

Plant injury due to oxygen deficiency in the root environment of soilless culture: A review

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Abstract

The deficiency of oxygen concentration in root environment linked to waterlogging conditions caused important injuries for plants. These effects could be reproduced by oxygen deficient nutrient solution. This bibliographical synthesis has been centered on experimental results obtained on plants cultivated in soilless culture. This review paper presents a methodology used to study oxygen depletion in a nutrient solution and to calculate root respiration rates. The main factors influencing root respiration are reviewed as well as the consequences of oxygen deficiency on roots and shoots functioning. This study would not be complete without some information on the main mechanisms of plant adaptation to oxygen deficiency.

Introduction

Many agronomic studies have shown that spring or winter flooding entailed asphyxiating conditions for root systems. These conditions may be the source of important reductions in the yield of winter cultures (Cannell and Belford, 1980). These effects are the consequence of a diminution in the concentration of oxygen available for roots (Guyot and Prioul, 1985a; Trought and Drew, 1980). Waterlogging of the pore space leads to a slowing down or even a rupture in gas exchange between the atmosphere and the rhizosphere: the oxygen concentration required for the respiration of the root system then becomes a limiting factor.

For physiological experiments, "anoxia" will be used to qualify the absence of oxygen and "hypoxia" will be reserved for situations in which the oxygen concentration is a limiting factor. These conditions may apply to all or part of the root system (Bousqué et al., 1992). In soil or in soilless culture, it is rare that the absence of oxygen concerns the entire root system. On the other hand, hypoxia localized on a part of the roots is more frequent.

Root asphyxiation studies are difficult to carry out in natural soil conditions due to the presence of three

phases (solid, liquid and gas). A simpler approach consists in using hydroponic cultures without substrate. Moreover, wheat plant experiments have shown that oxygen deficient nutrient solutions could reproduce the same effects as soil waterlogging. (Guyot and Prioul, 1985b). These hydroponic techniques also avoid the consequences of the presence of anaerobic micro-organisms in waterlogged soils (Drew and Lynch, 1980): fermentation products may accumulate to toxic levels.

The bibliographical synthesis presented here essentially concerns results obtained in soilless culture. This review paper presents (i) a methodology used to study oxygen depletion in a nutrient solution and to calculate root respiration rates, (ii) the main factors influencing root respiration, (iii) the consequent mechanism of injury to roots and shoots.

Root system respiration

Root system physiological activities require energy provided by glucidic substances produced in aerials parts and oxygen molecules. First, glucose is transformed into pyruvic acid by glycolysis. Then, pyruvic acid, oxidized in the Krebs cycle, is transformed into

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carbon dioxide. The electrons released in this cycle are transported to the oxygen molecules through the electron transport chain. At the same time as this energy is liberated inside mitochondria by the respiratory process, cell catabolism releases carbon dioxide. For glucose, the general equation is:



Hence, oxygen is continuously needed by root cells. It is supplied by the water flow and can be directly absorbed in gaseous form. Exogenous oxygen must be regularly supplied by the immediate root environment.

Oxygen can diffuse from aerial tissues to roots, but the amounts are usually not sufficient for the oxygen requirements of crops (except rice) and dry land plants (Veen, 1989). For wetland plants, internal oxygen transport can contribute significantly to root respiration under anoxic conditions (Laan et al., 1990).

In plants, the lack of aeration in roots does not result in the immediate death of the plant. Plant root physiology is characterized by an adapting response: Under non-aerated conditions, plants can survive in "standby" state, awaiting more favorable oxygen supply conditions. Depending on the species, this phase can last a few days or weeks without any visible symptoms. In this case, a fermentative metabolism seems to ensure root survival under anaerobic conditions (Drew, 1983; Saglio et al., 1980). These phenomena induce a decrease, then stopping of aerial growth and thus affect final crop yield.

When subjected to prolonged non-aerated conditions, plants will sooner or later die: this phenomenon arises in flooded zones and hydromorphic soils. However, if aerobic conditions are restored before this lethal stage, physiological functions can eventually be recovered.

Study methodology

In soilless culture, asphyxiating conditions can be induced by two processes:

- air dissolved in the nutrient solution can be replaced by another gas (nitrogen bubbling),
- roots placed in an airtight PVC tank containing nutrient solution are gradually asphyxiated by their own oxygen consumption.

This bibliographical review essentially concerns results obtained by this second system. This methodology is closer to natural conditions where oxygen depletion occurs gradually. However, results obtained by

this approach must be carefully translated to soil systems: morphology and anatomy of roots are slightly modified in soilless conditions (Morard, 1995).

