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

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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; Voesenek 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
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 μmol PAR m$^{-2}$ s$^{-1}$; day/night length 16 h/8 h) to >2 years in rather low light conditions (17 μmol PAR m$^{-2}$ 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 underwa-ter 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 import-ant 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 condi-tions 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 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 dissec-ted 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 special-ized 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 C$_3$ and C$_4$ 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 C$_3$ and C$_4$ 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 Wiegleb, 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 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 observed 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 (\( >50 \mu\text{L}^{-1} \)) and may not be reached under submerged conditions [given the data provided in the same paper, and the concentrations of 4–5 \( \mu\text{L}^{-1} \) 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 heterophyly) 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 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 short- age 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; Rasio *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 diffusion 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 photosynthetic 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 heterophyll 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.

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