

INFLUENCE OF SOIL OXYGEN SUPPLY ON ROOT GROWTH AND FUNCTIONING  
(REVIEW OF THE LITERATURE)

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**S y n o p s i s.** All problems connected with the role of soil oxygen in root growth and functioning are discussed in this review. There are: diffusion of oxygen to and within plant roots, root respiration and factors affecting it, metabolic activity of roots under anoxia, oxygen deficit and root growth and water and nutrient uptake by roots and adaptation of roots to oxygen stress.

1. INTRODUCTION

Soil aeration status, described in details in the book Soil Aeration and Its Role for Plants [96], is one of the most important factors influencing plant roots, which is shown clearly in Figure 1. As can be seen, among many components of the scheme, soil oxygen plays a fundamental role for plant roots functioning, through its availability by the root system, its direct effects connected with the physiological events occurring within the plants and indirect effects changing soil properties.

Most of the negative phenomena connected with oxygen deficiency in soil are caused solely and directly by lack of oxygen for metabolic processes. Indirect effects appear only when there is a long-lasting shortage of oxygen in the soil.

Plants vary widely in response to oxygen stress in the soil. In general, critical oxygen level in soil for plants begins in the range of 5-10%  $O_2$  by volume. Root growth of most plants is limited when less than 0.1 of the pore spaces in soil are filled with air and the oxygen diffusion rate (ODR) is less than  $35 \mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  [96].

Although few plants are subjected to complete anoxia, many are exposed to periods of oxygen deficiency caused by water-saturated (waterlogged or submerged)

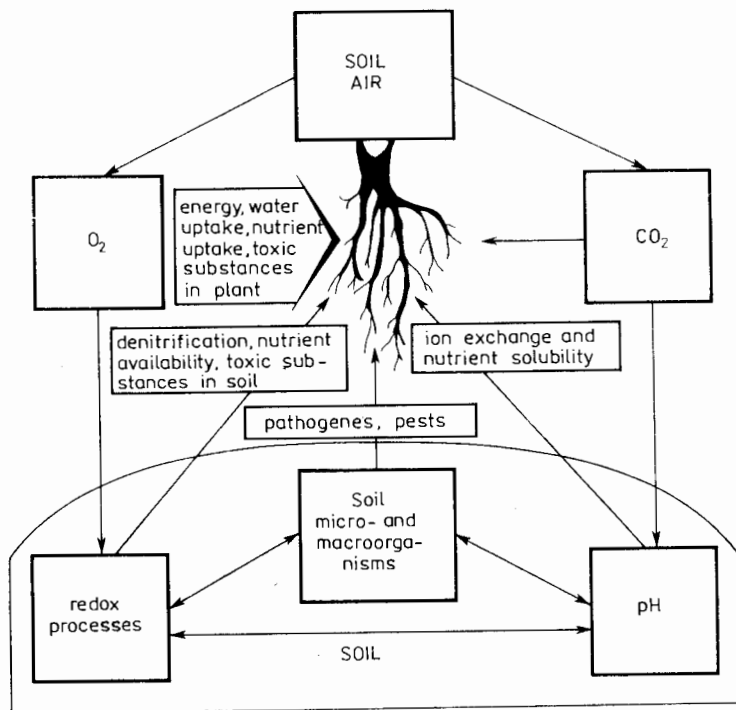


Fig. 1. A scheme of direct and indirect effects of soil air on plants [96]

Fig. 1. Schéma d'influence directe et indirecte de l'air du sol sur les plantes [96]

or compacted soils. The extreme case of oxygen deficiency for plant roots is that in which the soil air is almost completely replaced by water. Such conditions may be permanent (e.g., in bog or marsh soils), intermittent (e.g., in rice soils), or sporadic and of short duration [96].

As to the plant's tolerance to soil waterlogging, there is a whole spectrum of plants - from hygrophites adapted to permanent flooding (e.g., rice) to mesophytes among which significant differentiation exists. Hence, among these plants there are those moderately tolerant to flooding (most grasses and cultivated plants), as well as those very sensitive to it so that after only a few days of flooding they die away (e.g., tobacco, peas). Xerophytes have been investigated only to a limited extent. Even if their system is sensitive to oxygen deficiency, the fact is that some of them can live with a reduced root system, being capable of increasing their resistance to all stresses, and among them to an oxygen deficiency stress [96].

## 2. DIFFUSION OF OXYGEN TO AND WITHIN PLANT ROOTS

The final stage in the transport of oxygen from the soil to the respiring tissue of the plant root is the radial diffusion of oxygen from the root surface to its center. In turn, part of the carbon dioxide produced in the roots diffuses outwards, in a direction to the radial opposite to the radial movement of oxygen, and, part is transported upwards with the transpiration stream and also by longitudinal diffusion to the shoot where it can either be assimilated or released to the atmosphere.

### 2.1. Radial diffusion

Radial diffusion of oxygen from the soil into a root of radius  $R$  having uniform respiratory activity  $q_i$  and diffusion coefficient inside the root tissue  $D_i$ .

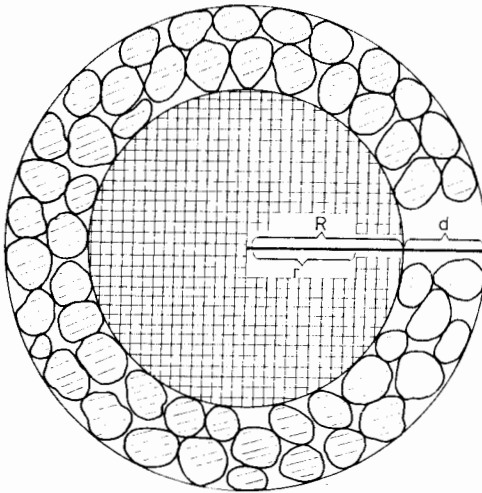


Fig. 2. Schematic cross-section of a root of radius  $R$ , surrounded by soil saturated with water of effective thickness  $d$ ,  $r$  - distance of a root element under consideration from the root axis [96]

Fig. 2. Section de la racine au rayon  $R$ , enrobé de sol saturé d'eau à l'épaisseur effective  $d$ ,  $r$  - la distance entre l'élément de racine considéré et l'axe racinaire [96]

and surrounded by a uniform form layer of water saturated soil of effective thickness  $d$  with an effective diffusion coefficient  $D_e$  and respiratory activity  $q_e$  (Fig. 2) has been lately considered under steady state conditions by de Willigen and van Noordwijk [72] and van Noordwijk and de Willigen [260]. Some more simplified situations without respiration within the saturated layer surrounding the root

( $q_e=0$ ) has been considered previously by Wanner [273], Lemon [166], Lemon and Wiegand [169] and Wiegand and Lemon [276].

The equations presented below are based on those reports especially on that of de Willigen and van Noordwijk [72] and de Willigen [260] giving the most general solutions. These authors have presented also non-steady state solution for radial oxygen distribution within the root without water saturated layer:

$$C_i(t) = C_o - \frac{q_i}{4D_i} (R^2 - r^2) + \frac{2q_i R^2}{D_i} \sum_{n=1}^{\infty} \frac{\exp(-\alpha_n t) J_0(\alpha_n \frac{r}{R})}{\alpha_n^3 J_1(\alpha_n)}, \quad (1)$$

where:

$C_i(t)$  is the concentration of oxygen within the root tissue at a distance  $r$  from the root centre after time  $t$  (assuming initial oxygen concentration within entire root as 0),

$C_o$  is external oxygen concentration,

$\alpha_n$  is the  $n$ -th positive root of  $J_0(\alpha)=0$ ,

$J_0$  and  $J_1$  are Bessel functions of the first kind and zeroth and first order, respectively.

The discussion of this solution by de Willigen and van Noordwijk [72] leads to the conclusion that steady-state situation in roots is approximated within about two minutes. Thus further considerations will concern only steady-state conditions:

$$\frac{\partial C}{\partial t} = D \nabla^2 C + q, \quad (2)$$

where:

$C$  is the gas concentration,

$q$  is the respiration rate per unit volume,

$D$  is the diffusion coefficient.

The general diffusion equation for oxygen, assuming the absence of longitudinal gradients in the cylindrical system for steady-state conditions, takes the following forms for the water film surrounding the root, and the root tissue, respectively:

$$D_e \left[ \frac{d^2 C_e}{dr^2} + \frac{1}{r} \frac{dC_e}{dr} \right] - q_e = 0 \quad (3)$$

and

$$D_i \left[ \frac{d^2 C_i}{dr^2} + \frac{1}{r} \frac{dC_i}{dr} \right] - q_i = 0. \quad (4)$$

The boundary conditions in this situation are as follows:

$$r = 0, \quad \frac{dC_i}{dr} = 0$$

$$r = R, \quad C_i = C_e = C_R \text{ and } D_e \frac{dC_e}{dr} = D_i \frac{dC_i}{dr} \quad (5)$$

$$r = R + d, \quad C_e = C_o.$$

The solution of equations (3) and (4), when  $q_i$  and  $q_e$  are not dependent on the oxygen concentration, is given by the two equations [72]:

$$C_e = C_o - \frac{q_e}{4D_e} \left[ (R + d)^2 - r^2 \right] - \frac{R^2(q_i - q_e)}{2D_e} \ln \frac{R+d}{r} \quad (6)$$

$$C_i = C_o - \frac{q_i}{4D_i} (R^2 - r^2) - \frac{R^2(q_i - q_e)}{2D_e} \ln \frac{R+d}{R} - \frac{q_e}{4D_e} \left[ (R+d)^2 - R^2 \right]. \quad (7)$$

The concentration of oxygen on the root-water film interface  $C_R$  can be obtained by putting  $r=R$  to either of the equations. Then we get:

$$C_R = C_o - \frac{R^2 (q_i - q_e)}{2D_e} \ln \frac{R+d}{R} - \frac{q_e}{4D_e} \left[ (R+d)^2 - R^2 \right]. \quad (8)$$

Combining equations (7) and (8) we obtain:

$$C_i = C_R - \frac{q_i(R^2 - r^2)}{4D_i}. \quad (9)$$

The values of  $q_i$  for roots may vary from 10 to 300  $\text{mg} \cdot \text{m}^{-3} \cdot \text{s}^{-1}$  and those of  $q_e$  from 0.1 to 10  $\text{mg} \cdot \text{m}^{-3} \cdot \text{s}^{-1}$  while  $D_e$  is between 0.3 and  $3.3 \cdot 10^{-10} \text{m}^2 \cdot \text{s}^{-1}$  [97]. The values of  $D_i$  for the roots are from 2.2 to  $9 \cdot 10^{-10} \text{m}^2 \cdot \text{s}^{-1}$  [169].

Oxygen concentration distribution both within the root and outside it calculated on the basis of the equations (6) and (7) for minimum respiration rate values and for maximum diffusion coefficient values likely to occur in roots and in soil is presented in Figure 3.

It should be emphasized that the above equations are valid only when the respiratory activity of the root does not depend on oxygen concentration i.e., when  $C_R \geq C'_R$ , where  $C'_R$  is a critical concentration of oxygen on the root surface.

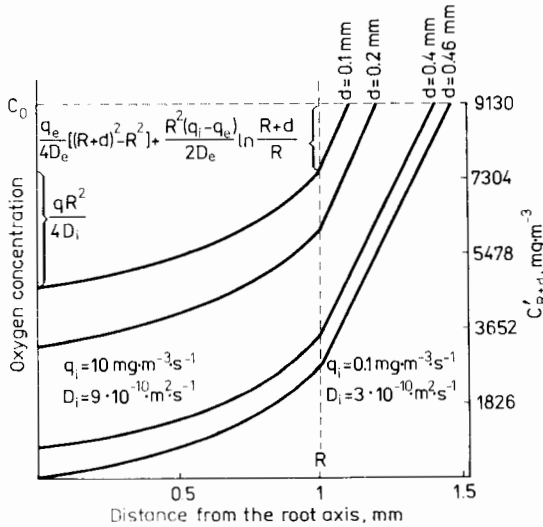


Fig. 3. Effect of water film thickness on oxygen distribution inside and outside the roots as a function of distance from the root centre for the minimum respiration rates and for the maximum diffusion coefficients likely to occur in the root and in the soil (calculated from eqs. 6 and 7)

Fig. 3. Effet d'épaisseur du film d'eau sur la distribution d'oxygène à l'intérieur et à l'extérieur des racines en fonction de la distance du centre de la racine pour les vitesses minimales de respiration et pour les coefficients de diffusion maximaux apparaissant dans la racine et dans le sol (calculé à partir des équations 6 et 7)

Equation (7) permits calculation of the oxygen concentration at the centre of the root  $C_{r=0}$ , by substituting  $r=0$ ; than:

$$C_{r=0} = C_0 - \frac{q_i R^2}{4D_i} - \frac{R^2(q_i - q_e)}{2D_e} \ln \frac{R+d}{R} - \frac{q_e}{4D_e} \left[ (R+d)^2 - R^2 \right] \quad (10)$$

and having included equation (8) we get:

$$C_{r=0} = C_R - \frac{q_i R^2}{4D_i} \quad (11)$$

If the oxygen concentration at the root axis reaches the critical value  $C'_{r=0}$ , below which respiration rate decreases the critical concentration on the root surface  $C'_R$  will be:

$$C'_R = C'_{r=0} + \frac{q_i R^2}{4D_i} \quad (12)$$

i.e., it is increased in relation to  $C'_{r=0}$  by the concentration drop inside the root.

The critical oxygen concentration at the exterior of the water or soil-water film surrounding the root  $C'_{R+d}$  is, obviously,  $C'_R$  increased by the difference in concentration across the film (cf. eq. (8) i.e.,

$$C'_{R+d} = C'_{r=0} + \frac{q_i R^2}{4D_i} + \frac{R^2(q_i - q_e)}{2D_e} \ln \frac{R+d}{R} + \frac{q_e}{4D_e} \left[ (R+d)^2 - R^2 \right]. \quad (13)$$

When the respiratory activity within the saturated layer around the root can be neglected, i.e.,  $q_e = 0$ , than equation (6-8), (10) and (13) are simplified as follows:

$$C_e = C_o - \frac{R^2 q_i}{2D_e} \ln \frac{R+d}{R} \quad (14)$$

$$C_i = C_o - \frac{q_i}{4D_i} (R^2 - r^2) - \frac{R^2 q_i}{2D_e} \ln \frac{R+d}{R} \quad (15)$$

$$C_R = C_o - \frac{R^2 q_i}{2D_e} \ln \frac{R+d}{R} \quad (16)$$

$$C_{r=0} = C_o - \frac{q_i R^2}{4D_i} - \frac{R^2 q_i}{2D_e} \quad (17)$$

$$C'_{R+d} = C'_{r=0} + \frac{q_i R^2}{4D_i} + \frac{R^2 q_i}{2D_e} \ln \frac{R+d}{R}. \quad (18)$$

As the affinity of cytochrome oxidase to oxygen is extremely high ( $K_M = 0.1 \mu\text{M}$ , i.e., 0.008 kPa) we can assume that the critical oxygen concentration inside the root, i.e., on cell level is close to zero. Than we can put  $C'_{r=0} = 0$  to equations (12), (13) and (18).

Having considered this we get formula for critical oxygen concentration on the root surface:

$$C'_R = \frac{q_i R^2}{4D_i} \quad (19)$$

and on the exterior of the soil-water film surrounding the root:

$$C'_{R+d} = \frac{q_i R^2}{4D_i} + \frac{R^2(q_i - q_e)}{2D_e} \ln \frac{R+d}{R} + \frac{q_e}{4D_e} \left[ (R+d)^2 - R^2 \right] \quad (20)$$

which in the case of  $q_e = 0$  (negligible respiration outside the root) is simplified to:

$$C'_{R+d} = \frac{q_i R^2}{4D_i} + \frac{R^2 q_i}{2D_e} \ln \frac{R+d}{R} \quad (21)$$

The values of critical external concentration of oxygen ( $C'_{R+d}$ ) calculated from equations (20) and (21) for different values of  $D_e$ ,  $D_i$ ,  $q_e$  and  $q_i$  are plotted vs.  $d$  - value in Figure 4.

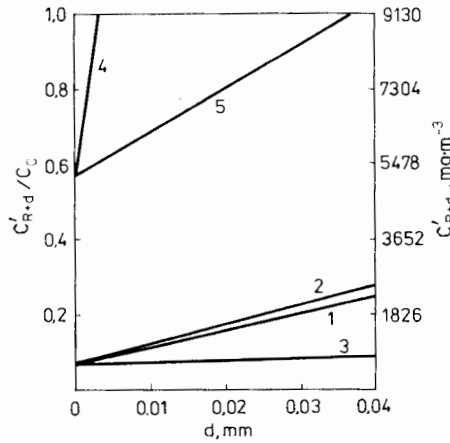


Fig. 4. Effect of water film thickness on actual oxygen concentration outside the water film surrounding the root ( $C'_{R+d}$ ) at extreme values of  $q_i$ ,  $D_i$ ,  $D_e$  likely to occur in roots and soils for the root of radius  $R=0.25$  mm (calculated from eq. 20)

1 -  $q_i \min = 10 \text{ mg}\cdot\text{m}^{-3}\cdot\text{s}^{-1}$ ,  $D_i \min = 2.2\cdot 10^{-10} \text{ m}^2\cdot\text{s}^{-1}$ ,  $q_e \min = 0.1 \text{ mg}\cdot\text{m}^{-3}\cdot\text{s}^{-1}$ ,  
 $D_e \min = 0.3\cdot 10^{-10} \text{ m}^2\cdot\text{s}^{-1}$ , 2 -  $q_i = 10 \text{ mg}\cdot\text{m}^{-3}\cdot\text{s}^{-1}$ ,  $D_i \min = 2.2\cdot 10^{-10} \text{ m}^2\cdot\text{s}^{-1}$ ,  
 $q_e \max = 10 \text{ mg}\cdot\text{m}^{-3}\cdot\text{s}^{-1}$ ,  $D_e \min = 0.3\cdot 10^{-10} \text{ m}^2\cdot\text{s}^{-1}$ , 3 -  $q_i = 10 \text{ mg}\cdot\text{m}^{-3}\cdot\text{s}^{-1}$ ,  $D_i \min =$   
 $= 2.2\cdot 10^{-10} \text{ m}^2\cdot\text{s}^{-1}$ ,  $q_e \max = 10 \text{ mg}\cdot\text{m}^{-3}\cdot\text{s}^{-1}$ ,  $D_e \max = 3.3\cdot 10^{-10} \text{ m}^2\cdot\text{s}^{-1}$ , 4 -  $q_i \max =$   
 $= 300 \text{ mg}\cdot\text{m}^{-3}\cdot\text{s}^{-1}$ ,  $D_i \max = 9\cdot 10^{-10} \text{ m}^2\cdot\text{s}^{-1}$ ,  $q_e \max = 10 \text{ mg}\cdot\text{m}^{-3}\cdot\text{s}^{-1}$ ,  $D_e \min = 0.3 \times$   
 $\times 10^{-10} \text{ m}^2\cdot\text{s}^{-1}$ , 5 -  $q_i = 300 \text{ mg}\cdot\text{m}^{-3}\cdot\text{s}^{-1}$ ,  $D_i \max = 9\cdot 10^{-10} \text{ m}^2\cdot\text{s}^{-1}$ ,  $q_e = 10 \text{ mg}\cdot\text{m}^{-3}\cdot$   
 $\times \text{s}^{-1}$ ,  $D_e \max = 3.3\cdot 10^{-10} \text{ m}^2\cdot\text{s}^{-1}$

Fig. 4. Influence d'épaisseur du film d'eau sur la concentration d'oxygène actuelle à l'extérieur du film d'eau sur la racine ( $C'_{R+d}$ ) et les valeurs extrêmes de  $q_i$ ,  $D_i$  et  $D_e$  ayant lieu dans les sols et racines au rayon  $R = 0,25$  mm (calculé à partir de l'équ. 20)

The knowledge of oxygen consumption in a unit of its volume  $q_i$  permits the calculation of a unit oxygen flow  $f_r$  related to a unit of root surface. If the root has a length  $l$  and a radius  $R$ :



$$f_r = \frac{R^2 l q_i}{2 R l} = \frac{R q_i}{2}, \quad (22)$$

which, after combining with equation (16), gives:

$$f_r = D_e \frac{C_{R+d} - C_R}{R \ln(1 + \frac{d}{R})}. \quad (23)$$

This has been presented by numerous authors, e.g., Lemon [166], Lemon and Erickson [167, 168], and Stolzy et al. [242].

The method of measuring the  $f_r$  value using polarographic method, which is also named Oxygen Diffusion Rate (ODR) has been elaborated by Lemon and Erickson [167, 168].

It should be emphasized here that during the measurement of the value of flow  $f_r$  by means of the polarographic method using a platinum electrode (simulating the root) it is assumed that  $C_R$  equals zero at a surface of the electrode. In the case of a root this is a simplification, as the critical concentrations of oxygen on the root surface are not lower than  $0.02-0.03 \text{ m}^3 \cdot \text{m}^{-3}$ .

In view of the analogy of the mathematical description of diffusion flow to electrical current flow where the intensity of diffusive flow corresponds to the intensity of electric current, and the difference between concentrations corresponds to the difference in the electric potential, in the design of electrical analogues of diffusion the concepts of diffusive permeability of a medium  $P_D$  [185] and its reciprocal known as diffusive resistance  $R_D$  [19] are introduced. These parameters are frequently used in the description of gas exchange in roots and in photosynthesis research.

In the case of uniaxial diffusion, diffusive permeability  $P_D$  is equal to a ratio of the diffusion coefficient  $D$  to the length of the diffusion path  $\Delta x$ :

$$P_D = \frac{D}{\Delta x} \quad (24)$$

and is expressed in  $\text{m} \cdot \text{s}^{-1}$ .

Fick's equation

$$f_x = -D \frac{dC}{dx} \quad (25)$$

for the diffusion flow  $f_x$  may, therefore, be written as follows:

$$f_x = P_D \Delta C, \quad (26)$$

where:

$\Delta C$  is a difference in the concentrations over the distance  $\Delta x$ ,

$P_D$  is a diffusive permeability of the medium.

