next the role of temperature and oxygen level of the water in a separate experiment. In contrast to previous studies (Klimesova, 1994; Siebel, 1998) we used an experimental design that allowed us to investigate the role of these factors both independently and in interaction with each other. At consecutive periods after the onset of flooding, we determined plant biomass and total non-structural carbohydrates in (tap)roots to determine flooding tolerance as the rate of biomass loss and overall anaerobic and aerobic respiration as the rate of decline in belowground carbohydrate reserves (Setter et al., 1987). The experiments were performed with three grassland species (i.e. *Rumex crispus* L., *Rumex acetosa* L. and *Daucus carota* L.) that represent a broad range of respiratory capacities in warm water (Laan, 1990) and occur in river floodplains at positions with different flooding probabilities (Van Eck, 2004).

2. Materials and methods

2.1. Experiment I: acclimation status and water temperature

2.1.1. Plant material

The selected species (*R. crispus* L., *R. acetosa* L. and *D. carota* L.) are representative for the different elevation ranges along flooding gradients of the River Rhine in the Netherlands. *R. crispus* occurs on low-elevation, frequently flooded sites, *R. acetosa* occupies intermediate sites along the flooding gradient. *D. carota* can mainly be found on dikes and river dunes that are rarely flooded (Voesenek, 1990; Van Eck, 2004). All species are hemicryptophytes with growth buds on or just below the soil surface.

Seeds were collected in 1999 from single populations in river forelands along the River Waal, the main branch of the River Rhine in the Netherlands (*D. carota*: 51°52′05″N 5°58′00″E, *R. acetosa*: 51°53′35″N 5°39′34″E and *R. crispus*: 51°52′53″N 5°45′06″E) and germinated on moist filter paper in petri dishes. Equally sized seedlings were selected and each seedling was transplanted to a 800 ml pot filled with a sand:clay (1:1 v/v) mixture. Seedlings were grown for 2 months in a greenhouse at 16 h daylight at a minimum temperature of 20 °C. Additional lighting was provided by 400 W high-pressure sodium lamps to maintain a minimum of 100 μmol m^{-2} s^{-1} at plant level. In October 1999, the plants assigned to the summer acclimation status (hereafter referred to as 'summer' plants) were allowed to continue growing for 8 weeks in the greenhouse. The plants assigned to the winter acclimation status (hereafter referred to as 'winter' plants) were transferred to an unheated greenhouse where day length and temperature followed outdoor winter conditions (pre-treatment *sensu* Andrews and Pomeroy (1989)). After 6 weeks (13 December 1999 to 2 February 2000), temperatures in this cold greenhouse were relatively high and winter plants were therefore grown for two more weeks in a climate chamber (6 °C, 8 h daylight of 100 μmol m^{-2} s^{-1}). All plants were watered with tap water when necessary and fertilised twice during the growth period with half-strength modified Hoagland nutrient solution (Johnson et al., 1957). The fraction of total biomass after the pre-treatment period that was allocated to below ground parts of both *Rumex* species was

Table 1
Total dry weight and dry weight allocation to roots, presented as the root weight ratio (RWR) in summer and winter acclimated plants, at the start of the flooding treatment (mean ± S.E., $n = 4$) and the results of t-test (p-values) for differences in RWR and total dry weight between seasonal acclimation

Species	Plant parameter	Summer plants	Winter plants	p-value
D. carota	Total dw (g)	0.48 ± 0.03	0.16 ± 0.05	0.001
	RWR	25.25 ± 1.97	30.86 ± 2.26	0.11
R. acetosa	Total dw (g)	0.95 ± 0.12	0.38 ± 0.05	0.004
	RWR	69.24 ± 1.74	78.65 ± 1.81	<0.001
R. crispus	Total dw (g)	0.51 ± 0.04	0.17 ± 0.04	<0.001
	RWR	13.08 ± 0.98	28.58 ± 3.18	0.003

significantly higher in winter- than in summer-acclimated plants (Table 1). In *D. carota,* the root weight ratio also tended to be higher in winter-acclimated plants, but not significantly so.

