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Root responses to flooding

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Soil water-logging and submergence pose a severe threat to plants. Roots are most prone to flooding and the first to suffer from oxygen shortage. Roots are vital for plant function, however, and maintenance of a functional root system upon flooding is essential. Flooding-resistant plants possess a number of adaptations that help maintain oxygen supply to the root. Plants are also capable of initiating organogenesis to replace their original root system with adventitious roots if oxygen supply becomes impossible. This review summarizes current findings on root development and *de novo* root genesis in response to flooding.

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Introduction

Plants are frequently exposed to water-logging and submergence, which reduce gas diffusion in the soil and flood water and consequently oxygen supply to the root. In addition, soil microorganisms compete with the root for the remaining oxygen rendering maintenance of energy supply by way of oxidative phosphorylation in mitochondria difficult or impossible. Fermentation provides a means for substrate-level ATP synthesis but carbohydrate input is high and the ATP yield is low with 2–4 ATP generated per glucose in fermentation versus 36 ATP per glucose in oxidative phosphorylation. Root carbohydrate reserves are considered a hallmark of flooding resistance [1••,2,3]. During hypoxic or anoxic conditions the starch reserves in the root are rapidly used up and maintenance of root growth and function becomes difficult or impossible. Mineral uptake by roots is crucial for a plant and can no longer be accomplished when energy supply, membrane integrity and ion transport in the root are impaired causing nutrient deficiency not only in the root but also in the shoot [4]. Hypoxic conditions can furthermore affect root hydraulic conductance because of the hypoxia-sensitive transcellular water movement via aquaporin activity [5]. In the shoot stomatal closure and wilting are consequences of reduced root water conductivity. Nutrient deficiency leads to premature plant senescence and ultimately to plant death. A major strategy of a flooded plant must hence be aimed to maintain aerobic metabolism in the root. This review focuses on the adaptive strategies of plants to maintain a functional root system during flooding.

Anatomical and morphological adaptations in the root improve oxygen status

A number of mechanisms have been described that help maintain root function through an improved oxygen supply during flooding. Among these is the establishment of a lateral diffusion barrier which minimizes radial oxygen loss from flooded roots to the soil. *Zea nicaraguensis* (teosinte) is a wild relative of *Zea mays* (maize) but unlike maize, it is tolerant to water logging. Enhanced deposition of lignin and suberin at outer cell layers of teosinte roots in response to soil water logging increases gas-impermeability at the root surface and results in a much reduced radial loss of oxygen from teosinte compared to maize roots [6]. Similarly, suberin deposition and lignification of the exodermis in *Oryza sativa* L. (rice) roots provide a barrier for radial oxygen loss [7••,8]. A reduced loss of oxygen from the root helps maintain cellular oxygen as long as oxygen is supplied continuously from an aerated shoot to the root which continuously consumes oxygen in respiration. Oxygen distribution from the shoot to the root and along the root is facilitated by the formation of internal gas spaces (aerenchyma). Water logging promotes aerenchyma formation in both, wetland and dryland species [9]. However, many semi-/aquatic or water logging-tolerant plants such as rice or *Juncus effusus* constitutively form root aerenchyma even in well-drained soils. In addition, gas spaces are formed more extensively in response to flooding in flooding-tolerant plants than in intolerant species as seen in teosinte compared to its domesticated relative maize [10].

Lysigenous aerenchyma develop as a consequence of programmed death of cortex cells and complete digestion of cell remnants [11]. This process not only results in the formation of a continuous gas space but at the same time reduces the number of oxygen-consuming cells. As a result, aerenchyma improve the oxygen balance in a dual fashion. In addition, digested cortex cells provide nutrients for the remaining cells. Analysis of teosinte roots revealed however that the apical 10–20 mm of the root tips are exempt from cell wall fortification and aerenchyma formation [10]. The region that lacks an enforced gas diffusion barrier and internal gas spaces extended even further in maize. Thus, the root apex with its quiescent center and its dual apical meristem that produces cells for the root proper from the proximal and lateral stem cells and root cap cells from distal stem cells [12••] is particularly prone to oxygen shortage. Limited gas diffusion in this cell-dense growth region further aggravates the problem of oxygen supply in the root apex. Particularly under long-term flooded conditions, the roots suffer from oxygen shortage even in well-adapted plants. This is manifest in root growth inhibition and eventually in roots that become dysfunctional. For a plant to survive, the root system in the soil must then be replaced.