Considering that:

$$P_D = \frac{1}{R_D} \quad (27)$$

Fick's equation may be expressed in a form analogous to Ohm's law, that:

$$f_x = \frac{\Delta C}{R_D}, \quad (28)$$

where:

$R_D$  is expressed in  $s \cdot m^{-1}$ .

The use of the concept of diffusion resistance is convenient in that it permits the summation of diffusion resistance values along the diffusion path, in a manner analogous to the summation of electrical resistances. This is important e.g., when determining the diffusion resistance of the whole plant, the complete root system, or individual roots, where we do not have an exact distribution of the diffusion coefficient which surely differs between the root epidermas and the internal tissues. In the literature there is a lack of empirical data concerning the values of the radial diffusion coefficient in the roots.

In roots with no air-filled spaces, the oxygen diffusion coefficient is undoubtedly less than  $2.1 \cdot 10^{-9} \text{ m}^2 \cdot \text{s}^{-1}$  (at  $20^\circ\text{C}$ ), i.e., below that for pure water, due to obstacles in the form of cell walls. Estimated values of this coefficient adopted by various authors are from  $2.2 \cdot 10^{-10}$  to  $9 \cdot 10^{-10} \text{ m}^2 \cdot \text{s}^{-1}$  [169].

As is known, plant root porosity may be considerable and occasionally even reach  $0.6 \text{ m}^3 \cdot \text{m}^{-3}$  [19]. It is difficult, however, to say whether and to what extent it effects an increase in the radial diffusion coefficient in roots because of the lack of data from direct measurements.

Radial diffusion permeability of adventitious roots of maize, as measured by Luxmoore et al. [185] was  $4.8 \cdot 10^{-6}$ , and for rice  $1-11 \cdot 10^{-6} \text{ m} \cdot \text{s}^{-1}$ , and in both cases decreased with increase in the distance from the root tips (Fig. 5). In this figure it can also be seen that, contrary to expectations, an increase in porosity with increase in the distance from the root tips is accompanied, not by an increase in the diffusive permeability, but by its decrease. This probably follows from the ageing of the root epidermas and decrease in their permeability.

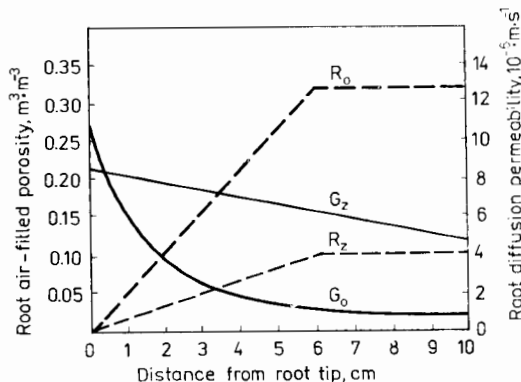


Fig. 5. Air-filled porosity of soil (G) and radial diffusive permeability (R) of maize (z) and rice (o) as a function of the distance from the root tip [96]

Fig. 5. Porosité à l'air de sol (G) et perméabilité diffusive radiale (R) du maïs (z) et du riz (o) en fonction de la distance du cône de croissance [96]

### 2.2. Longitudinal diffusion

It is well known that plant roots may contain free spaces filled with air [6, 12, 13, 19, 139, 264] the volume of which, in the case of aquatic plants, is comparable to the air-filled porosity of soils. These are intercellular space having continuity along the root down to a distance of 2-3 mm from the root tip. They are found in the suberized root tissue known as aerenchyma [77].

The porosity of mesophyte roots is slight (of the order of several per cent of the root volume), however, under conditions of soil inundation with water, even with these plants it is quite common to find the development of adventitious roots containing aerenchyma [79] and having a porosity much greater than in the primary roots [181]. This results in an increase in root porosity under conditions of insufficient oxygen supply from the soil (Table 1).

The existence of a continuous system of air spaces in root tissue makes an internal gas exchange possible both through diffusion and through mass flow. As to the relative contribution of the two mechanisms, in relation to roots all the considerations presented for soils [95] are applicable, including the general conclusion that diffusion is the fundamental mechanism of gas transport. This is true in relation to the transport of oxygen downwards in the roots, but the upward transport of carbon dioxide is also facilitated by the transpiration stream.

The existence of the diffusive transport of oxygen to the roots has been shown experimentally by mean of labelled oxygen for English bean [86], maize [134, 135] and barley [24, 135].

T a b l e 1. Root porosity  
T a b l e a u 1. Porosité de racine

Plant	Porosity, $m^3 \cdot m^{-3}$		Ref.
	abundance of oxygen in soil	oxygen deficiency in soil	
Rice	0.05	0.25-0.30	[24, 92]
Maize	0.06-0.07	0.12-0.17	[197, 287]
Festuca	0.02	0.06	[197]
Barley	0.03	0.04	[287]
Sunflower	0.06	0.12	[287]
Wheat	0.21-0.126	0.035-0.145	[2, 180, 231, 233, 263]
Tomato	0.05	0.08	[287]

Investigations of the transport of ethylene in rice have shown that it is proportional to the fresh mass of the plant and does not depend on illumination nor on illumination related changes in the transpiration stream [165], which indicates that the exchange of gas between the plant and the atmosphere is not a factor limiting the total process of gas transport in the plant. This is supported by the investigations by Ando et al. [10], Stelzer and Läuchli [238]. The latter authors have found that oxygen enters the root system mainly at the stem base. It has also been found that oxygen can diffuse from roots to the surrounding medium in the case of rice [15, 16, 261, 262], bog-bean [57], maize [134], barley [258] and bog plants [14].

In the case of bog plants internal gas transport suffices to cover the oxygen requirements of the whole root system, with mesophytes it constitute only a supplementary factor.

Quantitative determination of the role of internal longitudinal diffusion is complicated by the closing of stomata under conditions of insufficient oxygenation [130, 232, 233]. However, it follows from the publications quoted previously [165, 238] that changes in the diffusive resistance in leaves should not affect the resultant oxygen transport in the roots to any significant degree.

The distribution of oxygen concentration at a depth  $x$  in a straight vertical root of constant diameter and length  $L$ , under conditions of no radial transport to or from the surrounding medium, assuming that both the respiratory activity  $q$  and the oxygen diffusion coefficient  $D$  in the root are constant along the whole length of the root and that  $q$  is not a function of oxygen concentration, can be described in a manner analogous to soil [96] by the following equation:

$$C = C_0 - \frac{q(2Lx - x^2)}{2D}, \quad (29)$$

where:

$C_0$ , in this case, is the concentration of oxygen at the beginning of the root, i.e., at  $x = 0$ .

Oxygen concentration at the tip of the root, i.e., at  $x = L$ , is:

$$C_L = C_0 - \frac{qL^2}{2D}. \quad (30)$$

If we assume that the growth of roots stops when the critical concentration of oxygen,  $C'$ , is reached at the root tip, then the limit of root penetration into a soil innudated with water,  $L'$ , is:

$$L' = \sqrt{\frac{2D(C_0 - C')}{q}}. \quad (31)$$

The root oxygenation depth,  $L_{an}$ , can be calculated by means of equation (30) substituting values  $C_L = 0$  and  $L = L_{an}$ . Then:

$$L_{an} = \sqrt{\frac{2DC_0}{q}}. \quad (32)$$

Replacing the atmospheric concentration of oxygen  $C_0$  and the diffusion coefficient in the root  $D$  with partial pressure of oxygen in the atmosphere  $P_0$  and the diffusion constant in the root  $K$ , respectively [96] we get:

$$L_{an} = \sqrt{\frac{2KP_0}{q}}. \quad (33)$$

The length  $L_{an}$  can represent both the depth at which oxygen concentration in the roots drops to zero, and the limit depth of root penetration in an anoxic medium, if the growth of the roots ceases at an oxygen concentration level of zero. A graphic interpretation of this relationship has been presented in Figure 6, where the value  $K/K_0$ , as long as the diffusion takes place in the gaseous phase, is equivalent to  $D/D_0$ , and may be interpreted, in relation to root, as its effective porosity. We can see that when this porosity is below  $0.05 \text{ m}^3 \cdot \text{m}^{-3}$  at normal respiration values (approximately  $100 \text{ mg} \cdot \text{m}^{-3} \cdot \text{s}^{-1}$ ) in the absence of radial diffusion from the soil the oxygenated section of the roots is only about 7 cm, and therefore longitudinal transport is significant only for the part of the root system near the soil surface.

The literature of the subject does not quote any data concerning the longitudinal diffusion coefficient in the roots, hence it is difficult to use data from Figure 6 in practice. These difficulties are compounded by the simplifying assump-

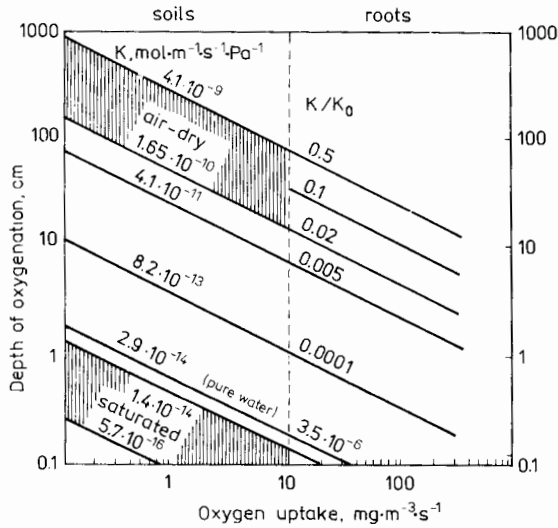


Fig. 6. Soil oxygenation depth under steady-state conditions as a function of respiration rate of soils and roots, calculated from eq. 33 [239]

$K_0$  - oxygen diffusion coefficient in air (equal to  $8.26 \cdot 10^{-9} \text{ mol} \cdot \text{m}^{-1} \cdot \text{s}^{-1} \cdot \text{Pa}^{-1}$  at  $20^\circ\text{C}$ )

Fig. 6. Profondeur d'aération du sol dans les conditions permanentes en fonction de la vitesse de respiration des sols et des racines calculée à partir de l'équ. 33 [239]

$K_0$  - coefficient de la diffusion d'oxygène à l'air

tions adopted in the development of the equations in this part of the text. The assumptions referred to are: no radial diffusion, constant values of the diffusion coefficient and of the respiratory activity of the root along its whole length, and  $q$  independent of oxygen concentration. All these assumptions are not met in reality, as  $q$  is greatest at the tip of the root (184) and decreases at oxygen concentrations below the critical value (96) and root porosity (and probably also the longitudinal diffusion coefficient) decrease in the direction of the growing tip of the root.

Calculations made by Luxmoore et al. [182-187] have shown that in the case of maize about 25% of the root requirement for oxygen is met by longitudinal internal transport. The investigations of Greenwood [101] involving 12 vegetable plants have shown that the internal aeration of their roots is significant for only a 5 cm section of root measured from the soil surface.

A similar evaluation of the significance of internal transport in mesophytes has been arrived at by Yu et al. [287], investigating the penetration depth for the roots of 5 plants in a soil completely saturated with water. Under these conditions the porosity of the roots of maize increased from 0.075-0.115 to 0.15-

$0.18 \text{ m}^3 \cdot \text{m}^{-3}$  while the depth of root penetration into the soil was 17 cm. For sunflower the porosity increased from 0.06 to  $0.11 \text{ m}^3 \cdot \text{m}^{-3}$ , and the penetration depth was 15 cm. The porosity of the roots of barley was about  $0.035 \text{ m}^3 \cdot \text{m}^{-3}$  and did not show any significant changes under the conditions of inundation with water, while their penetration depth was 12 cm. In the case of wheat the root porosity increased from 0.04 to  $0.08 \text{ m}^3 \cdot \text{m}^{-3}$ , and the penetration depth was 10 cm. Another wheat variety, however, increased its root porosity from 0.06 to  $0.15 \text{ m}^3 \cdot \text{m}^{-3}$  with a root penetration depth of only 5 cm. Tomato roots increased their porosity from 0.04 to  $0.08 \text{ m}^3 \cdot \text{m}^{-3}$  with a penetration depth of 6 cm.

The differences in the penetration depth of roots with similar porosity may be the result of differences in both their respiratory activity and in the values of their longitudinal diffusion coefficients. It seems, however, in view of the continuity of the intercellular pores, that the differences in the respiratory activity are probably more significant than in longitudinal diffusion.

Some other aspects of gas exchange in soil environment under flood conditions are treated elsewhere [239].

### 3. ROOT RESPIRATION AND FACTORS AFFECTING IT

Root respiration varies among plant species from that of several up to several hundreds and even up to  $1,600 \text{ cm}^3 \text{ O}_2$  or  $\text{CO}_2$  per kg of root fresh weight per hour (Table 2).

It is closely connected with root activity and especially with root growth (growth respiration), maintenance processes (maintenance respiration) and uptake and transport of ions - ion uptake respiration [106, 107, 160-164, 266, 267].

According to Szaniawski [244-246] the ratio of maintenance respiratory activity of the whole shoot to that of the entire root system remains for a given plant constant irrespective of growth temperatures (from 10 to  $30^\circ\text{C}$ ) and shoot to root ratios (from 2 to 7). It was equal about 1.1 for sunflower [244] and 1.75 for cucumber [245].

Root growth respiration is the amount of oxygen used to produce 1 g of dry mass. The values of root growth respiration measured for several plant species by Lambers and Steingröver [161, 162] has been found to be from 390 to 1430  $\text{mg O}_2$  per gram dry weight. It was also found that for the same plant (*Senecio aquaticus*) grown in anoxic conditions, root growth respiration was three times lower than in the aerated culture [161].

Root activities mutually influence each other. For instance, a decrease in root respiration under low oxygen conditions has a negative effect on ion uptake, whereas decrease in ion uptake by low ion concentrations has a negative influence on root respiration.

T a b l e 2. Respiratory activity of root fresh weight in  $\text{cm}^3 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$   
 T a b l e a u 2. Respiration des racines fraîches,  $\text{cm}^3 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$

Plant	O <sub>2</sub> or CO <sub>2</sub>	Respiration	Ref.
Bean	O <sub>2</sub>	250-325	[224]
Soybeans	O <sub>2</sub>	330-470	[200]
Maize	O <sub>2</sub>	360-580	[200]
Barley	O <sub>2</sub>	100-650	[44]
Oats	CO <sub>2</sub>	0-1,500	[87]
Carrot	O <sub>2</sub>	115-190	[200]
Onion	CO <sub>2</sub>	300-1,600	[31]
Potato tubers	O <sub>2</sub>	2.3-3.2	[235]
Alfalfa	CO <sub>2</sub>	112	[28]
Trefoil	CO <sub>2</sub>	114.2-136.6	[28]
Pears	CO <sub>2</sub>	24.9-133.2	[9]
Sugar maple	O <sub>2</sub>	134-245	[45]
" "	CO <sub>2</sub>	95-225	[45]
Red maple	O <sub>2</sub>	161-221	[45]
" "	CO <sub>2</sub>	113-191	[45]
Baldcypress	O <sub>2</sub>	168-226	[45]
"	CO <sub>2</sub>	119-202	[45]

Veen [267] examined during the 7 experimental days the relation between root respiration and root activity of a maize root system. He found oxygen consumption per unit of root growth equal to  $24.5 \text{ mg O}_2 \cdot \text{g}^{-1}$  and per unit of ion uptake equal to  $36.8 \text{ mg} \cdot \text{O}_2 \text{ meq.}^{-1} \cdot \text{NO}_3^{-1}$  ( $\text{NO}_3^{-1}$  was used as a measure of the total uptake).

The change of the light period (the amount of light supplied to the shoot) had a strong effect on the ion uptake, but only a small effect on root respiration (Fig. 7).

Studies by Hausen [106] revealed, however, that root respiration of *Lolium multiflorum* L. during 2 to 3 day periods of high illumination was 3 to 4 times higher than that of low illumination. After defoliation, root respiration decreased and was not affected by the illumination level until the regrowth of new leaves.

Under normal conditions ion uptake respiration is of considerable importance and amounts to 60% of the total root respiration, which is shown in Table 3.



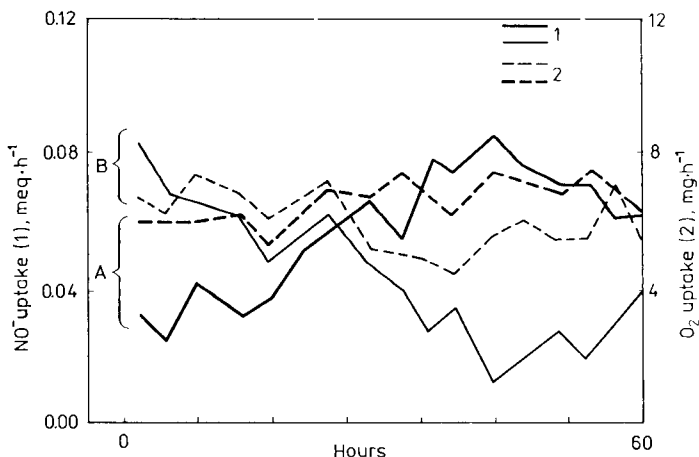


Fig. 7. Effect of increasing (A) and decreasing (B) the light period on NO<sub>3</sub><sup>-</sup> uptake (1) by maize roots and root respiration (2) [267]

Fig. 7. Influence de l'augmentation (A) et de la diminution (B) du temps d'illumination sur l'absorption de NO<sub>3</sub><sup>-</sup>(1) par les racines de maïs et sur la respiration racinaire (2) [267]

T a b l e 3. Relative energy consumption of uptake, growth and maintenance processes for roots of maize at light intensity 70 W·m<sup>-2</sup> [267]

T a b l e a u 3. Consommation relative d'énergie dans les processus d'absorption, de croissance et de maintenance dans les racines de maïs quand l'intensité de lumière est 70 W·m<sup>-2</sup> [267]

Day number	Per cent of total respiration used for		
	ion uptake	growth	maintenance
3	39	52	9
4	49	42	9
6	60	24	16

### 3.1. External factors

#### 3.1.1. Oxygen

Root respiration is the first process to be restricted by oxygen deficiency. Other disturbances of the vital functions of plants are the consequence of the respiration disturbances.

Anderson et al. [9] after examining the effect of root anaerobiosis of 6 plant varieties on their respiration found that respiration of feeder roots

Table 4. Effect of treatment (aerobic, anaerobic), incubation conditions (21% O<sub>2</sub> and 0.5% O<sub>2</sub>) and treatment duration (12, and 26 days) on root respiration on 3 "Barlett" grafted pear rootstocks [9]

Tableau 4. Effet du traitement (aérobie, anaérobie), des conditions d'incubation (21 % O<sub>2</sub> et 0,5 % O<sub>2</sub>) et de la durée de traitement (12 et 26 jours) sur la respiration des racines de 3 poiriers [9]

Treatment	Root respiration, cm <sup>3</sup> CO <sub>2</sub> ·kg <sup>-1</sup> ·h <sup>-1</sup> fr. wt.				
	incubation % O <sub>2</sub>	duration days	<i>P. betulaeifolia</i>	<i>P. callergana</i>	<i>P. communis</i>
Aerobic	0.5	12	40.0	41.7	52.7
		26	60.0	106.2	64.5
	21	12	72.1	99.5	87.6
		26	84.1	133.2	74.0
Anaerobic	0.5	12	41.7	30.2	40.3
		26	45.6	48.0	26.6
	21	12	62.4	35.6	53.4
		26	97.7	66.1	24.9

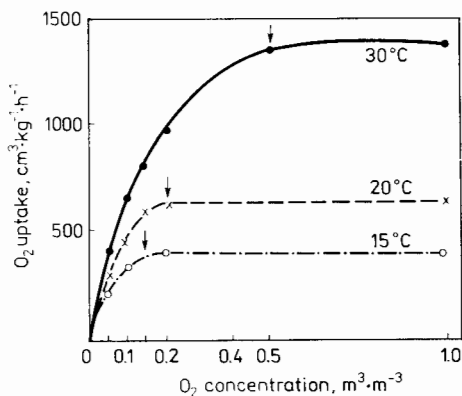


Fig. 8. Influence of oxygen concentration, at different temperatures, on the respiration of onion root-excised segments 0-5 mm from the tip. Arrows mark critical oxygen concentration, below which limitation of respiration by oxygen availability appears [96]

Fig. 8. Influence de la concentration d'oxygène à différentes températures sur la respiration des segments racinaires excisés d'oignon 0-5 mm du cône. Les flèches indiquent la concentration critique d'oxygène, au-dessous de laquelle on observe la limitation de respiration [96]

(< 2 mm diameter) in air (0.21 m<sup>3</sup>·m<sup>-3</sup>) of *Pyrus betulaeifolia*, *Pyrus calleryana*, *Pyrus communis* and *Cydonia oblonga* was reduced by no more than 50% after 26 days of anaerobiosis. In contrast, root respiration of *Prunus persica* was reduced by 80% with anaerobiosis, whereas that of *Salix discolor* increased. Respiration rates of anaerobically or

aerobically treated pear roots were inhibited by 25% to 50% when incubated in 0.5% O<sub>2</sub> compared to rates in air (Table 4).

The influence of oxygen concentration at different temperatures on the respiration rate of excised onion roots is shown in Figure 8. The curves in this Figure have two basic parts: the range of respiration limitation by oxygen concentration and a flat part where respiration rate is not dependent on oxygen concentration. Respiration rate in this range of oxygen concentrations achieves its maximum value for a given temperature and will be called maximum respiration ( $q_{\max}$ ). The critical oxygen concentration (COC) values increase with temperature and are, for excised onion roots, equal from 0.10 to 0.15 m<sup>3</sup>·m<sup>-3</sup> at 15°C [30, 31]. Equally high COC values for the respiration of excised roots were found for *Eriophorum angustifolium* - 0.15 m<sup>3</sup>·m<sup>-3</sup>, pea - about 0.20 m<sup>3</sup>·m<sup>-3</sup> [7], and *Senecio aquaticus* - 0.15 m<sup>3</sup>·m<sup>-3</sup> [160].

