

Flooding Stress on Plants: Anatomical, Morphological and Physiological Responses

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1. Introduction

Flooding is a natural disturbance affecting crop and forage production worldwide due to the detrimental effects that it provokes on most terrestrial plants (Bailey-Serres & Voesenek, 2008; Colmer & Voesenek, 2009). Over the last years, the Intergovernmental Panel on Climate Change (<http://www.ipcc.ch>) has informed that man-induced world climate change will increase the frequency of precipitations of higher magnitude as well as tropical cyclone activity. As a result, the occurrence of flooding events on flood plains (*i.e.* lowlands) and cultivated lands is expected to be higher (Arnell & Liu, 2001). On the other hand, the increasing world population, along with the intensification of agriculture have provoked a reduction in the arable land per capita, which has decreased over the last five decades from 0.32 ha to 0.21 ha, and it is expected to be further diminished up to 0.16 ha per capita by 2030 (FAO 2006 as cited in Mancuso & Shabala, 2010). As a consequence, marginal lands are being incorporated into production to cope with the rising food demand. These issues lead to the necessity to get highly productive crops in arable lands subjected to periodic events of water excess, and to introduce new (or improved) flood-tolerant forage species in flood-prone pastures (and grasslands) devoted to livestock production. So, the understanding of plant functioning under flooding conditions is crucial in order to achieve these goals.

Soil water excess determines a severe decrease in the oxygen diffusion rate into the soil because of the 10^4 lower diffusion of gases into water with respect to air (Armstrong, 1979; Ponnampuruma, 1972; 1984). Shortly after the soil is flooded, the respiration of roots and micro-organisms depletes the remnant oxygen and the environment becomes hypoxic (*i.e.* oxygen levels limit mitochondrial respiration) and later anoxic (*i.e.* respiration is completely inhibited; Blom & Voesenek, 1996; Bailey-Serres & Voesenek, 2008; Wegner, 2010). So, the first constraint for plant growth under flooding is the immediate lack of oxygen necessary to sustain aerobic respiration of submerged tissues (Armstrong, 1979; Vartapetian & Jackson, 1997; Voesenek et al., 2004). As flooding time increases, a second problem associated with water excess appears as a result of the progressive decrease in the soil reduction-oxidation potential (redox potential) (see Fig. 1; Pezeshki & DeLaune, 1998; Pezeshki, 2001). With the reduction of the soil redox potential potentially toxic compounds appear such as sulfides, soluble Fe and Mn, ethanol, lactic acid, acetaldehyde and acetic and formic acid (Kozłowski, 1997; Fiedler et al., 2007). Therefore, the lack of oxygen and later the accumulation of some potentially toxic compounds are the major constraints that plants suffer under flooding conditions.

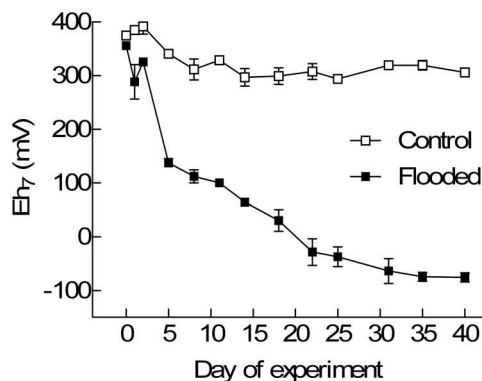


Fig. 1. Course of soil redox potential at pH 7 (EH_7) at control and flooded conditions by 40 days. [Reproduced from Striker et al. (2005) with permission from Springer].

In a broad sense, the term flooding is often used to depict different situations in which the water excess can range from water saturated soil (*i.e.* waterlogging) to deep water columns causing complete submergence of plants (Fig. 2). So, a first step is to accurately define the correct terms for each situation of water excess. Waterlogging corresponds to the full saturation of the soil pores with water, and with a very thin – or even without - a layer of water above the soil surface. Hence, under waterlogged conditions, only the root system of plant is under the anaerobic conditions imposed by the lack of oxygen, while the shoot is under atmospheric normal conditions. Flooding is the situation in which there is a water layer above the soil surface. This water layer can be shallow or deep, so that it can provoke partial or complete submergence of plants. It should be noted that, at the same water depth, the degree of plant submergence will depend on the developmental stage (*eg.* seedlings *vs.* adult plants) and plant growth habit (*eg.* creeping plant growth *vs.* erect plant growth), among other traits influencing plant height. Under partial submergence conditions, plants have a portion of their shoots underwater, besides having their roots completely immersed in water-saturated soil. Under complete submergence, plants confront the most stressful scenario because both, shoot and root plant compartments, are underwater, and in this case

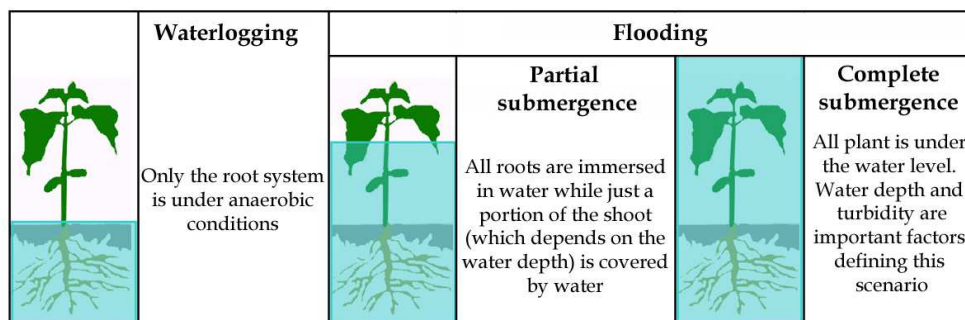


Fig. 2. Scheme of the different scenarios encountered by plants in front to increasing levels of water excess, ranging from waterlogging to complete submergence.

the chances to capture atmospheric oxygen and to continue with carbon fixation are restricted (but see plant strategies to deal with this stress on section 3.1). This situation is worsened in turbid water and/or with deep water columns above plants because the irradiance available to sustain underwater photosynthesis for survival is drastically reduced (Mommer et al., 2004; Colmer & Pedersen, 2008; Vashist et al., 2011).

Another crucial aspect that should be taken into account when defining ‘flooding’ is its duration (see Colmer & Voesenek, 2009). In this sense, flooding duration has been recognized as a major factor in determining plant survival following oxygen deprivation (Kozłowski & Pallardy, 1984; Armstrong et al., 1994; Lenssen et al., 2004). It is known that a single species of a similar age and size that is capable of surviving a short flooding period may perish if exposed to a longer one (Else et al., 1996; Crawford, 2003). In addition, a recent review of methodological aspects of flooding experiments highlighted the importance of also considering the type and age of the species tested (Striker, 2008; Fig. 3). This work showed that: (i) crop species are subjected to shorter flooding periods than non-crop species, and that (ii) seedlings of crops are exposed to even shorter periods than adult individuals; a fact that did not occur in experiments that used non-crop species (Fig. 3).

