

Is elongation-induced leaf emergence beneficial for submerged *Rumex* species?

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- **Background and Aims** Plant species from various taxa ‘escape’ from low oxygen conditions associated with submergence by a suite of traits collectively called the low oxygen escape syndrome (LOES). The expression of these traits is associated with costs and benefits. Thus far, remarkably few studies have dealt with the expected benefits of the LOES.
- **Methods** Young plants were fully submerged at initial depths of 450 mm (deep) or 150–240 mm (shallow). *Rumex palustris* leaf tips emerged from the shallow flooding within a few days, whereas a slight lowering of shallow flooding was required to expose *R. acetosa* leaf tips to the atmosphere. Shoot biomass and petiole porosity were measured for all species, and treatments and data from the deep and shallow submergence treatments were compared with non-flooded controls.
- **Key Results** *R. palustris* is characterized by submergence-induced enhanced petiole elongation. *R. acetosa* lacked this growth response. Upon leaf tip emergence, *R. palustris* increased its biomass, whereas *R. acetosa* did not. Furthermore, petiole porosity in *R. palustris* was twice as high as in *R. acetosa*.
- **Conclusions** Leaf emergence restores gas exchange between roots and the atmosphere in *R. palustris*. This occurs to a much lesser extent in *R. acetosa* and is attributable to its lower petiole porosity and therefore limited internal gas transport. Leaf emergence resulting from fast petiole elongation appears to benefit biomass accumulation if these plants contain sufficient aerenchyma in petioles and roots to facilitate internal gas exchange.

Key words: Submergence, emergence, enhanced shoot elongation, porosity, aerenchyma, *Rumex*, cost–benefit analysis, phenotypic plasticity.

INTRODUCTION

A variety of specialized plant species are able to complete their life cycle in flood-prone environments such as lake shores, river floodplains, peat bogs and swamps. These species are occasionally exposed to elevated water levels and are therefore characterized by traits that enable them to cope with the resulting hampered gas exchange between flooded plant organs and the air. This slow rate of gas diffusion in water dramatically reduces oxygen and carbon dioxide influx, causing an imbalance in a plant’s energy and carbon economy (Bailey-Serres and Voesenek, 2008; Jackson, 2008).

A suite of complementary traits, collectively called the low oxygen escape syndrome (LOES), facilitates escape from submergence stress in some species and thus avoids carbohydrate starvation and oxygen depletion (Gibbs and Greenway, 2003; Voesenek *et al.*, 2006; Bailey-Serres and Voesenek, 2008; Jackson, 2008; Voesenek and Pierik, 2008). The LOES includes upward growth of leaves (hyponastic growth), petiole/stem elongation, thinner leaves, cuticles and cell walls, re-orientation of chloroplasts, leaf gas envelopes, aerenchyma and a barrier for radial oxygen loss (Colmer, 2003; Cox *et al.*, 2003; Mommer *et al.*, 2005b, 2007; Colmer and Pedersen, 2008). The elongation traits are initiated by ethylene that accumulates in submerged plant tissues (Musgrave *et al.*, 1972; Kende *et al.*,

1998; Vreeburg *et al.*, 2005; Jackson, 2008). In the semi-aquatic plant *Rumex palustris*, ethylene accumulation is accompanied by an up-regulation of ethylene receptor and biosynthesis genes (Vriezen *et al.*, 1997, 1999; Rieu *et al.*, 2005) and a fast decline of the endogenous abscisic acid (ABA) concentration. This drop in ABA is regulated via a decrease in biosynthesis and an increase in catabolism (Benschop *et al.*, 2005). Down-regulation of ABA is necessary for fast underwater elongation because normal levels of ABA inhibit an increase of the growth-promoting hormone gibberellin (Benschop *et al.*, 2006). Next to this hormonal regulation, ethylene also directly causes an increase in the transcription of the cell-wall loosening gene *RpEXPA1* and accumulation of Expansin proteins (Vreeburg *et al.*, 2005). Finally, ethylene also induces a fast apoplastic acidification, which is presumably related to the pH optimum of Expansins between 3.5 and 4.5 (Vreeburg *et al.*, 2005).

Selection for a specific trait such as flooding-induced shoot elongation in a given environment is an expression of the balance between involved costs and the benefits raised by such a trait. Setter and Laureles (1996) demonstrated that, in rice, elongation growth under water goes at the expense of survival if the plants are unable to emerge from deep water. This shows that costs are involved in underwater elongation and explains why submergence-induced shoot elongation is only selected for in environments with relatively shallow but

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prolonged flooding events (Voeselek *et al.*, 2004). However, surprisingly little research attention has been given to the expected benefits of leaf emergence as a consequence of submergence-induced shoot elongation.