Atwell et al. [21] examining COC for respiration of excised root segments of maize found 0.117 and 0.065 mol O<sub>2</sub>·m<sup>-3</sup> in the expanding and expanded zones of the roots, respectively. In contrast, the COC exceeded 0.20 mol O<sub>2</sub>·m<sup>-3</sup> in the apex, suggesting that O<sub>2</sub> supply for metabolic processes is most likely to be sub-optimal in this zone. Their results show clearly that the adverse effects of low O<sub>2</sub> concentrations are unlikely to be a consequence of substrate shortage for either respiration or synthesis of macromolecules.

Because the activity of cytochrome oxidase decreases abruptly at very low oxygen concentrations (below 0.01 m<sup>3</sup>·m<sup>-3</sup>) one can assume that with a COC at the root surface, oxygen concentration at the root axis approaches zero.

COC depends not only on the maximum root respiration ( $q_{\max}$ ) but also on other factors, which is shown by the equation:

$$\text{COC} = \frac{q_{\max} R^2}{4D_i}, \quad (34)$$

where:

R is the root radius,

D<sub>i</sub> is the coefficient of radial diffusion of oxygen in root tissue.

The thicker the root and the lower the oxygen diffusion coefficient within it, the higher the COC value.

In addition to COC, a half respiration concentration of oxygen (HRC), analogous to Michaelis constant, is used. The HRC values for excised root segments are

within 0.07 to 0.12  $\text{m}^3 \cdot \text{m}^{-3}$  for maize, 0.05 to 0.25  $\text{m}^3 \cdot \text{m}^{-3}$  for rice at 25°C [184], and 0.025  $\text{m}^3 \cdot \text{m}^{-3}$  for *Senecio aquaticus* [160]. The HRC values estimated from data of Berry and Norris [31] for excised onion roots are within 0.04 to 0.11  $\text{m}^3 \cdot \text{m}^{-3}$ .

There is an opinion [19, 20] that those high COC and HRC values obtained in vitro for excised roots are an artifact of the measurement conditions due to filling of the intercellular air spaces by liquid. For an intact root system, the oxygen diffusion coefficient should be much higher, implying lower COC values (cf. equation 34).

This point of view is supported by the results obtained by Armstrong and Gaynard [20] who found, for roots of intact rice and *Eriophorum angustifolium* plants, COC values within 0.016 to 0.027  $\text{m}^3 \cdot \text{m}^{-3}$  and HRC values below 0.001  $\text{m}^3 \cdot \text{m}^{-3}$ .

It can be seen that these values are almost one order of magnitude lower than those quoted above for excised roots. The results of Armstrong and Gaynard [20] are more convincing, because the same authors found out that for excised roots of *Eriophorum angustifolium*, COC equals to 0.15  $\text{m}^3 \cdot \text{m}^{-3}$  and HRC equals to 0.03  $\text{m}^3 \cdot \text{m}^{-3}$ .

Additionally, Lambers and Smakman [161] reported, for intact root systems of six *Senecio* species grown in nutrient solution (but cut off from the tops), relatively low HRC values amounting to about 0.02  $\text{m}^3 \cdot \text{m}^{-3}$ , although their COC values are rather high (about 0.20  $\text{m}^3 \cdot \text{m}^{-3}$ ).

Similar HRC values (0.005 to 0.02  $\text{m}^3 \cdot \text{m}^{-3}$ ) for intact roots of mustard seedlings were reported by Greenwood [102], and Greenwood and Goodman [103].

The COC values obtained from roots grown in soil (Table 5) resemble those found for both excised and intact roots in solution.

However, HRC values for intact roots in soil are apparently lower than for excised roots. This is in agreement with the view of Armstrong and Gaynard [20] although the HRC values for intact roots are not so low as these authors suggest.

The most credible view seems to be that presented by Armstrong [19], Armstrong and Gaynard [20], and Greenwood [100] which proves right that root respiration does not decrease unless the oxygen partial pressure on the root surface is lower than 1 to 2 kPa. This is in agreement with physiological theory, as it has been established that cytochrome oxidase has a high affinity for oxygen.

On this basis, the higher values of COC found in the literature must be the result of the presence of water films on the root surface or the result of the diffusive resistance of the plant tissue. Nevertheless, the phenomenon of decreasing root respiration at a soil air oxygen pressure of a few kPa does in fact occur [226, 247].

The above picture is, however, a considerable simplification because condi-

Table 5. Comparison of the critical oxygen concentration (COC) and half respiration concentration (HRC) values for plant roots

Tableau 5. Comparaison de la concentration critique d'oxygène (COC) et de la concentration de demi-respiration (HRC) pour les racines

Roots	Plants	COC $\frac{3}{m^3 \cdot m^{-3}}$	HRC $\frac{3}{m^3 \cdot m^{-3}}$	Ref.
Excised	onion	0.10-0.50	0.04-0.11	[30, 31]
	Eriophorum			
	angustifolium	0.15	0.03	[19]
	peas	0.20		[7]
	maize	0.05-0.16		[21]
	maize		0.07-0.12	[184]
	rice		0.05-0.25	[184]
Whole in solution	Senecio	0.15-0.20	0.02-0.025	[161]
	E. angustifolium and rice	0.16-0.027	0.001	[19]
	mustard	~0.20	0.005-0.10	[102, 103]
Intact	maize	0.10	~0.02	[213]
	cotton	0.21	<0.01	[248]
	dwarf peas	0.15	0.02-0.04	[226]

tions of full oxygenation or of complete anoxia hardly ever, if ever, occur within plant roots. This is especially underlined by Crawford [64] who draws attention to the fact that root meristemes display some anoxic metabolism even in contact with atmospheric air. This is confirmed by the high respiratory quotients in meristemes and the presence of ethanol in them [64].

Because it is difficult to assess the thickness of the moisture films usually present on the root surface in soil conditions and their role in impeding the diffusion of oxygen, it is not easy to assign a value to the real oxygen concentration on root epidermas. This is the reason for the higher COC and HRC values observed in soil conditions as compared with those predicted by biochemistry or found with the use of special experimental techniques [20]. The involvement of the water films on root surface makes it difficult to directly relate root respiration and other plants responses to oxygen content in soil air which was treated more extensively in Chapter 5.

When the oxygen concentration in the root environment decreases the zone of anoxic metabolism localized in the meristeme expands to the other parts of the root system although rarely, if ever, occupying it entirely because its upper parts are supplied with oxygen through internal diffusion from the shoots.

Thus the physiological role of the decline in oxygen uptake by the root system as a whole, observed below the critical value of oxygen concentrations in the surroundings, may be of greater importance, than is implied by the relative value of this decline as these anoxic areas, although limited in size, are located in the parts which are most important for root functioning.

It should, however, be emphasized that a partial limiting of the root respiration rate does not necessarily mean a reduction in the root elongation rate [103].

It must be stressed that after a short anaerobic period which does not injure the roots permanently, an increased oxygen uptake by the roots appears (the so called "respiration rebound"). This phenomenon has been observed both in excised roots [288] and in intact roots [82, 282].

### 3.1.2. Carbon dioxide

The effect of carbon dioxide on root respiration has been little studied. Harris and van Bavel [108] reported that  $0.05 \text{ m}^3 \cdot \text{m}^{-3}$  of carbon dioxide in soil air entirely inhibited root respiration of tobacco, maize, and cotton. However, Norris et al. [199] found that onion root respiration is less sensitive to carbon dioxide than is microbial respiration.

### 3.1.3. NPK fertilization

Also the influence of mineral fertilization on root respiration has been little studied. Figliolia et al. [87] recorded that the respiration of oat roots in a nutrient solution was lowered by a deficiency on N and P, but was not influenced by K availability.

### 3.1.4. Ethylene

There are some papers [212, 235] indicating a stimulatory effect of ethylene on respiration of potato tubers, at concentrations which may occur in soil. A suppressing effect of  $5 \text{ cm}^3 \cdot \text{m}^{-3}$  of ethylene in soil air on respiration of grapevine roots was reported by Ishii et al. [125].

## 3.1.5. Temperature

Respiration of roots increases exponentially with temperature (Figure 9). Initially, this increase is rapid when the respiration rate is limited by biochemical reactions. At higher temperatures the transport of substrates and products of the metabolism (sugars, oxygen, carbon dioxide), based mainly on the diffusion process, becomes the limiting factor. At temperatures above 35°C the protoplasm system is starting to break down.

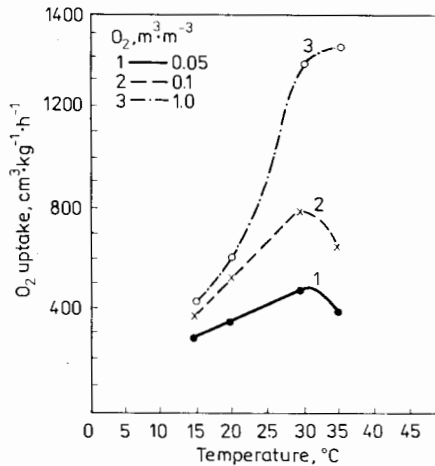


Fig. 9. Respiration of excised segments of onion roots (0-5 mm from tip), at different O<sub>2</sub> contents, as related to temperature [96]

Fig. 9. Respiration des segments racinaires excisés (0-5 mm du cône) à différentes teneur en oxygène, suivant la température [96]

Limitation of respiration through the physical processes of diffusive transport may also occur at lower temperatures if the oxygen concentration is low, which is shown in Figure 9 by the curves corresponding to 0.05 and 0.10 m<sup>3</sup>·m<sup>-3</sup> of oxygen. These curves have been plotted on the basis of the data from Figure 8.

The curves 1 and 2 corresponding to oxygen concentration below 0.1 m<sup>3</sup>·m<sup>-3</sup> illustrate the range of respiration limitation caused by oxygen, and the curve 3 concerning pure oxygen illustrates the limitation of respiration due to internal factors in the tissue.

In order to describe the influence of temperature on root respiration, the Arrhenius equation was applied:

$$\ln q = c + T \ln Q_{10}/10, \quad (35)$$

where:

$q$  is respiration rate at a temperature  $T$ ,

$c$  is constant,

$Q_{10}$  is the so-called  $Q$ -ten temperature coefficient, showing how many times the respiration intensity increases when the temperature increases by  $10^{\circ}\text{C}$ .

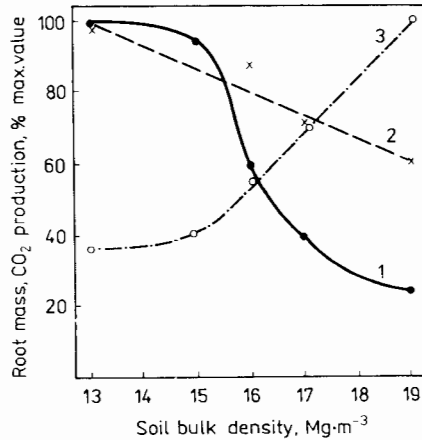


Fig. 10. Arrhenius plot for respiration of excised roots of barley (1) and maize (2) [96]

Fig. 10. Graphique d'Arrhenius pour la respiration des racines excisées d'orge (1) et de maïs (2) [96]

In most cases [31, 44, 67, 169] a change in the slope of the plot of  $\ln q$  vs.  $1/T$  was observed (Fig. 10). This change of the slope, which indicates a change of activation energy, denotes a change of the limiting factor with temperature. The values of activation energy for respiration of roots reported in the literature are very differentiated. Thus for onion roots, Berry and Norris [31] found values within 7 to 59  $\text{kJ mol}^{-1}$  roots, while Lemon and Wiegand [169] reported 45 to 75  $\text{kJ} \cdot \text{mol}^{-1}$ . In turn Carey and Berry [44] found 49 to 116  $\cdot \text{kJ mol}^{-1}$  for maize and 54  $\text{kJ} \cdot \text{mol}^{-1}$  for maize and 54  $\text{kJ mol}^{-1}$ .

### 3.1.6. Soil mechanical impedance

The plant roots need more energy while penetrating a compact soil layer. Thus their oxygen requirements in that situation should be higher. This has been proven in experiments on plants grown in nutrient solution with and without mechanical obstacles of glass beads, where oxygen uptake by bean roots has been studied [224], as well as in compacted soil in which carbon dioxide production by cotton roots was followed [248].



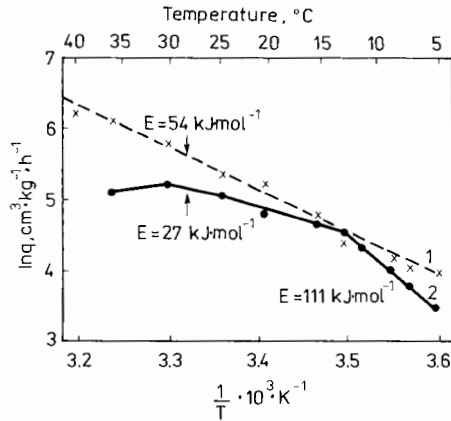


Fig. 11. Influence of soil compaction on the respiration rate and weight of cotton roots in the percent of maximum values [96]  
 1 - dry mass, 2 - total CO<sub>2</sub> production by root system, 3 - CO<sub>2</sub> evolution per root dry mass unit

Fig. 11. Influence du tassement de sol sur la vitesse de respiration et le poids des racines de cotonnier en pour cent des valeurs maximales  
 1 - matière sèche, 2 - la production totale de CO<sub>2</sub> par le système racinaire, 3 - dégagement de CO<sub>2</sub> par l'unité de matière sèche de racine

It should be emphasized, in the latter case, that although a fivefold increase in carbon dioxide production per root mass unit, resulting from soil compaction, was observed, the mass of the entire root system and its total carbon dioxide production were negatively correlated with soil bulk density (Fig. 11).

### 3.1.7. Soil salinity

One of the external factors influencing root respiration is soil salinity, though its effect has not been studied extensively. It was found [138] that the respiration rate of exised root segments of *Tamarix tetragyna* decreased linearly with the increase of NaCl concentration in the solution.

### 3.1.8. Redox potential and soil acidity

Anaerobic rice root respiration under controlled soil redox conditions and acidity was investigated by Tolley et al. [251]. Using the activity of the inducible enzyme alcohol dehydrogenase (ADH) as an indicator of anaerobic root respiration, they found a decrease in redox potential resulted in an increase in root ADH (Fig. 12). Soil acidity also seems to have had an effect since production of ADH at pH

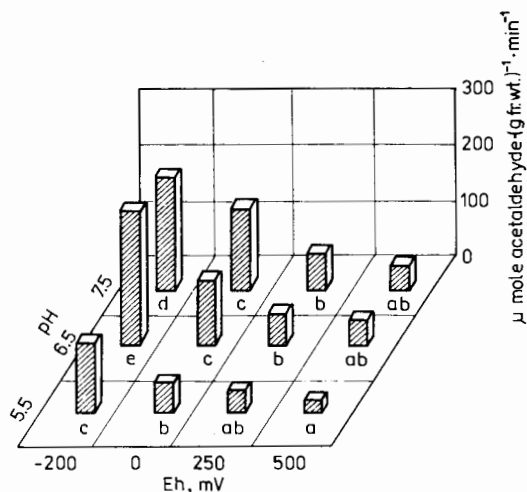


Fig. 12. Root ADH activity as affected by soil pH and redox conditions (Eh)[251]. Values followed by the same letter are not statistically different at the 5% level

Fig. 12. Activité de ADH de racine sous l'influence de pH et des conditions d'oxydoréduction du sol [251]. Les valeurs désignées par les mêmes lettres ne sont pas statistiquement différentes sur le niveau de confiance de 5 %

5.5 was lower than at 6.5 and 7.5. This was apparently due to the relationship which exists between redox potential and pH.

### 3.2. Internal factors

The limitation of root respiration by internal factors results from the properties of the respiring tissue (these being related to the genetic background and physiological age of the plant) as well as from the effect of the shoots.

It was found that the respiration intensity is highest in the apical part of the root and decreases with the distance from the root tip [30, 31, 184, 188], as shown in Figure 13.

Root respiration during the vegetation period undergoes specific changes independently of the effect of temperature or other external factors. Thus the root respiration of the perennial desert shrub *Atriplex confertifolia*, measured at constant temperature, showed spring and autumn maxima [113]. According to the authors of that paper, this phenomenon may be connected with the reflection of environmental preconditioning, as well as with an overall genetically based program of the plant development.

In the case of maize grown in controlled conditions [11], maximum respiration of the entire root system was  $800 \text{ cm}^3 \text{ CO}_2$  per plant per day during the appearance

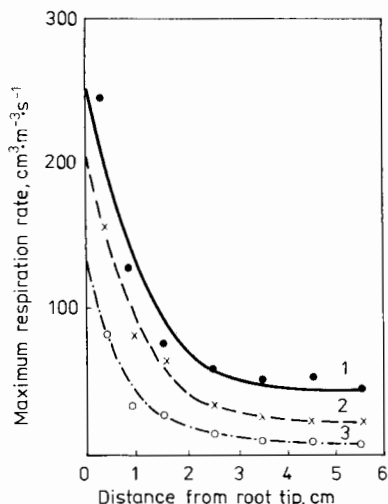


Fig. 13. Respiration rate of rice roots in the atmosphere containing the following concentration of oxygen: 1 -  $0.8 \text{ m}^3 \cdot \text{m}^{-3}$ , 2 -  $0.208 \text{ m}^3 \cdot \text{m}^{-3}$ , 3 -  $0.044 \text{ m}^3 \cdot \text{m}^{-3}$  [96]

Fig. 13. Vitesse de respiration des racines du riz dans l'atmosphère contenant les concentrations suivantes d'oxygène: 1 -  $0,8 \text{ m}^3 \cdot \text{m}^{-3}$ , 2 -  $0,208 \text{ m}^3 \cdot \text{m}^{-3}$ , 3 -  $0,044 \text{ m}^3 \cdot \text{m}^{-3}$  [96]

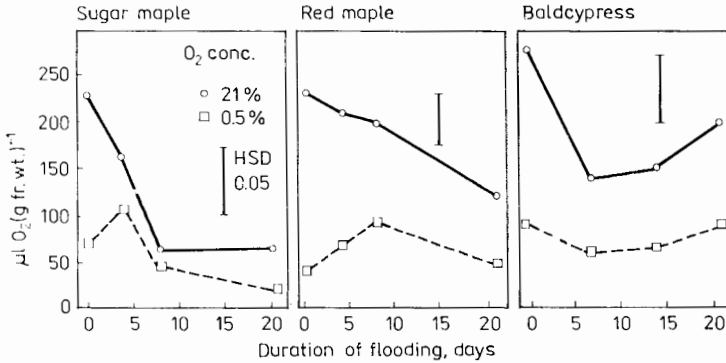
of panicles. Later the respiration rate decreased to about  $400 \text{ m}^3 \text{ CO}_2$  per day per plant, and oscillated around this value until plant senescence.

Besides seasonal dynamics, plant roots also exhibit a diurnal variation in respiration rate. Huck et al. [123] pointed out that the root respiration of plants (maize, soybean, *Derris elliptica*) grown at constant temperature was 25 to 50% higher during the day than at night. On the other hand, root segments excised from the plants at different times of the day and night showed no differentiation in respiratory activity. Also no correlation was found between respiration rate and sugar content in the root, which eliminates substrate level as a cause of the variation observed. The mechanism of the variation has not been fully explained, but it is undoubtedly connected with the action of light and the presence of shoots [106, 107].

Studies by Hansen [106] revealed that the root respiration of *Lolium multiflorum* L. during 2 to 3 day periods of high illumination was 3 to 4 times higher than at low illumination. After defoliation, root respiration decreased and was not affected by illumination level until the regrowth of new leaves.

Some differentiation in root respiration rate was also found among the plants of different climatic zones [67] Roots of plants of cool regions showed higher respiration rates, at the same temperature, as compared with plants of warmer

zones. According to Crawford and Palin [67] high respiration rates at low temperatures can be an advantage for an earlier resumption of growth but at high temperatures they can lead to an excessive consumption of carbohydrate reserves.



Rys. 14. Oxygen consumption rates by excised tree roots at three O<sub>2</sub> levels after 0 to 22 days of flooding [45]

Fig. 14. Vitesse de consommation d'oxygène par les racines excisées des arbres pour trois niveaux d'oxygène après 0-22 jour d'inondation [45]

Lambers [160] reported that the root respiration rate of *Senecio aquaticus* (flood-tolerant species) was, at 20°C, lower than that of *Senecio jacobaea* (flood-intolerant). This would suggest that the low respiratory activity of roots may be an adoptive feature of increasing plant tolerance to flooding.

The respiratory capacity of flood pretreated roots of flood-tolerant, and intolerant trees (baldcypress - *Taxodium distichum*, red maple - *Acer rubrum*, and sugar maple - *Acer saccharum*) was examined by Carpenter and Mitchell [45, 46]. They found that flooding reduced root respiration capacity in all species affecting intolerant species the most and tolerant the least (Fig. 14).

Roots of all three species utilized O<sub>2</sub> with similar efficiency prior to flood stress. However, the respiratory capacity of sugar maple roots declined substantially during the first 8 days of flooding, and more gradually from 8 to 22 days, at 0.21 or 0.05 m<sup>3</sup>·m<sup>-3</sup> O<sub>2</sub>. Red maple roots declined gradually in respiratory capacity over the entire flooding period at 0.21, but not at 0.05 m<sup>3</sup>·m<sup>-3</sup> O<sub>2</sub>. After an initial sharp decline, baldcypress roots gradually regained capacity to utilize O<sub>2</sub> from 8 to 22 days of flooding at all 3 levels of O<sub>2</sub>. When tested at 0.21 m<sup>3</sup> × m<sup>-3</sup> O<sub>2</sub> both red maple and baldcypress roots had 2 to 3 fold higher respiratory capacities than had sugar maple roots after 22 days of flooding.

RQ values (the volumetric ratio of carbon dioxide evolved to oxygen consumed) were similar for all three species at 0.21 m<sup>3</sup>·m<sup>-3</sup>, and all decreased after flooding. At 0.05 m<sup>3</sup>·m<sup>-3</sup> O<sub>2</sub>, RQ values were higher for red maple and baldcypress than for sugar maple on both day 0 and day 8 (Table 6).

