

REVIEW

Underwater Photosynthesis in Flooded Terrestrial Plants: A Matter of Leaf Plasticity

LIESJE MOMMER* and ERIC J. W. VISSER

Department of Experimental Plant Ecology, Radboud University Nijmegen,
Toernooiveld 1, 6525 ED Nijmegen, The Netherlands

Received: 15 November 2004 Returned for revision: 20 January 2005 Accepted: 14 February 2005 Published electronically: 15 July 2005

- **Background** Flooding causes substantial stress for terrestrial plants, particularly if the floodwater completely submerges the shoot. The main problems during submergence are shortage of oxygen due to the slow diffusion rates of gases in water, and depletion of carbohydrates, which is the substrate for respiration. These two factors together lead to loss of biomass and eventually death of the submerged plants. Although conditions under water are unfavourable with respect to light and carbon dioxide supply, photosynthesis may provide both oxygen and carbohydrates, resulting in continuation of aerobic respiration.

- **Scope** This review focuses on evidence in the literature that photosynthesis contributes to survival of terrestrial plants during complete submergence. Furthermore, we discuss relevant morphological and physiological responses of the shoot of terrestrial plant species that enable the positive effects of light on underwater plant performance.

- **Conclusions** Light increases the survival of terrestrial plants under water, indicating that photosynthesis commonly occurs under these submerged conditions. Such underwater photosynthesis increases both internal oxygen concentrations and carbohydrate contents, compared with plants submerged in the dark, and thereby alleviates the adverse effects of flooding. Additionally, several terrestrial species show high plasticity with respect to their leaf development. In a number of species, leaf morphology changes in response to submergence, probably to facilitate underwater gas exchange. Such increased gas exchange may result in higher assimilation rates, and lower carbon dioxide compensation points under water, which is particularly important at the low carbon dioxide concentrations observed in the field. As a result of higher internal carbon dioxide concentrations in submergence-acclimated plants, underwater photorespiration rates are expected to be lower than in non-acclimated plants. Furthermore, the regulatory mechanisms that induce the switch from terrestrial to submergence-acclimated leaves may be controlled by the same pathways as described for heterophyllous aquatic plants.

Key words: Flooding, gas exchange, heterophylly, hormonal regulation, leaf morphology, phenotypic plasticity, photorespiration, photosynthesis, *Rumex*, submergence, survival, wetlands.

INTRODUCTION

Complete submergence imposes considerable stress on plant functioning, predominantly by way of oxygen deprivation, and rapidly results in loss of biomass and ultimately in death of many plant species. However, not all species are equally vulnerable to submergence, and flooding therefore results in distinct distribution limits of plant species along the vertical elevation gradient of river floodplains (Sýkora *et al.*, 1988; Lenssen *et al.*, 1999; Silvertown *et al.*, 1999; Bockelmann *et al.*, 2002). As expected, flooding-sensitive species are generally restricted to high elevated sites in these floodplains where floods are rare, whereas most species growing at low elevated and more frequently flooded habitats are tolerant to flooding. Although this relationship may seem trivial, experimental data were not available until recently, when van Eck *et al.* (2004) found a strong relationship between the LT₅₀ of species, i.e. the time at which 50% of the plants had perished upon experimental submergence, and their vertical distribution in a floodplain. In particular, the depth and the duration of the floods appear strongly to determine the chances of plant survival (Klimešová, 1994; Blom and Voesenek, 1996; Toner and Keddy, 1997; van de Steeg and Blom, 1998; Casanova and Brock, 2000), even in flood-tolerant species.

Plants have evolved a number of mechanisms that are considered to reduce the negative effects of submergence, and which include both metabolic and morphological plasticity (Armstrong *et al.*, 1994a; Vartapetian and Jackson, 1997). Many of the traits of flood-tolerant plants are directed to amelioration of oxygen availability. A well-described example is elongation of the shoot (reviewed in Voesenek *et al.*, 2004), either by increased growth of petioles and lamina (e.g. in *Rumex palustris*; Voesenek *et al.*, 2003) or by stem elongation (e.g. in rice; *Oryza sativa*; Kende *et al.*, 1998), which can ultimately restore the contact of the plant with the atmosphere. Once oxygen enters the shoot, within-plant diffusion is enhanced by longitudinal air channels (aerenchyma) in shoot and roots (Visser *et al.*, 1996; Jackson and Armstrong, 1999; Colmer, 2003) and by development of a gas-tight barrier in the roots to prevent oxygen from diffusing into the anaerobic soil (Armstrong 1979; Colmer *et al.*, 1998; Visser *et al.*, 2000). Voesenek *et al.* (2004) showed, however, that only a subset of flooding-tolerant plant species was capable of significant shoot elongation. These species generally inhabit poorly drained habitats, where floodwater may remain stagnant for a substantial period of the growing season, and shoot elongation is at these sites an efficient solution to avoid oxygen deficiency. Many species, on the other hand, experience submerged conditions that are too deep for the shoot to reach

* For correspondence. E-mail L.Mommer@science.ru.nl

the surface. A straightforward way to reduce shortage of both oxygen and carbohydrates under such conditions would be the continuation of photosynthesis under water. As photosynthesis produces both oxygen and carbohydrates, it might alleviate stress considerably in completely submerged plants.

Our aim is to provide an overview of current knowledge on the importance of underwater photosynthesis for the survival of submerged terrestrial plants. The main factors that change in the underwater environment will be briefly discussed, after which we will summarize the effects of photosynthesis on internal oxygen concentrations.

Furthermore, we will focus on the morphological acclimation of the shoot that is often found in submerged plants, which is important for gas exchange between the leaves and the floodwater, and thus crucial for underwater photosynthesis. The relevance of these changes in leaf phenotype for plant performance will be shown by comparing them with the leaves of heterophyllous aquatic and amphibious species. The latter groups also show high plasticity in leaf morphology and have leaves specialized for photosynthesis in either air or water. We will conclude the review with some perspectives of what we believe are important questions that remain to be solved to increase our understanding of the importance and function of underwater photosynthesis further.

SUBMERGED CONDITIONS LIMIT THE AVAILABILITY OF OXYGEN, LIGHT AND CARBON

Submergence severely inhibits gas exchange between the plant and the environment due to a 10^4 times lower diffusion rate of gases in water than in air (Jackson, 1985). As a result of this hampered gas exchange, oxygen concentrations within the submerged plant may fall in darkness (Stünzi and Kende, 1989; Rijnders *et al.*, 2000). Such low oxygen levels will then limit aerobic respiration and other essential oxygen-dependent processes (Armstrong and Gaynard, 1976; Laan *et al.*, 1990). Anaerobic metabolic pathways, such as fermentation, may partly compensate the low ATP yield from impaired aerobic metabolism (Perata and Alpi, 1993; Gibbs and Greenway, 2003), but these pathways are far less efficient than aerobic respiration and thus reduce the pool of carbohydrate reserves rapidly (Laan and Blom, 1990; Guglielminetti *et al.*, 1997). Submergence-induced oxygen deficiency in terrestrial plants is, therefore, inevitably accompanied by energy and carbohydrate deficits.

Light quantity and quality are also different under water, compared with the conditions above water. Aquatic environments are generally considered to be shaded environments, since light is attenuated by surface reflection, back-scattering, and absorption by water and suspended particles (Holmes and Klein, 1987; Sand-Jensen, 1989). This particularly applies to river water, in which the load of suspended sediment is often very high, and thus light transmission is poor. For example, median transmission in the river Rhine is <1% in a flood of 1 m depth, even at the lowest levels of suspended loads observed during flooding (Vervuren *et al.*, 2003). Similarly, seasonally flooded rice

fields may also suffer from turbid conditions, with light penetrating <0.4 m deep into the floodwater (Ram *et al.*, 2002). Such low light conditions result in a particularly unfavourable environment for underwater photosynthesis.

