Plant Responses and Adaptation to Flooding

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Concept

Soil waterlogging and submergence (collectively termed flooding) are abiotic stresses that influence species composition and productivity in numerous plant communities, world-wide. Hydrological patterns can determine the vegetation in natural and man-made wetlands, since this is dependent on ecophysiological responses of species to flooding.

Causes of Waterlogging

- Over irrigation
- Canal irrigation in areas adjoining agricultural lands where subsoil water table steadily rises
- Inadequate drainage
- Surface flooding
- Presence of high water table
- During monsoon and soon after some areas remains totally submerged by the discharge of the rivers and accumulation of runoff from the surrounding catchment
- Waterlogging conditions are also caused in depressions along roads, canals and railway sides during rainy season
- Seawater comes to a particular area during high tidal surges.

Plant responses to flooding

<table>
<thead>
<tr>
<th>Waterlogging</th>
<th>Submergence</th>
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<tbody>
<tr>
<td>Only the root system is under anaerobic conditions</td>
<td>Partial submergence</td>
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<tr>
<td>All roots are immersed in water while just a portion of the shoot (which depends on the water depth) is covered by water</td>
<td>Complete submergence</td>
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<tr>
<td>All plant is under the water level. Water depth and turbidity are important factors defining this scenario</td>
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Fig. 1. Scheme of the different scenarios encountered by plants in front to increasing levels of water excess, ranging from waterlogging to complete submergence.

Most plant species cannot survive prolonged submergence or soil waterlogging. Crops are particularly intolerant to the lack of oxygen arising from submergence. A major constraint resulting from excess water, at least for poorly adapted species, is an inadequate supply of oxygen to submerged tissues; diffusion of oxygen through water is 10000-fold slower than in air. In addition to the threat of oxygen deficiency, excess water also leads to other changes in the soil that influence plants; levels of the plant hormone ethylene, and products of anaerobic metabolism (e.g. Mn²⁺, Fe²⁺, S²⁻, H₂S and carboxylic acids) can
accumulate. Moreover, when flooding results in complete submergence, and in normally submersed aquatic plants, availability to the shoots of carbon dioxide, light and oxygen typically diminish.

Impacts of flooding

- Hypoxia and anoxia of soils
- Loss of nitrogen fixing bacteria
- Toxic anaerobic substances
- Submerged plants have reduced availability of light and CO₂
- Decrease photosynthesis
- Decrease nutrient availability
- Altered metabolism

Physiological responses to soil waterlogging

One of the earliest plant physiological responses to soil flooding is a reduction in stomatal conductance (Fig. 2). Soil waterlogging may not only increase stomatal resistance but also limit water uptake, thus in term leading to internal water deficit. Low O₂ levels may also reduce hydraulic conductivity (Fig. 2) consequent to a decrease in root permeability. The reduced hydraulic conductivity throughout the plant under soil waterlogging conditions is most probably linked to inhibition of water transport. Other factors such as a decrease in leaf chlorophyll content, early leaf senescence and a reduction in leaf area may also contribute to inhibition of photosynthesis at a later stage. When the stress is prolonged it may lead to the inhibition of photosynthetic activity of the mesophyll, as well as reductions in the metabolic activity and the translocation of photoassimilates.

A common response to flooding is the reduction of plant carbon fixation (i.e. rate of photosynthesis). In the short term, photosynthesis can drop as a result of a restriction of CO₂ uptake due to stomata closing. 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. Both the content of Rubisco protein as well as its activation can be significantly reduced by flooding.

Fig. 2 Main physico-chemical events taking place in the rhizosphere during soil waterlogging and the resulting modifications in plant metabolism and physiology followed by the initiation of adaptive responses.
Morphological and anatomical adaptations to soil waterlogging

Plant has evolved various morphological and anatomical adaptation in response to flooding (Fig. 3)

A Root adaptations

1. Aerenchyma
   - Long interconnected gas-filled chambers.
   - Pathway for gas to diffuse from leaves to roots.
   - Allows aerobic respiration to continue in the roots.
   - Allows oxygenation of the soil surrounding roots.

2. Adventitious roots
   - Roots that grow above the soil.
   - Shallow roots
   - Help in gas transfer
   - Pneumatophores – root tips that stick up from the soil surface.

B. Shoot adaptations

1. Shoot elongation
   - Removes the shoots from complete submergence. It is happened by loosening of cell walls, intake of water, and synthesis of new polysaccharides

2. Submerged leaves
   - Thinner cuticles
   - Longer leaves
   - Physiological changes to cells

Fig. 3. Anatomical and morphological adaptations taking place during plant flooding.
C. Signaling and hormones

- Regulate the responses of plants to waterlogging and flooding
- Ethylene – most important
- Gibberellic acid
- Abscisic acid
- Auxins
- Hormones are interdependent, e.g., ethylene decreases abscisic acid concentrations which leads to an increase in gibberellic acid

D. Biochemical mechanism

Plants which can withstand waterlogging condition have mechanisms such as increased availability of soluble sugar, greater activity of glycolytic pathway and fermentation enzymes, and involvement of antioxidant defense mechanism to cope with the oxidative stress induced by waterlogging. Ethylene plays an important role in change of mechanisms of plants in deficiency of oxygen. It was also reported that ethylene induces the genes of enzymes associated with aerenchyma formation, glycolysis and fermentation pathway.

Main metabolic fermentative pathways in flooded plants

As \( O_2 \) levels decline, the fermentative pathway serves as a metabolic safe route. This is performed through two steps: carboxylation of pyruvate to acetaldehyde (catalysed by PDC) and the subsequent reduction of acetaldehyde to ethanol with concomitant oxidation of NADPH to NADP\(^+\), catalysed by alcohol dehydrogenase (ADH). In flooded plants, three main metabolic fermentative pathways are active: an ethanolic pathway, a lactic acid one and one involving alanine aminotransferase (Fig. 3). Glycolysis, linked principally to ethanol and to a lesser extent lactate fermentation is the principal means of recycling the NADH necessary to maintain glycolysis and ATP production. However, anaerobic fermentation is very inefficient, releasing a fraction of the ATP normally generated under aerobic conditions.

Anoxia tolerant species often share the following characteristics: i) a capacity to sustain ethanol fermentation, ii) release of ethanol and other by-products of anaerobic metabolism to the surrounding environment, iii) carbohydrate reserves allowing glycolysis to be maintained and iv) an ability to generate ATP through the adaptation of the TCA cycle. Although ethanolic and lactate fermentation do occur under limiting \( O_2 \) conditions, in most cases they are not sufficient for long term flooding tolerance.

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**Fig. 3** Schematic diagram of the three main metabolic fermentative pathways in flooded plants
Advances in rice research for flood tolerance

The identification of SUB1A as the determinant for submergence tolerance in rice allowed the breeding of flood-tolerant rice varieties, often called ‘scuba rice’. These varieties showed the same yield and quality traits as their non-Sub1 counterparts when grown under non-flooded conditions, but displayed yield advantages of 1 to more than 3 t ha⁻¹ after complete submergence for various durations. This is a great example of rapid translation of a scientific discovery into agricultural improvements in less than ten years since the discovery of SUB1A in 2006. Experimental evidence showing that SUB1A also contributes to drought tolerance in rice suggests that this trait will contribute to the development of rice varieties better adapted to climate changes. Incorporating flooding tolerance into crops other than rice will be very challenging, given the lack of accessions with flooding tolerance traits.