The experimental device, schematized in Figure 1 (Silvestre, 1992), includes:

- a PVC culture tank with an airtight screw cover, polyurethane mastic is used to ensure airtightness between plant collars and the cover;
- a nutrient solution formed with macronutrients (mmoles L⁻¹: K⁺ 7, Ca²⁺ 5, Mg²⁺ 1.5, NO₃⁻ 15, H₂PO₄⁻ 2, SO₄²⁻ 1.5) and micronutrients mg L⁻¹: Fe 15, Mn 0.49, Cu 0.06, Zn 0.11, B 0.26, Mo 0.01);
- several specific electrodes to continuously measure different parameters (pH, oxygen, nitrates, potassium, etc. . .);
- several inlet pipes with taps, which control air and water admission, as well as an internal pressure regulator system;
- a magnetic stirrer to homogenize the nutrient solution;
- an electronic scale placed under the experimental device to measure water losses due to plant transpiration.

Before beginning the experiments, the PVC tank must be closed hermetically. Then, the root system consumes the oxygen dissolved in the nutrient solution until it is depleted: asphyxiation occurs gradually via root cell consumption. To obtain comparative results, the entire device is placed in a culture chamber where temperature, humidity and lighting are controlled. The different parameters are regularly analyzed every few minutes without opening the closed system. Before each measurement, transpiration water losses are compensated for by deionized and degasified water.

Oxygen depletion by roots

Oxygen depletion has been studied on different species. Figures 2 and 3 show the evolution of the partial pressure of oxygen for wheat (Morard et al., 1990) and for cucumber (Schapira et al., 1990). Oxygen dissolved in the nutrient solution is depleted after around one hour, experimental conditions were approximately 25 g of fresh roots per liter of nutrient solution and 20 °C media temperature. Depletion curves are analogous and can be considered as exponentials, including three phases:

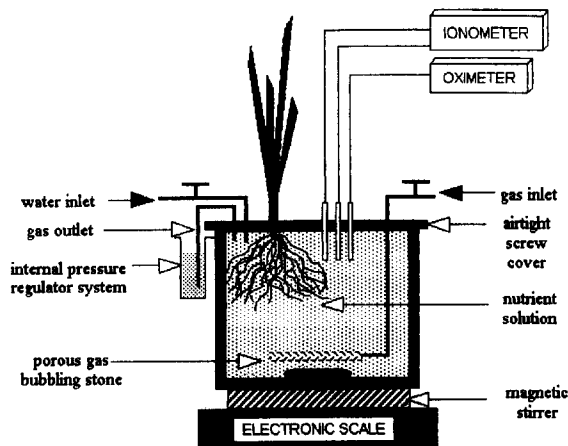


Figure 1. Experimental device used to study root gas exchanges.

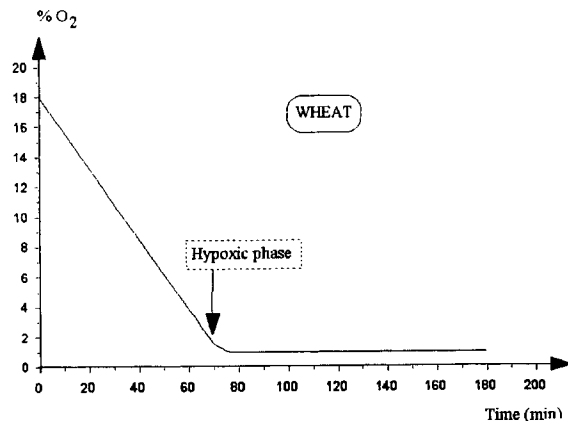


Figure 2. Depletion of dissolved oxygen in closed nutrient medium by wheat root system.

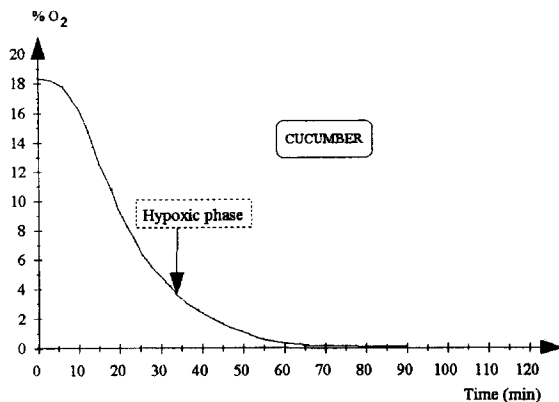


Figure 3. Depletion of dissolved oxygen in closed nutrient medium by cucumber root system.

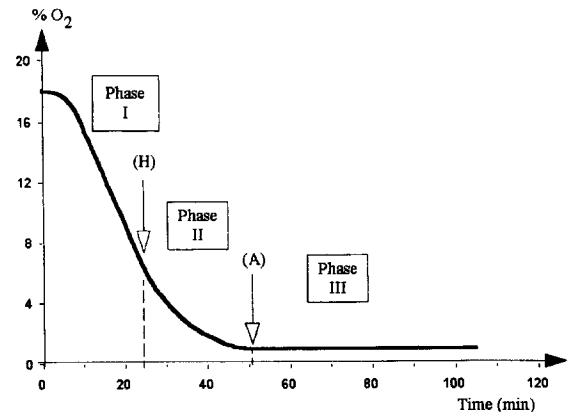


Figure 4. Model of dissolved oxygen depletion by root system in closed nutrient medium.