Additionally, photosynthesis will not only be limited by light during flooding, but also the availability of carbon dioxide is severely limited. Although this gas is approx. 28 times more soluble in water than oxygen, the slow diffusion rate in water will greatly hamper uptake rates by the leaves compared with those in air. Boundary layers around the leaves are likely to be several orders greater in water than in air, particularly in stagnant or slow flowing water (Smith and Walker, 1980). Additionally, carbon dioxide levels fluctuate strongly in time, in both diurnal and yearly cycles, with higher concentrations typically present at night and in the colder season, because of temperature effects on the solubility of gasses in water (Maberly, 1985). Floodwater may contain higher carbon dioxide concentrations if the pH is sufficiently low, but both rice fields (Setter *et al.*, 1987) and river forelands (van den Brink *et al.*, 1993) are commonly submerged with water containing little carbon dioxide, e.g. in the range of 3–100 μM .

LIGHT IMPROVES SURVIVAL DURING SUBMERGENCE

Because of the unfavourable light conditions and carbon dioxide concentrations described above, potentials for underwater photosynthesis would be expected to be very low in terrestrial plants. However, an increasing body of evidence points to a beneficial effect of light on plant survival. Vervuren *et al.* (2003) tested the survival of various floodplain species during prolonged submergence in different light environments. In all species tested, higher light conditions resulted in improved survival, independent from their flooding tolerance. Remarkable was the response of *Rumex crispus*, a perennial grassland species, whose survival increased from 4 months in nearly dark conditions ($0.4 \mu\text{mol PAR m}^{-2} \text{s}^{-1}$; day/night length 16 h/8 h) to >2 years in rather low light conditions ($17 \mu\text{mol PAR m}^{-2} \text{s}^{-1}$, day/night length 16 h/8 h). Clearly, not much light is needed to maintain surviving plant tissues, although total biomass usually decreases considerably under such conditions. Similar but less extreme responses were found for three other *Rumex* species (Nabben *et al.*, 1999), some terrestrial *Ranunculus* species (He *et al.*, 1999), a set of other river-accompanying species (Blom *et al.*, 1994) and rice (Adkins *et al.*, 1990; Ito *et al.*, 1999; Ram *et al.*, 2002). Even tall helophyte (Clevering *et al.*, 1995; Armstrong *et al.*, 1999) and tree species (Siebel *et al.*, 1998) may profit from underwater photosynthesis, when they are submerged during their establishment phase.

Improved survival of submerged plants in the presence of light was found to correlate with the carbohydrate status of the plants. Internal concentrations of soluble carbohydrates and starch in the shoots of submerged rice decreased in both light and shaded (i.e. 75% less light) conditions, but submerged plants in full light always contained more carbohydrates (30–160%, depending on the cultivar) than those submerged in shade (Ram *et al.*, 2002). *Rumex crispus*

showed a similar response, although in this case the total starch content, rather than the concentration, was considerably higher (approx. 70 %) in light-grown submerged plants (Laan and Blom, 1990). Such differences in carbohydrate levels are likely to result from carbon fixation and subsequent sucrose production, which in turn fuels respiration and thereby decreases the demand on stored carbon (i.e. starch). On the other hand, oxygen produced by photosynthesis may improve the aeration status of submerged plant organs (see the following section), and thus enable continued aerobic respiration, which is far more efficient in terms of carbohydrate use per unit ATP produced than anaerobic metabolism (Gibbs and Greenway, 2003). In this way, the depletion of the carbohydrate storage will also be slowed down considerably.

LIGHT INCREASES THE INTERNAL OXYGEN CONCENTRATIONS IN SUBMERGED PLANTS

As shown above, light, and therefore presumably underwater photosynthesis, may determine the survival of terrestrial plant species when flooded. Oxygen deficiency is commonly considered to be the main stress factor under these conditions, and one would therefore expect that one important result from photosynthesis is an improved oxygen status in the submerged leaves. Then, if the porosity of the tissues is sufficiently high, oxygen may be able to diffuse throughout the plant, including the root system. Such a mechanism has been shown for submerged *Eriophorum angustifolium* plants (Gaynard and Armstrong, 1987), where photosynthetically produced oxygen contributed to radial oxygen loss (ROL) from the roots to the sediment. Similarly, rice (Waters *et al.*, 1989), sea grasses (Pedersen *et al.*, 1998, 2004) and amphibious isoetid species (Pedersen *et al.*, 1995; Sorrell, 2004) showed substantially higher oxygen concentrations in the rhizosphere during the light period. Also, hydroponically grown *Rumex maritimus* plants that were completely submerged in the light showed lower oxygen uptake rates from the medium surrounding the roots compared with dark-submerged plants, due to the additional supply of photosynthetically derived oxygen (Laan and Blom, 1990). These indirect methods have in common that they all clearly point to increased oxygen concentrations in submerged plants when these were photosynthesizing, although they do not predict the actual internal oxygen concentration.

A more direct approach was used by Rijnders *et al.* (2000) and Mommer *et al.* (2004), who measured the internal oxygen concentration in the petioles of submerged *R. palustris* plants and found increased concentrations in the light (Fig. 1), even in the presence of very limited amounts of dissolved carbon dioxide in the floodwater (Mommer *et al.*, 2004). The internal oxygen concentrations observed in the study of Mommer *et al.* (2004) were more than sufficient to maintain aerobic respiration in the shoot in light, but also in darkness, indicating that hypoxic conditions are not always as prevalent as reported in the past. Putatively, such relatively high oxygen concentrations in the shoot provide a source to maintain at least part of the

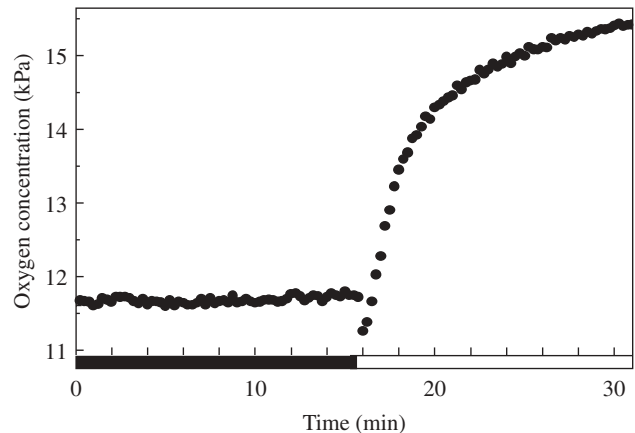


FIG. 1. Internal oxygen concentrations in the petiole of a submerged *Rumex palustris* plant, in the dark (closed bar) and in the light (open bar). Oxygen concentrations were measured with a microelectrode inserted in the petiole in close proximity to the leaf lamina (cf. Mommer *et al.*, 2004). Light conditions were saturating ($450 \mu\text{mol PAR m}^{-2} \text{s}^{-1}$ at the leaf level), and external dissolved carbon dioxide concentration was low ($8 \mu\text{M}$), at a temperature of 20°C .

root system well aerated (Armstrong *et al.*, 1994b; Sand-Jensen *et al.*, 2005).

