Mechanisms of waterlogging tolerance in wheat: Morphological and metabolic adaptations under hypoxia or anoxia

Md. Alamgir Hossain[1] and Sarder Nasir Uddin[2]*

[1]Department of Crop Botany, Bangladesh Agricultural University, Mymensingh-2202, Bangladesh
[2]Biotechnology and Genetic Engineering Discipline, Khulna University, Khulna-9208, Bangladesh

*Corresponding author: opunasir@gmail.com

Abstract

Waterlogging is a widespread limiting factor for wheat production throughout the world specially irrigated and high rainfall environments. The important biological consequence of waterlogging is the deficiency (hypoxia) or complete absence (anoxia) of oxygen in soil environment which restricts the growth, development and finally yield in wheat. The tolerant genotypes of wheat can adapt to transient waterlogging by developing mechanisms related to morphology and metabolism to cope with the stress. The morphological mechanisms include the development of adventurous roots with well formed aerenchyma and sometimes with a barrier for ROL. Aerenchyma is a continuous gas filled channel, which provides a low resistance internal pathway for the movement of O_2 from the aerobic shoots to anaerobic roots to respire aerobically under hypoxia or anoxia. However, lack of oxygen induces the anaerobic roots to shift the energy metabolism from aerobic to anaerobic mode. Greater activities of glycolytic and fermentative enzymes, increased availability of soluble sugars, and involvement of antioxidant defense mechanism against post-stress oxidative damages are the main metabolic mechanisms for waterlogging tolerance in wheat.

Keywords: aerenchyma, anoxia, carbohydrate reserves, hypoxia, oxidative stress, waterlogging tolerance, wheat.
Abbreviations: ASA, ascorbate; ACC, 1-aminocyclopropane-1-carboxylic acid; ADH, alcohol dehydrogenase; GSH, glutathione; HPT, hypoxic pre-treatment; LDH, lactate dehydrogenase; NADPH, nicotinamide adenine dinucleotide phosphate-reduced; PDC, pyruvate decarboxylase; ROL, radial oxygen loss; ROS, reactive oxygen species; SS, sucrose synthase; TCA, tri carboxylic acid.

Introduction

Waterlogging occurs over a vast regions throughout the world (Kozlowski, 1984) adversely affecting approximately 10% of the global land area (FAO, 2002). It usually occurs when rainfall or irrigation water deposits on the soil surface or subsoil for prolonged period of time. It can also occur when the amount of water added through rainfall or irrigation is more than what can percolate into the soil within one or two days. Waterlogging occurs in many wheat growing regions throughout the world, especially irrigated and high rainfall environments. About 10-15 million ha of the world's wheat growing areas are affected by waterlogging each year (Sayer et al., 1994) representing 15-20% of the 70 million ha annually cultivated for wheat production (Settler et al., 2003). The effects of waterlogging are most widespread in rice-wheat rotation commonly followed in south and south-east Asia including Bangladesh, Pakistan, India, Nepal and China (Samad et al., 2001). Soils are generally puddled to restrict water percolation for rice cultivation which leads to develop a soil pan. The soil pan is often left undisturbed at cultivation for wheat that follows rice and may create a barrier for water movement causing waterlogging in case of excessive irrigation or rainfall. Waterlogged plants are affected by various stresses, such as limitations to gas, and mineral nutrient deficiencies and microelement toxicities (Setter and Waters, 2003; Setter et al., 2009). The wheat plant responds to waterlogging by restricting root growth, reducing the dry matter accumulation, prematurely senescing leaves, reducing tillering, wilting, producing sterile florets, and lowering kernel weights and finally grain yield (Cannell et al., 1980; van Ginkel et al., 1992; Sayre et al., 1994;

Zhang et al., 2006; Jiang et al., 2008 Hossain et al., 2011)). These responses in wheat grown under natural conditions can be reproduced in a hypoxic or anoxic nutrient solution produced by continuous flushing with nitrogen gas (Trought & Drew, 1980a, b). Root hypoxia or anoxia is the major cause of reduced plant growth under waterlogging stress (Trought & Drew, 1980a, b; Drew, 1991; Huang et al., 1994a, b). Although wheat is one of the most intolerant crops to soil waterlogging (Thomson et al., 1992; Musgrave 1994) there is a wider genetic diversity in tolerance to soil waterlogging among cultivars of wheat (Thomson et al., 1992; Sayre et al., 1994; Settler and Waters, 2003). The tolerance of wheat to waterlogging depends on the ability to change its morphological and metabolic traits in response to the stress for its survival and growth. The intolerance of wheat to waterlogging presumably results from its lacking, or having only a low expression of traits associated with tolerance to waterlogging (Thomson et al., 1992; Huang et al., 1997). Here we attempted to review the mechanisms of tolerance of wheat to waterlogging emphasizing the morphological and metabolic adaptive mechanisms under oxygen deficit environment, hypoxia and anoxia.

Hypoxia and anoxia

Hypoxia or oxygen depletion is a phenomenon that occurs in soil environments as oxygen in soil air becomes reduced to a point below optimum level. In plant physiological studies, the term "hypoxia" is reserved for situations in which the oxygen

concentration is a limiting factor (Morard and Silvestre, 1996). It is the most common form of stress in wet soils and occurs during short-term flooding when the roots are submerged under water but the shoot remains in the atmosphere. It may also occur in roots near the surface of long-term flood water (Sairam et al., 2008). Anoxia, the extreme form of hypoxia, is used to qualify the complete lack of oxygen in physiological experiments (Morard and Silvestre, 1996). It is usual form of stress in soil that experiences long-term flooding or waterlogging. It occurs in plants completely submerged by water, and in deep roots below flood waters (Sairam et al., 2008).

How does waterlogging induce hypoxia and anoxia?

One of the most important properties of soil is soil aeration which relates to the ability of soils to exchange gases with the atmosphere. This exchange is usually achieved primarily through diffusion of gasses from and to the soil via pore spaces in the soil. In most well drained soils, the air-filled pore spaces make up 10 to 40% of total soil volume. Waterlogging eliminates these gas-filled pore spaces and cuts the supply of oxygen to the roots to a large extent (Ponnamperuma, 1972). In the waterlogged soil, micro channels for gas diffusion among soil particles or aggregations become sealed with water, which results the gas diffusivity in soil 10^4 times lower than in well-drained soil (Armstrong, 1979; Ponnamperuma, 1984). The lower gas diffusivity between ambient air and waterlogged soil results in low O_2 concentration (hypoxia) and high toxic gas concentration, such as CO_2 and reduced gases (Ponnamperuma, 1972, 1984). Moreover, gases formed by soil metabolism, including carbon dioxide, start to accumulate near root surfaces (Setter and Belford, 1990). The gas exchange between soil and atmosphere almost stops as soon as the waterlogging sets in. The soil microbes and plant roots use up the oxygen trapped in the soil and therefore, the roots may become exposed to complete lack of oxygen (anoxia) (Jackson and Drew, 1984). However, under natural conditions, oxygen concentration decreases gradually, and hence, anoxia is always preceded by hypoxia (Setter and Waters, 2003) in waterlogged environment.