- first, a regular and linear decrease in the oxygen concentration up to 4 to 6% of partial pressure (phase I),
- next, a progressive slope change corresponding to increasingly slower diminution (phase II),
- finally, an asymptote parallel to the abscissas corresponding to a 1% oxygen value (phase III).

Other oxygen depletion tests indicate the same process with winter oilseed rape (Silvestre, 1992), wheat (Bousqué, 1992), violet (Shan Sei Fan, 1993), tomato (Schapira, 1983), cucumber (Schapira, 1983). Thus, we can construct an oxygen depletion model comprising three successive phases (Figure 4).

Respiration rate

To compare these results obtained with different species, it is necessary to express the oxygen consumption value per unit of time and per unit of fresh root weight (for instance: milligrams of oxygen consumed per hour and per gram of dry root matter or μ moles of oxygen per hour and per fresh root matter). The derivative calculated between two successive measurements gives the respiration rate (Bertoni et al., 1993). The proposed model can also describe the different respiration rates: the three phases of oxygen depletion described in Figure 4 correspond, in fact, to three different rates (Figure 5).

- * Phase I – At the beginning of root system isolation, the linear decrease in oxygen concentration corresponds to a constant respiration rate: in this case, root cell requirements are satisfied and oxygen is not considered as a limiting factor.

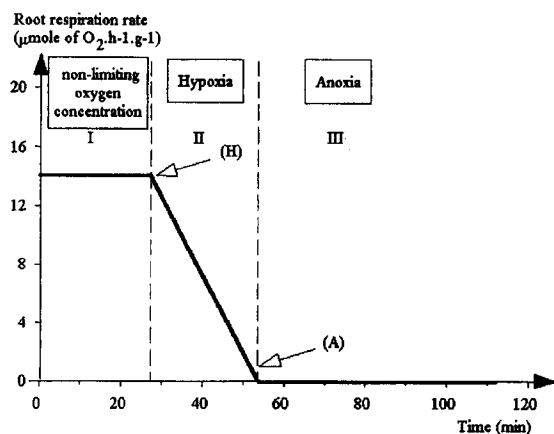


Figure 5. Calculated respiration rate of root system in closed nutrient medium.

* Phase II – The oxygen concentration in the nutrient solution becomes a limiting factor and the respiration rate decreases regularly (hypoxia).

* Phase III – the oxygen concentration stabilizes at around 1% of the partial pressure, which seems to be the limit capacity for dissolved oxygen use by root cells; the respiration rate tends towards zero (anoxia). These strict anoxic conditions occur in soil after long waterlogging periods or in soilless culture when substrate porosity is inadequate or when the nutrient solution is not sufficiently aerated.

Whatever the plant, these three phases are clearly delimited. They appear as changes of slope in the curves in Figures 4 and 5. They represent a difference in root metabolism functioning:

- “H” marks the beginning of the hypoxic phase and has been called the “critical oxygen pressure” C.O.P. (Drew, 1983);
- “A” indicates the total lack of available oxygen for the entire root system.

The calculation of the root respiration rate (phase II) also allows comparison of the requirements of different species, expressed per unit of fresh matter. Bibliographical data is rare in this area. Table 1 compiles the results obtained using soilless culture experimental systems, results which are close to those given in Figure 1. Under non-limiting oxygen concentration conditions, the roots of some plants, such as oilseed rape and corn require more oxygen than others (wheat, cucumber, tomato).

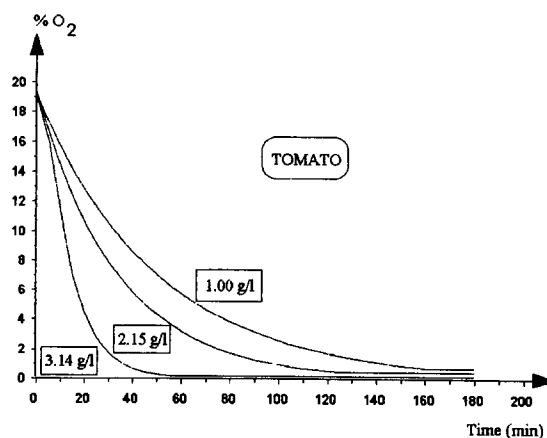


Figure 6. Depletion of dissolved oxygen in closed nutrient medium by three tomato plants (root weights are expressed per dry matter gram and per nutrient solution liter).

Factors influencing root respiration

Root oxygen needs differ depending on species (Table 1). Other factors also influence root respiration; the most important are described hereafter.

Root weight

Oxygen consumption is proportional to the quantity of roots colonizing the nutrient medium. Figure 6 shows the oxygen consumption of tomatoes having different root weights (Schapira et al., 1990): curves are homothetic and oxygen decrease is faster as root weight increases. Ablation of part of the plant roots does not affect the exponential nature of oxygen depletion.