CARBON DIOXIDE IS AN IMPORTANT LIMITING FACTOR FOR UNDERWATER PHOTOSYNTHESIS

As stated in a previous section, underwater photosynthesis will not only be limited by light, but also by a severely reduced inorganic carbon supply compared with photosynthesis above water, due to slower carbon dioxide diffusion rates (Bowes, 1987; Madsen and Sand-Jensen, 1994). Furthermore, the development of larger stagnant boundary layers around the leaves (Smith and Walker, 1980; Jones *et al.*, 2000) reduces carbon dioxide availability for photosynthesis under water even further. In terrestrial plants, which are not specialized for an aquatic life, underwater photosynthesis is, therefore, characterized by relatively low photosynthesis rates, high carbon dioxide compensation points and low uptake efficiency of carbon dioxide due to high diffusion resistance (Maberly and Madsen, 1998; Sand-Jensen and Frost-Christensen, 1999).

True aquatic plant species often have thin, highly dissected leaves, a morphology which is believed to be directed to the optimization of gas exchange underwater (Sculthorpe, 1967; Rascio *et al.*, 1999). These 'aquatic' leaves, such as in aquatic *Ranunculus* species (Bruni *et al.*, 1996) and *Elodea nuttallii* (Jones *et al.*, 2000), do not possess stomata. Instead, cuticles of these leaves are minimized or even lacking and, therefore, underwater gas exchange most probably occurs via the epidermal cells and cuticle layer.

Many aquatic plants not only rely on their highly specialized growth forms, but have also developed additional carbon dioxide-concentrating mechanisms, which enhance carbon gain under water (Bowes and Salvucci, 1989; Keeley and Santamaria, 1992; Maberly and Madsen, 2002). The most widespread mechanism to increase carbon dioxide

availability is the ability to use HCO_3^- in photosynthesis (Allen and Spence, 1981; Prins and Elzenga, 1989; Madsen, 1993). This may be achieved by proton extrusion at one side of the leaf, thereby lowering the pH and thus shifting the inorganic carbon equilibrium in favour of carbon dioxide over HCO_3^- (Prins *et al.*, 1982; Lara *et al.*, 2002). Alternatively, HCO_3^- itself may also be actively taken up (Elzenga and Prins, 1989; Lara *et al.*, 2002). The use of HCO_3^- is a carbon-concentrating mechanism, and often coupled to a C4 metabolism, as has been reported for *Hydrilla verticillata* (Holaday and Bowes, 1980; Spencer *et al.*, 1996; Magnin *et al.*, 1997; Reiskind *et al.*, 1997), *Elodea canadensis* (Elzenga and Prins, 1989) and *Egeria densa* (Browse *et al.*, 1979; Casati *et al.*, 2000). This type of metabolism generally relies on a spatial separation between the C₃ and C₄ carboxylating enzymes, but the characteristic Kranz or bundle sheath anatomy observed in terrestrial plants (Lambers *et al.*, 1998) is most often lacking in aquatic species (Magnin *et al.*, 1997; Reiskind *et al.*, 1997). Separation between the C₃ and C₄ carboxylating enzymes in aquatic species appears to occur at the cellular level at the chloroplasts (Reiskind *et al.*, 1997; Casati *et al.*, 2000; Rao *et al.*, 2002).

Another alternative carboxylation pathway is crassulacean acid metabolism (CAM), which is also observed in drought-adapted plant species. This alternative carboxylation pathway has a separation of the two carboxylation steps in time. CAM has only been observed in isoetids, such as *Lobelia dortmanna* and *Littorella uniflora* (Robe and Griffiths, 1990; Madsen *et al.*, 2002). These species can use carbon dioxide from the sediment, which contains high carbon dioxide concentrations as a result of microbial respiration (Wium-Andersen, 1971; Roelofs *et al.*, 1984; Pedersen *et al.*, 1995). This carbon dioxide diffuses from the soil into the roots and then further follows the concentration gradient into the shoot via aerenchymatous tissue. Future research will need to prove if these mechanisms can be induced in terrestrial wetland plants.

HETEROPHYLLY AS A STRATEGY TO INCREASE CARBON DIOXIDE UPTAKE IN CONTRASTING ENVIRONMENTS

Several aquatic and amphibious species growing in the transition from water to land, e.g. various *Potamogeton* species (Frost-Christensen and Sand-Jensen, 1995), *L. uniflora* (Hostrup and Wiegand, 1991; Robe and Griffiths, 1998) and *Ranunculus* species (Bruni *et al.*, 1996; Garbey *et al.*, 2004), show remarkable plasticity in leaf form, specialized for photosynthesis either in air or under water (Maberly and Spence, 1989; Sand-Jensen and Frost-Christensen, 1999). In order to acclimate successfully to flooding and improve underwater gas exchange, submerged terrestrial plants probably need to develop leaves with a fundamentally different morphology and anatomy. It is an intriguing question whether terrestrial plants can employ heterophyllous strategies similar to aquatic and amphibious species.

As mentioned above, typical aquatic-like leaves have a specialized leaf form with filamentous, dissected leaves with few or no stomata, which is entirely different from the



FIG. 2. Morphology of a control (left) and submerged (right) *Rumex palustris* plant. Submergence took place during 14 d in 0.7 m deep containers with circulating clear tap water, with light intensities of $100 \mu\text{mol PAR m}^{-2} \text{s}^{-1}$ at leaf level and a 16 h/8 h day/night cycle; temperature 20°C . Plants were 52 d old. Scale bar = 50 mm.

terrestrial form (Sculthorpe, 1967). Most aquatic leaves of amphibious plants, however, are simply more elongated and thinner and have a higher specific leaf area (SLA) than terrestrial leaves (Nielsen, 1993; Frost-Christensen and Sand-Jensen, 1995). Measurements on the terrestrial plant *R. palustris* also showed elongated leaves (Fig. 2) and an increased SLA (Mommer *et al.*, 2005), indicating decreased thickness and a relatively increased gas exchange area (Mommer *et al.*, 2004).

Leaf plasticity does not only occur at the level of species, but the ability to express differential leaf anatomy under different environmental conditions may also vary among populations of a single species (Lynn and Waldren, 2001; Lenssen *et al.*, 2004). Lynn and Waldren (2002) showed that populations of *Ranunculus repens* from frequently flooded habitats have a highly dissected leaf type, which was more favourable for underwater photosynthesis. In the case of another terrestrial *Ranunculus* species, *R. flammula*, the one population that had little leaf plasticity performed extremely poorly in a survival experiment under submerged conditions (10 % survival) compared with populations that could change their leaf morphology in response to submergence (75–100 % survival) (Cook and Johnson, 1967).

Aquatic leaf type formation in heterophyllous amphibious plants has been claimed to be regulated by the plant hormones ethylene and abscisic acid (ABA) (Kuwabara *et al.*, 2001; Minorsky, 2003). Leaves were narrow and contained fewer stomata when *Ludwigia arcuata* was submerged or when treated with ethylene (Kuwabara *et al.*, 2003). However, the ethylene concentrations needed to mimic the submergence response fully were exceptionally high ($>50 \mu\text{L L}^{-1}$) and may not be reached under submerged conditions [given the data provided in the same paper, and the concentrations of $4\text{--}5 \mu\text{L L}^{-1}$ ethylene in submerged *Rumex* plants found by Voesenek *et al.* (1993a)]. Exogenous supply of ABA was able to counteract the submergence response and switched on terrestrial leaf formation in *Marsilea quadrifolia* (Lin and Yang, 1999) and *L. arcuata* (Kuwabara *et al.*, 2003). Hsu *et al.* (2001) confirmed these results and, moreover, showed that the ABA response was correlated with a differential expression pattern of ABA-induced ABRH (ABA-responsive heterophylly) genes in *Marsilea*.