2.1.2. Experimental set-up

In February 2000, summer and winter plants were placed in four basins and completely submerged in either warm or cold tap water (two basins per temperature treatment), in a complete factorial design. Basins (diameter of 1.8 m; depth 1 m) were positioned in a greenhouse that followed outdoor conditions with respect to light period and temperature. The basins consisted of metal rings coated with foil at the inner side. Both warm- and cold-water basins were provided with a thermo-stated electric heating system at the bottom underneath the foil. Temperatures were measured every hour in each basin using a four-channel external H8 Hobo data logger (ONSET computer corporation, Bourne, Massachusetts) and ranged 20–22 °C in the warm-water basins and 6–10 °C in the cold-water basins. To prevent the establishment of temperature gradients a pump gently circulated the water in each basin. Oxygen was measured twice during the experiment with YSI oxygen device, model 54 with a Pt/Au electrode (Yellow Springs, Ohio). Oxygen concentrations ranged 7.8–8.4 ppm in the warm water basins and 9.6–10.8 ppm in the cold-water basins.

Plants of both acclimation stages were placed in four basins (two warm-water and two cold-water basins). Water level was kept 90 cm above the soil surface in the pots to realise complete submergence. The basins were covered with black plastic foil to exclude carbohydrate gain from photosynthesis so that changes in carbohydrates would accurately reflect respiration processes (Setter et al., 1987).

To assess the effects of water temperature and acclimation status on plant growth and survival, total plant biomass and total non-structural carbohydrate (TNC) reduction of the species were determined. Since summer and winter plants would inevitably differ in plant size and amount of carbohydrate storage, we chose depletion rates for biomass and TNC (taken as the slope of the curve of biomass or TNC versus time) instead of absolute amounts as a basis for comparison. Harvest dates were chosen in such a way that they would allow the fit of a reliable decay curve, and we therefore chose a shorter period and shorter harvest intervals for warm water than cold water, where decay was expected to be slower. In warm water, the plants were harvested after 3, 4, 7, 9, 11, 14 and 17 days flooding, whereas in cold

water, the plants were harvested after 4, 11, 17, 24, 31, 38 and 45 days flooding. Furthermore, for both summer and winter plants, non-submerged control plants were harvested just before the start of the flooding treatment ($t = 0$ days). At each harvest, four replicates (two per basin) of each species and acclimation status were taken out of the water and subsequently separated into roots and shoots after gently washing with tap water. Total plant dry weight was determined after 48 h drying at 70 °C.

Carbohydrate measurements were restricted to the roots because these parts are most likely to experience oxygen deficiency due to their distance from the oxygen-generating shoots and their fast rates of respiration (Vartapetian and Jackson, 1997). In addition, roots are the plant organs where reserve carbohydrates are mainly stored (Crawford, 1992; Yoshie, 1995). TNC were extracted out of 30 mg dried (tap)root material with acid hydrolysis (Poorter and Villar, 1997) using 4 ml demi and 2 ml 8 M HCl (1 h 100 °C). All soluble carbohydrates and glucose released from starch were measured using anthrone (Yemm and Willis, 1954) and will hereafter be referred to as TNC. TNC was calculated by multiplying total root dry weight and the measured concentration and therefore refers to the total weight (mg) of below ground carbohydrates.

2.2. Experiment II: oxygen concentration and water temperature

2.2.1. Experimental set-up

In order to separate the effects of oxygen concentration and water temperature, a second experiment was performed with *R. acetosa*. This species gave the clearest response to different water temperatures within a relatively short period (Van Eck, 2004). Seedlings of *R. acetosa* were grown in 40 ml pots for 8 weeks following the conditions of summer-acclimated plants in experiment I. The *R. acetosa* plants were then completely submerged in containers of 77 l (0.55 m × 0.40 m × 0.35 m) filled with tap water, in a factorial design with four different oxygen levels, and placed either in a warm or cold climate room. Each container contained 28 plants. Practical limitations prevented replication of climate rooms or containers. However, we could strictly control all parameters that might have affected plant responses to flooding, i.e. light, temperature and quality of the gas mixtures. In each climate room, we ran the experiment in two subsequent series, applying two different oxygen concentrations per series (1 and 6 ppm followed by 9 and 13 ppm, respectively).