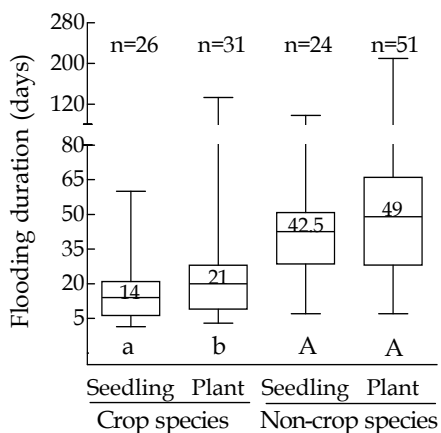


Fig. 3. Flooding duration in the experiments done on crop species and non-crop species. The end of the boxes defines the 25th and 75th percentiles, with a line at the median and error bars defining the 10th and 90th percentiles. Different letters indicate significant differences ($P < 0.05$) between medians based on the Mann-Whitney test. Lower case letters compare medians within the crop category while upper case letters compare medians within the non-crop category. [Adapted from Striker (2008) with permissions from Wiley-Blackwell]

2. Plant responses to partial submergence

Plants develop a suite of anatomical, morphological and physiological responses in order to deal with partial submergence imposed by flooding (Armstrong, 1979; Kozłowski & Pallardy, 1984; Vartapetian & Jackson, 1997; Striker et al., 2005; Colmer & Voesenek, 2009). The most common anatomical response is the generation of aerenchyma in tissues (Justin &

Armstrong, 1987; Seago et al., 2005), which facilitates the transport of oxygen from shoots to roots (Colmer, 2003a). At morphological level, usual responses to flooding include adventitious rooting and increases in plant height and consequently, in the proportion of biomass above water level (Naidoo & Mundree, 1993; Grimoldi et al., 1999). This also helps to facilitate the oxygenation of submerged tissues through the aerenchyma tissue (Laan et al., 1990; Colmer, 2003a). At physiological level, flooding modifies water relations and plants carbon fixation. Closing of stomata, with or without leaf dehydration, reduction of transpiration and inhibition of photosynthesis, are responses that can occur in hours or days, depending on the tolerance to flooding of each plant species (Bradford & Hsiao, 1982; Else et al., 1996; Insausti et al., 2001; Striker et al., 2005; Mollard et al., 2008; 2010). The following sections show the main plant responses at those levels associated with tolerance to flooding.

2.1 Anatomical traits of tolerance to partial submergence

Aerenchyma formation in the root cortex is the most studied plastic response to flooding (Smirnoff & Crawford, 1983; Justin & Armstrong, 1987; Colmer et al., 1998; Visser et al., 2000; McDonald et al., 2002; Evans, 2003; Grimoldi et al., 2005; Seago et al., 2005; Striker et al., 2007a). This aerenchymatic tissue provides a continuous system of interconnected aerial spaces (aerenchyma lacunae) of lower resistance for oxygen transport from aerial shoots to submerged roots, allowing root growth and soil exploration under anaerobic conditions (Armstrong, 1979; Colmer & Greenway, 2005).

The spatial arrangement of aerenchyma in the root cortex in response to flooding is variable among species (Smirnoff & Crawford, 1983; Justin & Armstrong, 1987; Visser et al., 2000; McDonald et al., 2002; Grimoldi et al., 2005; Seago et al., 2005). Different aerenchyma types arise from the combination of four general root structural types (Justin & Armstrong, 1987). Such four general root structural types - graminaceous, cyperaceous, *Apium*, and *Rumex* - have been described on the basis of the spatial arrangement of the aerenchyma tissue and the packing of the cells in the cortex (Justin & Armstrong, 1987; Seago et al., 2005). The shape of these root types resembles a bicycle wheel (graminaceous), a spider web (cyperaceous), a honeycomb (*Rumex*) and a non-organized structure with irregular aerenchyma lacunae (*Apium*) (Justin & Armstrong, 1987; Striker et al., 2007a; Fig. 4).

Three different origins of aerenchyma tissue generation have been recognized after the comprehensive review by Seago et al. (2005), namely: lysigeny, schizogeny and expansigeny. The most common is lysigeny, a process that involves the collapse and death of cells in the cortex zone, often coupled with cell separations preceding cell collapse (schizo-lysigeny). Within this aerenchyma origin, two distinct patterns leading to aerenchyma lacunae can be distinguished. The first one is called radial lysigeny, in which aerenchyma lacunae are generated by collapse of cells radially aligned in the cortex and separated by intact radial files of cells (or remnant cell walls). This type of aerenchyma is typical of many graminaceous species and resembles the shape of a bicycle wheel (Fig. 4a). The second one is termed tangential lysigeny, which implies cell separation and collapse in tangential sectors of the root cortex with intact radial files of cells, so that the resulting shape resembles a spider web. This aerenchyma type is typical of cyperaceous species (Fig. 4b). Sometimes, aerenchyma lacunae generated by cell lysis (lysigeny) does not present a regular and easily identifiable spatial pattern. The last case is that of species showing an irregular

non-organized location of aerenchyma lacunae in their root cortex (*Apium* root type; Fig. 4c). Schizogeny is the process of aerenchyma generation that involves the expansion of intercellular spaces into lacunae along radial sectors (*sensu* Seago et al., 2005). This origin often precedes the cell lysis (lysogeny) that increases the size of the lacunae generated and just in few cases, it appears as the only process generating aerenchyma. Expansigeny implies the generation of lacunae by cell division and cell enlargement but without cell death (lysigeny) or further separation (schizogeny). This type of aerenchyma generation is characterized by a honeycomb (hexagonal) appearance in root cross sections and it is called *Rumex* type (Fig 4d).

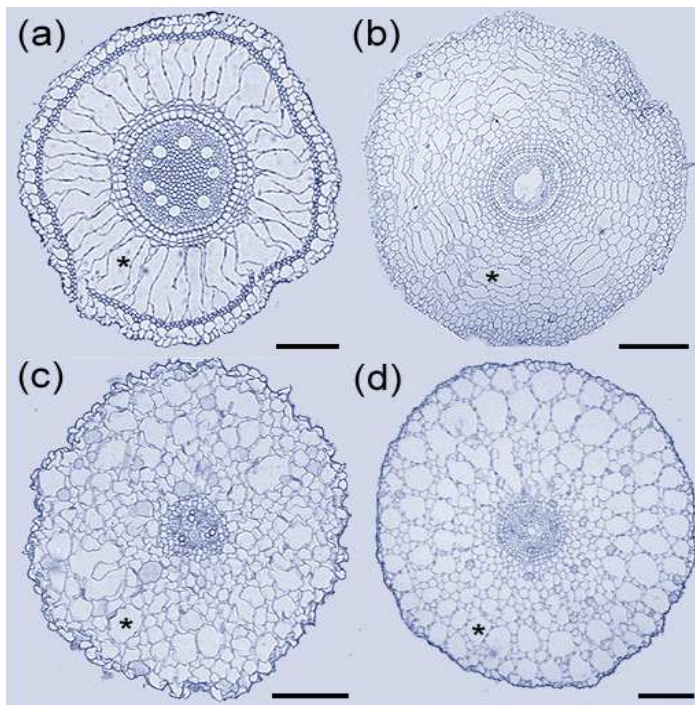


Fig. 4. Root cross sections showing the four main aerenchyma types: graminaceous in *Paspalum dilatatum* Poir. (a), cyperaceous in *Cyperus eragrostis* Lam. (b), *Apium* type in *Lotus tenuis* Waldst. & Kit. (c) and *Rumex* type in *Rumex crispus* L. (d). Asterisks indicate aerenchyma lacunae. Scale bars represent 150 μm . [Adapted from Striker et al. (2006, 2007a) with permissions from Wiley-Blackwell]