Contrasting evidence for ABA action originates from work on *Egeria densa*, where application of exogenous ABA induced expression of C4-like biochemical traits (Casati *et al.*, 2000). Thus, although ABA induces the terrestrial leaf morphology in *Marsilea* and *Ludwigia*, it induces the 'aquatic' photosynthesis type in *Egeria*. To increase complexity even further, *Eleocharis vivipara* also showed induction of C4 photosynthesis by ABA (Ueno, 1998), but in this species the C4 traits were expressed in air instead of under water, where it showed C₃ characteristics (Ueno, 2001). We conclude that ABA is likely to play an important role in inducing a heterophyllous switch (with many details still needing to be elucidated), but it remains difficult to extrapolate its role in leaf anatomy to its role in photosynthetic metabolism. Interestingly, ABA, in an interplay with ethylene, is also a key player in submergence-induced elongation growth responses in the terrestrial species *R. palustris* and rice (Kende *et al.*, 1998; Voesenek *et al.*, 2003), but this work focused on petioles and stems rather than on the leaf lamina. It therefore remains to be clarified whether these plant hormones are also responsible for changes in leaf morphology of submerged terrestrial plants.

LEAF ACCLIMATION ENHANCES GAS EXCHANGE FROM THE WATER COLUMN INTO THE LEAVES

Attempts to relate underwater photosynthesis to flooding tolerance have failed when non-acclimated plants were investigated at high carbon dioxide concentrations (Voesenek *et al.*, 1993b; He *et al.*, 1999; Vervuren *et al.*, 1999; Mommer *et al.*, 2005). We suggest, therefore, that it is not the photosynthesis capacity under water *per se* that determines survival under water, but photosynthetic performance under more natural conditions, where carbon dioxide availability is limited and thus low gas diffusion resistance becomes more important.

The degree to which plants are able to conduct underwater photosynthesis largely depends on the gas exchange

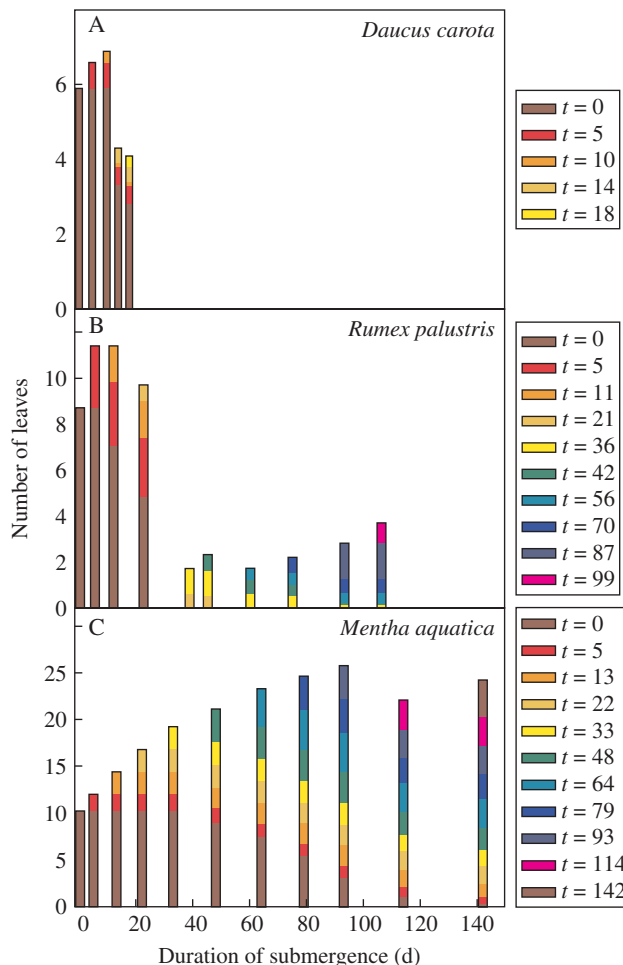


FIG. 3. Leaf longevity of submerged plants of three plant species contrasting in flooding tolerance. Species presented are (A) *Daucus carota*—flooding-intolerant; (B) *Rumex palustris*—flooding-tolerant; (C) *Mentha aquatica*—flooding-tolerant. New leaves present at the subsequent censuses ($t = x$ days) are represented by different colours. Leaves present at the onset of submergence are indicated as $t = 0$. Conditions of submergence were similar to those given at Fig. 2, but with lower light conditions ($30 \mu\text{mol PAR m}^{-2} \text{s}^{-1}$). Measurements were performed on ten plants per species. Standard errors were typically 5% of the mean.

capacity of their leaves under water. The development of new, acclimated leaves may therefore be crucial for survival under water. We observed that flooding-tolerant species generally continued to develop new leaves during complete submergence, whereas flooding-intolerant species, such as *Daucus carota*, were hardly able to develop new leaves under water (Fig. 3A). This inability of flooding-intolerant species to produce new leaves is probably related to shortage of energy, as illustrated by van Eck *et al.* (2005), who showed that intolerant species such as *D. carota* were unable to access stored carbohydrates in the taproot. Furthermore, internal aeration in these species may be poor and thus limits underwater plant performance. Flooding-tolerant species had different patterns of leaf formation under water. *Rumex palustris* showed a continuous turnover of leaves, compensating the loss of older leaves by formation of new acclimated leaves (Fig. 3B), whereas other species,

such as *Mentha aquatica*, had much lower turnover rates, but also continued leaf development (Fig. 3C). Another flood-tolerant species, *Oenanthe aquatica*, even developed highly dissected leaves under water (L. Mommer unpubl. res.), strongly resembling the submerged leaves of some aquatic heterophyllous *Ranunculus* species (Bruni *et al.*, 1996; Rascio *et al.*, 1999; Germ and Gaberscik, 2003; Garbey *et al.*, 2004).

The amount of data on the effect of leaf acclimation on the internal gas concentration is very limited. Experiments with microelectrodes measuring internal oxygen concentrations within the petioles of submerged *R. palustris* plants showed that, even in the dark when the only source of oxygen is uptake from the floodwater, the internal oxygen concentrations were considerably higher in submergence-acclimated plants than in non-acclimated plants (Mommer *et al.*, 2004). This passive diffusion of oxygen from the water column into the plant has been observed previously for aquatic macrophytes such as *L. uniflora* and *L. dortmanna* (Sand-Jensen *et al.*, 1982) and seagrasses (Pedersen *et al.*, 1998; Greve *et al.*, 2003; Pedersen *et al.*, 2004). It was remarkable that the internal oxygen concentrations of petioles of submergence-acclimated *Rumex* plants were almost similar to the oxygen concentrations of the water column (Mommer *et al.*, 2004). This shows clearly that shoot acclimation to submergence is particularly functional with respect to gas exchange capacity between the water column and the plant.

The data of Mommer *et al.* (2004) contrast to some extent with experiments of Rijnders *et al.* (2000) and Stünzi and Kende (1989), where internal oxygen concentrations decreased rapidly upon submergence. This contrast shows the importance of boundary layers under water. Oxygen concentrations remained stable and relatively high when plants were submerged in a stirred solution (Mommer *et al.*, 2004), whereas, without stirring, oxygen concentrations fell rapidly (Stünzi and Kende, 1989; Rijnders *et al.*, 2000).