The experimentally applied oxygen concentrations included both saturation concentrations of cold and warm water (13 and 9 ppm, respectively) and lower concentrations (1 and 6 ppm). These concentrations were realised by bubbling tap water in a PVC-cylinder (height: 1.5 m, diameter 0.2 m) with different mixtures of pressurised air and nitrogen or pressurised air and oxygen, obtained by HI-TEC E55N3 gas blenders (Bronkhorst HIGH TECH, Ruurlo, The Netherlands). Water with the adjusted oxygen concentration was gently circulated between the cylinders and the basins by a pump. The containers were covered with black foil.

Temperature and oxygen concentrations were measured twice a week with an YSI integrated oxygen/temperature device, model 54 with a Pt/Au electrode (Yellow Springs, Ohio). Temperature in the containers was 5.5 ± 0.1 °C ($n = 31$) and 22.6 ± 0.2 °C ($n = 35$) in the cold and warm climate room, respectively. For each oxygen treatment the adjusted oxygen concentrations of the water were equal in warm and cold water (Table 2).

Table 2
Mean values of oxygen levels (ppm) of the water (±S.E. and number of replicates) for the cold- and warm-water submergence treatment of *R. acetosa* in experiment II

O_2 level	Cold water	Warm water	*p*-value
1	1.4 ± 0.3, $n = 8$	1.4 ± 0.1, $n = 10$	0.062
6	6.2 ± 0.2, $n = 6$	6.5 ± 0.1, $n = 11$	0.107
9	9.8 ± 0.4, $n = 8$	9.0 ± 0.4, $n = 8$	0.065
13	12.3 ± 0.2, $n = 9$	11.5 ± 0.4, $n = 8$	0.077

Results of the Mann–Whitney rank sum test (*p*-values) for differences in oxygen-level between temperature treatments are presented as well.

Within a period of 25 days four plants per water temperature and oxygen level were taken out of the water at regular intervals. Subsequently, roots and shoots were gently washed with tap water, dead roots were removed and total plant dry weight (dried for 48 h at 70 °C) was determined. TNC was not determined because it was shown in experiment I that TNC responses followed biomass responses in *R. acetosa*.

2.2.2. Statistical analysis

For experiment I, linear regression of ln-transformed biomass and TNC data was carried out because previous research indicated that an exponential decay curve best describes changes in biomass and TNC for flooded plants (Clevering et al., 1995; Perata et al., 1996; Van Eck, 2004). Effects of flooding duration, species, acclimation and water temperature on total dry weight and TNC content in (tap)roots (ln-transformed data) were tested with ANOVA. In these analyses, flooding duration was included as a continuous variable and species, acclimation and water temperature as categorical variables. Differences between treatments on dry weight or TNC reduction rate would surface as significant interactions of flooding duration with the indicated categorical variable. A similar procedure was followed to analyse the effect of water temperature and oxygen concentration (experiment II).

3. Results

3.1. Experiment I: acclimation status and water temperature

Water temperature significantly affected decay rates in all three species (significant interaction between temperature and flooding duration in Table 3) and biomass loss was always faster in warm water than in cold water (Fig. 1).

Acclimation also explained a significant, but relatively small, part of the variation in biomass loss rates (Table 3). Its effect was most clear in warm water as also indicated by the significant three-way interaction between acclimation, water temperature and flooding duration (Table 3). In contrast to our expectations however, winter acclimated plants lost biomass faster than summer plants when flooded in warm water, particularly plants of *D. carota* and *R. acetosa* (Fig. 1).