Temperature

The temperature of the nutrient medium directly influences the root respiration rate (Boisseau et al., 1988) (Figure 7). For wheat, this relationship is linear between 9 and 20 °C (Figure 8). Successive oxygen depletion measurements were made at different root temperatures (9° to 20 °C) on the same wheat plant (Figure 7). These tests (numbered of 1 to 5) were carried out with the experimental device described in Figure 1 and under strictly identical conditions (active photosynthetic radiation, air temperature and humidity, nutrient solution).

The first test (no.1), on day 1, involved oxygen depletion at 20 °C (Figure 7); then the nutrient solution was aerated for 22 hours before conducting test no.2

Table 1. Root respiration rate of different species (in milligrams of oxygen hour⁻¹ gram⁻¹ of dry matter and in μ moles of oxygen hour⁻¹ gram⁻¹ of fresh matter)

Species	mg O ₂ hour ⁻¹ g ⁻¹ d.m.	μ mole O ₂ hour ⁻¹ g ⁻¹ f.m	References
Oilseed rape	2.50	7.80	Silvestre (1992)
Corn	2.00	6.24	Veen (1977)
Cucumber	0.86	2.70	Schapira (1983)
	1.29	4.02	Veen (1989)
Tomato	1.04	3.24	Schapira (1983)
	1.50	4.68	Veen (1989)
Wheat	1.25	3.90	Bousque (1992)
Violet	0.46	1.44	Shan Sei Fan (1993)
Strawberry	0.52	1.62	Morard (1995)

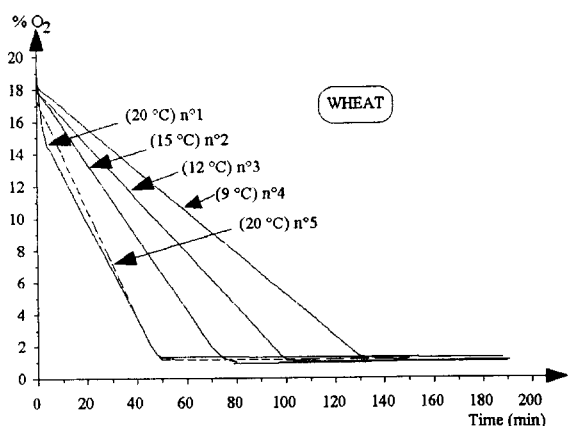


Figure 7. Depletion of dissolved oxygen in closed nutrient medium by wheat root system at different temperatures.

at 15 °C: the same experimental sequence was applied for each lower temperature (no.3 at 12 °C; no.4 at 9 °C). The fifth day (test no.5), the root system of the same wheat plant was again subjected to the conditions of test no.1 at 20 °C. The curve obtained is strictly analogous to that obtained in test no.1.

These results show that:

- oxygen consumption is directly dependent on root temperature (Figure 8),
- daily one-hour oxygen depletion repeated over several days does not affect metabolism or integrity of wheat roots. In other words, roots quickly recover normal cell functioning after a short anoxic period.

Transfer of glucide from aerial part

The supply of photosynthates from aerial parts influences root oxygen consumption: when tomato leaves

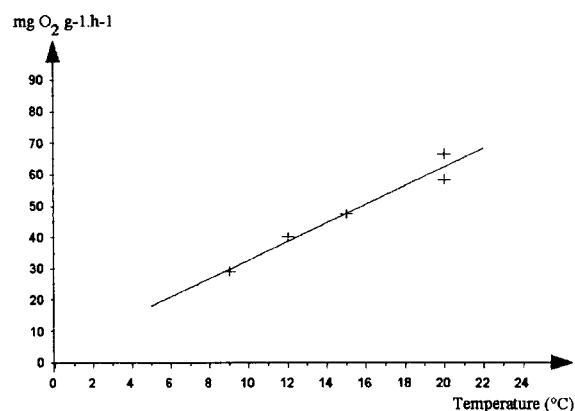


Figure 8. Evolution of respiration rate as function of wheat root temperature in closed nutrient medium.

receive 327 W m⁻² of light, their roots consume 12.10⁻² mg of O₂ min⁻¹ gram⁻¹ of dry matter but only 7. 10⁻² mg of O₂ min⁻¹ gram⁻¹ of dry matter when the illumination is reduced to 136 W m⁻² (Schapira, 1983).

Diminution of the glucide supply during the scotophase also explains why oxygen consumption decreases at night. Steiner (1985) provides respiration rates for the total root systems of producing tomato plants:

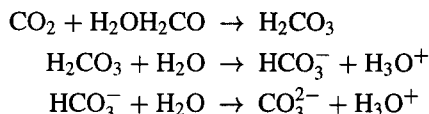
- 6. 7. 10⁻³ of O₂ second⁻¹ on a sunny day and only 2. 2. 10⁻³ of O₂ second⁻¹ in cloudy weather,
- respectively 2.5 and 1.1. 10⁻³ of O₂ second⁻¹ for the nights following these days.

In summary, at night the root system of the tomato plant consumes two to three times less oxygen than during the preceding day and oxygen consumption may decrease by 67% with low illumination of aerial parts.

This data also confirms that root respiration is linked to the photosynthetic activity of the aerial part.