Mechanisms of tolerance of wheat to waterlogging

Waterlogging tolerance is defined as the survival or the maintenance of plant growth at high rates under waterlogged conditions relative to well drained conditions. It may be defined as the maintenance of relatively high grain yields under waterlogged conditions relative to non- or less-waterlogged conditions (Setter and Waters, 2003). The plant species tolerant to waterlogging can develop some morphological traits or can alter the metabolism in response to oxygen shortage to survive or to maintain their growth. The mechanisms of waterlogging or hypoxia tolerance includes: i) the maintenance of high internal aeration through constitutive aerenchyma and creation of an oxidized zone around root tips through radial O_2 loss (Armstrong et al., 1994), ii) metabolic adaptation that maintain energy production under hypoxia (Brandle and Crawford, 1987) with the substantial storage of carbohydrates for fermentation under hypoxia (Brandle, 1991). Mechanisms of tolerance to waterlogging in wheat are discussed here in main two heads: (A) morphological adaptation, and (B) metabolic adaptation.

A. Morphological adaptation

i) Root growth

A common adaptation of plants to waterlogging is the survival and growth of seminal roots and production of numerous adventitious roots with aerenchyma (Belford, 1981; Trought and Drew, 1982; Drew, 1983; Smirnoff and Crawford, 1983; Justin and Armstrong, 1987; Barrett-Lennard et al., 1988; Thomson et al., 1992; Huang et al., 1994a). The root growth in waterlogging intolerant genotypes is drastically suppressed by waterlogging stress. However, the tolerant genotypes have the ability to continue their root growth under the stress in some extent. Huang et al. (1994a) reported a drastic decrease (42-50%) in length of the longest seminal root and also in total length of seminal roots by 14 d hypoxia for waterlogging intolerant genotypes (Bayles, BR34, Coker-9766 and FL302). The above hypoxic stress had no significant effect on the growth of seminal roots for tolerant genotypes (Gore and Savannah). Total root dry mass was reduced for all genotypes except for Savannah (Huang et al., 1994a). However, the waterlogging tolerance of a plant is determined not only by its capability to undergo morphological adaptations, but also by the ability to recover from transient waterlogging or hypoxia of the root system (Krizek, 1982; Huang et al., 1994a, 1997). The growth of many species that are tolerant to hypoxic conditions can also be reduced when the roots are waterlogged, but unlike sensitive ones, tolerant species rapidly resume their growth a short period after the resumption of aeration in roots (Crawford, 1982). In a hypoxic experiment with two Japanese cultivars, Daichinominori (adapted to wet areas in Japan and supposed to be a less waterlogging sensitive cultivar) and Haruyutaka (adapted to dry areas in Japan and supposed to be a more waterlogging sensitive cultivar), similar suppressive root growth was observed during 20d hypoxic stress for both cultivars. However, the difference in recovery between the cultivars was observed. The less sensitive cultivar, Daichinominori showed complete recovery in root growth while the more sensitive cultivar, Haruyutaka showed partial recovery by 10d after the resumption of aeration (recovery) (Hossain et al., unpublished data).

ii) Aerenchyma formation and increased root porosity

Aerenchyma is a special tissue which consists of continuous gas filled channels or much enlarged gas spaces, and root porosity is volume of gas-filled spaces in relation to the total tissue volume. Aerenchyma provides a low resistance internal pathway for the movement of O_2 from the shoots to the roots (Armstrong, 1979; Armstrong and Webb, 1985; Drew et al., 1985). Aerenchyma tissue in roots allows the roots to respire aerobically and to maintain growth under hypoxic conditions. Moreover, a part of oxygen transported to plant root tips through the aerenchyma leaks out into the surrounding soil and results in a small zone of oxygenated soil around the roots providing an aerobic environment for microorganisms that can prevent the influx of potentially toxic soil components (Visser et al., 1997; Armstrong and Armstrong 1988; Colmer, 2003) such as nitrites and sulphides of Fe, Cu and Mn. Therefore, aerenchyma formation is thought to be one of the most important morphological adaptations for the tolerance to hypoxic or anoxic stress. The aerenchyma in stems and roots can be distinguished into lysigenous and schizogenous aerenchyma on the basis of the process of formation (Jackson and Armstrong, 1999; Evans, 2003; Visser and Voesenek, 2004).