Biomass decay rate was also species dependent (Table 3) indicating that there were clear differences in flooding tolerance among the three species. The rate of biomass decay

Table 3
ANOVA for effects of flooding duration, species, temperature and seasonal acclimation on total dry weight and total non-structural carbohydrate content in the (tap)root (ln-transformed data)

Source of variation	Total dry weight		Total non-structural carbohydrate content	
	d.f.	%SS	d.f.	%SS
Flooding duration (F)	1	38.94[***]	1	43.17[***]
Species (Sp) × F	2	7.85[***]	2	1.51[*]
Temperature (T) × F	1	13.31[***]	1	7.71[***]
Seasonal acclimation (S) × F	1	3.97[***]	1	1.98[***]
Sp × T × F	2	5.56[***]	2	1.29[**]
Sp × S × F	2	0.23	2	0.01
T × S × F	1	0.88[***]	1	0.05
Sp × T × S × F	2	0.25	2	0.22
Residual	337	29.00	324	44.05

Flooding duration was included as a continuous variable and interactions with flooding duration therefore indicate rate of biomass or carbohydrate loss as affected by the indicated categorical variable. Table gives proportion of variation (%SS: sum of squares for source of variation relative to total sum of squares) and its significance. d.f. is degrees of freedom.

[*] $p < 0.05$.
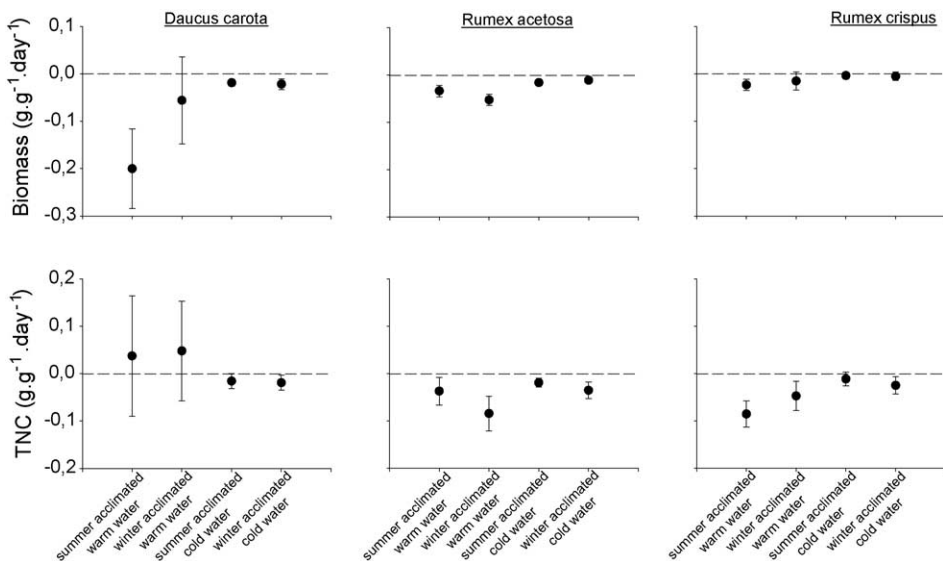[**] $p < 0.01$.
[***] $p < 0.001$.

Fig. 1. Total dry weight reduction rate and TNC reduction rate in (tap)roots in winter and summer acclimated plants of *D. carota*, *R. acetosa* and *R. crispus*, in both warm (20 °C) and cold (6 °C) water (with 95% confidence intervals). Reduction rates are based on linear regression of ln-transformed data.

corresponded with their respective elevational position. The high-elevated *D. carota* had the fastest loss, the intermediately elevated *R. acetosa* lost biomass more slowly, whereas the low elevated *R. crispus* also had the lowest rate of biomass decay (Fig. 1). Species differences in flooding tolerance were also dependent on water temperature (Table 3), but temperature merely affected the magnitude of species differences but did not seem to have reversed the hierarchy in flooding tolerance. In warm water, species clearly differed in rates of biomass loss, whereas in warm water differences between the intermediately tolerant *R. acetosa* and the highly tolerant *R. crispus* were less pronounced (Fig. 1). Differences among species in flooding tolerance were never affected by seasonal acclimation (Table 3). Hence, our study provided no evidence for the assumption that winter acclimation enhances flooding tolerance. Instead, low water temperature appeared the main factor mitigating effects of flooding during winter.