Carbon dioxide concentration

The effect of carbon dioxide in soilless cultures is often underestimated. In nutrient solutions, this gas is in equilibrium with carbonates:



The dissociation constants of these reactions strongly influence the pH of the nutrient solution. Carbon dioxide results partly from the root respiration process, in which glucides are oxidized, and partly from carbon dioxide from the air during exogenous aeration of the nutrient solution.

Deficient root aeration leads to an increase in the relative carbon dioxide concentration which is linked to oxygen depletion. The experimental system (Figure 1) can be used to modelize this causal relationship. Gas exchanges can be characterized by a respiratory quotient (RQ) determined by the ratio of O₂ absorbed to CO₂ released. The oxygen and carbonate concentrations in the nutrient solution are continuously measured using the experimental system described in Figure 1 (Figure 9).

Under aerated conditions, RQ=1, which corresponds to normal oxidation of a glucide molecule. When hypoxic conditions appear (point H in Figure 5 corresponds to 6% oxygen partial pressure in Figure 9), the RQ value is greater than 1 (point H : 8% in Figure 10) corresponding to a degraded glucide molecule.

In the experiment illustrated in Figure 9, gas exchanges show an RQ greater than 1 as of the beginning of hypoxia (6% of pressure ; Figure 4) and root carbon dioxide release is greater than root oxygen consumption. Substantiated by other experiments (Drew, 1983), this phenomenon can be explained by different hypotheses :

- limitation of oxygen distribution through root tissues (Berry and Norris, 1949),
- utilization of NO₃⁻ ions as final electron acceptors (Garcia Novo and Crawford, 1973),
- insaturation of a fermentation metabolism in roots (Saglio et al., 1980).

The most probable explanation is the third one: Carbon dioxide is released by this anaerobic metabolism when oxygen is depleted in the root medium (Figure 9)

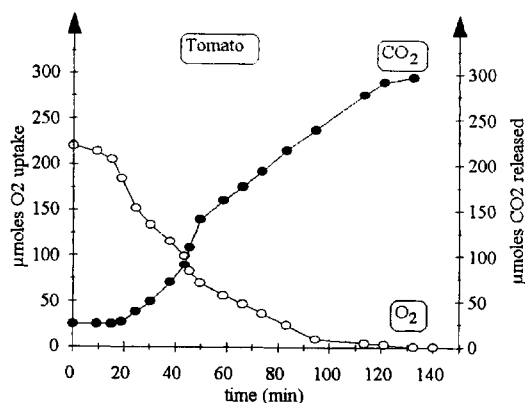


Figure 9. Evolution of oxygen uptake and carbon dioxide release by tomato root system in closed nutrient medium.

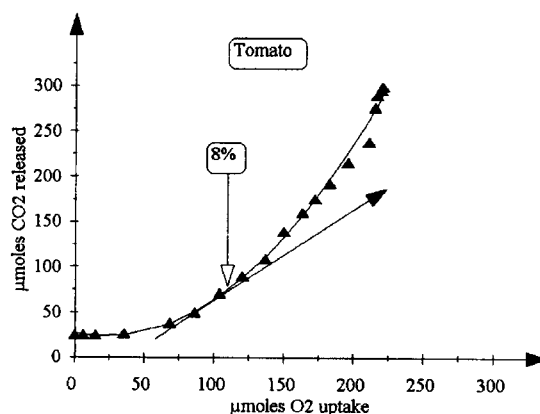
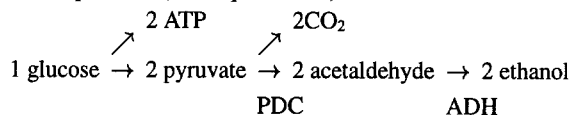


Figure 10. Respiratory quotient (RQ) evolution of tomato root system, determined by ratio of O₂ absorbed to CO₂ released in closed nutrient medium (point H : 8% oxygen partial pressure).

during the anoxic phase. Ethanol present in wheat roots and in the culture medium confirms this classic fermentative process (Bousqué, 1992):



These reactions require two enzymes: phosphoenolpyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH); their activities are stimulated by high CO₂ concentrations in asphyxiated tissues (Chang and Hammet, 1982).

The fermentative process produces two CO₂ molecules for each glucose molecule, which would explain the RQ>1 value obtained in the oxygen stress tomato experiment (Figure 10). During oxygen depletion, aerobic respiration is replaced by anaerobic res-

piration. This fermentative phase corresponds to an exceptional and transient period in root metabolism. In this case, only 2 ATP molecules are produced, instead of the 36 produced in aerobic conditions. This process ensures minimum energy production, which nevertheless seems inadequate for maintenance of cell metabolism in higher plant cells (Drew and Lynch, 1980).

Under poor aeration conditions, the decrease in cell ATP concentration reduces root release of protons into the nutrient solution. This phenomenon and carbon dioxide accumulation promote alkalization of the nutrient solution (Glinski and Stepniewski, 1985). On the other hand, after a long hypoxic period, root asphyxiation can entail acidification of the nutrient medium caused by organic acids from destroyed cells (Tret'yakov et al., 1990).