T a b l e 6. Respiratory quotient (RQ) for excised tree roots at two  $O_2$  levels ( $0.21$  or  $0.05 \text{ m}^3 \cdot \text{m}^{-3}$ ) and after 0 or 8 days of flooding [45]

T a b l e a u 6. Coefficient de respiration (RQ) des racines excisées d'arbre pour deux concentrations d'oxygène ( $0.21$  ou  $0.05 \text{ m}^3 \cdot \text{m}^{-3}$ ) et après 0 et 8 jours d'inondation [45]

$O_2$ concentration $\text{m}^3 \cdot \text{m}^{-3}$	Species	RQ	
		days flooded	
		0	8
0.21	sugar maple	0.92	0.71
	red maple	0.86	0.70
	baldcypress	0.89	0.71
0.05	sugar maple	1.45	1.37
	red maple	2.68	1.79
	baldcypress	1.69	1.70

3.3. Respiration of root nodules

Pankhurst and Sprent [201] examined in a pot experiment the effects of temperature and oxygen tension on the respiratory activity of soybean and French bean

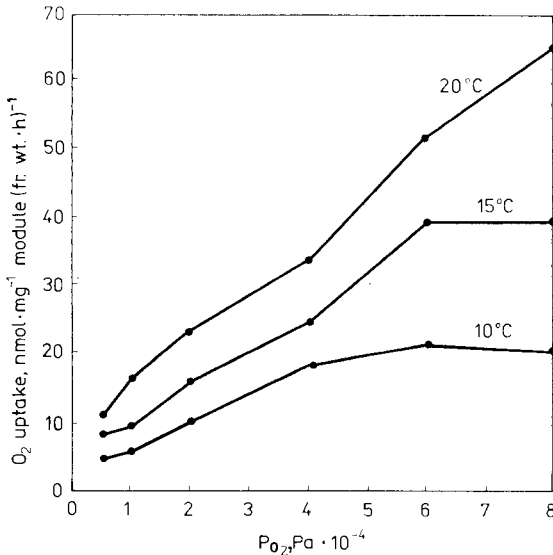


Fig. 15. Effect of increasing  $P_{O_2}$  on the respiratory activity of turgid soybean root nodules at 10, 15, and 20 °C. Each point is the mean of 4 replicates [201]

Fig. 15. Influence de  $P_{O_2}$  sur l'activité respiratoire des nodules de racines de soya à 10, 15 et 20°C. Chaque point est la moyenne de 4 répétitions [201]

nodules. They found an increase of the respiratory activity of turgid nodules with rising temperature over the range 10-30°C. However, below 10°C the activity decreased rapidly.

Respiration by soybean nodules was not inhibited by high  $P_{O_2}$  at low temperatures (Fig. 15), but was saturated at a  $P_{O_2}$  of 40 kPa at 10°C and of 60 kPa at 15°C. At 20°C, respiration by the nodules showed a rather linear increase with increasing  $P_{O_2}$ .

Tjepkema [250] noted that *Myrica gale* can transport  $O_2$  to the submerged nitrogen-fixing nodules through aerenchymatous nodule roots which emerge above the water surface.

#### 4. METABOLIC ACTIVITY AND ENERGY CHARGE OF ROOTS UNDER ANOXIA

Under anoxia carbon dioxide, fermentative metabolites such as ethanol, ethylene, and its precursor 1-aminocyclopropane-1-carboxylic acid (ACC), and some organic acids may appear in roots. Also the available energy is limited slowing absorption and translocation of water and nutrients in roots.

##### 4.1. Carbon dioxide production

Aerobic and anaerobic  $CO_2$  evolution was measured by Tripepi and Mitchell [252] who found 66% decline in  $CO_2$  production upon anaerobiosis by roots of river birch and European birch. Barta [28] studied the same problem on waterlogging-tolerant birdsfoot trefoil and waterlogging-sensitive alfalfa roots placed in nutrient solution. He found that  $CO_2$  evolution rate of waterlogged roots of both species showed significant declines relative to aerobic controls (similar to that reported by Tripepi and Mitchell - 252). However, the percentage decline, relative to the control, was significantly less for trefoil roots.

This smaller percentage decline is consistent with a previous work of Barta [27] showing that alcohol dehydrogenase (ADH) activity in waterlogged trefoil roots was stimulated to a level equal or greater than that found in waterlogged alfalfa roots. There was no effect of waterlogging duration (1-4 days) on  $CO_2$  evolution in either species which is a confirmation of previous results reported by Carpenter and Mitchell [45, 46].

4.2. Ethanol synthesis and loss from roots

Exclusion of oxygen from metabolism causes a change of this metabolism towards fermentation. A few types of fermentation are possible which is shown in Figure 16. In the case of plants the most common is alcohol fermentation [61, 64, 66, 119, 147].

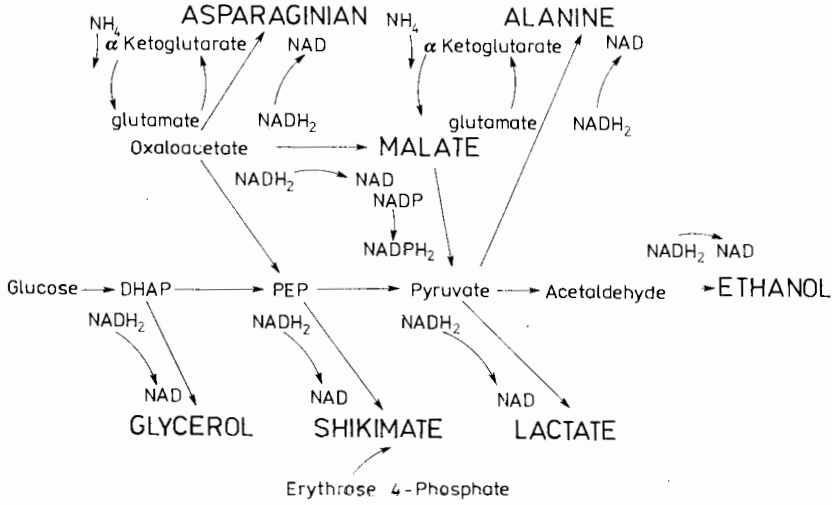


Fig. 16. Diagram illustrating the various means of proton disposal and the range of end-products of glycolysis found in plants capable of enduring prolonged periods of partial or total anoxia [96]

Fig. 16. Diagramme de la disposition de proton et le produit final de glycolysis dans les plantes résistantes à anoxémie prolongée, partielle ou totale [96]

Ethanol is found in the root meristemes, even if they are in contact with atmospheric air. In this case its concentration rapidly decreases with the increase in the distance from the root cap [63].

Ethanol formation in roots when in anoxic conditions, is connected with the plant's capability of surviving periods of flooding. During flooding root ethanol production and alcohol dehydrogenase which is positively correlated with ethanol content in the plant [27, 64, 119] are stimulated. In fact, high level of ADH activity and increased ethanol production has been used in classification of flood "tolerant" and "intolerant" plants.

Barta [27] in field experiments carried out on a fine, loamy soil with flooding 2-year-old stands of alfalfa and birdsfoot trefoil for 12 days found that root concentration of ethanol increased throughout the flooding regime in alfalfa roots from  $0.12$  to  $0.22 \mu\text{mol} \cdot (\text{g fr. wt.})^{-1}$ , and was significantly higher ( $0.91 \mu\text{mol} \cdot (\text{g fr. wt.})^{-1}$ ) in roots with shoots removed. This suggests that the shoots either inhibited root ethanol production or facilitated its removal from the root.

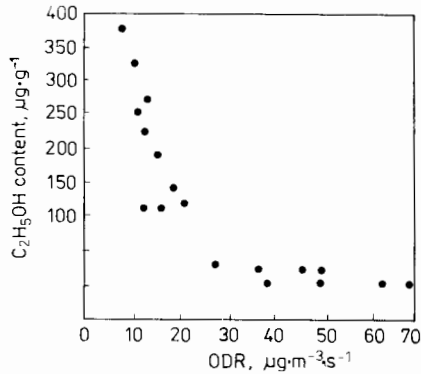


Fig. 17. Ethanol content in xylem exudate of tomato plants vs. soil ODR [96]

Fig. 17. Teneur en ethanol dans la sécrétion de xylème des tomates en fonction de l'ODR du sol [96]

It was confirmed by other authors [e.g., Soldatenkov and Chao Hsien-Tuan - 234] who suggested the positive effect of shoots on the inhibition of root ethanol production or its removal from the root reducing injury of flooded plants.

No ethanol was detected in any trefoil (flood tolerant species) root samples which is difficult to explain. It is possible that significant ethanol metabolism occurs in flooded trefoil roots and is an important mechanism in its removal from the root. This phenomenon was not found in pot experiments with the same plants [26, 27].

Atwell et al. [21] examining the concentration of ethanol in maize roots grown in solution at two levels of  $\text{O}_2$  concentration ( $0.25$  and  $0.04 \text{ mol}\cdot\text{m}^{-3}$ ) found a decrease of ethanol content in roots of 66 and 86% depending on the kind of nutrient solution.

The ethanol formation in plant roots is connected with environmental conditions. Fulton and Erickson [88] stated, that ethanol accumulation in flooded tomato plants was closely correlated with ODR values in the soil, which is shown in Figure 17. Further investigations of the relationship between ethanol accumulation in the plant and soil conditions showed that ethanol concentration is higher in plants subjected to sudden anoxic stress than in plants grown for a long time in conditions of insufficient oxygenation, and moreover, depends on the physiological age of the plants [22].

Examining the ethanol balance in the tomato plant, Bolton and Erickson [36] and Fulton and Erickson [88] found the maximum ethanol concentration in the bottom of the stem and in the top roots. Its highest concentrations in the plant were  $300$  to  $350 \mu\text{g}\cdot\text{g}^{-1}$ . The decrease of ethanol concentration in the lower part of the root explained by its secretion to the environment.



The possibility of toxic effects of ethanol on plant tissues depends on its concentration, which is the result of the ethanol formation processes, and of the processes of its removal by roots and shoots and also on the extent of its remethylization within the plant tissues.

Crawford [63] gives as an example rice and swamp tupelo trees (*Nyssa sylvatica*), which easily remove ethanol by adventitious roots and tolerate flooding well despite the fact that they show Pasteur effect (the phenomenon of increased substrate use in anoxic conditions) and that ethanol is a main product of anoxic respiration.

Injury caused by ethanol consists of a deleterious effect on the cell membranes [148] resulting in leakage of electrolyte, organic acids, amino acids, and sugars from the roots [104, 191]. This cell injury caused by ethanol explains acceleration of the rate of glycolysis (Pasteur effect) which is observed in flood-intolerant plants. This, in turn, results in a decreasing ATP level in the cells and, as a consequence, increasing ethanol production. This autocatalytic process, according to Crawford [63], explains the susceptibility of many plants even to oxygen stresses of short duration [84, 122].

According to Barta [27], the ethanol toxicity in plant roots has been definitively proved. It has never been demonstrated that the level of ethanol accumulation in flooded roots is sufficiently high to be lethal to the tissue. Jackson et al. [131] showed that the exposed pea roots to levels of ethanol up to 100-fold greater than that found in xylem sap of flooded roots had little toxic effect and failed to simulate flooding injury.

#### 4.3. Ethylene

Ethylene is always present in plants and its increased concentration is caused by various stresses: thermal, water, mechanical, chemical, and disease [1, 105]. Moreover, root oxygenation is a very important factor.

An increase of ethylene concentration in roots and other parts of waterlogged plants was found in broadbean [83], *Callitriche* [198], chrysanthemum [140], maize [78], eucalyptus [55], maple [190], radish [140], sunflower [140, 141, 272], sweet potato [202], tomato [37, 40, 127, 128, 130, 140, 141], and willow [51].

Ethylene concentration in waterlogged plants increases as the result of two processes: 1) anaerobic stimulation of ethylene production [37, 40, 127, 130, 143], and 2) the water-jacket effect of water in preventing ethylene diffusion out of the roots [78, 140, 142, 198].

Under flooded conditions ethylene becomes a growth promoting hormone for plants [41, 131, 145].

Generally, it is known that ethylene is formed in plant tissue under oxic conditions [177, 189]. This is true for the roots, as the presence of ethylene was observed, in amounts approximately  $0.9 \text{ cm}^3 \cdot \text{m}^{-3}$ , in the roots of intact maize plants grown in an aerated nutrient solution [78, 130]. In addition, Konings and Jackson [149] observed the evolution of ethylene from undisturbed root systems of rice, white mustard, and three varieties of tomato cut off from the shoots and incubated in a humid atmosphere containing  $0.21 \text{ m}^3 \cdot \text{m}^{-3}$  of oxygen.

The production of ethylene in this case was positively correlated to the rate of root elongation, thus rice roots, evolving ethylene in the amount of  $1.5 \times 10^{-3} \text{ mm}^3 \cdot (\text{g fr. wt.})^{-1} \cdot \text{h}^{-1}$ , elongated at a rate of about  $20 \text{ mm} \cdot \text{day}^{-1}$ , while the roots of mustard, producing ethylene at a rate of  $6.5 \cdot 10^{-3} \text{ mm}^3 \cdot (\text{g fr. wt.})^{-1} \cdot \text{h}^{-1}$ , elongated by about  $65 \text{ mm} \cdot \text{day}^{-1}$ .

On the other hand, other authors [78, 129] observed that the ethylene concentration in the roots of plants grown in a nonaerated solution (up to  $1.9 \text{ cm}^3 \cdot \text{m}^{-3}$ ) was twice as much as when grown in an aerated one ( $0.9 \text{ cm}^3 \cdot \text{m}^{-3}$ ). Also Kawase [146] reported an increase in the ethylene concentration in the roots of garden plants (chrysanthemum, sunflower, tomato, and radish) under the effect of flooding the roots in the soil with water.

The examples that reported an increase in the ethylene concentration in roots due to lack of aeration of the nutrient solution or flooding the soil with water cannot constitute a proof of an increase in the production of ethylene by roots under anoxic conditions, as these conditions cannot be considered anoxic. In the nonaerated nutrient solution oxygen concentration, as a result of internal oxygen transport through the plant was equivalent to approximately  $0.012 \text{ m}^3 \cdot \text{m}^{-3}$  in the air [78, 129]. In the case of the waterlogging garden plants mentioned [140] there must have also been certain amount of oxygen in the plant roots from the internal transport.

In turn, under anoxic conditions (in an atmosphere of nitrogen), no evolution of ethylene was observed during the incubation of excised roots [78, 130].

On the basis of the foregoing it can be stated that ethylene in the roots is only produced in the presence of oxygen, although the required oxygen content is low. The lower limit of oxygen concentration, as well as its optimum concentration for ethylene production, have not yet been determined.

Bradford et al. [38], Bradford and Yang [39] found that under the low oxygen conditions in the soil during flooding, tomato roots synthesize ACC, being the precursor of ethylene, and transport it in the xylem to the shoot, where it is rapidly converted to ethylene. Adams and Yang [3] identified this precursor in apple tissue. Inhibitors of the ethylene biosynthetic pathway are available for further testing of this ACC transport hypothesis: aminooxyacetic acid (AOA) or

aminoethoxyvinylglycine (AVG) block the synthesis of ACC, whereas  $\text{Co}^{2+}$  prevents its conversion to ethylene.

It is worth while to mention that some authors [e.g., 53] found the effect of salts on the ethylene production in *Virginia radiata* hypocotyl sections. In their experiments NaCl and KCl increase decreased ethylene production, when  $\text{CaCl}_2$  - increased.

Aerenchyma formation, and the growth of adventitious roots is favoured by increases in the ethylene content of roots exposed to poorly aerated aqueous environments [78, 126].

#### 4.4. Other anoxic metabolites

Besides metabolites discussed earlier, there are other substances which may appear in roots when the supply of oxygen is insufficient. Their formation and role are not yet fully explained.

Barta [28] summarizing the knowledge on the problem of metabolic responses of roots under anoxia, states that root anaerobiosis leads to rapid changes in membrane permeability, as evidenced by increased efflux of electrolytes and organic metabolites. Loss of  $\text{O}_2$  uptake has also been attributed to irreversible injury of membrane-bound oxidase enzymes. He found, for birdsfoot trefoil and alfalfa a significant lowering of glucose-6-phosphate in trefoil roots exudation of  $\text{K}^+$ , sugars and amino-N, especially during the first days of root anaerobiosis. Also alcohol dehydrogenase activity (ADH) increased several fold with flooding of roots of these two species [26]. This enzyme which catalyzes a step of the fermentation process that yields ethanol,  $\text{CO}_2$ , and energy from sugar has also been studied in plant roots under anoxic conditions by John and Greenway [136], Chang et al. [48], and Hook and Brown [114].

Crawford [60, 64] and Stolzy and Flühler [240] have reported that in anoxic conditions pyruvic, fumaric, acetic, aspartic, glutamic, propionic, butyric, malic, shikimic, glycolic, and  $\alpha$ -aminobutyric acids are formed in roots.

Visser et al. [268] observed that the amount of carbohydrates in apple roots decreased in the case of the nonaerated nutrient solution. Atwell et al. [21] found no major carbohydrate depletion due to  $\text{O}_2$  deficiency in the excised maize roots but the total soluble sugars and amino acid concentration in roots were generally greater at low ( $0.02\text{-}0.06 \text{ mol } \text{O}_2 \cdot \text{m}^{-3}$ ) rather than at high ( $0.16\text{-}0.25 \text{ mol } \text{O}_2 \cdot \text{m}^{-3}$ ) oxygen concentrations. This applied specifically to the root apices (0-2 mm) and expanding (2-15 mm) tissue.

In anaerobic stress during waterlogging the synthesis and translocation of growth regulators such as cytokinins (CK) and gibberellins (GA), are suppressed

in the roots. The rapid appearance of an anaerobic stress reduces root conductance of water flow but generally in waterlogged plants root conductance remains identical or often exceeds that of control roots [41].

Cellulase activity is also increased by waterlogging in roots of bean, Brussels sprout, celery, chrysanthemum, lettuce, mustard, pea, radish, and sunflower plants [145].

In tobacco, under anoxic conditions a decrease of the nicotine concentration in roots was noted [108].

The results obtained by Blevis et al. [35] show an increase of particulate viologen utilizing nitrate reductase (EC 1.9.6.1) in barley roots situated in sterile, anoxic conditions.

#### 4.5. Microbial colonization and activity

Trolldenier et al. [253-255] investigating microbe population accompanying wheat roots growing in aerated and unaerated nutrient solution has revealed that reduced root growth due to lack of aeration was accompanied by a higher root microbe population.

The mucilaginous material (slime) surrounding roots was absent in unaerated and abundant in aerated root tips. This missing or incomplete mucilaginous layer on root tips is associated with unfavourable growth factors such as heavy metal toxicity [109] and attacks by pathogens [217].

#### 4.6. Energy charge

Adenylate energy charge (EC) of plant tissues defined as follows  $EC = (ATP + 0.5 ADP) : (ATP + ADP + AMP)$  under aerobic conditions does not differ from that of animal tissues and microorganisms and is close to 0.9 [220, 221].

Saglio et al. [220-222] measured simultaneously energy production expressed as EC, soluble sugars, and glycolytic activity (as estimated both by sugar consumption and build-up of terminal products such as ethanol and lactic acid) in excised maize roots tips after various times of aging in air. The transition of root tips from air to  $N_2$  atmosphere induced a rapid drop of EC from a high value close to 0.9 in air to lower values ranging from 0.6 to 0.15. They concluded that, in anoxia, there is a quantitative relationship between the EC value and the level of metabolic activity via fermentation (Fig. 18).

Similar results obtained Barta [28] for trefoil and alfalfa roots under anaerobic stress. The energy status of both species showed a sharp decline in ATP/ADP ratios amounting to 40-60% after 1 day of anaerobiosis. The significantly

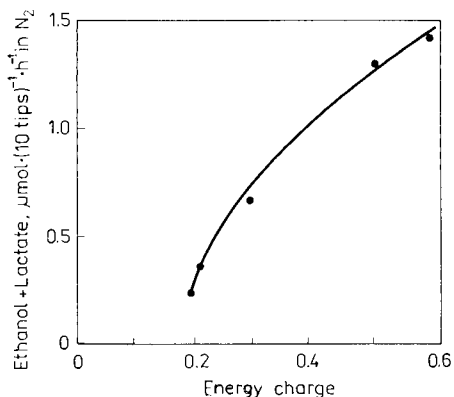


Fig. 18. Relationship between energy charge after 30 min. of anoxia and the rate of glycolysis (measured after 1 h anoxia) in excised maize root tips [220]  
 Fig. 18. Relation entre la charge énergétique après 30 min. d'anoxémie et la vitesse de glycolysis (après 1 h d'anoxémie) dans les cônes des racines de maïs excisées [220]

higher ATP/ADP ratios in trefoil in comparison to alfalfa support the earlier hypotheses [252], that the decline of EC during anaerobiosis is slower in waterlogging-tolerant species than in susceptible to waterlogging ones. It was found that waterlogging-tolerant rice is able to increase its EC with prolonged flooding, while wheat cannot [50].

The dependence of EC or ATP/ADP ratio on oxygen partial pressure [211, 223] was used to study internal transport in roots of maize [210, 223] and bulrush [237].

## 5. OXYGEN DEFICIT AND ROOT GROWTH AND WATER UPTAKE

### 5.1. Root growth rate

The reaction of roots to anoxic conditions manifests itself in various ways. Completely anoxic conditions stop root growth entirely within 2 to 3 min. This has been observed with cotton and soybean [122]. When the stress did not last longer than 30 min. the growth rate subsequently returned to normal. Anoxic stress lasting 3 h for cotton and 5 h for soybean killed the tap roots.

Roots of plants which are very sensitive to anoxic conditions (e.g.. tobacco, legumes) die after a few days of flooding [110, 150, 175, 284, 285], but the first symptoms of damage by waterlogging may appear after 1 to 2 h and permanent damage may appear after 24 h, especially on warm sunny days [152, 175].