The data described above suggest that shoot acclimation to submergence involves a reduction of the diffusion resistance to gases, which increases not only diffusion of oxygen into the plant, but also the influx of carbon dioxide, which enhances underwater photosynthesis. Such reduced gas diffusion resistance resulted in aquatic leaves of amphibious plant species exhibiting increased underwater photosynthesis rates and a higher carbon dioxide affinity compared with their terrestrial counterparts (Frost-Christensen and Sand-Jensen, 1992, 1995; Nielsen, 1993). The major factor determining carbon dioxide uptake efficiency under water is considered to be cuticle resistance (Frost-Christensen *et al.*, 2003). Frost-Christensen *et al.* (2003) showed that aquatic leaves of five amphibious species had a reduced cuticle thickness compared with terrestrial leaves, and an accompanying reduced diffusional resistance for gases such as oxygen. Hoffmann-Benning and Kende (1992) did not find differences in cuticle and epidermal cell wall thickness of submerged, elongated deepwater rice stem segments compared with non-flooded internodes, indicating that cuticle and cell wall synthesis can keep pace with the fast elongation growth (up to 5 mm h⁻¹)

that takes place in this and other terrestrial wetland species. However, ¹⁴C-labelled palmitic acid fed to fast elongating stem segments was incorporated into cutin polymers with different composition, as shown after reductive hydrolysis of the cuticle and subsequent fractioning on thin-layer chromatography (TLC) (Hoffmann-Benning and Kende, 1992). This analysis indicated that, tentatively, increased stem elongation was accompanied by a promotion of cutin monomer hydroxylation. Possibly, such changes in cuticle composition also take place in submerged leaves, thereby adding to a decrease in gas diffusion resistance.

Next to differences in diffusion resistance, differences at the biochemical level of photosynthesis have also been observed between the leaf types of amphibious plants, and therefore may also occur in submerged terrestrial plants. Chlorophyll contents (Frost-Christensen and Sand-Jensen, 1992; Nielsen, 1993), as well as concentrations of the carboxylation enzymes Rubisco and phosphoenolpyruvate carboxylase (Farmer *et al.*, 1986; Beer *et al.*, 1991), are lower in aquatic compared with terrestrial leaves of amphibious plants.

SUBMERGENCE LEADS POTENTIALLY TO HIGH PHOTORESPIRATION RATES

Underwater photosynthesis in terrestrial plants may be characterized by high photorespiration rates, as reduced gas diffusion rates under water will lead to relatively low internal carbon dioxide concentrations compared with the internal oxygen concentrations in the presence of light (Maberly and Spence, 1989; Jahnke *et al.*, 1991). High photorespiration rates may cause loss of assimilated carbon, which would add to the scarcity of carbon in submerged conditions.

Many aquatic macrophytes, however, such as *E. nuttallii* and *E. densa* do not suffer from high photorespiration rates, since they have low carbon dioxide compensation points or can even alter these under unfavourable (i.e. very low carbon dioxide) conditions as a result of their carbon-concentrating mechanisms (Van *et al.*, 1976; Salvucci and Bowes, 1981; Bowes *et al.*, 2002). This has been shown with enzyme assays and labelling studies of the photorespiratory cycle and the coupled C₄ metabolism (Hough, 1974; Salvucci and Bowes, 1983). Direct measurements of underwater photorespiration rates are lacking up to now. To our knowledge, the only data available on amphibious or terrestrial leaves are those of Lloyd *et al.* (1977), who showed that if the oxygen concentration doubles in water-saturated air, photosynthesis decreases by 50 % and thus photorespiration has increased. We suggest that submergence-acclimated leaves of terrestrial plant species will have decreased underwater photorespiration rates, because of the much higher CO₂ diffusion into these leaves relative to non-acclimated leaves.

PERSPECTIVES

As this review has shown, underwater photosynthesis is vital for survival of terrestrial plants during conditions of deep floods. Even rather low light conditions already result in increased survival. Changes in leaf morphology upon

submergence, which at least partly compensate the unfavourable gas exchange conditions under water by reducing the gas diffusion resistance, increase underwater photosynthesis rates, and also decrease photorespiration rates.

It would be particularly interesting to elucidate through which mechanisms the morphological changes of the leaves decrease the resistance to gas exchange. It could simply be the larger leaf surface area to volume ratio that increases the relative flux of carbon dioxide and oxygen from the water column into the plant. However, if the development of submergence-acclimated leaves is similar to heterophylly in aquatic and amphibious plants, terrestrial plants may be able to decrease cell wall and cuticle thickness in response to submergence, and even change the composition of the cuticle in order to decrease gas diffusion resistance (cf. Frost-Christensen *et al.*, 2003). Furthermore, acclimation to submergence may involve not only diffusion resistance, but also biochemical processes in the photosynthetic apparatus.

It is not yet known how the formation of submerged leaf types is induced in terrestrial plants. Data from aquatic and amphibious plants suggest the hormone ABA, and possibly ethylene, to be key players in morphological, anatomical and photosynthetic (biochemical) changes upon submergence (e.g. Kuwabara *et al.*, 2001, 2003; Minorsky, 2003). Interestingly, these hormones are also essential components of signalling cascades leading to enhanced shoot elongation during submergence in some terrestrial species (Kende *et al.*, 1998; Voesenek *et al.*, 2003). Incorporating plant hormones into underwater photosynthesis research in terrestrial plants will be a promising avenue of research to explore how changes in underwater gas exchange capacity of terrestrial plants are regulated.

ACKNOWLEDGEMENTS

We thank Ronald Pierik and Hans de Kroon for suggestions on drafts of the manuscript. Dick van Aalst produced the photograph of Figure 2.