The advantages of having adventitious roots

Flooding often results in complete or near complete loss of the roots in the soil. Flooding-tolerant herbaceous plants and trees produce adventitious roots in response to submergence to provide water, nutrients, and anchorage. The replacement of the sediment root system by adventitious roots from the stems of flooded plants was shown to improve plant growth in the perennial wetland species *Cotula coronopifolia* and *Meionectes brownii* [13]. Shoot-borne roots such as the adventitious roots of semi-aquatic rice that develop at the stem nodes reduce the distance over which oxygen has to be supplied. In general, the central cylinder of a root is most prone to oxygen deficiency because the endodermis with its thick suberized cell walls known as the Casparian strip, limits gas diffusion [14••]. The oxygen level in the stele of maize roots kept in solution drops to near zero [4]. Flooding of *Larix laricina* (tamarack) seedlings for six months resulted in a near complete loss of the primary root system and its replacement by adventitious roots [15]. These adventitious roots, which mostly remain under water, have a poorly developed endodermis that probably alleviates gas diffusion to the stele [15] revealing developmental plasticity in endodermis differentiation [16]. The aquatic roots of *C. coronopifolia* and *M. brownii* contain chlorophyll and are photosynthetically active, resulting in oxygen evolution. In addition photosynthesis may improve the energy balance even though the root biomass of *C. coronopifolia* and *M. brownii* did not differ between high and low light conditions [13]. In summary, adventitious roots minimize the distance for oxygen diffusion, are adapted to reduce radial oxygen loss, have improved gas diffusivity along and across the root, and occasionally have the ability for *in situ* oxygen evolution.

Adventitious root initiation

Soil water logging or submergence reduce gas diffusion from the soil or water column into the root rendering the root highly dependent on oxygen delivery from the non-submerged shoot. Submergence likewise reduces diffusion of endogenous gas into the surrounding flood waters by 10 000-fold with the consequence that the gaseous hormone ethylene accumulates in submerged tissues to physiologically active concentrations within a few hours [2,17]. Ethylene accumulation in submerged rice, maize, *Rumex palustris*, *Solanum lycopersicon* (tomato) or hypoxic *Arabidopsis thaliana* is enhanced by the induction of ethylene synthesis at the level of 1-aminocyclopropane-1-carboxylic acid (ACC) synthase (ACS) and ACC oxidase (ACO) gene expression and protein stability [18–22]. Owing to its near omnipresence in submerged tissue it is not surprising that ethylene acts as a key hormone that regulates many aspects of submergence adaptation in plants. Even though tomato is considered flooding-intolerant tomato plants nonetheless respond to flooding by hyponastic leaf movement and the formation of adventitious roots that relieve the submergence stress to some extent. While ethylene promotes the formation of adventitious roots in tomato, at the same time it inhibits lateral root formation favoring the generation of a shoot-borne root system [23••,24]. Ethylene auxin interactions also control root branching in *Arabidopsis* [25]. Induction of adventitious roots in tomato is dependent on the ethylene receptor Never ripe (Nr) [24]. Ethylene promotes *de novo* genesis of adventitious root primordia through auxin activity [26,27], which is increased by directing auxin flux toward the submerged stem [24,28]. Inhibition of auxin efflux with naphthylphthalamic acid (NPA) abolished adventitious root formation.

Well-adapted plants such as rice generate adventitious root primordia as an innate adaptation in the absence of a submergence signal [29]. The root primordia that are initiated at each node remain buried within the nodal tissue and are induced to emerge in response to submergence or ethylene [30]. CROWN ROOTLESS1 (CRL1)/ADVENTITIOUS ROOTLESS1 (ARL1), a LATERAL ORGAN BOUNDARIES DOMAIN (LBD)/ASYMMETRIC LEAVES2-LIKE (ASL) transcription factor controls the initiation of adventitious roots in rice. CRL1/ARL1 acts in the auxin signaling pathway downstream of AUXIN (AUX)/INDOLE-3-ACETIC ACID (IAA) and AUXIN RESPONSE FACTOR (ARF) transcription factors [31••,32]. The APETALA2 (AP2)/ETHYLENE RESPONSE FACTOR (ERF) transcription factor CRL5 may be a direct ARF target. *crl1/arl1* and *crl5* mutants possess fewer adventitious root primordia with additive phenotypes indicative of independent signaling pathways [33]. CRL5 is related to the *Arabidopsis* AINTEGUMENTA (AIL)/PLETHORA (PLT) proteins which are central regulators of root development. They control the transition from stem cell identity to meristem cell identity to cell differentiation in a dose-dependent manner thereby generating a developmental gradient in the apical root meristem by way of a concentration gradient [34,35,36••]. Overexpression of PLT genes results in ectopic root formation in *Arabidopsis* [34]. While CRL1/ARL1 is required for root initiation, the WUSCHEL-related homeobox gene *WOX11* was suggested to control early development and emergence of adventitious roots based