As already mentioned, plants which can survive an anoxic stress nevertheless decrease the rate of growth of their roots. This has been observed with tomato [128], maize [21, 90, 91, 95, 257], barley [89, 91], wheat [196, 228], pea [56, 89, 91], oak [227], snapdragon [242], tulips [280], sugar beets [277], bean [225], and mustard [103]. As a result of these root growth disturbances (due to an insufficient supply of oxygen to the roots) the mass of the root system decreases. This was observed with sorgo [118], barley [79], oats [43, 274], wheat [216, 256, 263, 274, 279], maize [76, 181], apple tree [268], sugar beets [275], lemon [156, 157, 241], orange [155, 241, 270], jojoba [214], avocado [159], grasses [170, 269], cotton [203], legumes [56], sugar cane [204], bean [225], broad bean, cabbage, and potato [279].

Under anoxic conditions the root mass of flood intolerant plants decreases earlier and to a higher degree than the mass of the shoots. Hence the ratio of shoots to roots is higher in anoxic conditions than in the presence on oxygen. This was found in the case of wheat [2, 256], lemon [154], jojoba [214], orange [270], and apple tree [268].

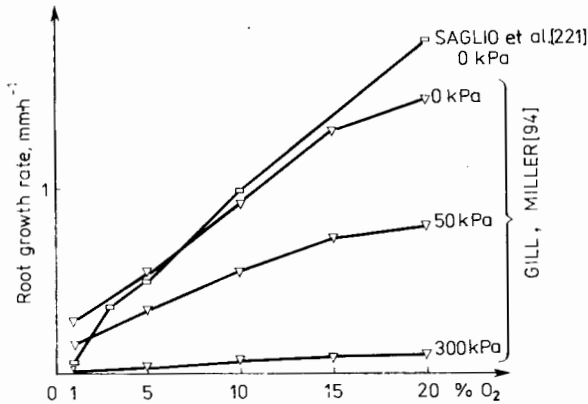


Fig. 19. Effect of oxygen concentration on growth rate of constrained and unconstrained roots [94]

Fig. 19. Influence de la concentration d'oxygène sur la vitesse de croissance des racines sans ou avec obstacle mécanique [94]

Roots growing in an environment with restricted oxygen supply are thicker, shorter, less branched, of light color [56, 269], have larger cells [206], and, in the case of legumes, possess fewer nodules [56].

Roots which are near to the anoxic zone in the soil show an ability to avoid this zone [228], which results in formation of a shallow root system [78, 178, 247], and in some cases the roots become aerotropic (negatively geotropic) and emerge from the soil [128, 269, 278]. The formation of the shallow root system results stimulation of the growth of lateral roots following the death of the

tap root tip [122]. The effect of oxygen concentration on the growth rate of constrained and unconstrained roots are shown in Figure 19.

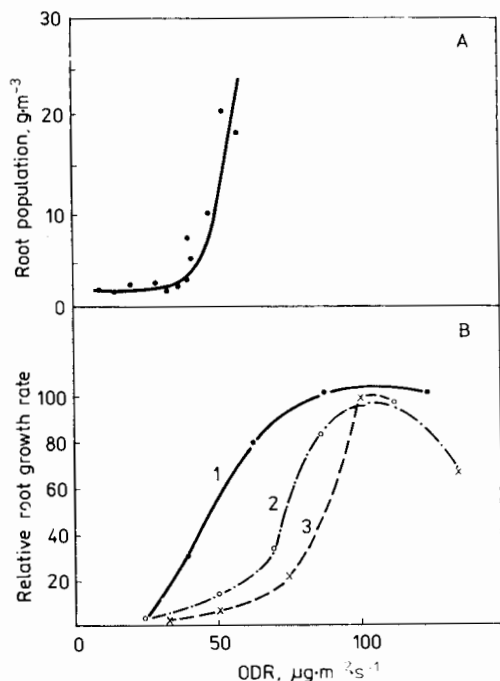


Fig. 20. Root response to ODR; (A) population of wheat roots in soil under field conditions. (B) relative root growth rate of three desert shrubs: *Franseria dumosa* (1), *Larrea tridentata* (2), *Artemisia tridentata* (3) [96]

Fig. 20. Réponse de la racine à l'ODR; (A) population des racines de blé dans le sol au champ, (B) vitesse relative de la croissance des racines de trois arbustes désertiques: *Franseria dumosa* (1), *Larrea tridentata* (2), *Artemisia tridentata* (3) [96]

It is widely agreed that the best indicator of soil oxygen availability for plant roots is the ODR. The reaction of roots of different plants to ODR is shown in Figure 20. We can see that the number of roots in the soil (Fig. 20A) already begins to be reduced at an ODR of  $50 \mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and drops rapidly to less than one fifth of the original number over the ODR interval 50 to  $40 \mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . The ODR value of  $40 \mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  may, accordingly, be accepted as critical, and  $50 \mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  as limiting for wheat root growth. Similarly, the root growth rate of desert shrubs is restricted at an ODR of  $50 \mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and is completely suppressed at an ODR of  $30$  to  $35 \mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Fig. 20B).

Blackwell and Wells [34] found  $15 \mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  as limiting value of ODR for the growth of winter oat. They also found a significant differentiation in root devel-

Table 7. Dry weight, numbers, diameters and lengths of winter oat roots after 8 days of growing in waterlogged and freely drained soils [34]

Tableau 7. Matière sèche, nombre, diamètre et longueur des racines d'avoine d'hiver après 8 jours de croissance dans les sols inondés et récemment drainés [34]

Root features	Plants in	
	waterlogged soil	freely drained soil
Average dry weight of roots, g.plant <sup>-1</sup>	0.021	0.024
Average diameter of roots, cm	0.066	0.039
Average number of lateral roots per plant	10	38
Different sized seminal roots, cm		
0-1	17.5	6
1-5	41	32.5
5-10	14.5	15
10-20	27	20
20 <sup>+</sup>	0	26.5

opments which is shown in Table 7. Decreasing rooting depth of potato, tomato and tulip growing in soil affected by low oxygen supply was indicated by Wiersum [281].

The critical ODR values for other plants are differentiated and (in  $\mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) are equal to 25 for barley [173], 42 and 20 for maize [33, 259], 33 for sunflower [171, 173], 33 for snapdragon [242], and 33 for cotton [171]. Growth of grasses was inhibited at an ODR of  $25\ \mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for turfgrass and  $17\ \mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for ryegrass [98, 170], 8 to  $15\ \mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for Kentucky bluegrass and  $33\ \mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for Newport Kentucky bluegrass [172]. Desert shrubs such as *Artemisia tridentata*, *Larrea tridentata*, and *Franseria dumosa* [179] have critical values of ODR in the range  $30$  to  $35\ \mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ .

Root growth of plants adapted to prolonged flooding (e.g., rice) is better in such conditions than when not flooded. This causes a decrease of shoot to root ratio due to flooding the soil [137, 181]. These plants generally have more porous roots and sometimes, e.g., black mangroves (*Avicennia nitida*), form special aerial roots (pneumatophores) containing aerenchyma, which supply oxygen to the normal roots.

## 5.2. Root growth force and pressure

The effect of oxygen on root growth pressure was studied by Eavis et al. [81] for peas and cotton using the dead-load technique. Average root growth pressure values did not change significantly for 3, 8 and 21%  $\text{O}_2$  treatments in the case of peas and ranged from 1.1 to 1.4 MPa, while those for cotton nodules decreased from 0.95 to 1.1 MPa at 8 and 21%  $\text{O}_2$  to 0.5 MPa at 3%  $\text{O}_2$ .



Souty and Stepniewski [236] measured root growth force and pressure for young (2-4 days) maize seedlings using a strain gauge technique at oxygen concentration

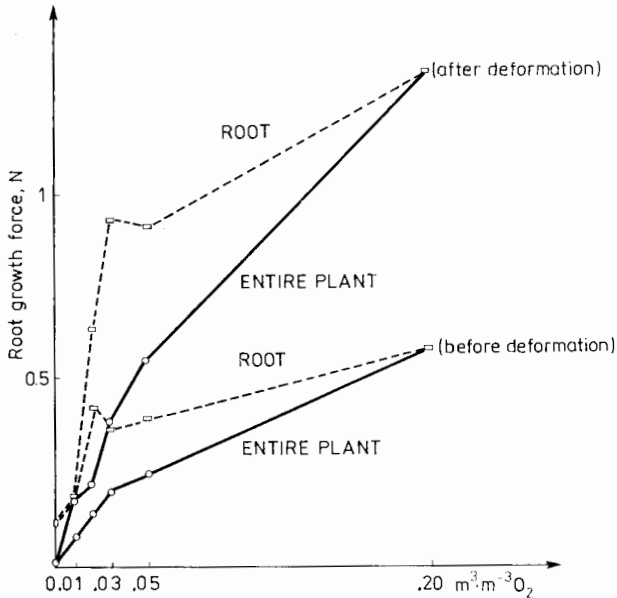


Fig. 21. Dependence of growth force of maize seminal roots before and after their deformation due to facing the obstacle (each point is a mean value of 4 seedlings) on oxygen concentration in the gas mixture surrounding the entire plant and the radicle only [236]

Fig. 21. Dépendence de la force de croissance des racines séminales de maïs avant et après leur déformation due à l'obstacle (chaque point est la moyenne de 4 brins) de la concentration d'oxygène dans le mélange de gaz entourant toute la plante et seulement la radicule [236]

ranging from 0 to 20%. The oxygen concentration was changed around the entire seedling or around its radicle only. Both root growth force and pressure as well as the growth rate decreased at oxygen concentrations below 3-5% (Fig. 21). As it can be seen the plant response was more pronounced when the entire seedling was in the gas mixture of lowered oxygen concentration. When only the plant radicle was exposed to oxygen stress the growth force (and thus pressure) was less affected, at least partly, due to possible oxygen diffusion through the plant tissue from the coleoptile to the radicle. The maximum mean root growth force of the radicles was 0.6 N before their deformation and 1.1 N after deformation of the impeded roots. This corresponded to the growth pressure 0.4 MPa and 0.65 MPa for undeformed and deformed roots, respectively.

### 5.3. Water uptake

It has been known that flooding the roots with water causes partial or complete inhibition of water uptake and transpiration [e.g., 2, 8, 42, 112, 128, 130, 175, 256, 282, 285].

A positive linear correlation has been found between oxygen uptake by roots and water use by plants with undamaged root systems [112].

The water conducting ability of *Lycopersicon esculentum* Hill. [41, 130, 150], *Nicotiana tabacum* L. [152] and several *Pyrus* species [8] was found to decline in response to flooding. Several authors suggested explanation that the decrease in the water permeability of the roots due to anoxia leads to a decrease in the water potential of the leaves and in consequence, the closure of stomata observed in numerous herbaceous and woody plant species [58, 130, 205, 232].

It is true that some authors [83, 93, 150, 152] have observed the intensification of water stress after flooding the roots. In many cases, however, this phenomenon was not confirmed, and even an opposite effect, i.e., an increase of water potential in leaves under conditions of root anoxia induced either by flooding [130, 205, 256] or by introducing nitrogen to the soil [233] has been revealed.

This means that the decreased water permeability of the roots is not the only factor reducing transpiration, as the cause-and-effect relationship between root permeability and stomata closure has not been proved. Thus further work is required to elucidate the nature of signals responsible for stomatal closure with root anoxia and to evaluate the role of root permeability in the decreased water uptake by the plants.

## 6. NUTRIENT CONTENT AND UPTAKE BY ROOTS UNDER OXYGEN STRESS

Oxygen stress in the soil causes the disturbances in the functioning of the root system, also in the nutrient uptake and content in the root.

A review of papers [56, 77, 133, 137, 154, 156-159, 176, 214, 230, 241, 268, 270, 279] on the changes of nitrogen, phosphorus, potassium, calcium, magnesium, sodium, chloride and some micronutrients (boron, zinc, copper, manganese and iron) content and uptake in roots of various plants under the influence of oxygen stress is presented in Tables 8-11.

As can be seen, the direction of the changes is different in different plant roots. In all cases uptake is decreased which is connected with a distinct decrease in the mass of the root exposed to oxygen deficiency [96]. Also almost in all cases a decrease in potassium, magnesium, chloride and ammonium [215] content in roots was found. A tendency in increasing manganese, iron and zinc in roots when oxygen concentration decreases is also visible.

T a b l e 8. Changes in N, P, and K content and uptake by roots of various plants under a shortage of oxygen in soil

T a b l e a u 8. Changements de teneur en N, P et K et d'absorption par les racines de diverses plantes dans le cas de déficit du sol en oxygène

Plant	Nitrogen			Phosphorus			Potassium		
	cont.	upt.	ref.	cont.	upt.	ref.	cont.	upt.	ref.
Lemon	+		[158]	0		[158]	0		[158]
	+	-	[154]	0		[154]	-		[154]
	+		[157]		-	[157]		-	[157]
Lemon and orange	-		[241]	-		[241]	-		[241]
Apple tree	-		[268]				-		[268]
Jojoba	+		[214]	-		[214]	-		[214]
Avocado	+		[159]	0		[159]	-		[159]
	-		[230]	0		[230]	-		[230]
Potato		-	[279]		-	[279]		-	[279]
Barley	-	-	[80]			[79]	-		[79]
Peas	-	-	[56]	-	-	[56]	-	-	[56]

Explanations: cont. = content, upt. = uptake, ref. = references, - = decrease, + = increase, 0 = insignificant changes.

Explications: cont. = teneur, upt. = absorption, ref. = références, - = diminution, + = augmentation, 0 = changements insignifiants.

T a b l e 9. Changes in Ca, Mg, and Na content and uptake by roots of various plants under a shortage of oxygen in soil

T a b l e a u 9. Changements de teneur en Ca, Mg et Na et d'absorption par les racines de diverses plantes dans le cas de déficit du sol en oxygène

Plant	Calcium			Magnesium			Sodium		
	cont.	upt.	ref.	cont.	upt.	ref.	cont.	upt.	ref.
Lemon	0		[158]	-		[158]	0		[158]
	-		[154]	0		[154]	+		[154]
		-	[157]		-	[157]		-	[157]
Lemon and orange	-		[241]	0		[241]			
Jojoba	0		[214]	-		[214]	-		[214]
Avocado	+		[159]	-		[159]	-		[159]
				-		[230]	+		[230]
Potato		-	[279]						
Broad bean		-	[279]						
Cabbage		-	[279]						
Wheat		-	[279]						
Peas		-	[56]	0	-	[56]			
Apple tree	-		[268]						

For explanations see Table 8. Explications v. tableau 8.

T a b l e 10. Changes in Cl, B, and Zn content and uptake by roots of various plants under a shortage of oxygen in soil

T a b l e a u 10. Changements de teneur en Cl, B et Zn et d'absorption par les racines de diverses plantes dans le cas de déficit du sol en oxygène

Plant	Chloride			Boron			Zinc		
	cont.	upt.	ref.	cont.	upt.	ref.	cont.	upt.	ref.
Lemon	-		[158]	0		[156]	+		[156]
	-		[154]	0		[158]	0		[158]
		-	[157]	+		[154]	+		[154]
					-	[157]		-	[157]
Lemon and orange	-		[241]	0		[241]	0		[241]
Avocado	-		[159]				+		[159]
	-		[230]						
Barley	-		[133]						
Jojoba				+		[214]	0		[214]

For explanations see Table 8. Explications v. tableau 8.

T a b l e 11. Changes in Cu, Mn, and Fe content and uptake by roots of various plants under a shortage of oxygen in soil

T a b l e a u 11. Changements de teneur en Cu, Mn et Fe et d'absorption par les racines de diverses plantes dans le cas de déficit du sol en oxygène

Plant	Copper			Manganese			Iron		
	cont.	upt.	ref.	cont.	upt.	ref.	cont.	upt.	ref.
Lemon	+		[156]	+		[156]	+		[156]
	0		[158]	0		[158]	0		[158]
	-		[154]	+		[154]	+		[154]
		-	[157]		-	[157]		-	[157]
Orange and lemon	+		[241]	+		[241]	+		[241]
Jojoba	0		[214]	+		[214]	+		[214]
Avocado	0		[230]	0		[230]	0		[230]

For explanations see Table 8. Explications v. tableau 8.

In flooding conditions the changes of the pH of medium may change the availability of some elements by roots. It has been recently revealed [74] that within 24 h the pH of the nutrient medium of sunflower plants in the flooded treatments was 1 pH unit higher than that of the nonflooded treatments and remained higher over several days.

## 7. ADAPTATION OF PLANT ROOTS TO ATMOSPHERIC STRESS IN THE SOIL

Atmospheric stress in the soil is referred to oxygen deficiency, waterlogging, and anaerobiosis [153]. All involve a build-up of carbon dioxide, ethylene, and other potentially toxic gases, and oxygen depletion which leads to a reduction of anaerobic respiration.

It is proved that no plant can survive under complete anoxia for prolonged periods. Although few plants are subjected to complete anoxia, many are exposed to periodical oxygen deficiency caused by water-saturated, compacted or surface sealed and crusted soils. In the case of waterlogging it should be noticed that it occurs not only when soil is inundated but also when water fills a critical proportion of the soil air spaces [145].

Anoxia intolerant plant species survive oxygen-free conditions for periods ranging from hours to days, or eventually degenerate [76]. This period for cotton tap root is in the range of 0.5-3 h [122] and for rice seminal roots of 96-120 h [32]. Anoxia tolerant plants or organs survive much more extended periods. Crawford [65] found that a number of wetland species that over-winter in anaerobic mud survived for a period of 2 months or more (*Scirpus maritima*) and for 1 month or more (*Schoenoplectus lacustris*, *S. tabernaemontani*, *Typha angustifolia*, *Phragmites australis* and *Iris pseudacorus*).

Waterlogging of the soil rapidly alters both the physical and biological environment of plant roots and drastically limits the diffusion of oxygen from the soil to the root system. It inhibits root growth, and root hair formation, increases susceptibility of roots to attack by predators and pathogens. Under prolonged flooding roots may blacken, die, and eventually rot [153].

Plants subjected to longlasting atmospheric stresses in the soil form some adaptative mechanisms, which allow them to grow, develop and yield. Plant tolerance to root flooding is relative and depends on their variety and stage of development. There is, however, controversy in the literature as to whether some phenomena e.g., adventitious roots or lignification are symptoms of flooding injury or a beneficial adaptation to waterlogging.

Numerous authors identified three different kinds of plant adaptation to anoxia in the soil viz. anatomical and morphological adaptation to internal transport, shallow rooting, and metabolic and physiological adaptation.

### 7.1. Anatomical adaptation

This adaptation has been reviewed by many authors, e.g., [4, 6, 12, 13, 17-19, 59, 73, 75, 77, 79, 93, 116, 117, 139, 181, 218].

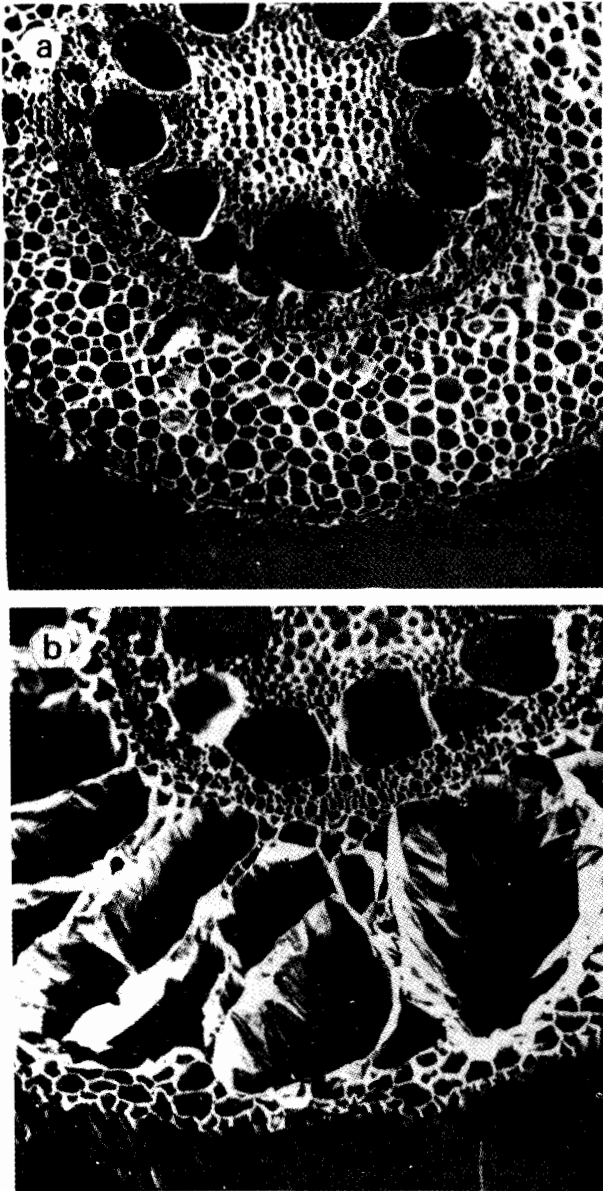


Fig. 22. Transverse sections of 2nd whorl adventitious roots in scanning electron microscope [78]

Fig. 22. Sections transversales des racines adventives sous le microscope à balayage [78]

It is mainly evaluated by the capability in taking  $O_2$  into the plants via the aerial parts, translocating  $O_2$  by the process of longitudinal diffusion to the root systems, and partly diffusing out of the root systems.

One of the most common anatomical adaptations is the formation of increased intercellular air spaces in root cortex that provide canals parallel to the axis of the root to a distance of 2 to 3 mm from the root tip through which gases can diffuse longitudinally (Fig. 22). They are found in the suberized root tissue known as aerenchyma [73, 77, 78, 145, 146].