LITERATURE CITED

- Adkins SW, Shiraishi T, McComb JA. 1990. Submergence tolerance of rice—a new glasshouse method for the experimental submergence of plants. *Physiologia Plantarum* 80: 642–646.
- Allen ED, Spence DHN. 1981. The differential ability of aquatic plants to utilize the inorganic carbon supply in the fresh waters. *New Phytologist* 87: 269–283.
- Armstrong W. 1979. Aeration in higher plants. In: Woolhouse HW, ed. *Advances in botanical research*. London: Academic Press, 226–328.
- Armstrong W, Gaynard TJ. 1976. The critical oxygen pressures for respiration in higher plants. *Physiologia Plantarum* 37: 200–206.
- Armstrong W, Brändle R, Jackson MB. 1994a. Mechanisms of flood tolerance in plants. *Acta Botanica Neerlandica* 43: 307–358.
- Armstrong W, Strange ME, Cringle S, Beckett PM. 1994b. Micro-electrode and modelling study of oxygen distribution in roots. *Annals of Botany* 74: 287–299.
- Armstrong J, Afreen-Zobayed F, Blyth S, Armstrong W. 1999. *Phragmites australis*: effects of shoot submergence on seedling growth and survival and radial oxygen loss from roots. *Aquatic Botany* 64: 275–289.
- Beer S, Sand-Jensen K, Madsen TV, Nielsen SL. 1991. The carboxylase activity of Rubisco and the photosynthetic performance in aquatic plants. *Oecologia* 87: 429–434.
- Blom CWPM, Voesenek LACJ. 1996. Flooding: the survival strategies of plants. *Tree* 11: 290–295.
- Blom CWPM, Voesenek LACJ, Banga M, Engelaar WMHG, Rijnders JGHM, Van de Steeg HM, *et al.* 1994. Physiological ecology of riverside species: adaptive responses of plants to submergence. *Annals of Botany* 74: 253–263.
- Bockelmann AC, Bakker JP, Neuhaus R, Lage J. 2002. The relation between vegetation zonation, elevation and inundation frequency in a Wadden Sea salt marsh. *Aquatic Botany* 73: 211–221.
- Bowes G. 1987. Aquatic plant photosynthesis: strategies that enhance carbon gain. In: Crawford RMM, ed. *Plant life in aquatic and amphibious habitats*. Oxford: Blackwell Scientific Publishers, 79–98.
- Bowes G, Salvucci E. 1989. Plasticity in the photosynthetic carbon metabolism of submerged aquatic macrophytes. *Aquatic Botany* 34: 233–266.
- Bowes G, Rao SK, Estavillo GM, Reiskind JB. 2002. C-4 mechanisms in aquatic angiosperms: comparisons with terrestrial C-4 systems. *Functional Plant Biology* 29: 379–392.
- van den Brink FWB, de Leeuw JPM, van der Velde G, Verheggen GM. 1993. Impact of hydrology on the chemistry and phytoplankton development in floodplain lakes along the lower Rhine and Meuse. *Biogeochemistry* 19: 103–128.
- Browse JA, Dromgoole FI, Brown JMA. 1979. Photosynthesis in the aquatic macrophyte *Egeria densa*. 3. Gas exchange studies. *Australian Journal of Plant Physiology* 6: 499–512.
- Bruni NC, Young JP, Dengler NC. 1996. Leaf developmental plasticity of *Ranunculus flabellaris* in response to terrestrial and submerged environments. *Canadian Journal of Botany* 74: 823–837.
- Casanova MT, Brock MA. 2000. How do depth, duration and frequency of flooding influence the establishment of wetland communities? *Plant Ecology* 147: 237–250.
- Casati P, Lara MV, Andreo CS. 2000. Induction of a C-4-like mechanism of CO₂ fixation in *Egeria densa*, a submersed aquatic species. *Plant Physiology* 123: 1611–1621.
- Clevering OA, van Vierssen W, Blom CWPM. 1995. Growth, photosynthesis and carbohydrate utilization in submerged *Scirpus maritimus* L. during spring growth. *New Phytologist* 130: 105–116.
- Colmer TD, Gibberd MR, Wiengweera A, Tinh TK. 1998. The barrier to radial oxygen loss from roots of rice (*Oryza sativa* L.) is induced by growth in stagnant solution. *Journal of Experimental Botany* 49: 1431–1436.
- Colmer TD. 2003. Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. *Plant Cell and Environment* 26: 17–36.
- Cook SA, Johnson MP. 1967. Adaptation to heterogeneous environments. 1. Variation in heterophylly in *Ranunculus flammula* L. *Evolution* 22: 496–516.
- van Eck WHJM, Van de Steeg HM, Blom CWPM, de Kroon H. 2004. Is tolerance to summer flooding correlated with distribution patterns in river floodplains? A comparative study of 20 terrestrial grassland species. *Oikos* 107: 393–405.
- van Eck WHJM, Lenssen JPM, Rengelink RHJ, Blom CWPM, de Kroon H. 2005. An experimental assessment of the effects of plant seasonal status, water temperature and oxygen concentration on plant response to flooding. *Aquatic Botany* 81: 253–264.
- Elzenga JTM, Prins HBA. 1989. Light-induced polar pH changes in leaves of *Elodea canadensis*. 1. Effects of carbon concentration and light intensity. *Plant Physiology* 91: 62–67.
- Farmer AM, Maberly SC, Bowes G. 1986. Activities of carboxylation enzymes in freshwater macrophytes. *Journal of Experimental Botany* 37: 1568–1573.
- Frost-Christensen H, Sand-Jensen K. 1992. The quantum efficiency of photosynthesis in macroalgae and submerged angiosperms. *Oecologia* 91: 377–384.
- Frost-Christensen H, Sand-Jensen K. 1995. Comparative kinetics of photosynthesis in floating and submerged *Potamogeton* leaves. *Aquatic Botany* 51: 121–134.
- Frost-Christensen H, Bolt Jørgensen L, Floto F. 2003. Species specificity of resistance to oxygen diffusion in thin cuticular membranes from amphibious plants. *Plant Cell and Environment* 26: 561–569.
- Garbey C, Thiebaut G, Muller S. 2004. Morphological plasticity of a spreading aquatic macrophyte, *Ranunculus peltatus*, in response to environmental variables. *Plant Ecology* 173: 125–137.