Water temperature also significantly accelerated loss of carbohydrates in storage organs (Table 3; Fig. 1). Again, there was a small impact of acclimation, due to the slightly faster loss of carbohydrates in winter plants, particularly when flooded in warm water (Fig. 1). Our data also revealed different modes of carbohydrate-use between species. The flood-sensitive *D. carota* had no significant decline of carbohydrates in the taproots (Table 3; Fig. 1), although there was significant but weak carbohydrate decline in winter plants in cold water ($R^2 = 0.19$; slope $= -0.02$). Carbohydrates declined in both *Rumex* species (Fig. 1), although differences between both species depended on water temperature (Table 3). In warm water carbohydrate decline was faster for *R. acetosa*, but differences between both species were hardly noticeable in cold water (Fig. 1).

3.2. Experiment II: effect of oxygen concentration and water temperature

In accordance with the first experiment biomass reduction in *R. acetosa* was faster in warm water than in cold water (Fig. 2). This temperature effect seemed also dependent on the oxygen concentration of the water as shown by the significant three-way interaction (Table 4). However, neither in warm nor in cold water was biomass loss clearly retarded at higher concentrations of oxygen (Fig. 2). Hence, this experiment provided no indication that higher oxygen concentrations of cold water are a cause of milder effects of winter floods.

4. Discussion

Our results strongly suggest that previously reported seasonal effects of flooding on species responses (Klimesova, 1994; Siebel, 1998; Crawford, 2003) are mainly due to water temperature rather than oxygen level or seasonal acclimation of the plants. In cold water, biomass decrease was slower than in warm water, but the rate of biomass decrease was never substantially reduced in winter-acclimated plants. Moreover, at least for *R. acetosa*, and within the range investigated by us, there was no clear effect of oxygen level of the water on the rate of biomass loss. Biomass responses, as measured in our study, only reflect effects of the flooding treatment on respiration since complete darkness prevented photosynthesis. During winter, respiration will be the predominant process determining a
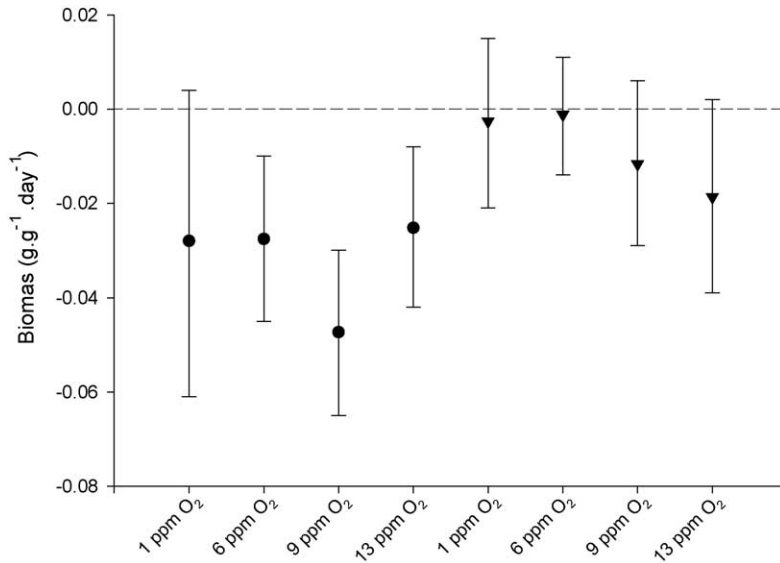
Fig. 2. Biomass reduction rate of *R. acetosa* during flooding in warm (20 °C, ●) and cold (6 °C, ▼) water at oxygen concentrations of 1, 6, 9 and 13 ppm (with 95% confidence intervals). Reduction rates are based on linear regression of ln-transformed data.

plant's response to flooding in the field since assimilation will be constrained by relatively small leaf area (Yoshie, 1995) or light extinction due to high sediment load of flood water (Vervuren et al., 2003).