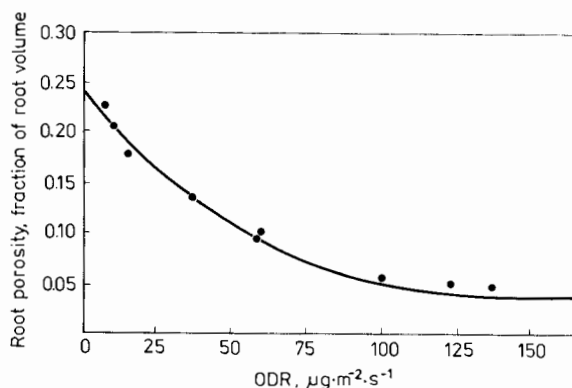


Fig. 23. Rice root porosity in active tillering phase as affected by soil air [96]

Fig. 23. Porosité de la racine du riz dans la phase de tallage sous l'influence de l'aération du sol [96]

The porosity of mesophyte roots is slight (of the order of several percent of the root volume). However, under conditions of soil inundation with water, even with these plants it is quite common to find the development of adventitious roots containing aerenchyma [79] and having a porosity much greater than in the primary roots [181] (Fig. 23). This results in an increase in root porosity under conditions of insufficient oxygen supply from the soil which was reported by many authors [2, 5, 24, 47, 124, 180, 197, 229, 231, 233, 263, 287].

Two kinds of aerenchyma has been described: lysigenous and schizogenous [85]. The first is formed when intercellular space arises through dissolution of entire cells. The second is connected with a separation of cell walls from each other along more or less extended areas of their contact.

McPherson [193] was the first who clearly defined lysigenous aerenchyma formation. He observed that aerenchyma formation in maize roots is preceded by the disappearance of protoplasm from the cell, bulging cells, death of cells, and by collapse of cell walls. He observed that: 1) aerenchyma formation in maize roots is prevented by  $\text{O}_2$  application, 2) increased respiration by raising temperature invariably increases aerenchyma formation, and 3) aerenchyma is never produced in the stelar tissue, but in the cortex, which is distal to the conducting tissue of the food. Based on these findings his stipulation is that death of the cells is

caused by starvation since anaerobic respiration is insufficient to maintain cellula integrity.

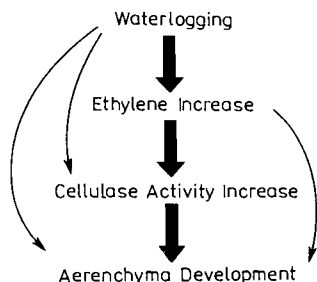


Fig. 24. Sequential steps in aerenchyma development [145]

Fig. 24. Degrés de développement d'aerenchyma [145]

The results described earlier suggested [144] to propose a chain of events in which waterlogging leads to aerenchyma development through elevation of ethylene concentration, which in turn increases cellulase activity (Fig. 24).

Beckel [29] examining *Bouteloua gracilis*, in which aerenchyma develops into root cortex under normal conditions, without waterlogging, found that plant has aerenchyma in the basal region of the root except for a short distance behind the growing point. Also, there is no aerenchyma near the tips of the adventitious roots formed in the water by waterlogged sunflower plants [146]. It seems that normal adventitious roots develop in sunflower plants even in water. If they are kept continuously in water, aerenchyma develops gradually as the roots increase in age. Philipson and Coutts [207] found that  $O_2$  diffuses at the bases and tips of lodgepole pine roots grown anaerobically, while it diffuses only at the bases of the roots grown aerobically. It shows that metabolically active root tips get a better  $O_2$  supply with this kind of aerenchyma development.

Williams and Barber [283] took the attention on the other role of aerenchyma. They stated that aerenchyma provides the greatest strength with the least tissue and that minimal tissue requires the minimum amount of  $O_2$  under anaerobic conditions. In other words it is a decreased demand for oxygen arising from the smaller number of cells present in aerenchymatous roots.

After investigating 2 types of aerenchyma (lysigenous and schizogenous) in waterlogged roots, Yamasaki [286] observed 2 types of radial cortical cell arrangement - columnar and oblique (Fig. 25). The columnar type had much more air space per unit area of cortex, as the oblique type provided that the cell sizes are equal. He found the columnar type (intensified by the development of lysigenous aerenchyma) to be more waterlogging-tolerant than the oblique type con-



nected with schizogenous aerenchyma). As examples: *Fagopyrum esculentum* (with oblique type of cortical cell arrangement) and *Polygonum thunbergii* (with columnar type) have been presented.

It is a general opinion that plants whose root do not readily form aerenchyma [e.g., peas 75] belong to the group which is most sensitive to flooding.

Some plant species develop specialized knee roots and pneumatophores, constituting a diffusion path for gases [93, 250].

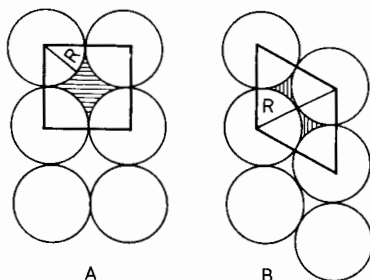


Fig. 25. Schematic illustration of cross section of root cortex describing 2 types of cortical cell arrangements: columnar (A) and oblique (B). R and shaded area indicate cell radius and intercellular space, respectively. Vertical line of each drawing is tangential to the root cross section [145]

Fig. 25. Présentation schématique de la section du cortex racinaire décrivant 2 types d'arrangement de cellule corticale: colonnaire (A) et oblique (B). R et espace hachuré indiquent respectivement le rayon de la cellule et l'espace intercellulaire. Ligne verticale de chaque dessin est tangente à la section de la racine [145]

In mangrove, a swamp plant roots possesses a specific mechanism for the entry of  $O_2$  into it - lenticels [115, 190, 207].

According to Yamasaki [286] also the lignification of cortex and epidermis which occurs more strongly in waterlogging-tolerant species than in nontolerant species may prove about plant adaptation to oxygen deficit. It may increase the mechanical strength of plant and increase disease resistance.

He suggests the classification of waterlogging-tolerance based on the lignification, cortical cell arrangement, and aerenchyma development in the roots (I - weakest and VIII - strongest):

- I. No lignification; oblique; less aerenchyma - Welsh onion, carrot, *Astragalus sinicus*.
- II. Lignified epidermis; oblique; potato, pepper, tomato, cosmos, buckwheat.
- III. Lignified epidermis and cortex; oblique; aerenchyma development - barley, wheat.
- IV. Lignified stele - rape, Japanese horseradish, sweet potato.

V. Tannin-like substance in root; oblique - *Saxifraga stolonifera*, *Equisetum arvense*, taro.

VI. Aerenchymatous epidermis; rarely lignified epidermis and cortex - *Polygonum Thunbergii*, *Acorus calamus*, *Cyperus microiria*, *Cyperus malaccensis*, *Eleocharis tuberosa*, *Sagittaria trifolia*, *Nalumbo nucifera*, *Oenanthe stolonifera*.

VII. Strongly lignified epidermis; large aerenchyma - rice, *Zizania latifolia*, *Beckmannia eruciformis*, maize, *Setaria italica*, Coix Ma-yuen, *Commelina communis*.

VIII. Lignified epidermis, cortex, and root hair; aerenchyma in cortex - *Juncus effusus*, *Juncus alatus*, *Iris laevigata*.

Krizek [153] has reported that fruit tree species have a wide-range of tolerance to long periods in water-saturated soils. The roots of apple, pear, and quince are relatively tolerant to flooding while those of peach, apricot, and almond are generally considered highly sensitive. „Myrobalan” plum is intermediate in tolerance [219].

While discussing the anatomical adaptation of plant roots to atmospheric stress it is worth to mention about the studies carried out by Trolldenier and Hecht-Buhholz [254] on the ultrastructure of wheat roots grown in aerated and unaerated nutrient solutions. They found that the ultrastructure of the root cap meristem cells of unaerated roots was similar to that of the aerated ones. The same was true for the central root cap cells. Differences occurred in the peripheral and subperipheral cells of the root cap. The cytoplasm of these cells appeared to contain less organelles in the unaerated roots than in the aerated ones.

A curious example of adaptation to flooding is floating or deep water rice grown in the floodplains of Southern Asia where the water can rise up to 6 m during the rainy season [209]. The distinguishing characteristics of this rice is its ability to elongate with rising waters, and the growth rates of 20-25 cm x x day<sup>-1</sup> have been recorded with the total plant height reaching up to 7 m. Its survival depends on the ability to keep tip of its foliage above the water surface and completely submerged plants cease to elongate and eventually die. Raskin and Kendle [209] found that in partially flooded deep water rice continuous air layers happend between the hydrophobic, compacted surface of the leaf blades and the surrounding water constitute the major path of gas transport. The total volume of the air layers on both sides of a leaf blade is about 45% of its volume. The conduction of gases through the internal air space of the leaf is negligible component to that through the external air layers. Gases move through the air layers both by diffusion and mass flow.

The air layers are vital for the survival of the partially submerged rice plants. Plants without air layers (e.g., washed with a surfactant solution) do

not grow in response to submergence and the submerged parts of the plant deteriorate as evident by rapid loss of chlorophyll and protein [209].

Another mechanism of gas exchange found in water plants is pressurised ventilation. This phenomenon was reported first in 1841 [208] in leaves of lotus (*Nelumbium*). Merget [195] demonstrated the physical nature of this phenomenon in an experiment with dead lotus leaves, which after remoistening exhibited their capacity for pressurisation. Recently this phenomenon was studied in detail in yellow water lily (*Nuphar luteum*) by Dacey [68, 69]. This plant, growing in lake sediments, has a rhizome measuring several meters in length and up to 10 cm in diameter and several rosettes of leaves that rise up through the water on petioles which may be 2 m long. The plant has an extensive system of continuous gas spaces or lacunae occupying about 60% of the petiole volume and up to 40% of the volume of the roots and rhizome [69]. It was found that young leaves of the water lily show a small overpressure of up to 0.2 kPa. Due to this pressure several litres of air per day move to  $50 \text{ cm} \cdot \text{min}^{-1}$  and then up the petioles of the older leaves to the atmosphere. The overpressure in the young leaves is created by purely physical processes of thermal transpiration and hygrometric pressure induced by the temperature difference between the leaf and the atmospheric air. It occurs only during the day when solar energy creates the temperature differences. This mechanism obviously not only supplies oxygen but also removes methane and carbon dioxide from plant tissues [70, 71]. It is not known how widespread this pressurised ventilation is among aquatic plants and further studies on this topic are necessary.

Due to the anatomical adaptation to internal gas transfer roots are able to oxidize the surrounding soil, leading to formation of oxidized coatings on root surface the amount of which is thought generally to be a function of the content of reduced Fe and Mn [49, 77, 99, 174, 249] and the oxidizing capacity of the roots [25, 194].

Good et al. [97] examined the composition of the green ash (*Fraxinus pennsylvanica* Marsh.) roots coating (Al, As, Ca, Fe, K, Mg, Mn, Ni, P and Zn) as the effect of soil wetness. They proposed first to use this root coating constituents as an indicator of rhizosphere oxidation.

## 7.2. Morphological adaptation

The basic method of morphological adaptation of herbaceous wetland species to tolerance flooding is the formation of adventitious roots containing aerenchyma that emerge from the base of the shoot (at and above the root collar) [19, 54, 145].

Clemens et al. [54] examining root systems of three young seedlings of *Eucalyptus* species during 7-10 weeks of waterlogging found that more than 90% of their root systems was replaced with new adventitious roots. They concluded that the

greater the adventitious root formation, the greater the waterlogging-tolerance of plants.

Adventitious roots were also found with 17 woody species by Hosner and Boyce [120], with sycamore, green ash, and water tupelo by Hook and Brown [114], with red maple and sugar maple by Maronek and Wott [190], with sunflower and tomato by Kramer [151], and Jackson [132], with cucumber and tomato by Hozumi [121].

There is a controversy as to the origin of adventitious roots - are they influenced due to the anaerobic effect causing the accumulation of auxin or by the "water effect" of waterlogging? [151, 271, 272].

### 7.3. Shallow rooting

Shallow rooting is a third way of plant adaptation to oxygen deficient media [96]. In this was the roots remain in the surface layer of the soil which is more abundant in oxygen than deeper horizons. Moreover, the path for internal diffusion in such roots, which are shorter than in plants grown in well-oxygenated media, is usually shorter. According to Huck [122] shallow horizontal rooting is explained by the death of the top roots after reaching the anoxic layer followed by stimulation of lateral root growth. Another mechanism responsible for shallow rooting is aerotropic root growth [269, 278] i.e., upward growth to better oxygenated soil layers. Due to this roots grow sometimes just at or even above soil surface [129].

### 7.4. Metabolic and physiological adaptation

Metabolic and physiological adaptation to withstand anoxia have been discussed recently by a number of authors [23, 25, 46, 48, 49, 63, 75, 76, 97, 114, 136, 194, 249, 275].

The mechanism of such adaptation, which seems to be important, at least during short term oxygen deficiency, is rather obscure. Such adaptation involves:

- a decrease of Pasteur effect,
- ethanol removal from roots,
- alternative metabolic path leading not to ethanol but to less toxic end products such as malate, lactate, shikimate, glutamate, the amino acids or glycerol.

The results of the study carried out by Carpenter and Mitchell [46] with flood-tolerant and flood-intolerant roots of 4 tree species indicate that roots of all these species possess CN-resistant as well as CN-sensitive  $O_2$  consumption mechanisms. Use of specific respiratory inhibitors: cyanide (KCN) and salicylhydroxamic acid (SHAM) also indicated that different species possess different proportions of the two pathways (oxic and anoxic), and that these proportions shift in response to flooding. The final statement is that cumulative flooding causes damage to the aerobic respiratory mechanism in roots of flood-intolerant species.

Lambers [160] reported that the root respiration rate of *Senecio aquaticus* (flood-tolerant species) was lower than that of *Senecio jacobaea* (flood-intolerant). This was confirmed by Carpenter and Mitchell [45, 46] with reference to roots of some tree species (*Acer saccharum*, *Acer rubrum*, *Taxodium distichum*, *Taxus cuspidata*). This would suggest that the low respiratory activity of roots may be an adaptive feature increasing root tolerance to flooding.

Several authors [59, 61, 62] try to explain why certain tree species are resistant to damage by waterlogged soils. One possibility is that enough  $O_2$  diffuses through lenticels and intercellular spaces to sustain aerobic respiration in submerged roots of tolerant species [59]. Alternatively, flood-tolerance in trees [61, 62] as in certain herbaceous species [192], may depend on the ability of roots to cope with products of anaerobic respiration. Such tolerance mechanisms need not be mutually exclusive, since flooded roots of *Fraxinus pennsylvanica* and *Nyssa aquatica* not only receive  $O_2$  internally from the shoot, but also accumulate ethanol [114].

Plant hormones have been shown to play also a role in adaptation of roots to flooding. In general, increased resistance to this stress is associated with a rise in endogenous abscisic acid (ABA) and a drop in gibberellins [153] which cause an increase in the root permeability to water through enhancement in hydraulic conductivity of the root.

Recently, attention has turned to the possibility that the composition of membrane lipids (especially in relation to the synthesis of unsaturated fatty acids which is dependent on molecular oxygen [243]) could play a key role in anoxia tolerance [52, 111, 265].

#### REFERENCES

1. Abeles F. B.: Ethylene in Plant Biology. Academic Press, New York, 1973.
2. Aceves-Novarro E., Stolzy L. H., Mehuys G. R.: Response of three semidwarf Mexican wheats to different aeration in the rooting medium at a constant salinity level. Soil Sci. Soc. Am. Proc., 39, 515, 1975.
3. Adams D. O., Yang S. F.: Ethylene biosynthesis: identification of 1-aminocyclopropane-1-carboxylic acid as an intermediate in the conversion of methionine to ethylene. Proc. Nat. Acad. Sci. (USA), 76, 170, 1979.
4. Agami M., Waisel Y.: The ecophysiology of roots of submerged vascular plants. Physiol. Veg., 24, 607, 1986.
5. Agnew M. L., Carrow R. N.: Soil compaction and moisture stress preconditioning in Kentucky Bluegrass. I. Soil aeration, water use, and root response. Agron. J., 77, 872, 1985.
6. Aimi R.: Cell-physiological study on the function root. IV. Active oxygen supply into the root from leaves in rice plant. Proc. Crop Sci. Soc. Jpn. 29, 51, 1960.
7. Amoore J. E.: Dependence of mitosis and respiration in roots upon oxygen tension. Proc. R. Soc., London, 154, 109, 1961.
8. Andersen P. C., Lombard P. B., Westwood M. N.: Effect of root anaerobiosis on the water relations of several *Pyrus* species. Physiol. Plant., 62, 245, 1984.
9. Andersen P. C., Montano J. M., Lombard P. B.: Root anaerobiosis, root respiration, and leaf conductance of peach, willow, quince, and several pear species. Hort. Sci., 20(2), 248, 1985.

10. Ando T., Yoshida S., Nishiyama I.: Nature of oxidizing power of rice roots. *Plant Soil*, 72, 57, 1983.
11. André M., Massimino D., Dagueuet A.: Daily patterns under the life cycle of a maize crop. I. Photosynthesis, transpiration, respiration. *Physiol. Plant.*, 43, 397, 1978.
12. Arashi K., Nitta H.: Studies on the lysigenous intercellular space as the ventilating system in the culm of rice and some other graminaceous plants. *Proc. Crop Sci. Soc. Jpn.*, 24, 78, 1955.
13. Arikado H.: Supplementary studies on the development of the ventilating system in various plants growing on lowland and on upland. *Bull. Fac. Agric., Mich Univ.*, 20, 1, 1959.
14. Armstrong W.: Oxygen diffusion from the roots of some British bog plants. *Nature (London)*, 204, 801, 1964.
15. Armstrong W.: The oxidizing activity of roots in waterlogged soils. *Physiol. Plant.*, 20, 920, 1967.
16. Armstrong W.: Rhizosphere oxidizing in rice: an analysis of intervarietal differences in oxygen flux from the roots. *Physiol. Plant.*, 22, 296, 1969.
17. Armstrong W.: Waterlogged soils, in *Environment and Plant Ecology*. Etherington, J.R. Ed., Wiley, New York, 1975, 181.
18. Armstrong W.: Root aeration in the wetland conditions. [In:] *Plant Life in Anaerobic Environments*. Hook D. D., Crawford. R.M.M. eds. *Ann Arbor Sci. Publ.* Ann Arbor, Mich., 1978, 269.
19. Armstrong W.: Aeration in higher plants. *Adv. Bot. Res.*, 7, 225, 1979.
20. Armstrong W., Gaynard I. J.: The critical oxygen pressures for respiration in intact plants. *Physiol. Plant.*, 37, 200, 1976.
21. Atwell B. J., Thomson C. J., Greenway H., Ward G., Waters I.: A study of the impaired growth of roots of *Zea mays* seedlings at low oxygen concentrations. *Plant, Cell and Environment*, 8, 179, 1985.
22. Aubertin G. M., Rickman R. W., Letey J.: Plant ethanol content as an index of the soil-oxygen status. *Agron. J.*, 58, 305, 1966.
23. Bacha R. E., Hossner L. R.: Characteristics of coatings formed on rice roots as affected by iron and manganese additions. *Soil Sci. Soc. Am. J.*, 41, 931, 1977.
24. Barber D. A., Ebert M., Evans N. T. S.: The movement of  $^{15}O_2$  through barley and rice plants. *J. Exp. Bot.*, 13, 397, 1962.
25. Barlett R. J.: Iron oxidation proximate to plant roots. *Soil Sci.*, 92, 372, 1961.
26. Barta A. L.: Regrowth and alcohol dehydrogenase activity on waterlogged alfalfa and birdsfoot trefoil. *Agron. J.*, 72, 1017, 1980.
27. Barta A. L.: Ethanol synthesis and loss from flooded roots of *Medicago sativa* L. and *Lotus corniculatus* L., *Plant, Cell and Environment*, 7, 187, 1984.
28. Barta A. L.: Metabolic response of *Medicago sativa* L. and *Lotus corniculatus* L. roots to anoxia. *Plant, Cell and Environment*, 9, 127, 1986.
29. Beckel D. K. B.: Cortical disintegration in the roots of *Bouteloua gracilis* (H.B.K.) Lag., *New Phytol.*, 55, 183, 1956.
30. Berry L. J.: The influence of oxygen tension on the respiration rate in different segments of onion roots. *J. Cell. Comp. Physiol.*, 33, 41, 1949.
31. Berry L. J., Norris W. E.: Studies of onion root respiration. Velocity of oxygen consumption in different segments of root of different temperatures as a function of partial pressure of oxygen. *Biochim. Biophys. Acta*, 3, 593, 1949.
32. Bertani A., Brambilla I., Menegas F.: Effect of anaerobiosis on rice seedlings growth, metabolic rate, and fate of fermentation products. *J. Exp. Bot.*, 31, 325, 1980.
33. Bertrand A. R., Kohnke H.: Subsoil conditions and their effects on oxygen supply and growth of corn roots. *Soil Sci. Soc. Am. Proc.*, 21, 135, 1957.
34. Blackwell P. S., Wells E. A.: Limiting oxygen flux densities for oat root extension. *Plant Soil*, 73, 129, 1983.
35. Blevins D. G., Lowe R. H., Staples L.: Nitrate reductase in barley root under sterile, low oxygen conditions. *Plant Physiol.*, 57, 458, 1976.