Lysigenous aerenchyma is created through cell disintegration (death) in the primary cortex of adventitious roots (Drew et al., 1979, 1981; Justin and Armstrong, 1991; Huang et al., 1997; Haque et al., 2010), whereas the schizogenous aerenchyma is formed by the separation of cells from each other, often accompanied by cell divisions and normal expansion (Jackson and Armstrong, 1999; Colmer et al., 2004). Under oxygen deficient condition, ethylene production is accelerated which in turn stimulates aerenchyma formation in adventitious roots and induces the growth of the roots (Drew et al., 1979; Jackson, 1989). The immediate precursor of ethylene is 1-amino cyclopropane 1-carboxylic acid (ACC), which is synthesized to a large extent in roots (Bradford and Yang, 1980). The activity of ACC synthase is stimulated in roots under flooding conditions (Cohen and Kende, 1987). However, the conversion of ACC to ethylene requires oxygen and the conversion reaction is blocked in an anaerobic root cell. The ACC is therefore, translocated from the anaerobic root cells towards the more aerobic portions of the root or to the shoot. The lower portions of the stems are usually the site of highest ACC accumulation and in the presence of oxygen ethylene is released (Sairam et al., 2008). Formation of aerenchyma has been observed in the roots of wheat when grown under low O_2 concentrations (Benjamin and Greenway, 1979; Trought & Drew, 1980b, c; Belford, 1981; Erdmann & Wiedenorth, 1986; Barrett-Lennard et al., 1988; Thomson et al., 1990, 1992; Drew, 1991; Huang et al., 1994a, b; Watkin et al., 1998; McDonald et al., 2001a, b; Haque et al., 2010). Aerenchyma formation increases the porosity of roots above the usual levels contributed by intercellular spaces (Colmer, 2003). The aerenchyma is usually formed within five to seven days of the onset of hypoxia in wheat (Thomson et al., 1990). Increased root porosity or anatomical investigation may be the evidence of aerenchyma formation. The increase in root porosity of tolerant genotypes in response to waterlogging stress could represent adaptation to anaerobic or hypoxic conditions. High porosity in root tissue increases the possibility of O_2 diffusion from shoots to roots (Haldemann & Brändle, 1983). Wheat genotypes with well-formed aerenchyma are more tolerant to waterlogging stress than genotypes with smaller aerenchyma (Huang et al., 1994a, b). The poorly developed adventitious root system and relatively low root porosity of hexaploid wheat are thought to contribute to its sensitivity to waterlogging (Thomson et al., 1992). Boru et al. (2003) reported 12 to 20% (v/v) root porosity for tolerant wheat genotypes (Ducula, Prl/Sara, and Vee/ Myna) and 6 to 8% for sensitive genotypes (Seri-82 and Kite/Glen) under hypoxia. They also reported that the root porosities of Ducula and Prl/Sara increased 425% and 493%, respectively under hypoxia. Under similar conditions, Huang and Johnson (1995) observed the increase in root porosity of waterlogging tolerant wheat genotype 'Jackson' and waterlogging sensitive genotype 'Coker 9835' by 185% and 53%, respectively. Barrett-Lennard et al. (1988) reported a two- to three-fold increase in root porosity of the cultivar Gamenya when grown hypoxically. Thomson et al. (1990) also observed similar increase in porosity in Gamenya. In cross sections of adventitious roots, aerenchyma occupies 19% and 30% of the cross sectional area in more waterlogging sensitive genotype 'Bayles' and less sensitive genotype 'Savannah', respectively under waterlogged sand culture (Huang et al., 1994).

iii) Barriers to radial oxygen loss

Oxygen in aerenchymatous roots may be consumed by respiration or be lost to the rhizosphere via radial diffusion from the root. The flux of oxygen from roots to rhizosphere is termed as radial oxygen loss (ROL) which usually oxygenates the rhizosphere of the plants growing in waterlogged soils (Armstrong, 1979). However, ROL decreases the amount of O_2 supply to the apex of roots that solely depends on aerenchymatous O_2 and, therefore, would decrease the root growth in hypoxic or anoxic environment (Armstrong, 1979; Jackson and Drew, 1984). The roots of many wetland plants contain a complete or partial barrier to ROL in their epidermis, exodermis or sub epidermal layers (Armstrong, 1971; Jackson and Drew, 1984; Jackson and Armstrong, 1999), whereas in non-wetland plants usually are lacking or having a partial barriers resulting considerable loss in aerenchymatous O_2 in root through ROL. Wheat plants can form aerenchymatous adventitious root, in response to waterlogging, which contains a partial barrier to ROL and can consume only 20% of the total O_2 entering a root through aerenchyma (Thomson et al., 1992). It is suggested that the loss in internal O_2 contributes the poor growth of adventitious roots and intolerance of wheat to waterlogged soil (Thomson et al., 1992). In contrary, waterlogging tolerant rice not only has a larger volume of aerenchyma, but it also has a strong barrier to ROL in basal regions of its adventitious roots and therefore deeper root penetration into waterlogged soil (Armstrong, 1971; Thomson et al., 1992; Colmer et al., 1998). However, some wheat genotypes can increase suberin or lignin on epidermis or exodermis of root which may acts as barriers to ROL and results in increased tolerance to waterlogging (Arikado, 1959; Jackson and Drew, 1984; Watkin et al., 1998; McDonald et al., 2001b).

B. Metabolic adaptation

The plant tissue under hypoxia or anoxia suffers from energy crisis (Gibbs and Greenway, 2003) due to reduced root respiration in both waterlogging-tolerant and intolerant plants (Marshall et al., 1973; Lambers, 1976; Drew 1983, 1990). The tolerant plant species cope with the energy crisis through metabolic adaptation to oxygen deficiency. The metabolic adaptations to oxygen deficiency includes: anaerobic respiration, maintenance of carbohydrate supply for anaerobic respiration, avoidance of cytoplasmic acidification and development of anti-oxidative defense system (Davies, 1980; Armstrong et al., 1994; Drew, 1997; Setter et al., 1997).