This paper presents the results of an experimental study on the benefits of leaf emergence from initial submergence expressed in terms of biomass accumulation. Two *Rumex* species were selected for study. The results demonstrate that elongation-mediated leaf tip emergence stimulates biomass accumulation in *R. palustris*. However, artificial emergence of leaf tips does not enhance growth of submerged *R. acetosa*, a species that by itself is unable to resurface after submergence. This difference in the ability of the two species to benefit from leaf emergence is hypothesized to be related to a higher capacity for internal gas diffusion in *R. palustris* than in *R. acetosa*.

MATERIALS AND METHODS

Seeds of *Rumex palustris* and *R. acetosa* were sown on polyethylene beads floating in water in a transparent container and allowed to germinate for 10 d at $70 \mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically active radiation (12 h light at 25°C and 12 h dark at 20°C). Seedlings were then transplanted to 175-mL pots containing a 2 : 1 mixture of potting soil and river sand, supplemented with 40 mL nutrient solution (for mineral components see Cox *et al.*, 2003). Plants were grown on pots for 25 d at $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ (16 h light, 8 h dark, relative humidity 70 %, 21°C). After 3 d under glass to prevent dehydration, pots of transplanted seedlings were placed on irrigation mats that were automatically watered twice a day (0700 and 1900 h). Fifteen days after potting, the plants received a further 20 mL of nutrient solution and submergence treatments were started 25 d after potting.

The aim was to determine the extent to which plants benefit from restoring aerial contact with the longest leaves through enhanced petiole elongation. Therefore, the biomass of fully submerged plants was compared with that of plants which were initially fully submerged but able to regain contact with the aerial environment by means of accelerated petiole extension. Previous work on submergence responses has revealed that biomass accumulation shows a good correlation with fitness traits such as survival (Van Eck *et al.*, 2006). To this end, plants were completely submerged in glass tanks. However, half of the plants were submerged to a depth of 450 mm, which is too deep for *R. palustris* to re-emerge through petiole elongation (deep submergence). The remaining plants were submerged in 160 mm (*R. acetosa*) or 240 mm (*R. palustris*) of water (shallow submergence). This shallow depth was outgrown in 5 d through submergence-induced petiole elongation by *R. palustris*, but not by *R. acetosa*, which fails to elongate underwater. Therefore, to observe the effect of re-emergence in *R. acetosa* it was necessary to lower the water level by 30 mm to expose the longest leaves to the air after 5 d. This allowed us to study whether this species could also benefit from restored contact with the atmosphere. In both species the laminae of 2–3 leaves thus re-emerged after 5 d in the shallow submergence treatment, whereas all leaves remained submerged for the entire 21 d in the deeper submergence treatment.

All submergence treatments lasted 21 d and were paralleled by plants that remained in aerated non-flooded control conditions. At the start of treatments ($t = 0$) and again 3 weeks later plants were harvested and petiole porosity, maximum petiole length and shoot dry weight were determined. Furthermore, plant height was recorded every 2–3 d during the 21-d experiment. Petiole porosity measurements were made as described by Raskin (1983) and the equations defined in Thomson *et al.* (1990). Each treatment for both species was carried out with ten replicate plants and the entire experiment was performed twice with comparable outcomes. Measurements made after 21 d of treatment were analysed with a one-way ANOVA and Tukey's *post-hoc* comparison using the SPSS 14 software package. Biomass data were ln transformed to meet the ANOVA requirements (equal variances and normal distribution of the data).

RESULTS

Two Rumex species differ in flooding-induced petiole elongation

Maximum plant height was used as a plant trait to describe the maximum shoot elongation capacity to flooding regimes. *R. palustris*, a species from environments with long-lasting floods, responded to both complete and partial submergence with a strong increase in maximum plant height. The largest maximum height was attained upon complete submergence. This resulted in leaf emergence from the shallow flood (240 mm depth) after 4 d of submergence (Fig. 1A). In contrast, *R. acetosa*, a species from rarely flooded field sites, is characterized by a lower final plant height during both submergence treatments compared with control, non-submerged conditions (Fig. 1B). The increased maximum plant height of submerged *R. palustris* plants results from a strong increase in maximum petiole length and involves only a marginal contribution of leaf lamina elongation (data not shown). The lack of increased petiole elongation upon submergence and an earlier cessation of elongation growth as compared with control conditions in *R. acetosa* explains the low plant height in submerged plants of this species (Fig. 2A). In both species the total number of leaves did not differ between partial and complete submergence and was lower than in the non-submerged control plants (Table 1).