   Although earlier work suggests differences in respiration rate between summer and winter acclimated plants (Pollock, 1990), our results indicate no effect of acclimation when plants are flooded. Moreover, a shift in allocation towards belowground structures as they occurred in winter acclimated plants, did also not result in reduced respiration. Such allocation patterns may mainly have evolved as protection against aboveground

Table 4
ANOVA for effects of flooding duration, water temperature and oxygen concentration on total dry weight (ln-transformed data) of *R. acetosa*

Source of variation	d.f.	%SS
Flooding duration (F)	1	33.94[***]
Oxygen (O) × F	3	20.28[***]
Temperature (T) × F	1	4.82[***]
O × T × F	3	4.23[***]
Residual	163	36.73

Flooding duration was included as a continuous variable and interactions with flooding duration therefore indicate rate of biomass as affected by the indicated categorical variable. Table gives proportion of variation (%SS: sum of squares for source of variation relative to total sum of squares) and its significance. d.f. is degrees of freedom.
[***] $p < 0.001$.

disturbances during the winter season, i.e. storms or ice scour. As indicated here, more allocation to belowground organs may be ineffective against disturbances such as floods that also affect the belowground compartment.

Remarkably, *R. acetosa* did not benefit from higher oxygen levels in the water during complete submergence in the dark. Possibly, oxygen concentration was already limiting for *R. acetosa* at water-saturated concentrations, which may explain the lack of response to a decrease of oxygen concentration below the saturation point (i.e. 13 mg l^{-1} in cold water). *R. acetosa* is likely to have experienced strongly hypoxic conditions at any applied oxygen level treatment since oxygen rapidly disappears in flooded soils (Ponnamperuma, 1984). In darkness, flooded plants may counteract reduction of the rhizosphere through oxygen uptake by the shoot (Rijnders et al., 2000; Mommer et al., 2004) and subsequent transport via air channels (aerenchyma) to belowground compartment (Jackson and Armstrong, 1999). In *R. acetosa* gas diffusion into flooded leaves does not seem to be limited (Vervuren et al., 1999), but oxygen transport may be strongly impeded by low porosity of petioles and roots (Jackson and Armstrong, 1999). The inability to benefit from higher oxygen levels in cold water may therefore also apply to a larger group of terrestrial plant species that lack the capacity for internal gas transport when flooded, but the picture is different for aerenchymatous species (Jackson and Armstrong, 1999).

Although lower water temperatures decreased the rate of carbohydrate use, our carbohydrate measurements in combination with rate of biomass loss strongly suggest that access and respiration of carbohydrates is still necessary for survival in cold water. The extremely flood-sensitive *D. carota* suffered high biomass loss during submergence and appeared unable to access its reserve carbohydrates from the taproots, probably because it lacks the specific enzymes required for mobilising carbohydrates during flooding (Guglielminetti et al., 1995; Perata et al., 1996). On the other hand, both *Rumex* species had a significant decline of carbohydrates and therefore seemed to be able to respire their taproot reserves in warm as well as in cold water. However, carbohydrate decline was faster in the relative flood-sensitive *R. acetosa* than in the flood-tolerant *R. crispus*, indicating a different efficiency in carbohydrate use.

In conclusion, (lower) water temperature surfaced as the most important explanation for the milder impact of winter floods on plant persistence. Although lower temperature reduced respiratory losses, the ability to access stored carbohydrates and the efficiency of carbohydrate use (i.e. species respiration rates) still appeared to be the key traits determining how long (winter) floods can be endured. The importance of carbohydrate reserves for survival of winter floods implies that plants with small carbohydrate reserves, such as juveniles or heavily grazed individuals (Whittaker, 1982) may be particularly vulnerable to (winter) floods. Our results further suggest that species such as *D. carota*, that lack the ability to access their carbohydrate reserves when flooded, will suffer from both summer and winter floods and will therefore always be restricted to the highest positions in river floodplains. If species have the capacity to access their carbohydrates when flooded (*R. acetosa* and *R. crispus*), winter floods will hardly affect their elevational position. For this group of species, interspecific differences in respiration rate in warm water may be the predominant cause of different distribution along flooding gradients.

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