Cell death and lysis leading to aerenchyma lacunae development are attributed to low pressures of oxygen (hypoxia) and ethylene accumulation (Jackson et al., 1985; Evans, 2003; but see Visser & Bögemann, 2006). However, aerenchyma development is identical independently of being promoted by hypoxia or by ethylene (Gunawardena et al., 2001). This suggests that the cell death programme generating aerenchyma is common but it can be triggered by a variety of stimuli (Evans, 2003), also including soil mechanical impedance (Engelaar et al., 1995; Striker et al., 2006) and phosphorus deficiency (Fan et al., 2007; Postma

& Lynch, 2011). Pioneer experiments by He et al. (1994) demonstrated that the application of low oxygen or high ethylene concentrations provoked an increase of the cellulase activity in the root apex, which is likely to contribute to cell wall breaking down (final step in lysigenous aerenchyma generation) (see review by Visser & Voesenek, 2004). The events of aerenchyma formation can be described in five stages (*sensu* Evans, 2003). The first stage is the perception of hypoxia and the initiation of ethylene biosynthesis; the second stage corresponds to the perception of the signal of increasing ethylene by cells located in the root cortex (especially in the mid cortex). The third stage starts with the beginning of cell death during which ions are lost from the cell into the apoplast, the plasma membrane invagination commences and the first changes in the cell walls structure can be detected. In the fourth stage, the condensation of the chromatin to nuclear periphery is produced, cell organelles are surrounded by bilipid membranes and a marked increase in cell wall hydrolytic enzymes takes place. Finally, in the fifth stage the cell wall breakdown and cell lysis occur, and then immediately the cell content is absorbed by the surrounding cells (Schussler & Longstreth, 2000; Evans, 2003).

In herbaceous plants, oxygen transport through aerenchyma along relatively short distances (*i.e.* from shoots to roots) is mostly attributed to diffusive mechanisms. In contrast, transportation of O₂ at longer distances (metres; for instance along flooded rhizomes) is theoretically most likely to occur by convective mechanisms (see a detailed review on this topic in Colmer, 2003a; Wegner, 2010). Diffusion of oxygen under flooding conditions is established by the generation of a longitudinal gradient towards the root apex. This gradient is produced by O₂ consumption due to respiration along the root, and by the radial oxygen loss towards the rhizosphere (hereafter referred to as ROL). Both processes act as a sink of O₂ in the waterlogged soil, determining a low oxygen concentration in the root apex and consequently the generation of the mentioned gradient. It should be noticed that a higher aerenchyma generation by lysogeny (cell death in root cortex) determines a lower respiratory demand, favouring the supply of more oxygen to the root apex, at the same time that it facilitates the O₂ transport due to the lower resistance for O₂ diffusion, associated to the bigger size of the aerenchyma lacunae. In addition, the magnitude of radial oxygen loss regulates the O₂ reaching the apex, which is expected to be low if the ROL is higher (Colmer, 2003a; Colmer & Voesenek, 2009; see further on in section 2.2.3).

2.2 Morphological responses conferring plants tolerance to partial submergence

Flooding induces morphological changes in roots and shoots. In roots, the formation of adventitious roots is highlighted as a common response of flood-tolerant species. These adventitious roots, which have high porosity, help plants to continue with water and nutrient uptake under flooding conditions, replacing in some way the functions of older root system (Kozłowski & Pallardy, 1984). It is frequent that these adventitious roots are positioned near the better-aerated soil surface. Following the review by Jackson (2004), there are three mechanisms for generating these 'replacement' root systems: (i) stimulation of the outgrowth of pre-existing root primordia in the shoot base (Jackson et al., 1981), (ii) induction of a new root system that involves initiation of root primordia and their subsequent outgrowth (Jackson & Armstrong, 1999; Shimamura et al., 2007; Fig. 5a) and (iii) placing roots at the soil surface involving the re-orientation of the root extension as seen for

woody species by Pereira & Kozłowski (1977) and for herbaceous species by Gibberd et al. (2001). The two first mechanisms appear to be triggered by ethylene, which is thought to increase the sensitivity of plant tissues to auxin (Bertell et al., 1990; Liu & Reid, 1992). In *Rumex palustris*, it was established that application of exogenous ethylene stimulated the production of adventitious roots without changing the root levels of indole acetic acid (IAA, an auxin). These results indicate that adventitious rooting is due to an increased sensitivity of tissues to auxin and not due to an increase in its concentration (Visser et al., 1995; 1996). Complementarily, Mc-Donald & Visser (2003) showed for *Nicotiana tabacum* (tobacco) that the application of naphthaleneacetic acid (NPA) – an auxin transport inhibitor – to wild type plants reduced the adventitious root formation to the level of ethylene-insensitive transgenic plants. These antecedents strongly demonstrate that cooperation between both hormones is important in defining adventitious rooting (see also the review by Visser & Voeselek, 2004).

It is predictable that stress from soil flooding on roots also alters shoot morphology because of the close functional interdependence between both of them. In this way, flooded plants of tolerant species are often taller than their non-flooded counterparts (Fig. 5b) as a result of increases in the insertion angles and length of their aerial organs. These responses were well characterized in the dicotyledonous *Rumex palustris* by Cox et al. (2003; 2004) and Heydarian et al. (2010) among others. The faster response is the increase in the petiole angle, called hyponastic growth, where maximum angle (70-80°, an almost vertical position) is reached just in four hours (Cox et al., 2003). Next to the change in the insertion petiole angle, an increase in petiole length follows (Cox et al., 2003; Heydarian et al., 2010) in order to maximize the leaf area above the water level (Laan et al., 1990). Such lengthening of petioles is associated with the cell wall loosening due to an increase in the expression and action of expansins (Vriezen et al., 2000). It was proved that both the increase in petiole angle and lengthening, are well mimicked by treating plants with ethylene, so that this hormone appears to be involved in regulating those responses (Vriezen et al., 2000; Heydarian et al., 2010). In graminaceous species the morphological responses are analogous to those developed by dicots. For instance, in the grass *Paspalum dilatatum* the first morphological response to flooding is the increase in the tiller insertion angle (Insausti et al., 2001) followed by the elongation of the leaf sheaths, and lastly (but not always) elongation of leaf blades (Insausti et al., 2001; Mollard et al., 2008; 2010). The higher leaf sheath length of flooded plants is the result of a higher number of longer parenchymatic cells with respect to control plants (Insausti et al., 2001).