36. Bolton E. F., Erickson A. E.: Ethanol concentration in tomato plants during soil flooding. *Agron. J.*, 62, 220, 1970.
37. Bradford K. J., Dilley D. R.: Effects of root anaerobiosis on ethylene production, epinasty, and growth of tomato plants, *Plant Physiol.*, 61, 506, 1978.
38. Bradford K. J., Hsiao T. C., Yang, S. F.: Inhibition of ethylene synthesis in tomato plants subjected to anaerobic root stress. *Plant Physiol.*, 70, 1503, 1982.
39. Bradford K. J., Yang S. F.: Xylem transport of l-aminocyclopropane-l-carboxylic acid, an ethylene precursor, in waterlogged tomato plants. *Plant Physiol.*, 65, 322, 1980.
40. Bradford K. J., Yang S. F.: Stress-induced ethylene production in the ethylene-requiring tomato mutant diageotropia. *Plant Physiol.*, 65, 327, 1980.
41. Bradford K. J., Yang S. F.: Physiological responses of plants to waterlogging, *Proc. of the Workshop on Adaptation to Water Stress in Plants*, Hort. Sci. (special insert), 16(1), 25, 1981.
42. Cambell C. A., Ferguson W. S.: Influence of air temperature, light intensity, soil moisture stress, and soil aeration on moisture use by wheat. *Can. J. Plant Sci.*, 49, 129, 1969.
43. Cannel R. Q., Belford R. K., Blackwell P. S., Govi G., Thomson R. J.: Effects of waterlogging on soil aeration and on root and shoot growth and yield of winter oats (*Avena sativa* L.). *Plant Soil*, 85, 361, 1985.
44. Carey R. W., Berry J. A.: Effects of low temperature on respiration and uptake of rubidium ions by excised barley and corn roots. *Plant Physiol.*, 61, 858, 1978.
45. Carpenter J. R., Mitchell C. A.: Root respiration characteristics of flood-tolerant and intolerant tree species, *J. Amer. Soc. Hort. Sci.*, 105, 684, 1980.
46. Carpenter J. R., Mitchell C. A.: Flood-induced shift of electron flow between cyanide-sensitive and alternative respiratory pathways in roots of tolerant and intolerant tree species. *J. Am. Soc. Hort. Sci.*, 105, 688, 1980.
47. Carrow R. N.: Influence of soil compaction on three turfgrass species. *Agron. J.*, 72, 1038, 1980.
48. Chang L. A., Hammett L. K., Pharr D. M.: Carbon dioxide effects on ethanol production, pyruvate decarboxylase, and alcohol dehydrogenase activities in anaerobic sweet potato roots. *Plant Physiol.*, 71, 59, 1983.
49. Chen C. C., Dixon J. B., Turner F. T.: Iron coatings on rice roots: Morphology and models of development. *Soil Sci. Soc. Am. J.*, 44, 1113, 1980.
50. Chirkova T. V.: Some regulatory mechanisms of plant adaptation to temporal anaerobiosis. [In:] *Plant Life in Anaerobic Environments*. Hook D. O., Crawford R. M. M. Eds., Ann Arbor Sci., Ann Arbor Mich., 1978, 137.
51. Chirkova T. V., Gutman T. S.: Physiological role of branch lenticels in willow and poplar under conditions of root anaerobiosis. *Sov. Plant Physiol.*, 19, 289, 1972.
52. Chirkova T. V., Khoang K. I., Blyudzin Y. A.: Effect of anaerobic conditions on fatty acid composition of wheat and rice root phospholipids. *Fiziol. Rast.*, 28, 358, 1981.
53. Chromiński A., Khan M. A., Weber D. J., Smith B. N.: Ethylene and ethern productions in response to salinity stress. *Plant, Cell and Environment*, 9, 687, 1986.
54. Clemens J., Kirk A. M., Mills P. D.: The resistance to waterlogging of three *Eucalyptus* species. Effect of waterlogging and an ethylene-releasing growth substance on *E. robusta*, *E. grandis* and *E. saligna*. *Oecologia*, 34, 125, 1978.
55. Clemens J., Pearson C. J.: The effect of waterlogging on the growth and ethylene content of *Eucalyptus robusta* Sm. (Swamp mahogany). *Oecologia*, 29, 249, 1977.
56. Cline R. A., Erickson A. E.: The effect of oxygen diffusion rate and applied fertilizer on the growth, yield, and chemical composition of peas. *Soil Sci. Soc. Am. Proc.*, 23, 333, 1959.
57. Coult D. A., Vallance K. B.: Observations on the gaseous exchanges which take

- place between *Manyanthes trifoliata* L. and its environment. *J. Exp. Bot.*, 9, 384, 1958.
58. Coutts M. P.: Effects of waterlogging on water relations of actively growing and dormant Sitka spruce seedlings. *Ann. Bot.*, 47, 747, 1981.
  59. Coutts M. P., Armstrong W.: Role of oxygen transport in the tolerance of trees to waterlogging. [In:] *Tree Physiology and Yield Improvement*. Cannell M.G.R., Last F.T. Eds., Academic Press, New York, 1976, 361.
  60. Crawford R. M. M.: Physiological ecology: a comparison of adaptation to oxygen poor environment in plants and animals (German, English summary). *Flora*, 161, 209, 1972.
  61. Crawford R. M. M.: Tolerance of anoxia and the regulation of glycolysis in tree roots. [In:] *The Physiology and Yield Improvement*, Cannell M.G.R., Last E.T. Eds., Academic Press, London, 1976.
  62. Crawford R. M. M.: Tolerance of anoxia and the metabolism of ethanol in tree roots. *New Phytol.*, 79, 519, 1977.
  63. Crawford R. M. M.: Metabolic indicators in the prediction of soil anaerobiosis. [In:] *Nitrogen in the Environment*. Vol. 1, Nielsen D. R., Mc Donald J. G., Eds., Academic Press, New York, 1978, 427.
  64. Crawford R. M. M.: Biochemical and ecological similarities in marsh plants and diving animals (Russian, English summary). *Izv. Akad. Nauk SSSR, Ser. Biol.*, 1, 77, 1981.
  65. Crawford R. M. M.: The anaerobic retreat as a survival strategy for aerobic plants and animals. *Trans. Bot. Soc. Edinb.*, 44, 57, 1982.
  66. Crawford R. M. M., Baines M. A.: Tolerance of anoxia and the metabolism of ethanol in intact roots and seeds. *New Phytol.*, 79, 519, 1977.
  67. Crawford R. M. M., Palin M. A.: Root respiration and temperature limits to North-South distribution of four perennial maritime plants. *Flora*, 171, 338, 1981.
  68. Dacey J. W. H.: Internal winds in water lilies: An adaptation for life in anaerobic sediments. *Science*, 210, 1017, 1980.
  69. Dacey J. W. H.: Pressurised ventilation in the yellow water lily, *Ecology*, 62, 1137, 1981.
  70. Dacey J. W. H., Klug M. J.: Methane efflux from lake sediments through water lilies. *Science*, 203, 1253, 1979.
  71. Dacey J. M. H., Klug M. J.: Tracer studies of gas circulation in Nuphar: oxygen-18 and carbon-14 dioxide transport. *Physiol. Plant.*, 56, 361, 1982.
  72. De Willigen P., van Noordwijk M.: Mathematical models on diffusion of oxygen to and within plant roots, with special emphasis on effects of soil - root contact. I. Derivation of the models. *Plant Soil*, 77, 215, 1984.
  73. De Wit M. C. J.: Morphology and function of roots and shoot growth of crop plants under oxygen deficiency. [In:] *Plant Life in Anaerobic Environment*. Hook D. D., Crawford R. M. M. Eds, Ann Arbor Science Publ., Ann Arbor, Mich., 1978, 333.
  74. Drakeford D. R., Reid D. M.: Changes in the ability of plants to alter the pH of the flooding medium as an early symptom of flooding stress in *Helianthus annuus*. *Can. J. Bot.*, 62, 2417, 1984.
  75. Drew M. C.: Plant responses to anaerobic conditions in soil and solution culture. *Curr. Adv. Plant Sci.*, 36, 1, 1979.
  76. Drew M. C.: Plant injury and adaptation to oxygen deficiency in the root environment: A review, *Plant Soil*, 75, 179, 1983.
  77. Drew M. C., Channel A., Garec J. P., Fourcy A.: Critical air spaces (aerenchyma) in roots of corn subjected to oxygen stress: structure and influence on uptake and translocation of <sup>86</sup>Rb ions. *Plant Physiol.*, 65, 506, 1980.
  78. Drew M. C., Jackson M. B., Giffard S.: Ethylene-promoted adventitious rooting and development of cortical air spaces (aerenchyma) in roots may be adaptive response to flooding in *Zea mays* L., *Planta*, 147, 83, 1979.
  79. Drew M. C., Sisworo E. J.: The development of waterlogging damage in young barley plants in relation to plant nutrient status and changes in soil properties. *New Phytol.*, 82, 301, 1979.



80. Drew M. C., Sisworo E. J., Saker L. R.: Alleviation of waterlogging damage to young barley plants by application of nitrate and a synthetic cytokinin, and comparison between the effects of waterlogging, nitrogen deficiency and root excision, *New Phytol.*, 82, 315, 1979.
81. Eavis B. W., Ralliff L. E., Taylor H. M.: Use of a dead-load technique to determine axial root growth pressure. *Agron. J.*, 61, 640, 1969.
82. Effer W. R., Ranson S. L.: Respiratory metabolism in buckwheat seedlings. *Plant Physiol.*, 42, 1042, 1967.
83. El-Beltagy A. S., Hall M. A.: Effect of water stress upon endogenous ethylene levels in *Vicia faba*. *New Phytol.*, 73, 4, 1974.
84. Erickson A. E.: Short-term oxygen deficiencies and plant responses. [In:] *Conf. Proc. Am. Soc. Agric. Eng. Drainage and Efficient Crop Production*. Chicago, 1965, 17.
85. Esan K.: *Plant Anatomy*, 2nd Ed., Wiley, New York, 1965.
86. Evans N. T. S., Ebert M.: Radioactive oxygen in the study of gas transport down the root of *Vicia faba*. *J. Exp. Bot.*, 11, 246, 1960.
87. Figliolia A., Izza C., Pagliara S.: Effect of some nutritive elements on *Avena sativa* root respiration (Italian, English summary). Note I, *Istituto Sperimentale per la Nutrizione delle Piante*, Rome 1977, 1.
88. Fulton J. M., Erickson A. E.: Relation between soil aeration and ethyl alcohol accumulation in xylem exudate of tomatoes. *Soil Sci. Soc. Am. Proc.*, 28, 610, 1964.
89. Geisler G.: Interactive effects of CO<sub>2</sub> and O<sub>2</sub> in soil on root and top growth of barley and peas. *Plant Physiol.*, 42, 305, 1967.
90. Geisler G.: The influence of oxygen and carbon dioxide concentration on growth of roots and shoots of winter barley, maize and peas (German, English summary). *Bayer, Landwirtsch. Jahrb.*, 45, 259, 1969.
91. Geisler G.: The influence of carbonic acid (CO<sub>2</sub> + HCO<sub>3</sub><sup>-</sup>) in the range of low oxygen concentration (O<sub>2</sub>) in soil air on shoot and root growth of cultivated plants (German, English summary). *Z. Acker Pflanzenbau*, 130, 1, 1969.
92. Ghildyal B. P.: Nature, physical properties and management of submerged rice soils, *Trans. 12th Int. Congr. Soil Sci.*, New Delhi, India, in *Vertisols and Rice Soils of the Tropics. Symposium papers II*, Shri S. N. Mehta, New Delhi, India, 1982, 121.
93. Gill C. J.: The flooding tolerance of woody species - a review. *For. Abstr.*, 31, 671, 1970.
94. Gill W. R., Miller R. D.: A method for study of the influence of mechanical impedance and aeration on the growth of seedling roots. *Soil Sci. Soc. Am. Proc.*, 20, 154, 1956.
95. Ginrich J. R., Russell M. B.: Effect of soil moisture tension and oxygen concentration on the growth of corn roots. *Agron. J.*, 48, 517, 1956.
96. Gliński J., Stepiński W.: *Soil Aeration and Its Role for Plants*. CRC Press, Inc., Boca Raton, Florida, 1985.
97. Good B. J., Faulkner S. P., Patrick W. H. Jr.: Evaluation of green ash root responses as a soil wetness indicator. *Soil Sci. Soc. Am. J.*, 50, 1570, 1986.
98. Gradwell M. W.: Soil physical conditions of winter and the growth of ryegrass plants. 1. Effects of compaction and puddling. *N. Z. J. Agric. Res.*, 8, 238, 1965.
99. Green M. S., Etherington J. R.: Oxidation of ferrous iron by rice (*Oryza sativa* L.) roots: a mechanism for waterlogging tolerance. *J. Exp. Bot.*, 28, 678, 1977.
100. Greenwood D. J.: The effect of oxygen concentration on the decomposition of organic materials in soils. *Plant Soil*, 14, 360, 1961.
101. Greenwood D. J.: Studies on the transport of oxygen through the stems and roots of vegetable seedlings. *New Phytol.*, 66, 337, 1967.
102. Greenwood D. J.: Root growth and oxygen distribution in soil. [In:] *Trans. 9th Int. Congr. Soil Sci.*, Adelaide, Australia, I, 823, 1968.
103. Greenwood D. J., Goodman D.: Studies on the supply of oxygen to the roots of mustard seedlings (*Sinapis alba* L.). *New Phytol.*, 70, 85, 1971.

104. Grineva G. M.: Alcohol formation and excretion by plant roots under anaerobic conditions (Russian, English summary). *Fiziol. Rast.*, 10, 361, 1963.
105. Guinn G.: Nutritional stress and ethylene evolution by young cotton balls. *Crop Sci.*, 16, 89, 1976.
106. Hansen G. K.: Utilization of photosynthates for growth, respiration, and storage in tops and roots of *Lolium multiflorum*. *Physiol. Plant.*, 42, 5, 1978.
107. Hansen G. K., Jensen C. R.: Growth and maintenance respiration in whole plants, tops and roots of *Lolium multiflorum*. *Physiol. Plant.*, 39, 275, 1977.
108. Harris D. G., van Bavel C. H. M.: Root respiration of tobacco, corn, and cotton plants. *Agron. J.*, 49, 182, 1957.
109. Hecht-Buchholz C., Foy C. D.: Effect on aluminium toxicity on root morphology of barley. *Plant Soil*, 63, 93, 1981.
110. Heinrichs D. H.: Root-zone temperature effects of flooding tolerance of legumes. *Can. J. Plant Sci.*, 52, 985, 1972.
111. Hetherington A. M., Hunter M. I. S., Crawford R. M. M.: Contrasting effects of anoxia on rhizome lipids in *Iris* species. *Phytochem.*, 21, 1275, 1982.
112. Holder C. B., Brown K. W.: The relationship between oxygen and water uptake by roots of intact bean plants. *Soil Sci. Soc. Am. J.*, 44, 21, 1980.
113. Holthausen R. S., Caldwell M. M.: Seasonal dynamics of root system respiration in *Altriplex confertifolia*. *Plant Soil*, 55, 307, 1980.
114. Hook D. D., Brown C. L.: Root adaptation and relative flood tolerance of five hardwood species. *Forest Sci.*, 19, 225, 1973.
115. Hook D. D., Brown C. L., Kormanik P. P.: Inductive flood tolerance in swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walt.) Sagr.). *J. Exp. Bot.*, 22, 78, 1971.
116. Hook D. D., Brown C. L., Wetmore R. H.: Aeration in trees. *Bot. Gaz.*, 133, 443, 1972.
117. Hook D. D., Scholtens J. R.: Adaptations and flood tolerance of tree species. [In:] *Plant Life in Anaerobic Environments*. Hook D. D., Crawford R. M. M. Eds., Ann Arbor Science Publ., Ann Arbor, Mich., 1978, 299.
118. Hopkins R. M., Patrick W. H.: Combined effects of oxygen concentration and soil compaction on root penetration. *Soil Sci.*, 108, 408, 1969.
119. Horlacher R., Poskuta J.: The influence of oxygen deficiency in roots on contents of ethanol, lactate and glucose and activities of ADH and LDH of wheat seedlings (German, English summary). *Biol. Plantarum*, 28, 130, 1986.
120. Hosner J. F., Boyce S. G.: Tolerance to water saturated soil of various bottomland hardwoods. *Forest Sci.*, 8, 180, 1962.
121. Hozumi K.: Water tolerance of vegetable crops (in Japanese). *Nogyo Gijyutsu*, 26, 352, 1966.
122. Huck M. G.: Variation in taproot elongation rate as influenced by composition of the soil air. *Agron. J.*, 62, 815, 1970.
123. Huck M. G., Hageman R. H., Hanson J. B.: Diurnal variation in root respiration. *Plant Physiol.*, 37, 371, 1962.
124. Idso S. B., Jackson R. D., Pinter P. J., Jr., Reginato R. J., Hatfield J. L.: Normalizing the stress-degree-day parameter for environmental variability. *Agric. Meteorol.*, 24, 45, 1981.
125. Ishii T., Fusao K., Mizutani K., Kadoya K.: Ethylene evolution in the rhizosphere of grapevines, and growth disorders as affected by ethylene. *Mem. Coll. Agric. Ehime Univ.*, 2, 97, 1982.
126. Jackson M. B.: Ethylene as a growth promoting hormone under flooded conditions. [In:] *Plant Growth Substances*, Wareing P. F., Ed., Academic Press. London, 1982, 291.
127. Jackson M. B., Campbell D. J.: Waterlogging and petiole epinasty in tomato: the role of ethylene and low oxygen. *New Phytol.*, 76, 21, 1976.
128. Jackson M. B., Campbell D. J.: Effects of benzyladenine and gibberelic acid on the response of tomato plants to anaerobic root environments and to ethylene. *New Phytol.*, 82, 331, 1979.
129. Jackson M. B., Drew M. C., Giffard S. C.: Effects of applying ethylene to

- the root system of *Zea mays* on growth and nutrient concentration in relation to flooding tolerance. *Physiol. Plant.*, 52, 23, 1981.
130. Jackson M. B., Gales K., Campbell D. J.: Effect of water-logged soil conditions on the production of ethylene and on water relationships in tomato plants. *J. Exp. Bot.*, 29, 183, 1978.
  131. Jackson M. B., Herman B., Goodenough A.: An examination of the importance of ethanol in causing injury flooded plants, *Plant, Cell and Environment.* 5, 163, 1982.
  132. Jackson W. T.: The role of adventitious roots in recovery of shoots following flooding of the original root systems. *Amer. J. Bot.*, 42, 816, 1955.
  133. Jacobson L., Cooper B. R., Volz, M. G.: The interaction of pH and aeration in Cl uptake by barley roots. *Physiol. Plant.*, 25, 432, 1971.
  134. Jensen C. R., Letey J., Stolzy L. H.: Labelled oxygen transport through growing corn roots. *Science*, 144, 530, 1964.
  135. Jensen C. R., Stolzy L. H., Letey J.: Tracer studies of oxygen diffusion through roots of barley, corn and rice. *Soil Sci.*, 103, 23, 1967.
  136. John C. O., Greenway H.: Alcoholic fermentation and activity of some enzymes in rice roots under anaerobiosis. *Aust. J. Plant. Physiol.*, 3, 325, 1976.
  137. Jugsujinda A., Patrick W. H.: Growth and nutrient uptake by rice in a flooded soil under controlled aerobic-anaerobic and pH conditions. *Agron. J.*, 69, 705, 1977.
  138. Kalir A., Poljakoff-Mayber A.: Effect of salinity on respiratory pathways in root tips of *Tamarix tetragyna*. *Plant Physiol.*, 57, 167, 1976.
  139. Katayama T.: Studies on the intercellular spaces in rice. I. *Proc. Crop Sci. Soc. Jpn.*, 29, 229, 1961.
  140. Kawase M.: Effect of flooding on the ethylene concentration in horticultural plants. *J. Am. Soc. Hortic. Sci.*, 97, 584, 1972.
  141. Kawase M.: Role of ethylene in induction of flooding damage in sunflower. *Physiol. Plant.*, 31, 29, 1974.
  142. Kawase M.: Ethylene accumulation in flooded plants. *Physiol. Plant.* 36, 236, 1976.
  143. Kawase M.: Anaerobic elevation of ethylene concentrations in waterlogged plants. *Amer. J. Bot.*, 65, 736, 1978.
  144. Kawase M.: Role of cellulase in aerenchyma development in sunflower. *Amer. J. Bot.*, 66, 183, 1979.
  145. Kawase M.: Anatomical and morphological adaptation of plants to waterlogging. *Hort. Sci.*, 16(1), 31, 1981.
  146. Kawase M., Whitmoyer R. E.: Aerenchyma development in waterlogged plants. *Amer. J. Bot.*, 67, 18, 1980.
  147. Kenefick D. G.: Formation and elimination of ethanol in sugar beet roots. *Plant Physiol.*, 37, 434, 1962.
  148. Kiyosawa W.: Studies on the effects of alcohols on membrane water permeability of *Nitella*. *Protoplasma*, 86, 243, 1975.
  149. Konings H., Jackson M. B.: A relationship between rates of ethylene production by roots and the promoting or inhibiting effects of exogenous ethylene and water on root elongation. *Z. Pflanzenphysiol.*, 92, 385, 1979.
  150. Kramer P. J.: Causes of injury to plants resulting from flooding of the soil. *Plant Physiol.*, 26, 722, 1951.
  151. Kramer P. J.: *Plant and Soil Water Relationships: A Modern Synthesis*. McGraw-Hill, New York, 1969.
  152. Kramer P. J., Jackson, W. T.: Causes of injury to flooded tobacco plants. *Plant Physiol.*, 29, 241, 1954.
  153. Krizek D. T.: Plant response to atmospheric stress caused by waterlogging. [In:] *Breeding Plants for Less Favourable Environments*. Chap. 10, Wiley, 1982, 293.
  154. Labanauskas C. K., Letey J., Stolzy L. H., Valoras N.: Effects of soil-oxygen and irrigation on the accumulation of macro- and micronutrients in citrus seedlings (*Citrus sinensis* var. Osbeck). *Soil Sci.*, 101, 378, 1966.
  155. Labanauskas C. K., Stolzy L. H., Handy M. F.: Protein and nonprotein amino