i) Anaerobic respiration

Plant cells produce energy in presence of oxygen through aerobic respiration which includes glycolysis, TCA or Krebs cycle and oxidative phosphorylation (Fig. 1). In absence of oxygen (under anoxic condition), Krebs cycle and oxidative phosphorylation are blocked, and cells inevitably undergo anaerobic respiration to fulfill the demand for energy (Davies, 1980). Anaerobic respiration includes glycolysis and fermentation (Fig 1). Generation of energy under anaerobic condition is largely achieved through glycolysis. For the continued operation of glycolytic pathway, the regeneration of NAD^+, a cofactor from NADH is essential (Drew, 1997). Large quantities of pyruvate generated in glycolysis as an end-product must be converted to alternative products to recycle NADH to NAD^+. Ethanolic Fermentation or lactate fermentation is the most important process by which NADH can be recycled to NAD^+ during oxygen deficiency (Kennedy et al., 1992; Perata and Alpi, 1993; Ricard et al., 1994). In ethanolic fermentation, pyruvate is the substrate of pyruvate decarboxylase (PDC) yielding CO_2 and acetaldehyde, which reduced to ethanol with the oxidation of NADH to NAD^+ by alcohol dehydrogenase (ADH). In lactic fermentation, pyruvate is the substrate of lactate dehydrogenase (LDH) yielding lactate with the oxidation of NADH to NAD^+. The efficacy of energy production by glycolysis and fermentation is much lower than
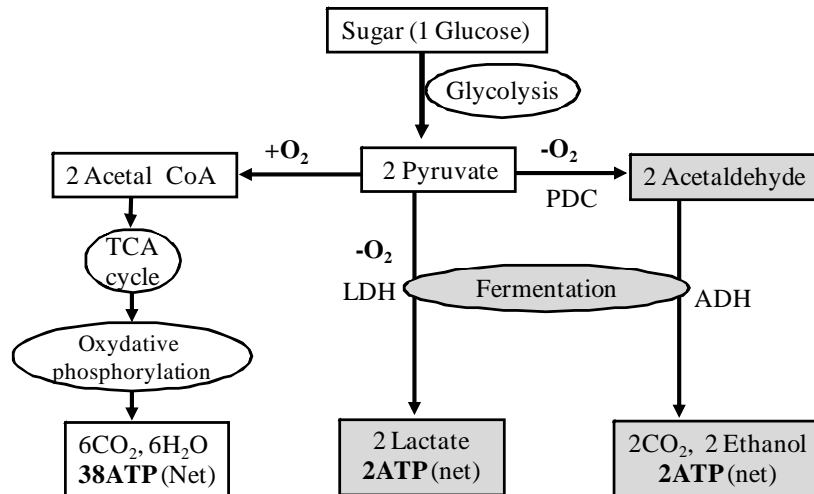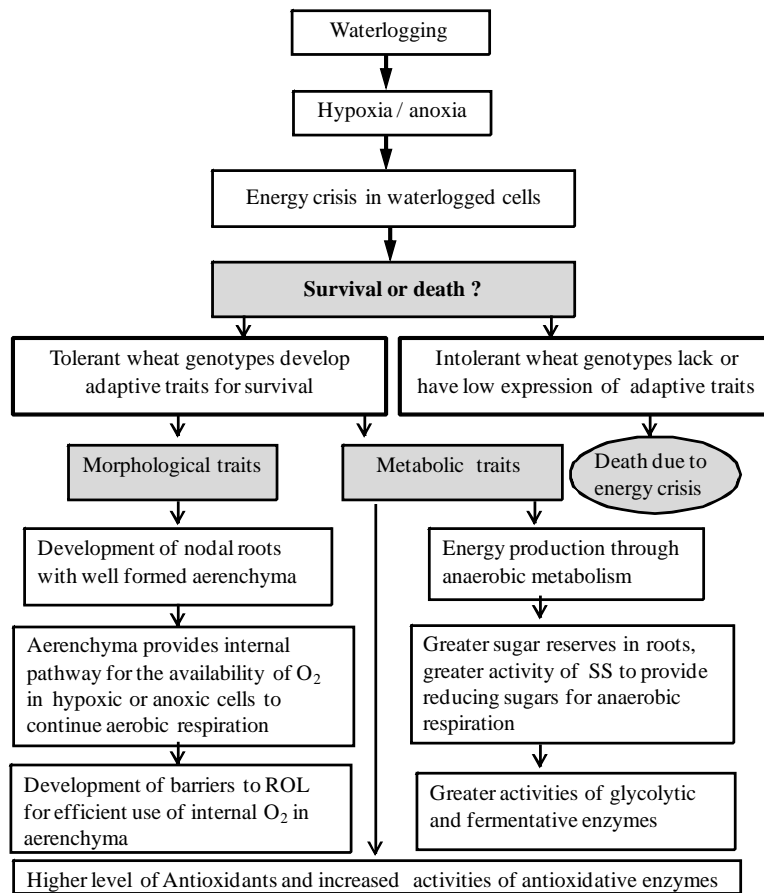
Fig 1. Shift of aerobic respiration to anaerobic respiration

that of aerobic respiration (Fig. 1). Moreover, the end-products of glycolytic and fermentative pathway, such as ethanol, lactic acid and carbon dioxide pose an additional hazard to the cell. It is well reported that the maintenance of an active glycolysis and an induction of fermentative metabolism are adaptive mechanisms for plant tolerance to anoxia (Kennedy et al., 1992; Ricard et al., 1994; Drew, 1997; Sairam et al., 2008). In waterlogged environment, anoxia is always preceded by hypoxia (Setter and Waters, 2003) and hypoxia is considered as hypoxic pre-treatment (HPT) before exposing the plants to anoxia (Waters et al., 1991). Hypoxia accelerates the induction of glycolytic and fermentative enzymes, for example aldolase and enolase (Bouny and Saglio, 1996; Germain et al., 1997), ADH and PDC (Johnson et al., 1989; Albrecht et al., 2004). This induction can improve or at least sustain the glycolytic rate in anoxic plants contributing higher tolerance to anoxia. In wheat, increased activities of ADH and PDC have been found in response to hypoxia resulting higher ethanol production contributing greater tolerance to anoxia (Waters et al., 1991). Anoxic cells may undergo lactic fermentation rather ethanolic fermentation onset of anoxia, though ethanol rather than lactate is the less deteriorating end product of fermentation (Davies, 1980). An accumulation of lactate promotes acidification of the cytoplasm (Roberts et al., 1984) of anoxia sensitive plants, such as maize, wheat and barley (Menegus et al., 1989, 1991). However, the enhanced lactate transport out of the roots into the surrounding medium may help to avoid cytoplasmic acidification (Xia and Saglio, 1992). Moreover, lowered cytoplasmic pH leads to the activation of PDC and inhibition of LDH (Davis, 1980) resulting a shift from lactate fermentation to ethnolic fermentation.

ii) Increased availability of soluble sugars

Due to shifting of energy metabolism from aerobic to anaerobic mode under hypoxia or anoxia the energy requirements of the tissue is greatly restricted as very few ATPs are generated per molecule of glucose. A high level of anaerobic metabolism in hypoxic or anoxic roots is therefore very important to supply the energy charge high enough which can sustain metabolism in roots for the survival of plants (Jackson and Drew, 1984). Thus, maintaining adequate levels of readily metabolizable (fermentable) sugars in hypoxic or anoxic roots is one of the adaptive mechanisms to waterlogging or oxygen deficient environment (Setter et al., 1987; Xia and Saglio, 1992; Sairam et al., 2009). The amount of root sugar reserve and activity of sucrose hydrolyzing enzymes are important determinants for waterlogging tolerance of crop plants (Sairam et al., 2009). Zeng et al. (1999) reported that of the two enzymes involved in sucrose hydrolysis, the activity of invertase is down-regulated, while that of sucrose synthase (SS) is up-regulated in hypoxic maize seedlings. The roots of comparatively tolerant genotypes contain greater sugar content (total, reducing and non-reducing sugar) than in susceptible genotypes of pigeon pea. Moreover, waterlogging induces to increase the content of reducing sugar through increased activity of SS in tolerant genotypes. The tolerant genotypes show increased expression of mRNA for SS while susceptible genotypes show very little expression under waterlogged condition (Sairam et al., 2009). Therefore, the availability of sufficient sugar reserves in the roots with the increased activity of SS to provide reducing sugars for anaerobic respiration is one of the important mechanisms of waterlogging tolerance. The concentration of soluble carbohydrate in roots and shoots of wheat is increased when the crop is subjected to long-term oxygen deficit (Barret-Lennard et al., 1988; Albrecht et al., 1993). In anoxic wheat roots, carbohydrates accumulate during HPT (Waters et al., 1991; Albrecht et al., 1993, 2004; Mustroph and Albrecht, 2003). The accumulation of sugars has been attributed to the fact that growth is inhibited in hypoxically treated roots, while photosynthetic reactions are still active in the less challenged leaves (Mustroph and Albrecht, 2003). Wheat genotypes tolerant to waterlogging accumulate more sugar in their roots in response to hypoxia compared to sensitive genotypes (Huang and Johson, 1995). This carbohydrate accumulation might support fermentation of HPT roots over a long period of anoxic stress, and could enhance tolerance against oxygen deficiency leading to a higher tolerance to anoxia. Moreover, exogenous supply of glucose prolongs the retention of root elongation potential under anoxic condition (Waters et al., 1991). The ratio of the root to shoot sugar increases for waterlogging tolerant wheat genotypes under hypoxia (Huang and Jonhson, 1995). The relatively large amount of sugars transported to root facilitates the energy supply for root respiration and ion uptake (Huang, 1997).