The effects of exogenous CO₂ bubbling in the nutrient solution were tested on tomatoes in a soilless culture. The experimental system (Figure 1) provides the following informations.

- * CO₂ saturation of the nutrient medium provokes tomato plant wilting after 5 days.
- * Bubbling of a gas mixture containing 50% O₂ and 50% CO₂ almost completely impedes root respiration.
- * According to Chang and Loomis (1945), respiration disturbance occurs as of 10% carbon dioxide (result related to decrease in relative O₂ concentration). So, water and mineral nutrient uptake are reduced. These phenomena are linked to an increase in nutrient solution pH due to the stopping of protons pumps (Tret'yakov et al., 1990) and to a modification of the chemical equilibrium between carbon dioxide and carbonates.

Effects of oxygen depletion on root system activity

Total or partial oxygen deprivation entails a disturbance in the functioning of this organ, with repercussions on water and mineral nutrient uptake in the entire plant.

Water uptake

Bibliographic sources present different interpretations of the effect of oxygen depletion on water uptake: for some researchers root asphyxia leads to reduced transpiration (Bradford and Hsiao, 1982; Bousqué et al.,

1992), while for others there is little or no modification (Saglio et al., 1980).

In fact, apart from differences in experimental conditions, asphyxiation duration and periods (day/night) constitute important parameters (Bradford and Hsiao, 1982). For short durations (a few hours), the effects on aerial part transpiration are not measurable: for wheat, the maximum duration can be estimated between 2 hours (Morard et al., 1990) and 6 hours (Trought and Drew, 1980); for tomatoes, it can be as long as a day (Lesaint et al., 1983). When root asphyxiation occurs over more than a day, a significant reduction is generally observed on different species; snapdragon (Letey et al., 1961); corn (Lesaint et al., 1983); tomato (Bradford, 1983a; Lesaint et al., 1983; Schapira, 1983); cucumber (Schapira, 1983); wheat (Bousqué, 1992); oilseed rape (Silvestre and Morard, 1994).

Transpiration reduction is related to stomatal closure which induces a water content increase in aerial parts: this result is confirmed by reduction of stomatal conductance and higher hydric potential values measured in tomato leaves under hypoxic conditions (Bradford, 1983a; Trought and Drew, 1980). The mechanism responsible for stomatal closure may be a hormonal signal. Indeed, root oxygen deprivation entails a diminution of root cytokinin synthesis (Bradford, 1983a) as well as an increase in endogenous abscissic acid (Setter et al., 1980; Bradford 1983b; Jackson and Hall, 1987).

After prolonged asphyxiation periods, visible symptoms appear before the lethal phase: wilting, followed by defoliation of the aerial part. Resistance to root asphyxiation varies depending on the plant species: ranging, for instance, from a few days for lupin to a few weeks for wheat. The plant can recover normal physiological activities if root aeration is restored before the lethal phase.

Uptake of mineral nutrients

Under oxygen-deficient conditions, the root cell energy pool is greatly decreased. This energy is necessary for plant uptake of mineral nutrients by active processes. Hence, phosphate (Hopkins, 1956), nitrate (Rao and Rains, 1976) and potassium uptake (Hiatt and Lowe, 1967) are decreased. Over longer deficiency periods, passive uptake mechanisms of minerals such as calcium and magnesium (Harris and Van Bavel, 1957; Trought and Drew, 1980) are also disturbed. The synthesis of our research, confirmed by the results of other authors (Harris and Van Bavel, 1957), allows us to

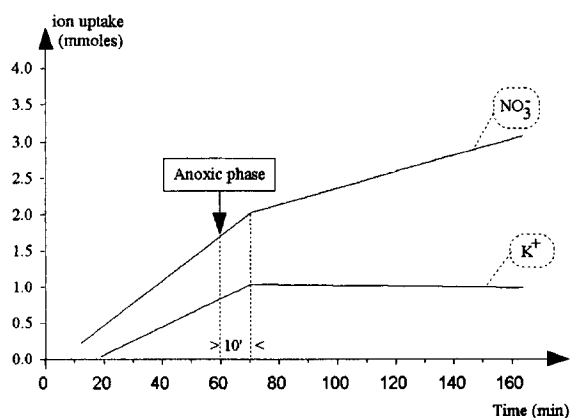


Figure 11. Cumulative nitrate and potassium uptake by wheat root system in closed nutrient medium.

classify, in the following order, the depressive effects of root asphyxiation on hydromineral uptake for the entire plant: $K > N > P > H_2O > Mg-Ca$.