Another specific change at shoot level implies stem hypertrophy (Fig. 5a), which is a white spongy tissue with large volumes of intercellular gas spaces (Armstrong et al., 1994). This tissue is secondary aerenchyma that forms externally from a phellogen and is homologous to cork (Shimamura et al., 2010; Teakle et al., 2011). Its role seems to be increasing air space which allows for increased movement of gases between water and plant tissues (Teakle et al., 2011). Some species with capacity to develop stem hypertrophy are *Lythrum salicaria* (Stevens et al., 1997), *Lotus uliginosus* (James & Sprent, 1999), *L. tenuis* (Striker et al., 2005; Fig. 5a), *Glycine max* (Shimamura et al., 2010) and *Melilotus siculus* (Teakle et al., 2011). In woody plants, an important morphological trait developed by tolerant species is lenticels hypertrophy at the stem base (Kozłowski, 1997). It is supposed that these special structures, functionally analogous to hypertrophied stem tissue, allow oxygen entrance into shallow roots through aerenchyma and intercellular spaces (Kozłowski, 1997; Shimamura et al.,

2010). This idea was based on studies where the blocking of lenticels of waterlogged plants with lanolin determined a marked reduction in the root aeration, so that lenticels appeared as points of air entrance to the root system (Shimamura et al., 2003). In spite of the above-discussed, there is controversy about the function of hypertrophied lenticels because, in several cases, they tend to be more developed below water (Parelle et al., 2006). Hence, this location does not support the idea of enablers of oxygen entry toward the root system. Some authors proposed that it is more likely that lenticels may help maintain plant water status during flooding, by partially supplying water for the shoots and thus replacing the less-functional roots (Pezeshki, 1996; Folzer et al., 2006). The recovery of stomatal conductance of flooded plants matching in time with the appearance of hypertrophied lenticels supports the belief that they contribute to the plant water homeostasis under flooding conditions (Groh et al., 2002; Parent et al., 2008). Finally, it was proposed that hypertrophic lenticels may also allow dissipation of metabolically generated volatile compounds like ethanol, ethylene and acetaldehyde, although the physiological significance of this fact for plant performance and survival has not been assessed to date (Jackson, 2004).

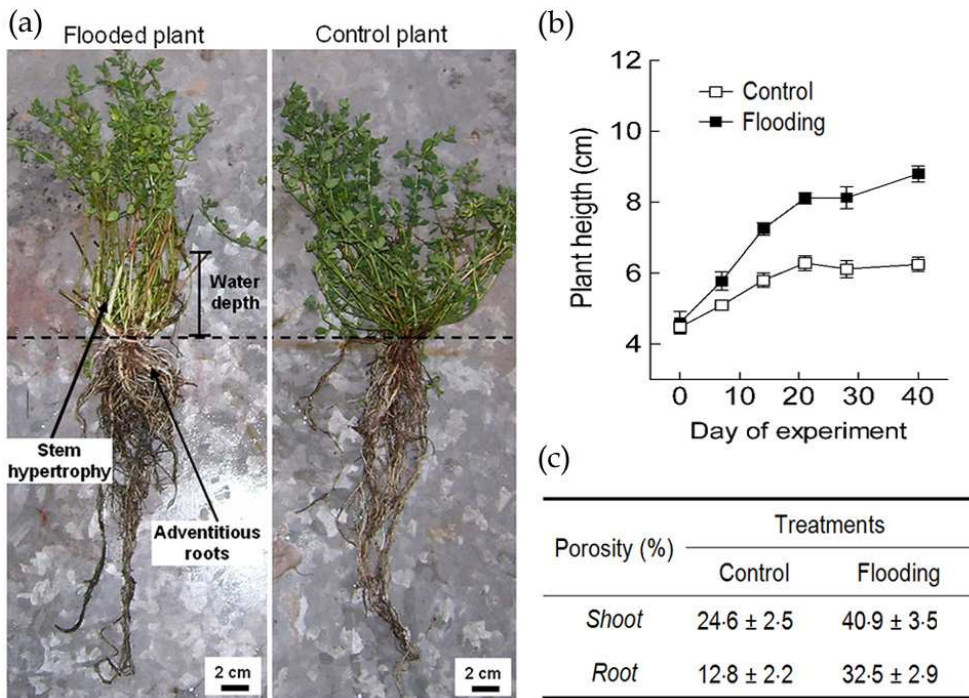


Fig. 5. Plant morphology (a) and plant height evolution (b) of *Lotus tenuis* subjected to 6 cm water depth flooding for 40 days (left photograph, note stem hypertrophy and adventitious rooting) and to control conditions (right photograph). (c) Shoot and root porosity of control and flooded plants of *L. tenuis* after 30 days of treatment. [(b) Adapted from Striker et al. (2011a) with permissions from Springer, (c) Adapted from Manzur et al. (2009) with permissions from Oxford University Press]

2.3 Physiological responses of plants to partial submergence by flooding

2.3.1 Plant water relations

In flood sensitive species like *Solanum lycopersicum*, *Pisum sativum*, *Helianthus annuus* and *Nicotiana tabacum*, a few hours after the soil becomes flooded, the water uptake by roots is reduced (Bradford & Hsiao, 1982; Jackson & Drew, 1984). Here, the reduction of water absorption under flooding is a consequence of a reduction of the root hydraulic conductivity (Else et al., 1995; Else et al., 2001; Islam & McDonald, 2004) that seems to be associated with the acidification of the cell cytoplasm and the gating of aquaporins (Tournarie-Roux et al., 2003). It appears that the excess of protons provoking such acidification, determines conformational changes of the mentioned water channels that trigger their closure (Tournarie-Roux et al., 2003; Verdoucq et al., 2008). So, the reduction of water uptake under water excess of the soil in flooding sensitive species shows the paradoxical response of wilting of leaves (Bradford & Hsiao, 1982; Else et al., 1996), as it can be seen under drought. In this type of species, unable to tolerate short-term flooding, plants die (without recovery) when the water recedes.

In flood-tolerant plants, the plant water relations during flooding can vary depending on the season of occurrence and naturally on species-specific responses (Crawford, 2003; Lenssen et al., 2004). For example, the grass *Paspalum dilatatum* and the legume *Lotus tenuis* are able to grow during periods of soil water excess in summer season (Insausti et al., 2001; Striker et al., 2006; 2007b; 2008; Mollard et al., 2008; 2010), although the impact of oxygen deprivation on the plant water status differs between species (Fig. 6). In *P. dilatatum*, flooding had no major effects on leaf water potential (Ψ_w), stomatal conductance (g_s) and transpiration rate (E) (see Figs 6a, c, e). Moreover, flooded plants registered a better plant water status than control ones on dates with higher water evaporative demand (VPD_{air} ; Fig. 6g). By contrast, in *L. tenuis* flooding had negative effects on Ψ_w , g_s and E that increased over time and provoked 40%, 55% and 60% reductions, in relation to control plants at the end of flooding period (day 15; Figs 6b, d, f). In this sense, decreases in g_s and transpiration rate by stomatal closing in response to flooding have been proposed as a mechanism to regulate the water balance of plants and prevent leaf dehydration (Bradford & Hsiao, 1982; Ashraf, 2003; Striker et al., 2005). Here, it should be noticed that the negative effects of hypoxia in a flood tolerant species like *L. tenuis* occurred after almost a week of flooding and not in the lapse of hours, as it happened in flood-sensitive species. Importantly, when flooding was discontinued, pre-flooded plants of *L. tenuis* recovered their water status (Ψ_w) during the first five days, and showed stomatal behaviour and transpiration rates similar to control plants until the end of the recovery phase. So, plant performance during flooding alone is not conclusive for assessments of its tolerance – post-flooding recovery also needs to be appraised (Malik et al., 2002; Striker, 2008; Striker et al., 2011b). In the case of the grass *P. dilatatum*, the lack of effects of flooding on its water relations reflects its high flood-tolerance documented in several works (Loreti & Oesterheld, 1996; Insausti et al., 2001; Mollard et al., 2008; 2010; Striker et al., 2006; 2008; 2011a). The ability of this species to maintain its leaf water status similar to controls (and even better than controls, at high evaporative demand, *i.e.* high DPV_{air}) indicates a high capacity to continue with water uptake under flooded soil conditions. Such capacity seems to be associated with its high porous root system allowing oxygen conduction for sustaining aerobic root respiration and functionality (Insausti et al., 2001).