- Gaynard TJ, Armstrong W. 1987. Some aspects of internal plant aeration in amphibious habitats. In: Crawford RMM, ed. *Plant life in aquatic and amphibious habitats*. Oxford: Blackwell Scientific Publishers, 303–320.
- Germ M, Gaberscik A. 2003. Comparison of aerial and submerged leaves in two amphibious species, *Myosotis scorpioides* and *Ranunculus trichophyllus*. *Photosynthetica* 41: 91–96.
- Gibbs J, Greenway H. 2003. Mechanisms of anoxia tolerance in plants. I. Growth, survival and anaerobic catabolism. *Functional Plant Biology* 30: 1–47.
- Greve TM, Borum J, Pedersen O. 2003. Meristematic oxygen variability in eelgrass (*Zostera marina*). *Limnology and Oceanography* 48: 210–216.
- Guglielminetti L, Wu Y, Boschi E, Yamaguchi J, Favati A, Vergara M, et al. 1997. Effects of anoxia on sucrose degrading enzymes in cereal seeds. *Journal of Plant Physiology* 150: 251–258.
- He JB, Bögemann GM, Van de Steeg HM, Rijnders JHGM, Voeseek LACJ, Blom CWPM. 1999. Survival tactics of *Ranunculus* species in river floodplains. *Oecologia* 118: 1–8.
- Hoffmann-Benning S, Kende H. 1992. On the role of abscisic acid and gibberellin in the regulation of growth in rice. *Plant Physiology* 99: 1156–1161.
- Holaday AS, Bowes G. 1980. C4 acid metabolism and dark CO₂ fixation in a submersed aquatic macrophyte (*Hydrilla verticillata*). *Plant Physiology* 65: 331–335.
- Holmes MG, Klein WH. 1987. The light and temperature environments. In: Crawford RMM, ed. *Plant life in aquatic and amphibious habitats*. Oxford: Blackwell Scientific Publishers, 3–22.
- Hostrup O, Wiegand G. 1991. Anatomy of leaves of submerged and emergent forms of *Littorella uniflora* (L.) Ascherson. *Aquatic Botany* 39: 195–209.
- Hough RA. 1974. Photorespiration and productivity in submersed aquatic vascular plants. *Limnology and Oceanography* 19: 912–927.
- Hsu TC, Liu HC, Wang JS, Chen RW, Wang YC, Lin BL. 2001. Early genes responsive to abscisic acid during heterophyllous induction in *Marsilea quadrifolia*. *Plant Molecular Biology* 47: 703–715.
- Ito O, Ella E, Kawano N. 1999. Physiological basis of submergence tolerance in rainfed lowland rice ecosystem. *Field Crops Research* 64: 75–90.
- Jackson MB. 1985. Ethylene and responses of plants to soil water-logging and submergence. *Annual Review of Plant Physiology* 36: 145–174.
- Jackson MB, Armstrong W. 1999. Formation of aerenchyma and the processes of plant ventilation in relation to soil flooding and submergence. *Plant Biology* 1: 274–287.
- Jahnke LS, Eighmy TT, Fagerberg WR. 1991. Studies of *Elodea nuttallii* grown under photorespiratory conditions. I. Photosynthetic characteristics. *Plant Cell and Environment* 14: 147–156.
- Jones JJ, Eaton JW, Hardwick K. 2000. The effect of changing environmental variables in the surrounding water on the physiology of *Elodea nuttallii*. *Aquatic Botany* 66: 115–129.
- Keeley JE, Santamaría L. 1992. Carbon: freshwater plants. *Plant Cell and Environment* 15: 1021–1035.
- Kende H, Van der Knaap E, Cho H-T. 1998. Deepwater rice: a model plant to study stem elongation. *Plant Physiology* 118: 1105–1110.
- Klimešová J. 1994. The effects of timing and duration of floods on growth of young plants of *Phalaris arundinacea* L. and *Urtica dioica* L.: an experimental study. *Aquatic Botany* 48: 21–29.
- Kuwabara A, Tsukaya H, Nagata T. 2001. Identification of factors that cause heterophylly in *Ludwigia arcuata* Walt. (Onagraceae). *Plant Biology* 3: 670.
- Kuwabara A, Ikegami K, Koshihara T, Nagata T. 2003. Effects of ethylene and abscisic acid upon heterophylly in *Ludwigia arcuata* (Onagraceae). *Planta* 217: 880–887.
- Laan P, Blom CWPM. 1990. Growth and survival responses of *Rumex* species to flooded and submerged conditions: the importance of shoot elongation, underwater photosynthesis and reserve carbohydrates. *Journal of Experimental Botany* 41: 775–783.
- Laan P, Tosserams M, Blom CWPM, Veen BW. 1990. Internal oxygen transport in *Rumex* species and its significance for respiration under hypoxic conditions. *Plant and Soil* 122: 39–46.
- Lambers H, Chapin FS, Pons TL. 1998. *Plant physiological ecology*. New York: Springer.
- Lara MV, Casati P, Andreo CS. 2002. CO₂-concentrating mechanisms in *Egeria densa*, a submersed aquatic plant. *Physiologia Plantarum* 115: 487–495.
- Lenzen JPM, Menting FBJ, Van der Putten WH, Blom CWPM. 1999. Control of plant species richness and zonation of functional groups along a freshwater flooding gradient. *Oikos* 86: 523–534.
- Lenzen JPM, van Kleunen M, Fischer M, de Kroon H. 2004. Local adaptation of the clonal plant *Ranunculus reptans* to flooding along a small-scale gradient. *Journal of Ecology* 92: 696–706.
- Lin BL, Yang WJ. 1999. Blue light and abscisic acid independently induce heterophyllous switch in *Marsilea quadrifolia*. *Plant Physiology* 119: 429–434.
- Lloyd NDH, Canvin DT, Bristow JM. 1977. Photosynthesis and photorespiration in submerged aquatic vascular plants. *Canadian Journal of Botany* 55: 3001–3005.
- Lynn DE, Waldren S. 2001. Morphological variation in populations of *Ranunculus repens* from the temporary limestone lakes (Turloughs) in the West of Ireland. *Annals of Botany* 87: 9–17.
- Lynn DE, Waldren S. 2002. Physiological variation in populations of *Ranunculus repens* L. (creeping buttercup) from the temporary limestone lakes (turloughs) in the west of Ireland. *Annals of Botany* 89: 707–714.
- Maberly SC. 1985. Photosynthesis by *Fontinalis antipyretica*. 2. Assessment of environmental factors limiting photosynthesis and production. *New Phytologist* 100: 141–155.
- Maberly SC, Madsen TV. 1998. Affinity for CO₂ in relation to the ability of freshwater macrophytes to use HCO₃⁻. *Functional Ecology* 12: 99–106.
- Maberly SC, Madsen TV. 2002. Freshwater angiosperm carbon concentrating mechanisms: processes and patterns. *Functional Plant Biology* 29: 393–405.
- Maberly SC, Spence DHN. 1989. Photosynthesis and photorespiration in freshwater organisms: amphibious plants. *Aquatic Botany* 34: 267–286.
- Madsen TV. 1993. Growth and photosynthetic acclimation by *Ranunculus aquatilis* L. in response to inorganic carbon availability. *New Phytologist* 707–715.
- Madsen TV, Sand-Jensen K. 1994. The interactive effects of light and inorganic carbon on aquatic plant growth. *Plant Cell and Environment* 17: 955–962.
- Madsen TV, Olesen B, Bagger J. 2002. Carbon acquisition and carbon dynamics by aquatic isoetids. *Aquatic Botany* 73: 351–371.
- Magnin NC, Cooley BA, Reiskind JB, Bowes G. 1997. Regulation and localization of key enzymes during the induction of Kranz-less, C-4-type photosynthesis in *Hydrilla verticillata*. *Plant Physiology* 115: 1681–1689.
- Minorsky PV. 2003. The hot and the classic. *Plant Physiology* 133: 1671–1672.
- Mommer L, Pedersen O, Visser EJW. 2004. Acclimation of a terrestrial plant to submergence facilitates gas exchange under water. *Plant Cell and Environment* 27: 1281–1287.
- Mommer L, de Kroon H, Pierik R, Bögemann GM, Visser EJW. 2005. A functional comparison of acclimation to shade and submergence in two terrestrial plant species. *New Phytologist* 167: 197–206.
- Nabben RHM, Blom CWPM, Voeseek LACJ. 1999. Resistance to complete submergence in *Rumex* species with different life histories: the influence of plant size and light. *New Phytologist* 144: 313–321.
- Nielsen SL. 1993. A comparison of aerial and submerged photosynthesis in some Danish amphibious plants. *Aquatic Botany* 27–40.
- Pedersen O, Sand-Jensen K, Revsbech NP. 1995. Diel pulses of O₂ and CO₂ in sandy lake sediments inhabited by *Lobelia dortmanna*. *Ecology* 76: 1536–1545.
- Pedersen O, Borum J, Duarte CM, Fortes MD. 1998. Oxygen dynamics in the rhizosphere of *Cymodocea rotundata*. *Marine Ecology Progress Series* 169: 283–288.
- Pedersen O, Binzer T, Borum J. 2004. Sulfide intrusion in eelgrass (*Zostera marina* L.). *Plant Cell and Environment* 27: 595–602.
- Perata P, Alpi A. 1993. Plant responses to anaerobiosis. *Plant Science* 93: 1–17.
- Prins HBA, Snel JFH, Zanstra PE, Helder RJ. 1982. The mechanism of bicarbonate assimilation by the polar leaves of *Potamogeton* and *Elodea*: CO₂ concentrations at the leaf surface. *Plant Cell and Environment* 5: 207–214.