Waterlogging

↓

Hypoxia / anoxia

↓

Energy crisis in waterlogged cells

↓

Survival or death ?

↓ ↓

Tolerant wheat genotypes develop adaptive traits for survival | Intolerant wheat genotypes lack or have low expression of adaptive traits

↓ ↓

Morphological traits | Metabolic traits | Death due to energy crisis

↓ ↓

Development of nodal roots with well formed aerenchyma | Energy production through anaerobic metabolism

↓ ↓

Aerenchyma provides internal pathway for the availability of O_2 in hypoxic or anoxic cells to continue aerobic respiration | Greater sugar reserves in roots, greater activity of SS to provide reducing sugars for anaerobic respiration

↓ ↓

Development of barriers to ROL for efficient use of internal O_2 in aerenchyma | Greater activities of glycolytic and fermentative enzymes

Higher level of Antioxidants and increased activities of antioxidative enzymes

Fig 2. Schematic diagram showing morphological and metabolic adaptive traits for waterlogging tolerance in wheat

iii) Antioxidant activities

Exposure of plants to most adverse conditions like hypoxia or anoxia causes oxidative stress, which affects plant growth due to the production of reactive oxygen species (ROS) such as superoxide radicals, hydroxyl radicals and hydrogen peroxide (Mittler et al., 2004). These ROS are very reactive and cause severe damage to membranes, DNA and proteins (Bowler et al., 1992; Foyer et al., 1997). Hypoxia stress triggers the formation of ROS and induces oxidative stress in plants (Yan et al., 1996; Geigenberger, 2003; Narayanan et al., 2005). Moreover, re-exposure to air after a period of oxygen deprivation can induce such stress causing serious injury (Monk et al., 1987; Crawford, 1992). To counter the hazardous effects of oxygen radicals, all aerobic organisms evolve a complex antioxidative defense system consisting of both antioxidants like ascorbate (AsA), glutathione (GSH), phenolic compounds, etc., and antioxidative enzymes such as superoxide dismutase, catalase, peroxidases, gluthatione reductase and ascorbate peroxidase (Zhang and Kirkham, 1994; Foyer et al., 1997; Garnczarska, 2005). A higher level of antioxidants and an increase in the activity of antioxidative enzymes are assumed to be adaptive mechanisms in overcoming certain stress situations (Foyer et al., 1995; Mishra et al., 1995). The tolerance to the stress may be improved by increased antioxidant capacity. Many recent attempts to improve stress tolerance in plants have been made by introducing and expressing genes encoding enzymes involved in the antioxidative defense system (Gupta et al.,

1993 ; Foyer et al., 1995). The roots of young wheat plants are able to cope with the deleterious effects of oxygen radical generation induced by re-aeration after anoxia by means of their antioxidative defense system including increased capacity to scavenge radicals and elevated activities of enzymes of the AsA-GSH cycle to enable the restoration of the essential, highly reduced state of the antioxidants, AsA and GSH (Albrecht and Wiedenroth, 1994; Biemelt et al., 1998).

Conclusion and future perspectives

Hypoxia or anoxia, consequences of waterlogging, results energy crisis in waterlogged cells which triggers the tolerant genotypes to develop different traits associated with waterlogging tolerance at least to survive under the stress as summarized in Fig. 2. The study of regulatory mechanisms and signaling events responsible for triggering responses to hypoxia or anoxia in wheat plants is a prospective area of research. Many questions remain to be answered about the response of individual cells. What might be the basis for the differential response between waterlogging-tolerant and intolerant wheat genotypes? Do these responses differ in cellular signaling and response mechanisms? It needs to be understood what signaling transduction pathways are involved to control adaptive responses? How do cells in roots and shoot communicate over a long distance when there is an energy crisis in the root cells? Understanding the cell to cell and

long-distance signaling mechanisms which determine the organ and whole plant response to hypoxia or anoxia, *viz.*, aerenchyma formation and adventitious root growth is another interesting area for research. So far we only know a little part of the unfolded story, with many more phenomena still unknown. Exploring these phenomena will be of relevance to waterlogging tolerance of wheat and will provide knowledge of the fundamental nature of the crops under anaerobiosis.

References

Albrecht G, Kammerer S, Praanik W, Wiedenroth EM (1993) Fructan content of wheat seedling (*Triticum aestivum* L.) under hypoxia and following re-aeration. New Phytol 123: 471- 476

Albrecht G, Mustroph A, Fox TC (2004) Sugar and fructan accumulation during metabolic adjustment between respiration and fermentation under low oxygen conditions in wheat roots. Plant Physiol 120: 93-105

Arikado H (1959) Supplementary studies on the development of the ventilating systems in various plants growing on low land and on upland. Bull Fac Agric Mie Univ 20: 1- 24

Armstrong W, Brändle R, Jackson MB (1994) Mechanisms of flood tolerance in plants. Acta Bot Neerl 43: 307-358

Armstrong W (1971) Radial oxygen losses from intact rice roots as affected by distance from the apex, respiration and waterlogging. Physiol Plant 25: 192- 197

Armstrong W (1979) Aeration in higher plants. Adv Bot Res 7: 225 - 332

Armstrong W, Webb T (1985) A critical oxygen pressure for root extension in rice. J Exp Bot 36: 1573-1582

Barrett-Lennard EG, Leighton P, Buwalda F, Gibbs J, Armstrong W, Thomson CJ, Greenway H (1988) Effects of growing wheat in hypoxic nutrient solutions and of subsequent transfer to aerated solutions I. Growth and carbohydrate status of shoots and roots. Aust J Plant Physiol 15: 585- 598