A more detailed study was carried out under hydroponic conditions (Figure 1) on the whole root systems of wheat (Morard et al., 1990) and cucumber (Bertoni et al., 1993): ten minutes after the beginning of hypoxia (COP), a potassium efflux appears in the nutrient solution as well as a 40% drop in the nitrate absorption rate (Figure 11). This potassium efflux is attributed to depolarization of root cell membranes, a direct consequence of H^+ -ATP-ase inhibition (Buwalda et al., 1988; Cheeseman and Hanson, 1979): a test carried out on beet root cells showed that after 5 hours of hypoxia the membrane electrical potential drops from -156 mV to -95 mV (Zhang et al., 1992). This is confirmed by an increase in tissue electrical conductivity, indicating a loss of membrane permeability (Cernohorska et al., 1989). In this case, the normal efflux of K^+ ions is not compensated by root cell active influx of these ions.

After short asphyxiation periods, return to normal aeration conditions leads to practically instantaneous restoral of the initial electrical potential of the cell membrane (Zhan et al., 1992), followed by the re-establishment of potassium influx ten minutes after the end of the hypoxic phase (Bertoni et al., 1993; Silvestre, 1992).

Transient oxygen deprivation does not seem to induce irreversible nutritional stress in plants, as was already shown in the previous study of water and temperature effects.

Root excretions in culture medium

Oxygen deficiency provokes the accumulation of different metabolites in the root: ethanol (Chang and Hammet, 1982), abscissic acid (Davies and Zhang, 1991), ethylene precursors (Bradford, 1983b) and succinic acid (Duthion, 1976); some of these products can be excreted in nutrient solution.

Ethanol, considered as a very toxic product for plants (Chang et al., 1983; Perata and Alpi, 1991), is produced in the roots, then migrates to the rhizosphere (Bolton and Erickson, 1970) or to aerial parts (Barta, 1984). The presence of ethanol in leaves enabled development of a root asphyxiation test by enzymatic dosage for wheat (Bousqué, 1992).

Effects of asphyxiation on aerial part metabolism

Metabolic disturbances linked to root asphyxiation affect the aerial part of plants: growth and development are reduced, thus leading to diminished final crop yield.

The main physiological consequence of root asphyxiation seems to be stomatal closure of leaves, leading to a reduction in transpiration (Bradford and Hsiao, 1982) then a reduction of photosynthesis. The decrease in photosynthetic activity seems to be related to a reduction in the number of photosystems and in the quantity of chlorophyll a and b in leaves (Ashraf and Mehmood, 1990) as well as to a diminution of RuBisCO (Zakrzhevskii and Ladygina, 1989).

Obviously, the reduction in photosynthates has direct repercussions on root growth and aerial part development (Trought and Drew, 1980; Voeselek et al., 1989; Guyot and Prioul, 1985b). Whatever the cultivated species, root asphyxiation entails a reduction in leaf area and therefore a decrease in growth rate and fresh weight (Cannell et al., 1985; Silvestre and Morard, 1994) at harvest, yield is significantly reduced (Bousqué, 1992; Cannell et al., 1980, 1985; Silvestre, 1992; Trought and Drew, 1980). For example, for winter oilseed rape, an asphyxiation period of 15 days during the stem elongation stage leads to several reductions (% of control value) (Silvestre and Morard, 1994):

- leaf area: -30%,
- dry weight of aerial parts: -33%,
- dry weight of root system: -72%,
- yield: -52%.

Yield reduction of least 50% was verified in early and later development stages.

Adaptation mechanisms

This bibliographical synthesis has been centered on experimental results obtained on plants cultivated in soilless culture. This study would not be complete without some information on the main mechanisms of plant adaptation to oxygen deficiency.

Some plants can develop processes for adapting to oxygen deficiency. Rice is the most well known of these plants. These adaptations can be anatomical, morphological or even metabolic.

Anatomical and morphological adaptations

For some plants, oxygen deficiency tolerance can express itself as an increase in root porosity related to degeneration of cortical cells provoked by ethylene (Drew, 1983; Kawase, 1978), or even by production of adventitious aerenchymatous roots (Laan et al., 1989) (Figure 12). The comparison of hypoxia-sensitive and hypoxia-tolerant winter wheat varieties shows that root porosity is respectively 3 to 8% (Yu et al., 1969) and 5 to 15% (Jensen et al., 1969). Rice is characterized by 27 to 36% root porosity (Jensen et al., 1969).

This increase of root porosity enables internal transport of oxygen from aerial parts to the roots (Mingeau, 1977). Amounts can reach more than 50% of the oxygen requirements of wetland species such as *Rumex maritimus* (Laan et al., 1990). For corn roots exposed to hypoxic conditions, oxygen diffuses across aerenchyma only to cortex cells. On the other hand, stele cells are characterized by fermentative metabolism (Thomson and Greenway, 1991).

Furthermore, oxygen deficiency entails an increase in the synthesis of ethylene precursors in roots; after migration of these precursors to aerial parts, ethylene promotes leaf epinasty phenomena that modify the angle between stem and petiole. Thus, the reduction of the leaf intercept area temporarily limits leaf overheating (Bradford and Hsiao, 1982; Marschner, 1990).

These two mechanisms allow the plant to limit water loss and leaf wilting provided that climatic conditions are not too dry.