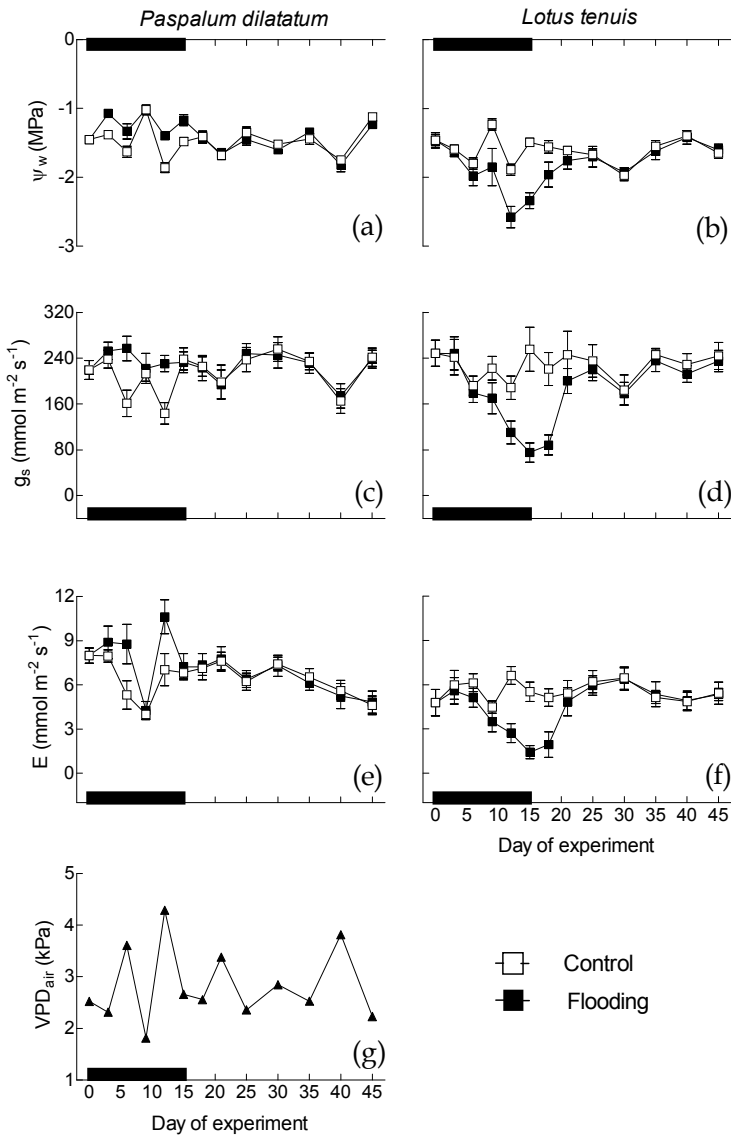


Fig. 6. Leaf water potential (Ψ_w), stomatal conductance (g_s) and transpiration rate (E) of *Paspalum dilatatum* (a, c, e) and *Lotus tenuis* (b, d, f) plants grown under different treatments: control and flooding. (g) Air vapour pressure deficit (VPD_{air}) at the moment of each measurement. Horizontal closed bars indicate the duration of the experimental flooding (15 days at 6 cm water depth). Values are means \pm SE of five replicates.

2.3.2 Photosynthesis responses

A common response to flooding is the reduction of plant carbon fixation (*i.e.* rate of photosynthesis; Jackson & Drew, 1984). In the short term, photosynthesis can drop as a result of a restriction of CO₂ uptake due to stomata closing (Jackson & Hall, 1987; Huang et al., 1994; 1997; Pezeshki & DeLaune, 1998; Malik et al., 2001; Striker et al., 2005; Mollard et al., 2010). Several works have shown correlation between stomatal conductance and carbon fixation in flooded plants indicating that stomatal aperture can be a limiting factor for photosynthesis (Vu & Yelenosky, 1991; Liao & Lin, 2001; Mielke et al., 2003). Stomata closing under flooding can occur in response to leaf dehydration where the guard-cells lose their turgor (Bradford & Hsiao, 1982; Striker et al., 2007b; Fig. 6b,d), but it can also occur without noticeable changes in the leaf water potential responding to a hormonal (non-hydraulic) regulation (Jackson & Hall, 1987; Jackson, 2002; Striker et al., 2005). In the last case, the available evidence supports the idea of stomatal closure mediated by action of abscisic acid (ABA) in leaves (Else et al., 1996; Jackson et al., 2003), but not synthesized and transported from the roots, as it happens under drought stress (Davies & Zhang, 1991).

If flooding continues in time, a decrease in the photosynthetic capacity of mesophyll cells *per se* (Liao & Lin, 1994; Yordanova & Popova, 2001) leads to a further reduction of photosynthesis. Such lower photosynthetic capacity can be attributed to a (i) lower leaf chlorophyll content (Yordanova & Popova, 2001; Manzur et al., 2009; *cf.* leaf greenness of flooded *vs.* control plant in Fig. 5), (ii) a reduced activity of carboxylation enzymes, and (iii) an oxidative damage on photosystem II by reactive oxygen species (Yordanova et al., 2004). In this respect, Liao & Lin (1994) registered in *Momordica charantia* (bitter melon) a lower activation level of Rubisco (enzyme that catalyses the initial reaction during CO₂ assimilation) as flooding time increases until reaching 59% of controls values after a week of treatment. In the same experiment, these authors also registered a reduction on leaf soluble protein including Rubisco (Liao & Lin, 1994). So, both the content of Rubisco protein as well as its activation can be significantly reduced by flooding (Liao & Lin, 1994; 2001). In addition, the low photon utilization of flooded plants (Titarenko, 2000 as cited in Yordanova et al., 2004) could result in the production of reactive oxygen species (ROS) (Asada and Takahashi, 1987). The main ROS are superoxide, single oxygen, hydrogen peroxide and hydroxyl radical, which are very reactive and provoke damage to lipid membranes and proteins (see reviews by Foyer et al., 1994; Noctor & Foyer, 1998). To manage the level of ROS for protecting cells, plants have antioxidants like ascorbate, glutathione and tocopherols, and enzymes (*i.e.* peroxidases, superoxide dismutase, glutathione reductase, catalase) with ability to scavenge ROS and regenerate the antioxidants (Asada, 2006; Murchie & Niyogi, 2011). However, under flooding stress, the scavenging capacity can be over passed due to the higher production of ROS, thus generating oxidative damage on the proteins of the photosynthetic apparatus (Yordanova et al., 2004).