Belford RK (1981) Response of winter wheat to prolonged waterlogging under outdoor conditions. J Agric Sci Camb 97: 557- 568

Biemelt S, Keetman U, Albrecht G (1998) Re-aeration following hypoxia or anoxia leads to activation of the antioxidative defense system in roots of wheat seedlings. Plant Physiol 116: 651-658

Boru G, van Ginkel M, Trethowan RM, Boersma L, Kronstad WE (2003) Oxygen use from solution by wheat genotypes differing in tolerance to waterlogging. Euphytica 132: 151-158

Bouny JM, Saglio PH. Bowler C, Montagu MV, Inze D (1992) Glycolytic flux and hexokinase activities in anoxic maize root tips acclimated by Superoxide dismutase and stress tolerance. Annu Rev Plant Physiol Plant Mol Biol 43: 83- 116

Bowler C, Montagu MV, Inze D (1992) Superoxide dismutase and stress tolerance. Annu Rev Plant Physiol Plant Mol Biol 43: 83-116

Bradford KJND, Yang SF (1980) Xylem transport of 1-aminocyclopropane-1-carboxylic acid, an ethylene precursor, in waterlogged tomato plants. Plant Physiol 65: 322- 326

Brandle RA (1991) Flooding resistance of rhizomatous amphibious plants. In: Jackson MD, Davies DD, Lambers H (eds) Plant life under oxygen deprivation. Academic Publisher, The Hague. pp 35-46

Brandle R, Crawford RMM (1987) Rhizome anoxia tolerance and habitat specialisation in wetland plants. In: Crawford RMM (ed) Plant life in aquatic and amphibious habitats. Blackwell, Oxford pp 397- 410

Cannell RQ, Belford RK, Gales K, Dennis CW, Prew RD (1980) Effects of waterlogging at different stages of development on the growth and yield of winter wheat. J Sci Food Agric 31: 117–132

Cohen E, Kende H (1987) *In vivo* 1-aminocy- clopropane- 1-carboxylate synthase activity in internodes of deep water rice: Enhancement by submergence and low oxygen levels. Plant Physiol 84: 282- 286

Colmer TD (2003) Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. Plant Cell Environ 26: 17- 36

Colmer TD, Gibberd MR, Wiengweera A, Tinh TK (1998) The barrier to radial oxygen loss from roots of rice (*Oryza sativa* L.) is induced by growth in stagnant solution. J Exp Bot 49: 1431-1436

Colmer TD, Peeters AJM, Wagemaker CAM, Vriezen WH, Ammerlaan A, Voesenek LACJ (2004) Expression of -expansin genes during root acclimations to O_2 deficiency in *Rumex palustris*. Plant Mol Biol 56: 423- 437

Crawford, RMM (1982) Physiological responses to flooding. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Encyclopedia of plant physiology, new series, vol. 12B, Physiological plant ecology II. Springer, Berlin, Germany. pp 453- 477

Davies DD (1980) Anaerobic metabolism and the production of organic acids. In: Davies DD (ed) The biochemistry of plants, Vol. 2. Academic Press, NY, USA. pp 581- 611

Drew MC (1983) Plant injury and adaptation to oxygen deficiency in the root environment: a review. Plant Soil 75: 179- 199

Drew M C (1991) Oxygen deficiency in the root environment and plant mineral nutrition. In: Jackson MB, Davies DD, Lambers H (eds) Plant life under oxygen deprivation. Academic Publisher, The Hague, The Netherlands. pp 303-316

Drew MC (1990) Sensing soil oxygen. Plant Cell Environ 13: 681- 693

Drew MC, Jackson MB, Giffard S (1979) Ethylene- promoted adventitious rooting and development of cortical air spaces (aerenchyma) in roots may be adaptive responses to flooding in *Zea mays* L. Planta 147: 83- 88

Drew MC, Jackson MB, Giffard SC, Campbell R (1981) Inhibition by silver ions of gas space (aerenchyma) formation in adventitious roots of *Zea mays* L. subjected to exogenous ethylene or to oxygen deficiency. Planta 153: 217- 224

Drew MC (1997) Oxygen deficiency and root metabolism: injury and acclimation under hypoxia and anoxia. Annu Rev Plant Physiol Plant Mol Bio 48: 223- 250

Drew MC, Saglio PH, Pradet A (1985) Larger adenylate energy charge and ATP/ADP ratios in aerenchymatous roots of *Zea mays* in anaerobic media as a consequence of improved internal oxygen transport. Planta 165: 51- 58

Erdmann B, Wiedenroth EM (1986) Changes in the root system of wheat seedlings following root anaerobiosis. II. Morphology and anatomy of evolution forms. Ann Bot 58: 607- 616

Evans DE (2003) Aerenchyma formation. New Phytol 161: 35- 49

FAO (2002) Agriculture. Available online at: http://www.fao.org/waicent/FAOINFO/AGRICULT/ag1/ag11/gaez//nav.html (Accessed March 18, 2009)

Foyer CH, Looez-Delgado H, Dat JF, Scott IM (1997) Hydrogen peroxide and glutathione-associated mechanisms of acclamatory stress tolerance and signaling. Physiol Plant 100: 241- 254

Foyer CH, Souriau N, Perret S, Lelandais M, Kunert KJ, Pruvost C, Jounanin L (1995) Overexpression of glutathione reductase but not glutathione synthetase leads to increases in antioxidant capacity and resistance to photoinhibition in poplar trees. Plant Physiol 109: 1047- 1057

Garnczarska M (2005) Response of the ascorbate–glutathione cycle to re-aeration following hypoxia in lupine roots. Plant Physiol Biochem 43: 583- 590

Geigenberger P (2003) Response of plant metabolism to too little oxygen. Curr Opin Plant Biol 6: 247- 256

Germain V, Ricard B, Raymond P, Saglio PH (1997) The role of sugars, hexokinase and sucrose synthase in the determination of hypoxically induced tolerance to anoxia in tomato roots. Plant Physiol 114: 167- 75

Gibbs J, Greenway H (2003) Mechanisms of anoxia tolerance in plants. I. Growth, survival and anaerobic catabolism. Funct Plant Biol 30: 1- 47

Gupta A, Webb RP, Holaday AS, Allen RD (1993) Overexpression of superoxide dismutase protects plants from oxidative stress: Induction of ascorbate peroxidase in superoxide dismutase overexpressing plants. Plant Physiol 103: 1067 - 1073