Biomass accumulation and aerenchyma

Rumex palustris plants exposed to 21 d of complete submergence neither lost nor gained shoot dry weight. However, when leaf parts of *R. palustris* emerged from the water surface a significant increase in shoot dry weight was observed as compared with plants that remained completely submerged. Such an increase was not observed in *R. acetosa* (Fig. 3). A possible benefit of elongation-induced leaf emergence is increased inward diffusion of oxygen and carbon dioxide from the atmosphere and enhanced outward diffusion of accumulated gases to the air. The internal diffusion depends on the porosity of the petioles. When petiole porosity was measured under control and submerged conditions for both species, porosity in *R. palustris* was twice that of *R. acetosa*.

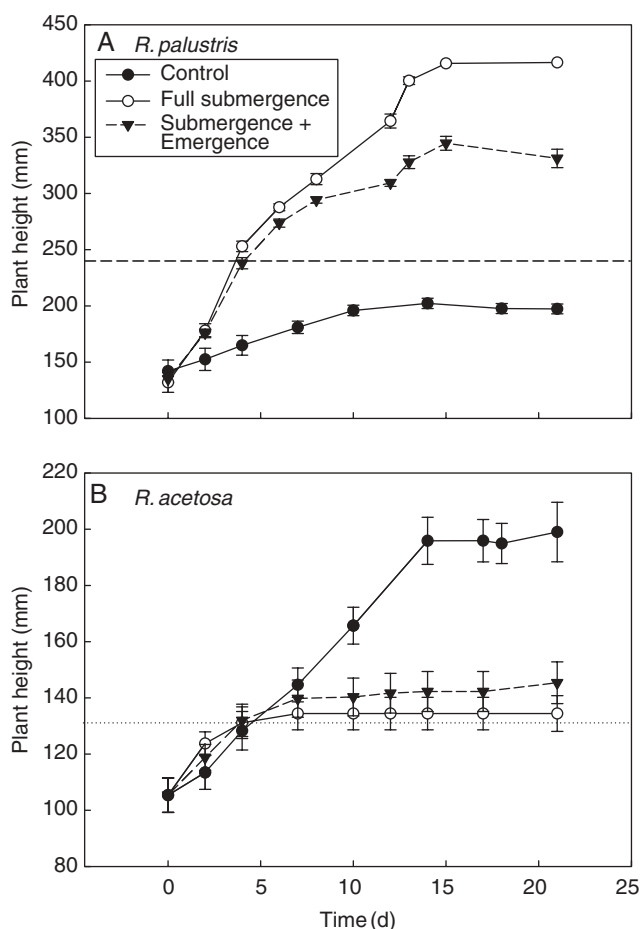


FIG. 1. Changes in shoot height of (A) *Rumex palustris* and (B) *R. acetosa* during 21 d of submergence. Dotted lines indicate the depth of the water in the shallow submergence treatment, and in the case of *R. acetosa* this indicates the level after lowering it to 130 mm after 5 d to expose leaf tips to the air. Plants of *R. palustris* were allowed to emerge above the water level by fast underwater extension. Controls were non-submerged plants grown in well-drained soil. Data are means \pm s.e. ($n = 8-10$).

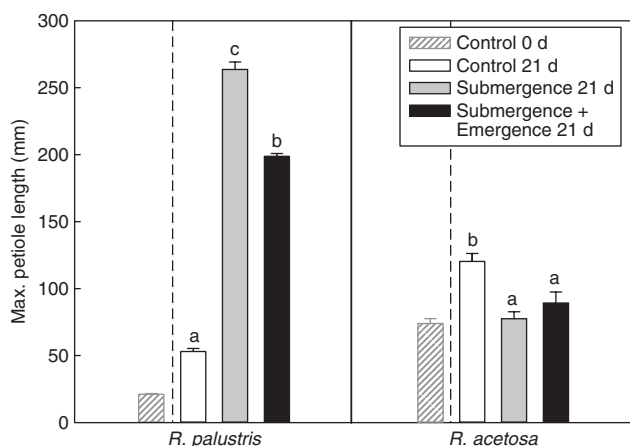


FIG. 2. Maximum petiole length of *Rumex palustris* and *R. acetosa* at the end of 21 d of submergence as described in Fig. 1. Control values at the start of the treatments (control $t = 0$) are shown for comparison. Data are means \pm s.e. ($n = 8-10$). Within each bar graph, means with different letters are statistically significantly different ($P \leq 0.05$).

