



Plant responses to flooding stress

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Most plant species cannot survive prolonged submergence or soil waterlogging. Crops are particularly intolerant to the lack of oxygen arising from submergence. Rice can instead germinate and grow even if submerged. The molecular basis for rice tolerance was recently unveiled and will contribute to the development of better rice varieties, well adapted to flooding. The oxygen sensing mechanism was also recently discovered. This system likely operates in all plant species and relies on the oxygen-dependent destabilization of the group VII ethylene response factors (ERFVIs), a cluster of ethylene responsive transcription factors. An homeostatic mechanism that controls gene expression in plants subjected to hypoxia prevents excessive activation of the anaerobic metabolism that could be detrimental to surviving the stress.

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Introduction

Although plants produce oxygen through photosynthesis, the lack of an efficient system to transport oxygen to non-photosynthetic organs implies that these organs can be deprived of oxygen if their anatomy limits oxygen diffusion from outside [1,2]. Additionally, complete submergence of the plant by flooding events may also lead to low-oxygen availability in the aboveground organs, especially when water turbidity limits photosynthesis [3]. When oxygen becomes limiting for respiration plants experience hypoxia, whilst the complete absence of oxygen (anoxia) is even more detrimental to plant survival. Both hypoxia and anoxia trigger extensive reprogramming of gene expression, with induction of the fermentative metabolism, allowing the plant to use glycolysis for ATP production [1]. Climate changes will lead to extremes in water availability that will cause severe drought in some areas, while

flooding due to extreme rainfall events will affect other geographical areas [4]. Unless new crop varieties able to withstand abiotic stresses are developed, productivity will be gravely affected. Until a decade ago little was known about the genes that confer tolerance to submergence, and it is only during recent years that light has been shed on the molecular mechanisms behind oxygen sensing and signalling in plants [2]. In this review we will highlight the most recent findings in the field of plant anaerobiosis, from ecophysiology of plants growing in wetlands to the translation of discoveries made in *Arabidopsis* to crops.

Flooding in the wild

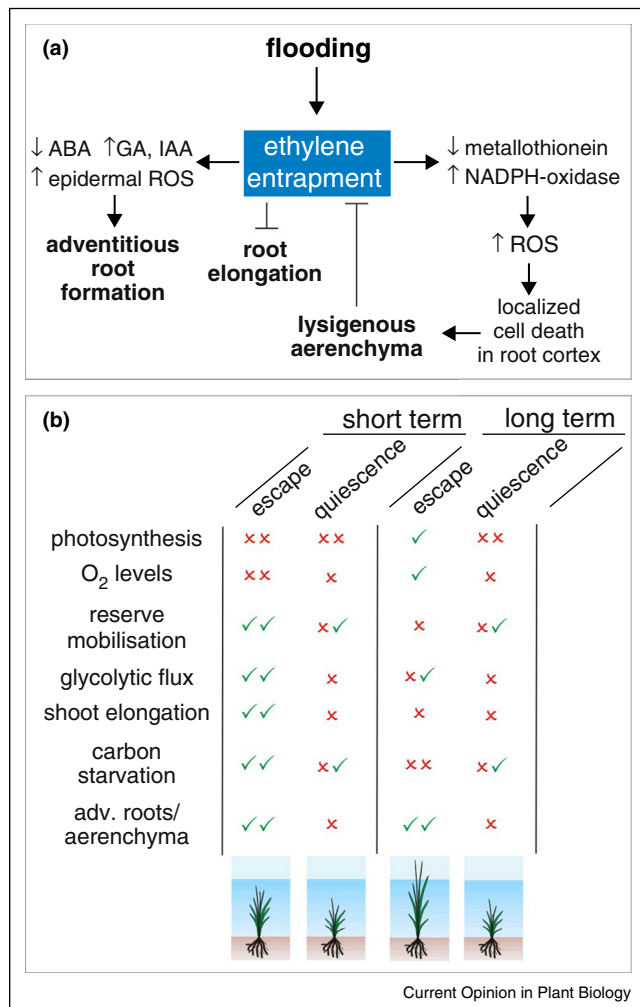
Flooding is a natural occurrence in many ecosystems and therefore many wild species are superbly adapted to watery conditions. Here improved gas exchange with the environment is essential to avoid hypoxia within the plant. To this end, plants can induce and/or constitutively develop aerenchyma, longitudinal connected gas spaces, which provide a rapid means of aerial gas exchange over long distances within the plant [5]. This is usually combined with a change in root architecture to minimize the distance (and therefore diffusive resistance) between the aerial surface and the flooded root tips [6], for instance via adventitious roots, which can create a collection of air conducting snorkels originating from the hypocotyl or stem into the anaerobic substrate. Often aerenchyma are combined with a barrier that prevents oxygen leakage into the surrounding anaerobic soil, which drastically improves flooding tolerance [7].