Haldeman C, Brandle R (1983) Avoidance of oxygen deficit stress and release of oxygen by stalked rhizomes of *Schoenoplectus lacustris*. Physiol Veg 21: 109- 113

Haque ME, Abe F, Kawaguchi K (2010) Formation and extension of lysigenous aerenchyma in seminal root cortex of spring wheat (*Triticum aestivum* cv. Bobwhite line SH 98 26) seedlings under different strength of waterlogging. Plant Root 4: 31- 39

Hossain MA, Araki H, Takahashi T (2011) Poor grain filling induced by waterlogging is similar to that in abnormal early ripening in wheat in Western Japan. Field Crops Res 123: 100–108

Huang B, Johnson JW, Nesmith DS, Bridges DC (1994a) Root and shoot growth of wheat genotypes in response to hypoxia and subsequent resumption of aeration. Crop Sci 34: 1538- 1544

Huang B, Johnson JW (1995) Root respiration and carbohydrate status of two wheat genotypes in response to hypoxia. Ann Bot 75: 427- 432

Huang B, Johnson JW, Nesmith S, Bridges DC (1994b) Growth, physiological and anatomical responses of two wheat genotypes to waterlogging and nutrient supply. J Exp Bot 45: 193- 202

Huang B, Johnson JW, Box JE, Nesmith S (1997) Root characteristics and physiological activities of wheat in response to hypoxia and ethylene. Crop Sci 37: 812- 818

Huang B (1997) Mechanisms of plant resistance to waterlogging. In: Basra AS, Basra RK (eds) Mechanisms of environmental stress resistance in plants. Harwood Academic Publishers, The Netherlands. pp 59- 82

Jackson MB, Armstrong W (1999) Formation of aerenchyma and the processes of plant ventilation in relation to soil flooding and submergence. Plant Biol 1: 274- 287

Jackson MB and Drew MC (1984) Effects of flooding on growth and metabolism of herbaceous plants. In: Kozlowski TT (ed) Flooding and plant growth. Academic Press, New York. pp 47- 128

Jackson MB (1989) Regulation of aerenchyma formation in roots and shoots by oxygen and ethylene. In: Osborn DJ, Jackson MB (eds) Cell separation in plants. Springer-Verlag, Berlin. pp 263- 274

Jiang D, Fan X, Dai T, Cao W (2008) Nitrogen fertilizer rate and post- anthesis waterlogging effects on carbohydrate and nitrogen dynamics in wheat. Plant Soil 304: 301- 314

Johnson JR, Crobb BG, Drew MC (1989) Hypoxic induction of anoxia tolerance in root tips of *Zea mays*. Plant Physiol 91: 837- 41

Justin SHFW, Armstrong W (1987) The anatomical characteristics of roots and plant response to soil flooding. New Phytol 106: 465- 495

Justin SHFW, Armstrong W (1991) Evidence for the involvement of ethene in aerenchyma formation in adventitious roots of rice (*Oryza sativa*). New Phytol 118: 49- 62

Kawase M, Whitmoyer RE (1980) Aerenchyma development in waterlogged plants. Am J Bot 67: 18- 22

Kennedy RA, Rumpho ME, Fox TC (1992) Anaerobic metabolism in plants. Plant Physiol 100: 1- 6

Kozlowski TT (1984) Extent, causes, and impact of flooding. In: Kozlowski TT (ed) Flooding and plant growth. Academic Press, New York. pp 1- 7

Krizek DT (1982) Plant response to atmospheric stress caused by waterlogging. In: Christiansen MN, Lewis CF (eds) Breeding plants for less favorable environments. John Willey & Sons Inc, New York. pp 293- 335

Lambers H (1976) Respiration and NADH oxidation of the root of flood- intolerant *Senecio* species as affected by anaerobiosis. Plant Physiol 37: 117- 122

Marshall DR, Broue P, Pryor AJ (1973) Adaptive significance of alcohol dehydrogenase isozymes in maize. Nature 244: 16- 17

McDonald MP, Galwey NW, Colmer TD (2001a) Waterlogging tolerance in the tribe Triticeae: The adventitious roots of *Critesion marinum* have a relatively high porosity and a barrier to radial oxygen loss. Plant Cell Environ 24: 585- 596

McDonald MP, Galwey NW, Ellneskog-Staam P, Colmer TD (2001b) Evaluation of *Lophopyrum elongatum* as a source of genetic diversity to increase waterlogging tolerance of hexaploid wheat (*Triticum aestivum*). New Phytol 151: 369- 380

Menegus F, Cattaruzza L, Chersi A, Fronza G (1989) Differences in the anaerobic lactate- succinate production and in the changes of cell sap pH for plants with high and low resistance to anoxia. Plant Physiol 90: 29- 32

Menegus F, Cattaruzza L, Mattana M, Beffagna N, Ragg E (1991) Response to anoxia in rice and wheat seedlings. Changes in the pH of intracellular compartments, glucose- 6- phosphate level, and metabolic rate. Plant Physiol 95: 760- 767

Mishra PN, Fatma T, Singhal GS (1995) Development of antioxidative defence system of wheat seedlings in response to high light. Physiol Plant 95: 72–82

Mittler R, Vanderauwera S, Gollery M, Breusegem FV (2004) Reactive oxygen gene network of plants. Trends Plant Sci 9: 490- 498

Monk LS, Fagerstedt KV, Crawford RMM (1987) Superoxide dismutase as an anaerobic polypeptide. A key factor in recovery from oxygen deprivation in *Iris pseudacorus*? Plant Physiol 85:1016- 1020

Morard E, Silvestre J (1996). Plant injury due to oxygen deficiency in the root environment of soilless culture: a review. Plant Soil 184: 243- 254

Musgrave ME (1994) Waterlogging effects on yield and photosynthesis in eight winter wheat cultivars. Crop Sci 34: 1314- 1318

Mustroph A, Albrecht G (2003) Tolerance of crop plants to oxygen deficiency stress: fermentative activity and photosynthetic capacity of entire seedlings under hypoxia and anoxia. Physiol Plant 117: 508- 520.