TABLE 1. Total leaf number per plant for non-submerged control plants, for plants that were submerged for 5 d and then re-emerged and for plants that remained fully submerged throughout the experiment of *Rumex palustris* and *R. acetosa* after 21 d of treatment

Species	Control	Submergence + emergence	Submergence
<i>R. palustris</i>	37.2 \pm 0.9	12.3 \pm 0.7	12.9 \pm 0.5
<i>R. acetosa</i>	23.7 \pm 1.8	13.1 \pm 1.5	9.5 \pm 1.1

Values are means \pm s.e. ($n = 8-10$).

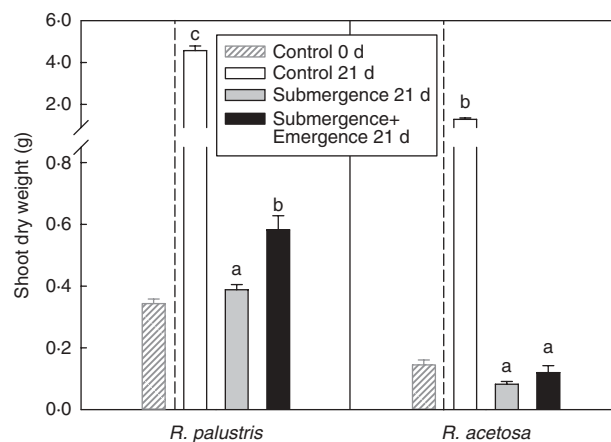


FIG. 3. Final shoot dry weight of *Rumex palustris* and *R. acetosa* after 21 d of submergence as described in Fig. 1. Controls were non-submerged plants grown in well-drained soil. Control values at the start of the treatments (control $t = 0$) are shown for comparison. Data are means \pm s.e. ($n = 8-10$). Within each bar graph, means with different letters are statistically significantly different ($P \leq 0.05$).

TABLE 2. Petiole porosity (% by volume) in non-submerged and fully submerged plants of *Rumex palustris* and *R. acetosa* after 21 d underwater

Species	Control	Submergence
<i>R. palustris</i>	24.1 \pm 0.3	23.4 \pm 0.7
<i>R. acetosa</i>	10.7 \pm 0.4	9.4 \pm 0.3

Values are means \pm s.e. ($n = 4-8$).

Furthermore, in neither species was petiole porosity enhanced by submergence for 21 d (Table 2).

DISCUSSION

Enhanced petiole and/or stem elongation is an important plant trait in the so-called LOES (Bailey-Serres and Voisenek, 2008; Jackson, 2008). It brings leaves to the water surface and it is particularly relevant to survival in shallow, long-lasting floods (Voisenek *et al.*, 2004). The present study shows that leaf emergence of *R. palustris* results in a significant increase of shoot dry weight compared with fully submerged plants. Furthermore, emergence of *R. acetosa*, a

species with lower petiole porosity, does not lead to increased biomass accumulation.