An extensive aerenchyma system is extremely effective under waterlogged conditions where the shoot remains in aerial contact and can thus funnel air down to the root. During complete submergence, however, the shoot does not make aerial contact oxygen, their effectiveness in funnelling air towards the roots is greatly compromised. In such cases, some wetland plant species, in an attempt to regain aerial shoot contact, display rapid vertical elongation of leaves, internodes or petioles to snorkel for air. This escape strategy is observed in some rice varieties (see below), as well as in several other plant species [8]. In an alternative strategy the plant aims to enter a state of inactivity (quiescence), to be revived once the flood recedes [9,10]. This is also a difficult tactic as energy and carbon utilisation should be kept to a minimum to make reserves last a long time, whilst they should simultaneously be sufficient to maintain cellular integrity (Figure 1a).

The submerged plant: low oxygen and high ethylene

Because of its gaseous nature ethylene hardly leaves the plant under flooded conditions and thus rapidly

Figure 1



Ethylene is a pivotal regulator growth survival strategies **(a)** and root development **(b)** during submergence and waterlogging. During complete submergence, ethylene induced growth strategies are paramount to survival (a), but both have different short term and long term effects on plant performance, especially since under long term submergence escaping plants will have regained aerial contact. Naturally, photosynthesis is severely reduced by flooding, but through an escape strategy some photosynthesis can be recovered through the re-establishment of aerial contact. This subsequently reduces the need for reserve mobilisation and limits oxygen shortage via aerenchyma. Initially, escaping plants will have low internal O₂ levels, due to their high metabolic activity which is fuelled by a strong glycolytic flux and reserve mobilisation. These high demands, generally mean escaping plants suffer strongly from carbon starvation. Though all these effects are ameliorated once aerial contact is made. Because quiescent plants have low activity, their requirements on reserves and energy are limited. Subsequently, internal O₂ levels would be at a higher steady state and carbon shortage would be considerable lower. However, quiescent plants still rely on reserve mobilisation to sustain cellular functions, both during short term and long term flooding. Root development is also essential to survive flooded conditions. The aqueous environment prevents ethylene to readily leave the plant tissues through gas diffusion. This ethylene entrapment starts a cascade that leads a change in root architecture (b), through for instance the formation of adventitious roots. This includes a hormonal cascade and ROS induced epidermal cell death.

accumulates inside the plant. It is therefore a highly reliable and rapid cue for plants to detect their predicament [11]. Another signal is the oxygen availability. The internal level of these gases is a balance between consumption, production and diffusive resistance. Therefore active, heterotrophic or compact tissue, such as meristems and roots, will rapidly experience low oxygen upon flooding. In photosynthetic tissue the consumption and production of oxygen is dependent on light conditions, and thus also the oxygen availability.

Ethylene is the primary signal for most adaptations to flooding. Ethylene modulates a hormonal cascade of ABA, GA and ultimately auxin to induce adventitious rooting in tomato, *Solanum dulcamarum*, and rice, and [12–14]. However, root emergence also requires ethylene induce ROS formation in the epidermal cells, leading to their cell death to allow root penetration [15]. Similarly, lysigenous aerenchyma formation, which is formed by apoptosis of specific cells in the cortex, involves an ethylene dependent drop in antioxidant activity. The subsequent increase in ROS leads to the required cell death [16–18]. Interestingly, the important suberin based oxygen barrier is not affected by ethylene, but likely causal genes involved in its formation have been identified [19]. The escape strategy to reach the water surface is also ethylene driven. However, downstream signalling is considered divergent in the plant kingdom, as it was found to act via group VII ERFs in rice (see below), but via genes typical of low light induced elongation in *Rumex palustris* [20–22]. Remarkably, ethylene pre-treatment induced anoxia tolerance of *Rumex palustris* was associated with enhanced hypoxia related gene expression. A behaviour that was absent in *Rumex acetosa*, a species that experience fewer flooding events and employs a quiescence instead of an escape strategy [20]. This highlights the importance of a link between ethylene and hypoxic signalling pathways.

The high levels of ethylene associated with flooding inhibit root elongation, but through the formation of aerenchyma the excessive ethylene is easily removed. However, species that are ineffective in producing aerenchyma therefore experience strong root growth reduction under flooded conditions [23]. The strong dose dependency of ethylene signalling [24] might play an important role in its contrasting developmental roles during flooding (Figure 2). To avoid detrimental effects associated with high levels of ethylene, some of the species that continuously occupy aquatic or flood-prone environments have

Simultaneously, high levels of ethylene in submerged roots, inhibit root elongation. However, ethylene also leads to a drop in the antioxidant metallothionein and an increase NADPH oxidase, which together leads to an accumulation of ROS. ROS acts as a signal for programmed cell death of specific cortex cells, eventually leading to the formation of lysigenous aerenchyma. As a result, the improved gas diffusion can remove high ethylene levels and thus releases the inhibition on root elongation.

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