If it is scaled up, the negative effects of flooding on photosynthesis from the leaf level to the plant level can lead to a low growth rate in flooded plants. Such a reduction in growth, determines a low demand of triose phosphate for sucrose biosynthesis as well as a slowdown on the phloem transport of this sugar (Pezeshki, 1994; Pezeshki, 2001; Sachs & Vartapetian, 2007). Consequently, starch starts to accumulate in the chloroplasts (Wample & Davies, 1983) leading to a negative feedback on photosynthesis rate (Liao & Lin, 2001). In addition, early leaf senescence (Grassini et al., 2007) and a reduction in leaf area may also

lead to a drop of carbon fixation at plant level (Striker et al., 2005). In this scenario, plants have to draw on their carbohydrate reserves in order to maintain their metabolic activity. In consequence, the level of reserve carbohydrates may be crucial in determining the tolerance to long term flooding (Schlüter & Crawford, 2001; Ram et al., 2002; Manzur et al., 2009; Striker et al., 2011a).

2.3.3 Radial oxygen loss (ROL), root apex oxygenation and root elongation

Under partial submergence (or under waterlogging), at least part of the shoots are above water and the capture of atmospheric oxygen by leaves is possible. This oxygen needs to be transported to the roots in order to avoid root anoxia. Root apex oxygenation is crucial for continuing with root elongation and soil exploration under flooding conditions (Armstrong, 1979). In plant species having (or developing) aerenchyma as a prerequisite for facilitating oxygen movement along roots, the magnitude of oxygen reaching the apex depends on the effectiveness of its longitudinal transport. When tissue respiratory demands are satisfied along the root, such effectiveness is mostly dependent on the loss of oxygen towards the rhizosphere (ROL; see review by Colmer, 2003a). The loss of oxygen from the root depends on the presence of barriers impeding its leakage towards the soil (Fig. 7). There are species possessing high aerenchyma proportion but not a barrier against ROL (or they have a slight barrier), so a considerable amount of oxygen is lost along the root, limiting the oxygen diffusion to the apex. Hence, in these species, the apex is poorly oxygenated and the root elongation is constrained (Fig. 7a). Other species, specially those inhabiting wetland sites, have barriers in the layers of the outer root cortex which prevent the loss of oxygen from the roots. In these cases, the longitudinal oxygen diffusion is enhanced, which increases the aeration of the root apex and allows root elongation and a flooded soil deeper exploration (Fig. 7b). The 'ROL barrier' can be constitutive like in *Juncus effusus* (Visser et al., 2000) or it can be induced by stagnant conditions like in *Caltha palustris* (Visser et al., 2000), *Lolium multiflorum* (McDonald et al., 2002) and some rice cultivars (Colmer et al., 1998; Colmer, 2003b). Studies on the spatial pattern of ROL along roots revealed that the barrier is preferentially located in the basal regions of the root while there is no barrier at the apex (Colmer et al., 1998; Visser et al., 2000; McDonald et al., 2002; Colmer, 2003b). So, even in species having a strong barrier against ROL, some oxygen is released through the tip zone, which generates an aerobic zone around it (Fig. 7b). It is supposed that such aerobic zone prevents the accumulation of potentially toxic compounds, like the reduced forms of iron (Fe^{2+}), manganese (Mn^{2+}) and sulfides, in the region of the sensitive root apex (Armstrong, 1979; Soukup et al., 2002; Pedersen et al., 2004; Armstrong & Armstrong, 2005).

Suberin is the most likely candidate to function as barrier to oxygen leakage (Colmer, 2003a,b; Colmer et al., 2006; Kotula et al., 2009; Shiono et al., 2011; Ranathunge et al., 2011). It should be mentioned that some authors consider that lignin cannot be discarded as part of the barrier to ROL, although evidence from De Simone et al. (2003) suggests that lignin does not accomplish such a function. Indeed, Shiono et al. (2011) indicate that suberin deposits may also be of more importance than lignin, as suberin increased prior to changes in lignin based on a detailed histochemical work. Besides, in species where the barrier against ROL is induced by stagnant conditions, there is an extra suberin deposition in the cell walls of the outer cortex, which denotes its importance in reducing ROL (Colmer, 2003b). On the other hand, it is interesting that in rice, the most studied species regarding this topic, the barrier to

ROL is triggered in a matter of hours and that the timing of generation also depends on the root length at the time of flood occurrence. Recently, Shiono et al. (2011) demonstrated that formation of the barrier to ROL commenced quickly in long adventitious roots (105 to 130 mm length) and that the barrier was completed within 24 hours. By contrast, barrier formation in short roots (65 to 90 mm length) took more than 2 days. These authors also showed that the timing of aerenchyma formation (see section 2.1) was similar between short and long roots. So, these root acclimations to deal with flooding, aerenchyma formation and the barrier to ROL, appear to be differentially regulated (see also Colmer et al., 2006).

Finally, the knowledge accomplished on the characteristics and functioning of the physical barrier against ROL has practical importance for improving the flood-tolerance of crops like wheat. This fact was recently demonstrated by Malik et al. (2011), who achieved a successful transfer of the barrier to ROL (and higher root porosity) from *Hordeum marinum* to wheat through wide hybridization and the production of *H. marinum*-wheat amphiploids.

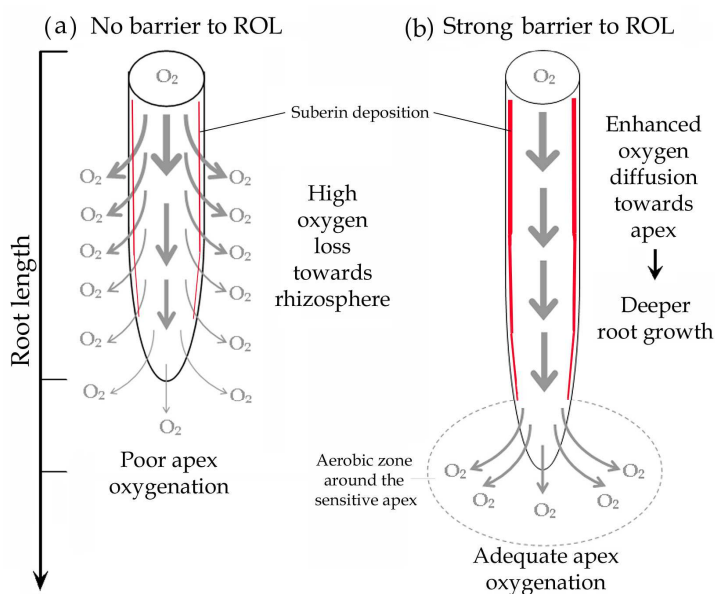


Fig. 7. Scheme showing two different patterns of radial oxygen loss (ROL) from roots. In these hypothetical examples, the root aerenchyma is considered a non-limiting factor for oxygen transport. (a) Root without barrier to ROL in the outer cortex, which loses oxygen along all positions resulting in a deficient apex oxygenation, and short roots in anoxic soils. (b) Root having a strong barrier to ROL, so that oxygen is transported efficiently to the apex allowing deeper root growth in flooded soils. The loss of oxygen is circumscribed to the apex, which generates an aerobic zone that diminishes entry of potentially toxic compounds (Fe^{2+} , Mn^{2+} , sulfides) in highly-reduced soils. The physical barrier to ROL is due to suberin deposition in the cell walls of the outer root cortex and/or the exodermis as it is indicated by red lines of different thickness between root types in (a) and (b). The thickness of the grey colour arrows indicates the amount of oxygen available. Figure re-drawn on the basis of Colmer & Voeseinek (2009).