Narayanan S, Ruma D, Gitika B, Sharma SK, Pauline T, Ram MS, Ilavazhagan G, Sawhney RC, Kumarand D, Banerjee PK (2005) Antioxidant activities of seabuckthorn (*Hippophae rhamnoides*) during hypoxia induced oxidative stress in glial cells. Mol Cell Biochem 278: 9- 14

Perata P, Alpi A (1993) Plant response to anaerobiosis. Plant Sci 93: 1- 7

Ponnamperuma FN (1984) Effects of flooding on soils. In: Kozlowski TT (ed) Flooding and plant growth. Academic Press, Orlando. pp 9- 45

Ponnamperuma FN (1972) The chemistry of submerged soil. Adv Agron 24: 29- 96

Ricard B, Couee I, Raymond P, Saglio PH, Saint-Ges V, Pradet A (1994) Plant metabolism under hypoxia and anoxia. Plant Physiol Biochem 32:1- 10

Roberts JKM, Callis J, Wemmer D, Walbot V, Jardetzky O (1984) Mechanism of cytoplasmic pH regulation in hypoxic maize root tips and its role in survival under hypoxia. Proc Natl Acad Sci USA 81: 3379- 3383

Sairam RK, Kumutha D, Ezhilmathi K, Deshmukh PS, Srivastava GC (2008) Physiology and biochemistry of waterlogging tolerance in plants. Biol Plant 52: 401- 412

Sairam RK, Kumutha D, Chinnusamy V, Meena RC (2009) Waterlogging- induced increase in sugar mobilization, fermentation, and related gene expression in the roots of mung bean (*Vigna radiata*). J Plant Physiol 166 : 602- 616

Samad A, Meisner CA, Saifuzzaman M, van Ginkel M (2001) Waterlogging tolerance. In: Reynolds MP, Ortiz -Monasterio JI, McNab A (eds) Application of Physiology in wheat breeding. CIMMYT, Mexico. pp 136- 144

Sayre KD, Van Ginkel M, Rajaram S, Ortiz- Monasterio I (1994) Tolerance to waterlogging losses in spring bread wheat: Effect of time of onset on expression. Annu Wheat Newsl 40: 165-171

Setter TL, Belford RK (1990) Waterlogging: How it reduces plant growth and how plants can overcome its effect. West Aust J Agric 31: 51- 57

Setter TL, Ellis M, Laureles EV, Ella ES, Senadhira D, Mishra SB, Sarkarung S, Datta S (1997) Physiology and genetics of submergence tolerance in rice. Ann Bot 79 (Suppl. A): 67- 77

Settler TL, Waters I (2003) Reviews of prospects for germplasm improvement for waterlogging tolerance in wheat, barley and oats. Plant Soil 253: 1- 34

Setter TL, Waters I, Sharma SK, Singh KN, Kulshreshtha N, Yaduvanshi NPS, Ram PC, Singh BN, Rane J, McDonald G, Khabaz- Saberi H, Biddulph TB, Wilson R, Barclay I, McLean R, Cakir M (2009) Review of wheat improvement for waterlogging tolerance in Australia and India: the importance of anaerobiosis and element toxicities associated with different soils. Ann Bot 103: 221- 235

Smirnoff N, Crawford RMM (1983) Variation in the structure and response to flooding of root aerenchyma in some wetland plants. Ann Bot 51: 237- 249

Thomson CJ, Colmer TD, Watkin ELJ, Greenway H (1992) Tolerance of wheat. (*Triticum aestivum* cv. Gamenya and

Kite) and triticale (*Triticosecale* cv. Muir) to waterlogging. New Phytol 120: 335- 344

Thomson CJ, Armstrong W, Waters I, Greenway H (1990) Aerenchyma formation and associated oxygen movement in seminal and nodal roots of wheat. Plant Cell Environ 13: 395- 403

Trought MCT, Drew MC (1980a) The development of waterlogging damage in wheat seedlings (*Triticum aestivum* L.) I. Shoot and root growth in relation to changes in concentration of dissolved gases and solutes in the soil solutions. Plant Soil 54: 77- 94

Trought MCT, Drew MC (1980b) The development of waterlogging damage in wheat seedlings (*Triticum aestivum* L.) II. Accumulation and redistribution of nutrients by the shoot. Plant Soil 56: 187- 199

Trought MCT, Drew MC (1980c) The development of waterlogging damage in young wheat plants in anaerobic solution cultures. J Exp Bot 31: 1573- 1585

Trought MCT, Drew MC (1982) Effects of waterlogging on young wheat plants (*Triticum aestivum* L.) and on soil solutes at different temperatures. Plant Soil 69: 311- 326

van Ginkel M, Rajaram S, Thijssen M (1992) Waterlogging in wheat: Germplasm evaluation and methodology development. In: Tanner DG, Mwangi W (eds) The Seventh Regional Wheat Workshop for Eastern, Central and Southern Africa. Nakuru, Kenya: CYMMYT. pp 115- 124

Visser EJW, Voesenek LACJ (2004) Acclimation to soil flooding - sensing and signal - transduction. Plant Soil 254: 197- 214

Visser EJW, Nabben RHM, Blom CWPM, Voesenek LACJ (1997) Elongation by primary lateral roots and adventitious roots during conditions of hypoxia and high ethylene concentrations. Plant Cell Environ 20: 647- 653

Waters I, Kuiper PJC, Watkin E, Greenway H (1991a) Effects of anoxia on wheat seedlings I. Interaction between anoxia and other environmental factors. J Exp Bot 42: 1427- 1435

Waters I, Morrell S, Greenway H, Colmer TD (1991b) Effects of anoxia on wheat seedlings II. Effects of O_2 supply prior to anoxia on tolerance to anoxia, alcoholic fermentation and sugars. J Exp Bot 42: 1437- 1447

Watkin ELJ, Thomson CJ, Greenway H (1998) Root development in two wheat cultivars and one triticale cultivar grown in stagnant agar and aerated nutrient solution. Ann Bot 81: 349- 354

Xia JH, Saglio PH (1992) Lactic acid efflux as a mechanism of hypoxic acclimation of maize root tips to anoxia. Plant Physiol 100: 40- 46

Yan B, Dai Q, Liu X, Huang S, Wang Z (1996) Flooding induced membrane damage, lipid oxidation and activated oxygen generation in corn leaves. Plant Soil 179: 261- 268

Zeng Y, Avigne WT, Koch KE (1999) Rapid repression of maize invertase by low oxygen: Invertase/sucrose synthase balance, sugar signaling potential and seedling survival. Plant Physiol 121: 599- 608

Zhang H, Turner NC, Poole ML, Simpson N (2006) Crop production in the high rainfall zones of southern Australia - potential, constraints and opportunities. Aust J Exp Agric 46:1035- 1049

Zhang J, Kirkham MB (1994) Drought- stress-induced changes in activities of superoxide dismutase, catalase, and peroxidase in wheat species. Plant Cell Physiol 35: 785- 791