Leaf emergence above the water line can be expected to promote gas exchange between submerged plant organs and the atmosphere. This can have a number of potential benefits. First, inward diffusion of oxygen will aerate potentially anoxic tissues such as apical and central stellar zones and relieve the energy crisis (Armstrong *et al.*, 1999; Colmer, 2003; Gibbs and Greenway, 2003; Fukao and Bailey-Serres, 2004). Secondly, this influx may enhance the oxygen concentration in plant zones characterized by so-called micro-aerobic conditions (0.1–0.75 % oxygen). These micro-aerobic conditions are thought to be responsible for the generation of reactive oxygen species and thus peroxidation of lipid membranes (Santosa *et al.*, 2007). A third benefit of leaf emergence is enhanced potential for photosynthesis as a result of access to atmospheric CO₂, which will be discussed in the next section. A final potential benefit would be the ventilation of accumulated gaseous components such as ethylene, which, at high concentration, interferes with normal root growth (Visser *et al.*, 1997; Visser and Pierik, 2007). These benefits all depend on fast gas diffusion. The rate of gas diffusion in submerged plant organs is inversely related to path length, loss of oxygen along the path and tortuosity of the air channels, and positively correlated with the porosity of the organ (Armstrong *et al.*, 1994; Colmer, 2003). Petiole porosity was found to be much higher in petioles of flood-tolerant *R. palustris* than in those of *R. acetosa*. The low petiole porosity in *R. acetosa* is therefore predicted to hamper fast gas exchange between emerged leaf parts and the root system, thereby preventing significant benefits from leaf emergence. This is further strengthened by the very low root porosity in *R. acetosa* (3–9 % by volume; Laan *et al.*, 1989; Visser *et al.*, 1996) compared with *R. palustris* (24–37 %; Visser *et al.*, 1996). The limited internal aeration this low porosity inevitably brings about will probably restrict aerobic respiration especially in roots and rhizomes and this, in turn, would suppress root growth, nutrient uptake and root-dependent processes of the shoot. This conceptual picture highlights the capacity for internal aeration as a major determinant of submergence tolerance and one that underpins the effectiveness of other traits, such as shoot elongation. This is in agreement with a recent study by Mommer *et al.* (2006) on the importance of various ecophysiological traits in determining submergence tolerance in a variety of species. It was found that capacity for internal aeration is a strong determinant of submergence tolerance (Mommer *et al.*, 2006). They also proposed that a high porosity may have coevolved with the ability for submergence-induced shoot elongation given that the coupling of the two traits appears to maximize the chances of survival by aerating the whole plant effectively.

An important benefit of leaf emergence is related to photosynthesis. When still fully submerged *R. palustris* can already fix some external carbon dioxide, using a variety of submergence-induced leaf acclimations (e.g. thinner cuticles and cell walls) that decrease the diffusion resistance for CO₂ and increase the affinity for CO₂ and thus enhance underwater maximum rates of photosynthesis (Mommer *et al.*, 2005b). Underwater photosynthesis in *R. palustris* (Mommer *et al.*, 2005b) will result in enhanced internal oxygen levels, thereby increasing the efficiency of respiration. The

combination of these two benefits probably prevented a decline in shoot dry weight observed in *R. palustris* during 21 d of complete submergence. However, much higher rates of photosynthesis would presumably be possible in leaves that re-emerge from the submerged environment and restart aerial photosynthesis. The net gain in biomass by *R. palustris* plants that emerged from the water by petiole extension is probably the combined result of the occurrence of aerial photosynthesis in the emerged leaves and enhanced aerobic respiration elsewhere in the plant. Internal transport of carbon dioxide to still submerged parts of leaves may also benefit from the faster ingress of carbon dioxide by virtue of the low porosity/low diffusion resistance pathway. The expected increase in the rate of photosynthesis in *R. acetosa* when emerging a few leaves into an aerated environment did not lead to an increase in shoot dry weight. This suggests that the lack of biomass increase in this species is strongly determined by the poor capacity of this species for internal gas diffusion related to its low overall tissue porosity.

The developmental context of the present study is as follows. Plasticity for petiole elongation in *R. palustris* incorporates an ability for fast extension growth under stressful submerged conditions, a prime example of adaptive phenotypic plasticity. A similar adaptive effect has also been shown for shoot elongation responses to shade imposed by competing neighbours, where the ability to elongate and outgrow adjacent plants stimulates growth in dry matter and reproduction in dense stands (Schmitt *et al.*, 1995; Schmitt, 1997). Interestingly, shoot elongation responses to submergence resemble elongation responses to shade imposed by competing neighbours and both involve a key role for the plant hormone ethylene (Pierik *et al.*, 2005; Mommer *et al.*, 2005a). The picture is emerging of ethylene as an essential modifier of a variety of plant growth adjustments to environmental fluctuations (Pierik *et al.*, 2007) and thus a key mediator of adaptive phenotypic plasticity.

In summary, the data presented indicate that, in *R. palustris*, leaf emergence arising from fast underwater petiole elongation restores gain in dry mass, this being the probable outcome of improved gas exchange between the atmosphere and the plant. This will contribute to the high survival rates and more seed production (Voesenek *et al.*, 1992) that is denied to plants that are fully submerged for long periods. However, even if closely related *R. acetosa* were capable of regaining contact with the air by means of fast petiole elongation (which it is not), this by itself would not ensure that growth in dry matter would ensue. This is because its low tissue porosity would hinder restoration of the rapid gas exchange needed to sustain basic energy-generating processes in the remaining submerged lower sections of the plant. This impediment will, ultimately, accelerate plant death even when parts of leaves were emerged above the water surface (Voesenek *et al.*, 1992).

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