3. Plant responses to complete submergence

Complete submergence is one of the most stressful scenarios that plants can confront in environments prone to soil flooding (Blom, 1999; Mommer & Visser, 2005; Colmer & Voesenek, 2009). In addition to oxygen deficiency for roots occurring during water excess in soil, plants subjected to complete submergence are restricted from obtaining enough oxygen for sustaining tissue aeration, even though in some species, oxygen can partially be supplied by underwater photosynthesis (Mommer et al., 2004; Colmer & Pedersen, 2008; Vashist et al., 2011). As a result, aerobic metabolism for energy production shifts to the much less efficient anaerobic/fermentative pathways (Gibbs & Greenway, 2003; Voesenek et al., 2006; Kulichikhin et al., 2009). Besides, depending on the turbidity of the water, light reduction can constrain carbon gain by photosynthesis (Sand-Jensen, 1989; Colmer & Pedersen, 2008). Therefore, complete submergence can cause a drastic energy and carbohydrate crisis that can threaten plant survival (Voesenek et al., 2006; Bailey-Serres & Voesenek 2008; 2010).

According to Colmer & Voesenek (2009), this stress can be classified depending on water depth and duration of the submergence. With respect to water, shallow floods are those of less than 0.5-1 meter of water column, in which submerged plants have chances to surpass the water level if they respond elongating their shoots (Setter & Laureles, 1996; Lynn & Waldren, 2003; Hattori et al., 2007). Shallow submergence can be found in lowland flat areas of the world, as in the Flooding Pampa grasslands (Soriano, 1991), as well as in lowland rice areas. On the other hand, deep floods are those of more than 1 m of water column, in which the effort of trying to de-submerge the plant shoots is useless, because the chances to surpass the water are non-existent. In these cases, the pursued benefit of developing a shoot elongation response is not outweighed by the incurred cost, because the plant exhausts its carbohydrates reserves, dying before reaching the water surface. In contrast, plants that remain quiescent are able to succeed in front to deep submergence, surviving by using carbohydrates reserves to maintain a basal metabolism until water subsides (Schlüter & Crawford, 2001; Ram et al., 2002; Manzur et al., 2009; Striker et al., 2011b). Deep submergence can be found in areas of Asia devoted to deepwater rice cultivation, river forelands of Europe (Bloom et al., 1994), and the Amazonia of South America (Parolin, 2009). Submergence can be considered of short duration generally when it is no longer than two weeks and it occurs during flash-flooding events. If submergence period is longer than two weeks (often of a month or more), it can be regarded as of long duration (see Colmer & Voesenek, 2009 and Fig. 3 of this chapter). Although this classification can appear as arbitrary, it is useful in order to understand the strategies used by plants to deal with each combination of water depth and duration of the submergence.

3.1 Plants facing submergence. What to do, escape from water or stay quiescent?

Plants cope with complete submergence by means of one of the two major strategies reported in plant submergence responses (*sensu* Bailey-Serres & Voesenek, 2008; 2010; Fig. 8). The first is an escape strategy – called LOES: low oxygen escape syndrome – and the second is a sit-and-wait strategy – called LOQS: low oxygen quiescence syndrome (Bailey-Serres & Voesenek, 2008; 2010; Hattori et al., 2010). The LOES implies shoot elongation in order to restore leaf contact with the atmosphere, while the LOQS is based on maintaining steady energy conservation without shoot elongation (Bailey-Serres & Voesenek, 2008). It has been postulated that LOES offers plants better chances to survive under shallow long-

term flooding, where shoot de-submergence is easily plausible (Fig. 8a). In contrast, LOQS is more likely to be adopted by species coping with deep short-term flooding (< 2 weeks) where shoot emergence seems to represent a higher cost of energy and might compromise eventual recovery when the water recedes (Colmer & Voeselek, 2009; Fig. 8b).

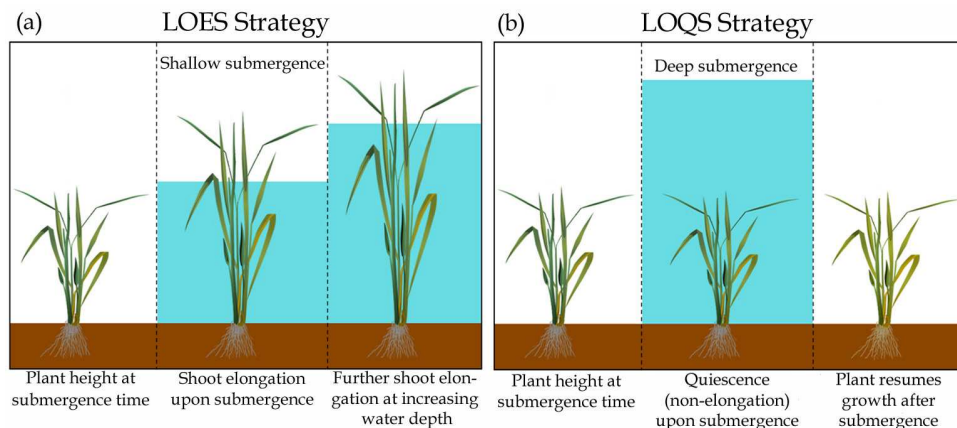


Fig. 8. Main strategies used by plants to deal with complete submergence. (a) Plant escaping from water by means of upward shoot elongation is the typical response of the 'low oxygen escape syndrome' (LOES). Plants using this strategy are able to continue elongating their shoots if the water depth increases (b) Quiescent plant under deep submergence surviving at expenses of its carbohydrates reserves depicts the 'low oxygen quiescence syndrome' (LOQS). It should be mentioned that plants escaping from water change their morphology for being taller, but their growth (in terms of biomass accumulation) is lower than that of the non-submerged plants.