- Prins HBA, Elzenga JTM. 1989. Bicarbonate utilization: function and mechanism. *Aquatic Botany* 34: 59–83.
- Ram PC, Singh BB, Singh AK, Ram P, Singh PN, Singh HP, et al. 2002. Submergence tolerance in rainfed lowland rice: physiological basis and prospects for cultivar improvement through marker-aided breeding. *Field Crops Research* 76: 131–152.
- Rao SK, Magnin NC, Reiskind JB, Bowes G. 2002. Photosynthetic and other phosphoenolpyruvate carboxylase isoforms in the single-cell, facultative C-4 system of *Hydrilla verticillata*. *Plant Physiology* 130: 876–886.
- Rascio N, Cuccato F, Dalla Vecchia F, La Rocca N, Larcher W. 1999. Structural and functional features of the leaves of *Ranunculus trichophyllus* Chaix., a freshwater submerged macrophyte. *Plant Cell and Environment* 22: 205–212.
- Reiskind JB, Madsen TV, VanGinkel LC, Bowes G. 1997. Evidence that inducible C-4-type photosynthesis is a chloroplastic CO₂-concentrating mechanism in *Hydrilla*, a submersed monocot. *Plant Cell and Environment* 20: 211–220.
- Rijnders JGHM, Armstrong W, Darwent MJ, Blom CWPM, Voeselek LACJ. 2000. The role of oxygen in submergence-induced petiole elongation in *Rumex palustris*: in situ measurements of oxygen in petioles of intact plants using micro-electrodes. *New Phytologist* 147: 479–504.
- Robe WE, Griffiths H. 1990. Photosynthesis of *Littorella uniflora* grown under two PAR regimes: C3 and CAM gas exchange and the regulation of internal CO₂ and O₂ concentrations. *Oecologia* 85: 128–136.
- Robe WE, Griffiths H. 1998. Adaptations for an amphibious life: changes in leaf morphology, growth rate, carbon and nitrogen investment, and reproduction during adjustment to emersion by the freshwater macrophyte *Littorella uniflora*. *New Phytologist* 140: 9–23.
- Roelofs JGM, Schuurkes JAAR, Smits AJM. 1984. Impact of acidification and eutrophication on macrophyte communities in soft waters: 2. Experimental studies. *Aquatic Botany* 18: 398–411.
- Salvucci E, Bowes G. 1981. Induction of reduced photorespiratory activity in submersed and amphibious aquatic macrophytes. *Plant Physiology* 67: 335–340.
- Salvucci ME, Bowes G. 1983. Two photosynthetic mechanisms mediating the low photorespiratory state in submersed aquatic angiosperms. *Plant Physiology* 73: 488–496.
- Sand-Jensen K. 1989. Environmental variables and their effect on photosynthesis of aquatic plant communities. General features of aquatic photosynthesis. *Aquatic Botany* 34: 5–25.
- Sand-Jensen K, Frost-Christensen H. 1999. Plant growth and photosynthesis in the transition zone between land and stream. *Aquatic Botany* 63: 23–35.
- Sand-Jensen K, Prah C, Stokholm H. 1982. Oxygen release from roots of submerged aquatic macrophytes. *Oikos* 38: 349–354.
- Sand-Jensen K, Pedersen O, Binzer T, Borum J. 2005. Contrasting oxygen dynamics in the freshwater isoetid *Lobelia dortmanna* and the marine seagrass *Zostera marina*. *Annals of Botany* 96: 613–623.
- Sculthorpe CD. 1967. *The biology of aquatic vascular plants*. London: Edward Arnold.
- Setter TL, Kupkanchankul T, Kupkanchankul K, Bhekasut P, Wiengweera A, Greenway H. 1987. Concentrations of CO₂ and O₂ in floodwater and in internodal lacunae of floating rice growing at 1–2 metre water depths. *Plant Cell and Environment* 10: 767–776.
- Siebel HN, van Wijk M, Blom CWPM. 1998. Can tree seedlings survive increased flood levels of rivers? *Acta Botanica Neerlandica* 47: 219–230.
- Silvertown J, Dodd ME, Gowing DJG, Mountford JO. 1999. Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature* 400: 61–63.
- Smith FA, Walker NA. 1980. Photosynthesis by aquatic plants: effects of unstirred layers in relation to assimilation of CO₂ and HCO₃⁻ and to carbon isotopic discrimination. *New Phytologist* 86: 245–259.
- Sorrell BK. 2004. Regulation of root anaerobiosis and carbon translocation by light and root aeration in *Isoetes alpinus*. *Plant Cell and Environment* 27: 1102–1111.
- Spencer WE, Wetzel RG, Teeri J. 1996. Photosynthetic phenotype plasticity and the role of phosphoenolpyruvate carboxylase in *Hydrilla verticillata*. *Plant Science* 118: 1–9.
- van de Steeg HM, Blom CWPM. 1998. Impact of hydrology on floodplain vegetation in the lower Rhine system: implications for nature conservation and nature development. In: Nienhuis PH, Leuven RSEW, Ragas AMJ, eds. *New concepts for sustainable management of river basins*. Leiden, The Netherlands: Backhuys Publishers, 131–144.
- Stünzi JT, Kende H. 1989. Gas composition in the internal air spaces of deepwater rice in relation to growth induced by submergence. *Plant Cell Physiology* 30: 49–56.
- Sýkora KV, Scheper E, van der Zee F. 1988. Inundation and the distribution of plant communities on Dutch river dikes. *Acta Botanica Neerlandica* 37: 279–290.
- Toner M, Keddy P. 1997. River hydrology and riparian wetlands: a predictive model for ecological assembly. *Ecological Applications* 7: 236–246.
- Ueno O. 1998. Induction of Kranz anatomy and C-4-like biochemical characteristics in a submerged amphibious plant by abscisic acid. *Plant Cell* 10: 571–583.
- Ueno O. 2001. Environmental regulation of C₃ and C₄ differentiation in the amphibious sedge *Eleocharis vivipara*. *Plant Physiology* 127: 1524–1532.
- Van TK, Haller WT, Bowes G. 1976. Comparison of the photosynthetic characteristics of three submersed aquatic plants. *Plant Physiology* 58: 761–768.
- Vartapetian BB, Jackson MB. 1997. Plant adaptations to anaerobic stress. *Annals of Botany* 79: 3–20.
- Vervuren PJA, Beurskens SMJH, Blom CWPM. 1999. Light acclimation, CO₂ response and long-term capacity of underwater photosynthesis in three terrestrial plant species. *Plant Cell and Environment* 22: 959–968.
- Vervuren PJA, Blom CWPM, De Kroon H. 2003. Extreme flooding events on the Rhine and the survival and distribution of riparian plant species. *Journal of Ecology* 91: 135–146.
- Visser EJW, Blom CWPM, Voeselek LACJ. 1996. Flooding-induced adventitious rooting in *Rumex*: morphology and development in an ecological perspective. *Acta Botanica Neerlandica* 45: 17–28.
- Visser EJW, Colmer TD, Blom CWPM, Voeselek LACJ. 2000. Changes in growth, porosity, and radial oxygen loss from adventitious roots of selected mono- and dicotyledonous wetland species with contrasting types of aerenchyma. *Plant Cell and Environment* 23: 1237–1245.
- Voeselek LACJ, Banga M, Thier R, Mudde CM, Harren FJM, Barendse GWM, et al. 1993a. Submergence-induced ethylene synthesis, entrapment, and growth in two plant species with contrasting flooding resistances. *Plant Physiology* 103: 783–791.
- Voeselek LACJ, Van Oorschot FJMM, Smits AJM, Blom CWPM. 1993b. The role of flooding resistance in the establishment of *Rumex* seedlings in river flood plains. *Functional Ecology* 7: 105–114.
- Voeselek LACJ, Benschop JJ, Bou J, Cox MCH, Groeneveld HW, Millenaar FF, et al. 2003. Interactions between plant hormones regulate submergence-induced shoot elongation in the flooding tolerant dicot *Rumex palustris*. *Annals of Botany* 91: 205–211.
- Voeselek LACJ, Rijnders JGHM, Peeters AJM, Van de Steeg HM, de Kroon H. 2004. Plant hormones regulate fast shoot elongation under water: from genes to communities. *Ecology* 85: 16–27.
- Waters I, Armstrong W, Thompson CJ, Setter TL, Adkins S, Gibbs J, et al. 1989. Diurnal changes in radial oxygen loss and ethanol metabolism in roots of submerged and non-submerged rice seedlings. *New Phytologist* 113: 439–451.
- Wium-Andersen S. 1971. Photosynthetic uptake of free CO₂ by the roots of *Lobelia dortmanna*. *Physiologia Plantarum* 25: 245–248.