Physiological adaptations

In sensitive plants, hypoxia usually increases the glycolysis rate and ethanol production. In tolerant plants, only glycolysis reactions are accelerated and malate, produced from phosphoenolpyruvate, is increased instead of ethanol (Crawford and Bains, 1977). This secondary reaction would detoxify root cells.

In winter wheat, several days of asphyxiation increase the fructosan content (5 to 7 times the control value) in root and stem cells (Albrecht et al., 1993). This compound characterized by low synthesis energy, is rapidly used as substrate by the respiration process after culture medium re-aeration. This mechanism is analogous to the cold adaptation process developed by some plants.

Nitrates could be used as final electron acceptors, instead of/or in complement of oxygen (Garcia Novo and Crawford, 1973). Furthermore, the reduction of nitrates to nitrites would allow root cells to create reducing power that could be used by the glycolysis process (Lambers, 1976).

Hypoxia entails cytoplasm acidification related to the accumulation of protons and organic acids (Roberts et al., 1985). According to these same authors, pH regulation would be essential to maintain root cell integrity.

Conclusions

A minimum oxygen concentration (above Critical Oxygen Pressure) is necessary for normal root activities. An oxygen concentration under the COP value becomes a factor limiting root cell metabolism (hypoxia). At a partial pressure less than 1%, roots are not able to take up oxygen (anoxia).

The oxygen consumption of a root system depends on different factors: species, temperature, glucide supply, carbon dioxide concentration in nutrient solution.

Oxygen deficiency interferes with the root's supply of nutrients to the plant for example, an efflux of K^+ appears ten minutes after the onset of wheat root anoxia; over a day water uptake is significantly reduced.

To conclude, temporary and short oxygen deficiency (a few hours) does not induce irreversible nutritional stress in plants. On the other hand, long periods of hypoxia (several days) provoke a decrease in growth that results in significant reduction in crop yield.

In spite of the information collected in this review of the bibliography, more research is needed to better

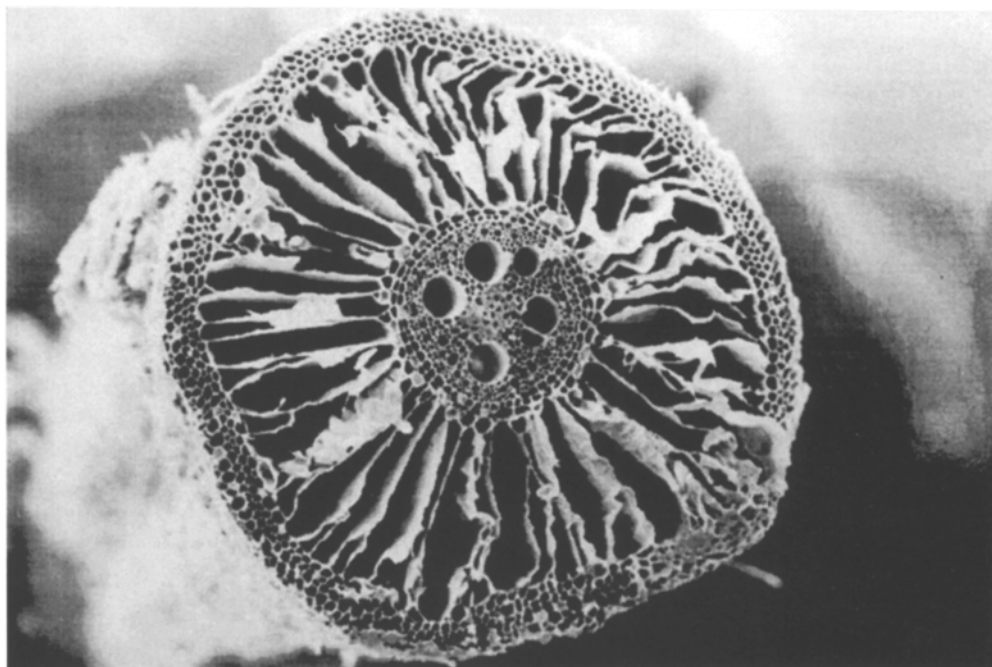


Figure 12. Cross section of aerenchymatous reed root scanning by electron microscopy ($\times 2000$). (With the permission of R Loveridge, Univ of Portsmouth, UK).

understand the effect of oxygenation on the root system of plants grown in soilless culture. The four following points need to be more clearly explained :

- 1) A more in-depth study of the effects of asphyxiation on the absorption of water and certain indispensable elements (Ca, P, micronutrients) should be carried out.
- 2) It is likely that there exists an asphyxiation signal transduction system from the roots to the aerial part. In this case, it is necessary to show that there is a molecular marker, for example inducing closure of stomata in plants subject to root asphyxiation.
- 3) Species and different varieties react differently to root asphyxiation: the respiration speed of the main cultivars, as well as the critical oxygen pressure (COP) under strictly comparable conditions must be defined.
- 4) Part of the results obtained during soilless culture may be used under natural conditions. However, this data cannot be directly translated to soil systems, where the problems are far more complex (micro-organisms, root colonization of the medium) without prior validation.

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