Fast shoot elongation (LOES) allows plants to restore the contact of their leaves with the atmosphere under shallow submergence (Grimoldi et al., 1999; Voeselek et al., 2006; Striker et al., 2011b). So, emerged leaves can function as 'snorkels' facilitating the entrance of oxygen and ventilation of gases (ethylene, methane, CO_2) accumulated in the submerged tissues (Colmer, 2003a; Colmer & Voeselek, 2009). The shoot elongation can happen in petioles (as in *Rumex* species, see Voeselek et al., 1990; Chen et al., 2009; 2011), or internodes (as in rice, see Hattori et al., 2009; 2010) depending on the growth form of the plant. It has been established, using rice and *Rumex palustris* as model species, that one of the first signals triggering the shoot elongation is the ethylene accumulation in submerged tissues (Voeselek et al., 1993; Jackson, 2008). Ethylene accumulates in submerged tissues due to a highly restricted outward diffusion in water (Armstrong, 1979), and the upregulation of enzymes associated with its biosynthesis (eg. ACC synthase and ACC oxidase; Vriezen et al., 2000). Under complete submergence, concentrations of ethylene increase, which downregulates the abscisic acid levels, and upregulates those of gibberellins (Jackson, 2008). Increased gibberellins level promotes the expression of genes encoding cyclins and expansins, associated with cell division and cell extension (respectively), which lead to a fast shoot elongation underwater (Jackson, 2008). Besides, the increase in endogenous ethylene produces a lower pH in the apoplast that favours the action of expansins provoking the cell wall loosening as a necessary step that precedes cell extension (Jackson, 2008).

Quiescence syndrome of plants (LOQS) under complete submergence – of short duration but deep water column – were reported in some rice varieties (Setter & Laureles, 1996), ecotypes of *Ranunculus repens* (Lynn & Waldren, 2003), *Rumex crispus* (Voeseenek et al., 1990), *Rumex acetosa* (Pierik et al., 2009), and *Lotus tenuis* (Manzur et al., 2009). In rice, pioneer studies have advanced in the understanding of this behaviour by comparing traits between tolerant accessions (eg. FR13A) and non-tolerant ones (eg. Liaogeng, IR42 and M202). Later, genetic studies have provided evidence that the shoot extension is controlled by a polygenic locus (*SUB1*) located at chromosome 9 (Xu et al., 2009). In this locus, rice has two or three genes –*SUB1A*, *SUB1B* and *SUB1C* –depending on the cultivar (or accession). Among these genes, it was established that the expression of the *SUB1A-1* is what confers submergence tolerance through the repression of shoot elongation and conservation of reserve carbohydrates, which prolongs underwater survival of plants (see review by Bailey-Serres & Voeseenek, 2008). In this respect, *SUB1A-1* acts specifically by limiting the ethylene-induced shoot extension, which involves the reduction of the expansins levels related to cell wall loosening, and the reduction of sucrose and starch consumption, among other responses (Fukao et al., 2006; Fukao & Bailey-Serres, 2008; Fig. 9).

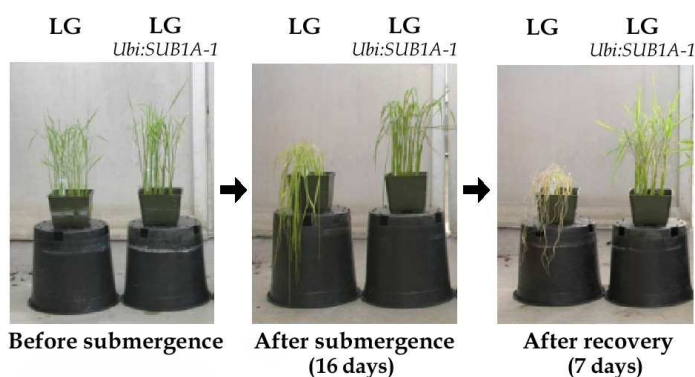


Fig. 9. Aspect of *Oryza sativa* plants of Liaogeng cultivar (LG, submergence intolerant) and of a transgenic line with constitutively expressed *Sub1A-1* (*ubi:SUB1A-1* with background genotype LG). Plants before submergence (left photographs), plants after 16 days of submergence (center photographs), and plants after 7 days of recovery (right photographs). It should be noticed that plants with similar genetic background (LG), but expressing *Sub1A-1* are tolerant to submergence. Reproduced with modifications from Fukao & Bailey-Serres (2008) with permission granted by The National Academy of Sciences, U.S.A.

In addition to the above mentioned traits associated to LOQS, there are other ones enabling plant survival when submergence time further extends. These traits are mainly associated with the improvement of photosynthesis underwater (Mommer et al., 2004; Mommer & Visser, 2005; Colmer & Pedersen, 2008). Underwater photosynthesis is enhanced in some species due to the presence of a thin gas layer (called 'plant plastron') retained at the surface of submerged leaves, which increases the thickness of the gas-liquid interface between leaves and the surrounding water. This allows stomata to remain open when submerged, which facilitates that carbon dioxide and oxygen bypass the cuticle resistance. As a result, the levels of available CO_2 and O_2 are higher, which improve photosynthesis and

oxygenation of shoots underwater (Colmer & Pedersen, 2008). Besides, some species are able to develop aquatic leaves with higher potential for carbon gain underwater. These aquatic leaves present characteristics that favour light interception underwater for improving photosynthesis, as higher specific leaf area (thin leaves), thin cuticles, thin cell walls and location of chloroplasts toward the epidermis (Mommer et al., 2004; Mommer & Visser, 2005; Bailey-Serres & Voeselek, 2010).

4. Conclusions

Floods entail different stressful conditions for plants, which mainly depend on water depth and its duration. Adaptive traits of plants enabling survival under soil waterlogging and partial submergence, are those directed to oxygenation of submerged tissues (*i.e.* parts of shoots and entire root system), and the location of leaves above water to continue with carbon fixation. Aerenchyma formation and development of adventitious roots, with barriers to radial oxygen loss, appear as the most important features facilitating longitudinal oxygen transport to sustain root aeration, and thus continue with water absorption in anaerobic soils. Both the reorientation and lengthening of shoots towards a vertical position, determine a higher proportion of leaves surpassing the water level in order to capture oxygen and continue photosynthesizing. Maintenance of stomatal conductance on mild days guarantees the uptake of CO₂ for carbon fixation, although on days of high atmospheric evaporative demand, the stomatal closure can be useful to regulate plant water homeostasis, which depends on the balance between water losses by transpiration and water uptake by roots. When water depth increases and plants are completely submerged, they can adopt two main strategies, namely LOES (low oxygen escape syndrome) and LOQS (low oxygen quiescence syndrome). The first involves the upward shoots elongation, which facilitates restoration of leaf contact with the atmosphere, and it is relevant for plants species (or ecotypes) selected in environments with shallow, prolonged floods. The second is a sit and wait strategy, where the plant remains quiescent during the submergence period by using its reserve carbohydrates conservatively for plant survival. When water subsides, plants showing LOQS resume their growth. The selection of this strategy is favoured in environments prone to deep, short floods. Future experiments assessing waterlogging and submergence responses of plants should include the combination of different flooding regimes. This would contribute to a better understanding of the costs and benefits related to particular combinations of traits conferring tolerance in variable flooding scenarios. Thus, a better comprehension of plant functioning under water excess, in a context that indicates a higher flooding occurrence during the years to come, would help to assist breeding programs as well as to define better management decisions for cultivation of crops and forage species in lands prone to flooding.

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