- acids in citrus leaves as affected by *Phytophthora* spp. root infestation and soil oxygen content. *J. Am. Soc. Hortic. Sci.*, 97, 433, 1972.
156. Labanauskas C. K., Stolzy L. H., Handy M. F.: Concentrations and total amounts of nutrients in citrus seedlings (*Citrus sinensis* var. Osbeck) and in soil as influenced by differential soil oxygen treatments. *Soil Sci. Soc. Am. Proc.*, 36, 454, 1972.
  157. Labanauskas C. K., Stolzy L. H., Klotz L. J., De Wolfe T. A.: Effects of soil temperature and oxygen on the amounts of macronutrients in citrus seedlings (*Citrus sinensis* var. Bessie). *Soil Sci. Soc. Am. Proc.*, 29, 60, 1965.
  158. Labanauskas C. K., Stolzy L. H., Klotz L. J., De Wolfe T. A.: Soil oxygen diffusion rates and mineral accumulation in citrus seedlings (*Citrus sinensis* var. Osbeck). *Soil Sci.*, 11, 386, 1971.
  159. Labanauskas C. K., Stolzy L. H., Zentmyer G. A., Szuszkiewicz T. E.: Influence of soil oxygen and soil water on the accumulation of nutrients in avocado seedlings (*Persea americana* Mill.). *Plant Soil*, 29, 391, 1968.
  160. Lambers H.: Respiration and NADH-oxidation of the roots of flood-intolerant *Senecio* species as affected by anaerobiosis. *Physiol. Plant.*, 37, 117, 1976.
  161. Lambers H., Smakman G.: Respiration of the roots of flood-tolerant and flood-intolerant *Senecio* species: affinity for oxygen and resistance to cyanide. *Physiol. Plant.*, 42, 163, 1978.
  162. Lambers H., Steingröver E.: Efficiency of root respiration of a flood-tolerant *Senecio* species as affected by low oxygen tension. *Physiol. Plant.*, 42, 179, 1978.
  163. Lambers H., Steingröver E.: Growth respiration of a flood-intolerant *Senecio* species: correlation between calculated and experimental values. *Physiol. Plant.*, 43, 219, 1978.
  164. Lambers H., Szaniawski R. K., de Visser R.: Respiration for growth, maintenance and ion uptake. An evaluation of concepts, methods, values and their significance. *Physiol. Plant.*, 58, 556, 1983.
  165. Lee K. K., Holst R. W., Watanabe I., App A.: Gas transport through rice. *Soil Sci., Plant Nutr.*, 27, 151, 1981.
  166. Lemon E. R.: Soil aeration and plant relations. I. Theory. *Agron. J.*, 54, 167, 1962.
  167. Lemon E. R., Erickson A. E.: The measurement of oxygen diffusion in the soil with a platinum microelectrode. *Soil Sci. Soc. Am. Proc.*, 16, 160, 1952.
  168. Lemon E. R., Erickson A. E.: Principles of the platinum microelectrode as a method of characterizing soil aeration. *Soil Sci.*, 79, 383, 1955.
  169. Lemon E. R., Wiegand C. L.: Soil aeration and plant relations II. Root respiration. *Agron. J.*, 54, 171, 1962.
  170. Letey J., Morgan W. C., Richards S. J., Valoras N.: Physical soil amendments, soil compaction, irrigation, and wetting agents in turfgrass management. III. Effects on oxygen diffusion rate and root growth. *Agron. J.*, 58, 531, 1966.
  171. Letey J., Stolzy L. H., Blank G. B., Lunt O. R.: Effect of temperature on oxygen diffusion rates and subsequent shoot growth, root growth and mineral content of two plant species. *Soil Sci.*, 92, 314, 1961.
  172. Letey J., Stolzy L. H., Lunt O. R., Younger V. B.: Growth and nutrient uptake of Newport bluegrass as affected by soil oxygen. *Plant Soil*, 20, 143, 1964.
  173. Letey J., Stolzy L. H., Valoras N., Szuszkiewicz T. E.: Influence of oxygen diffusion rate on sunflower growth at various soil and air temperatures. *Agron. J.*, 54, 316, 1962.
  174. Levan M. A., Riha S. J.: The precipitation of black oxide coatings on flooded conifer roots of low internal porosity. *Plant Soil*, 95, 33, 1986.
  175. Levan M. A., Riha S. J.: Response of root systems of northern conifer transplants to flooding. *Can. J. For. Res.*, 16, 42, 1986.
  176. Leyshon A. J., Sheard R. W.: Influence of short-term flooding on the growth and plant nutrient composition of barley. *Can. J. Soil Sci.*, 54, 463, 1974.
  177. Liberman M., Kunishi A., Mapson L. W., Wardale D. A.: Stimulation of ethylene production in apple tissue slices by methionine. *Plant. Physiol.*, 41, 376, 1966.

178. Lundegoård H. G.: Carbon dioxide evolution of soil and crop growth. *Soil Sci.*, 23, 417, 1927.
179. Lunt O. R., Letey J., Clark S. B.: Oxygen requirements for root growth in three species of desert shrubs. *Ecology*, 54, 1356, 1973.
180. Luxmoore R. J., Sojka R. E., Stolzy L. H.: Root porosity and growth responses of wheat to aeration and light intensity. *Soil Sci.*, 113, 354, 1972.
181. Luxmoore R. J., Stolzy L. H.: Root porosity and growth responses of rice and maize to oxygen supply. *Agron. J.*, 61, 202, 1969.
182. Luxmoore R. J., Stolzy L. H.: Oxygen diffusion in the soil-plant system. V. Oxygen concentration and temperature effects on oxygen relations predicted for maize roots. *Agron. J.*, 64, 720, 1972.
183. Luxmoore R. J., Stolzy L. H.: Oxygen diffusion in the soil-plant system. VI. A synopsis with commentary. *Agron. J.*, 64, 725, 1972.
184. Luxmoore R. J., Stolzy L. H., Letey J.: Oxygen diffusion in the soil-plant system. I. A model. *Agron. J.*, 62, 317, 1970.
185. Luxmoore R. J., Stolzy L. H., Letey J.: Oxygen diffusion in the soil-plant system. II. Respiration rate, permeability, and porosity of consecutive excised segments of maize and rice roots. *Agron. J.*, 62, 322, 1970.
186. Luxmoore R. J., Stolzy L. H., Letey J.: Oxygen diffusion in the soil-plant system. III. Oxygen concentration profiles, respiration rates, and the significance of plant aeration predicted for maize roots. *Agron. J.*, 62, 325, 1970.
187. Luxmoore R. J., Stolzy L. H., Letey J.: Oxygen diffusion in the soil-plant system. IV. Oxygen concentration profiles, respiration rates and radial oxygen losses predicted for rice roots. *Agron. J.*, 62, 329, 1970.
188. Machlis L.: The respiratory gradient in barley roots. *Am. J. Bot.*, 31, 281, 1944.
189. Mapson L. W.: Biogenesis of ethylene. *Biol. Rev.*, 44, 155, 1969.
190. Maronek D. M., Wott J. A.: Morphological and physiological responses of *Acer rubrum* L., and *Acer saccharum* Marsh. to inundation. *Hort. Sci.*, 10, 316, 1975.
191. Matthews S., Whitebread R.: Factors influencing preemergence mortality in peas. *Plant Physiol.*, 17, 11, 1968.
192. McManmon M., Crawford R. M. M.: A metabolic theory of flooding tolerance: the significance of enzyme distribution and behavior. *New Phytol.*, 70, 299, 1971.
193. McPherson D. C.: Cortical air spaces in the roots of *Zea mays* L. *New Phytol.*, 38, 190, 1939.
194. Mendelssohn I. A., Postek M. T.: Elemental analysis of deposits on the roots of *Spartina alterniflora* Loisel. *Am. J. Bot.*, 69, 904, 1982.
195. Merget A.: Sur la reproduction artificielle des phénomènes de thermodiffusion gazeuse des feuilles, par les corps poreux et pulvérulents humides. *Comptes Rendus, Academie des Sciences, Paris*, 78, 884, 1874.
196. Meyer W. S., Barrs H. D., Smith R. C. G., White N. S., Heritage A. D., Short D. L.: Effect of irrigation on soil oxygen status and root and shoot growth of wheat in a clay soil. *Aust. J. Agric. Res.*, 36, 171, 1985.
197. Mingeau M.: Root porosity and tolerance to flooding (French, English summary). *Ann. Agron.*, 28, 171, 1977.
198. Musgrave A., Jackson M. B., Ling E.: Callitriche stem elongation is controlled by ethylene and gibberellin. *Nature New Biol.*, 238, 93, 1972.
199. Norris W. E., Wiegand C. L., Johanson J.: Effect of carbon dioxide on respiration of excised onion root tips in high oxygen atmosphere. *Soil Sci.*, 88, 144, 1959.
200. Ohmura T., Howell R. W.: Inhibitory effect of water on oxygen consumption by plant materials. *Plant Physiol.*, 35, 184, 1960.
201. Pankhurst C. E., Sprent J. I.: Effect of temperature and oxygen tension on the nitrogenase and respiratory activities of turgid and water-stressed soybean and French bean root nodules. *J. Exp., Bot.*, 27, 96, 1976.

202. Paterson D. R., Earhart D. R., Fuqua M. C.: Effects of flooding level on storage root formation, ethylene production and growth of sweet potato. *Hort-Science*, 14, 739, 1979.
203. Patrick W. H., Delaune E. D., Engler E. M.: Soil oxygen content and root development of cotton in Mississippi river alluvial soils. *La., Agric. Exp. Stn., Bull.*, 673, 1973.
204. Patrick W. H., Turner F. T., Delaune R. D.: Soil oxygen content and root development of sugar cane. *La., Agric. Exp. Stn., Bull.*, 641, 1969.
205. Pereira J. S., Kozłowski T. T.: Variations among woody angiosperms in response to flooding. *Physiol. Plant.*, 41, 184, 1977.
206. Pitman M. G.: Adaptation of barley roots to low oxygen supply and its relation to potassium and sodium uptake. *Plant Physiol.*, 44, 1233, 1969.
207. Philipson J. J., Coutts M. P.: The tolerance of tree roots to waterlogging, III. Oxygen transport in lodgepole pine and Sitka spruce roots of primary structure. *New Phytol.*, 80, 341, 1978.
208. Raffineau-Delile A.: Evidence du mode respiratoire des feuilles de *Nelambium*. *Annales des Sciences Naturelles. II Serie*, 16, 328, 1841.
209. Raskin I., Kende H.: How does deep water rice solve its aeration problem. *Plant Physiol.*, 72, 447, 1983.
210. Raymond P., Bruceau E., Pradet A.: Etude du transport d'oxygène des parties aériennes aux racines à l'aide d'un paramètre du métabolisme. *La charge énergétique*, *CR Acad. Sci.*, 286, 1061, 1978.
211. Raymond P., Pradet A.: Stabilization of adenine nucleotide ratios at various values by an oxygen limitation of respiration in germination lettuce (*Lactuca sativa*) seeds. *Biochem. J.*, 190, 39, 1980.
212. Reid M. S., Pratt H. K.: Effects of ethylene on potato tuber respiration. *Plant Physiol.*, 49, 252, 1972.
213. Report 1975 IVW, Wageningen, The Netherlands, Mededeling 153, 1975, 54.
214. Reyes D. M., Stolzy L. H., Labanauskas C. K.: Temperature and oxygen effects in soil on nutrient uptake in jojoba seedlings. *Agron., J.*, 69, 647, 1977.
215. Rosen C. J., Carlson R. M.: Influence of root zone oxygen stress on potassium and ammonium absorption by Myrobalan plum rootstock. *Plant Soil*, 80, 345, 1984.
216. Ross D. J., Campbell I. B., Bridger B. A.: Biochemical activities of organic soils from subantarctic tussock grasslands on Campbell Islands. I. Oxygen uptakes and nitrogen mineralization. *N.Z.J. Sci.*, 22, 161, 1979.
217. Rovira A. D., Campbell R.: A scanning microscope study of interactions between microorganisms and *Gaeumannomyces graminis* (Syn. *Ophiobolus graminis*) on wheat roots. *Microb. Ecol.*, 2, 177, 1975.
218. Rowe R. N., Beardsell D. V.: Waterlogging of fruits trees. *Hort. Abstr.*, 43, 533, 1973.
219. Rowe R. N., Catlin J. B.: Differential sensitivity to waterlogging and Cyanogenesis by peach, apricot. and plum roots. *J. Am. Soc. Hort. Sci.*, 96, 305, 1971.
220. Saglio P. H., Pradet A.: Soluble sugars, respiration and energy charge during aging of excised maize root tips. *Plant Physiol.*, 66, 516, 1980.
221. Saglio P. H., Rancillac M., Bruzan F., Pradet A.: Initial oxygen pressure for growth and respiration of excised and intact roots. *Plant Physiol.*, 76, 151, 1984.
222. Saglio P. H., Raymond P., Pradet A.: Metabolic activity and energy charge of excised maize root tips under anoxia control by soluble sugars. *Plant Physiol.*, 66, 1053, 1980.
223. Saglio P. H., Raymond P., Pradet A.: Oxygen transport and root respiration of maize seedlings. *Plant Physiol.*, 72, 1035, 1983.
224. Schumacher T. E., Smucker A. J. M.: Mechanical impedance effects on oxygen uptake and porosity of drybean roots. *Agron. J.*, 73, 51, 1981.
225. Schumacher T. E., Smucker A. J. M.: Effect of localized anoxia on *Phaseolus vulgaris* L. root growth. *J. Exp. Bot.*, 35, 156, 1984.
226. Scotter D. R., Thurtell G. W., Tanner C. B.: Measuring oxygen uptake by the roots of intact plants under controlled conditions. *Soil Sci.*, 104, 374, 1967.

227. Sikes D. A., Pattit R. D.: Soil temperature, oxygen, and water level effects on sand shinnery oak. *Soil Sci.*, 130, 344, 1980.
228. Silberbush M., Gornat B., Goldberg D.: Effect of irrigation from a point source (trickling) on oxygen flux and on root extension in the soil. *Plant Soil*, 52, 507, 1979.
229. Sills M., Carrow R. N.: Turfgrass growth, N use, and water use under soil compaction and N fertilization. *Agron. J.*, 75, 488, 1983.
230. Slowik K., Labanauskas C. K., Stolzy L. H., Zentmyer G. A.: Influence of rootstocks, soil oxygen, and soil moisture on the uptake and translocation of nutrients in young avocado plants. *J. Am. Soc. Hortic. Sci.*, 194, 172, 1979.
231. Sojka R. E., Joseph H. A., Stolzy L. H.: Wheat response to short-term heat stress and to soil oxygen stress at three stages of growth. *Agron. J.*, 64, 450, 1972.
232. Sojka S. E., Stolzy L. H.: Soil-oxygen effects on stomatal response. *Soil Sci.*, 130, 350, 1980.
233. Sojka R. E., Stolzy L. H., Kaufmann M. R.: Wheat growth related to rhizosphere temperature and oxygen levels. *Agron. J.*, 67, 591, 1975.
234. Soldatenkov S. V., Chao Hsien-Tuan: The role of bean and corn leaves in re-spiration of oxygen-deprived roots. *Fizjologiya Rastenii*, 8, 385, 1961.
235. Solomos T., Laties G. G.: The mechanisms of ethylene and cyanide action in triggering the rise in respiration in potato tubers. *Plant Physiol.*, 55, 73, 1975.
236. Souty N., Stępniewski W.: The influence of external oxygen concentration on axial root growth force of maize radicals. *Agronomy* 8(4), 295, 1988.
237. Steinman F., Brandla R.: Die Überflutungstoleranz der Seebinse (*Schoenoplectus Lacustris* (L.) Palla). III. Beziehungen zwischen der Sauerstoffkonzentration in der Umgebung. *Flora*, 171, 307, 1981.
238. Stelzer R., Läuchli A.: Salt- and flooding tolerance of *Puccinellia peisonis*, IV. Root respiration and the role of aerenchyma in providing atmospheric oxygen to the roots. *Z. Pflanzenphysiol.*, 97, 171, 1980.
239. Stępniewski W., Gliński J.: Gas exchange and atmospheric properties of flooded soils. [In:] *The Ecology and Management of Wetlands*. Hook D. D., et al. Eds., Croom Helm LTD, Beckenham, Kent, UK, 1987, 269.
240. Stolzy L. H., Flühler H.: Measurement and prediction of anaerobiosis in soils. [In:] *Nitrogen in the Environment*. Vol. 1. Nielsen D. R., McDonald A. G., Eds., Academic Press, New York, 1978, 363.
241. Stolzy L. H., Labanauskas C. K., Klotz L. J., De Wolfe T. A.: Nutritional responses and root rot of *Citrus limon* and *Citrus sinensis* under high and low soil oxygen supplies in the presence and absence of *Phytophthora* spp., *Soil Sci.*, 119, 136, 1975.
242. Stolzy L. H., Letey J., Szuszkiewicz T. E., Lunt O. R.: Root growth and diffusion rates as functions of oxygen concentration. *Soil Sci. Soc. Am. Proc.*, 25, 463, 1961.
243. Stumpf P. K.: Biosynthesis of saturated and unsaturated fatty acids. [In:] *The Biochemistry of Plants*. 4 Ed. Stumpf, P.K., Academic Press, New York, 1980, 177.
244. Szaniawski R. K.: Adaptation and functional balance between shoot and root activity of sunflower plants grown at different root temperatures. *Ann. Bot.*, 51, 453, 1983.
245. Szaniawski R. K.: Homeostasis in cucumber plants during low temperature stress. *Physiol. Plant.*, 64, 212, 1985.
246. Szaniawski R. K.: Plant, stress and homeostasis. *Plant. Physiol., Biochem.*, 25, 63, 1987.
247. Tackett J. L., Pearson R. W.: Oxygen requirements of cotton seedlings roots for penetration of compacted soil cores. *Soil Sci. Soc. Am. Proc.*, 28, 600, 1964.
248. Tackett J. L., Pearson R. W.: Effect of carbon dioxide on cotton seedling root penetration of compacted soil cores. *Soil Sci. Soc. Am. Proc.*, 28, 741, 1964.

249. Taylor G. J., Crowder A. A., Rodden R.: Formation and morphology of an iron plaque on the roots of *Typha latifolia* L. grown in solution culture. *Am. J. Bot.*, 71, 666, 1984.
250. Tjepkema J.: The role of oxygen diffusion from the shoots and nodule roots in nitrogen fixation by root nodules of *Myrica gale*. *Can. J. Bot.*, 56, 1365, 1978.
251. Tolley M. D., DeLaune R. D., Patrick W. H., Jr.: The effect of sediment redox potential and soil acidity on nitrogen uptake, anaerobic root respiration, and growth of rice (*Oryza sativa*). *Plant Soil*, 93, 323, 1986.
252. Tripepi R. R., Mitchell C. A.: Metabolic response of river birch and European birch roots to hypoxia. *Plant Physiol.*, 76, 31, 1984.
253. Trolldenier G.: Einfluss der Stickstoff- und Kaliumernährung von Weizen sowie der Sauerstoffversorgung der Wurzeln auf Bakterienzahl, Wurzelatmung und Denitrifikation in der Rhizosphäre (German, English summary). *Zbl. Bakteriell. Ab. II*, 126, 130, 1971.
254. Trolldenier G., Hecht-Buchholz C.: Effect of aeration status of nutrient solution on microorganisms, mucilage and ultrastructure of wheat roots. *Plant Soil*, 80, 381, 1984.
255. Trolldenier G., von Rheinbaben W.: Root respiration and bacterial population of roots. I. Effect of nitrogen source, potassium nutrition and aeration of roots. *Z. Pflanzenernähr. Bodenkd.*, 114, 366, 1981.
256. Throught M. C. T., Drew M. C.: The development of water-logging damage in wheat seedlings (*Triticum aestivum* L.). I. Shoot and root growth in relation to changes in the concentrations of dissolved gases and solutes in the solution. *Plant Soil*, 54, 55, 1980.
257. Unger P. W., Danielsen R. E.: Influence of oxygen and carbon dioxide on germination and seedling development of corn (*Zea mays* L.). *Agron. J.*, 57, 56, 1965.
258. Van der Heide H., Boer-Bolt B. M., van Raalte M. H.: The effect of a low oxygen content of the medium on the roots of barley seedlings. *Acta Bot. Neerl.*, 12, 231, 1963.
259. Van Diest A.: Effect of soil aeration and compaction upon yield, nutrient uptake and variability in a greenhouse fertility experiment. *Agron. J.*, 54, 515, 1962.
260. Van Noordwijk M., de Willigen P.: Mathematical models on diffusion of oxygen to and within plant roots, with special emphasis on effects of soil-root contact. II. Applications, *Plant Soil*, 77, 233, 1984.
261. Van Raalte M. H.: On the oxygen supply of rice roots. *Ann. Bot., Gard. Buitenzorg*, 51, 43, 1941.
262. Van Raalte M. H.: On the oxidation of the environment by the roots of rice (*Oriza sativa* L.). *Hortus botanicus, Bogotiensis, Java, Syokubutu-Iho*, 1, 15, 1943.
263. Varade S. B., Stolzy L. H., Letey J.: Influence of temperature, light intensity, and aeration on growth and root porosity of wheat, *Triticum aestivum*. *Agron. J.*, 62, 505, 1970.
264. Vartapetian B. B., Andreeva I. N., Maslova I. P., Davtian N. G.: The oxygen and ultrastructure of root cells. *Agrochimica*, XV, 1,1, 1970.
265. Vartapetian B. B., Mazliak P., Lance C.: Lipid biosynthesis in rice coleoptiles grown in the presence or in the absence of oxygen. *Plant Sci. Lett.*, 13, 321, 1978.
266. Veen B. W.: The uptake of potassium, nitrate, water and oxygen by a maize root system in relation to its size. *J. Exp. Bot.*, 28, 1389, 1977.
267. Veen B. W.: Relation between root respiration and root activity. *Plant Soil*. 63, 73, 1981.
268. Visser J., Locher J. Th., Brouwer R.: Effects of aeration and mineral supply on growth and mineral content of shoots and roots of apple trees (var. "Golden Delicious" on M IX). *Neth. J. Agric. Sci.*, 19, 125, 1971.
269. Waddington D. V., Bakker J. H.: Influence of soil aeration on the growth and chemical composition on three grass species. *Agron. J.*, 57, 253, 1965.



270. Wallihan E. F., Garber N. J., Sharpless R. G., Printy W. L.: Effect of soil oxygen deficit on iron nutrition of orange seedlings. *Plant Physiol.*, 36, 425, 1961.
271. Wample R. L., Reid D. M.: Effect of aeration on the flood-induced formation of adventitious roots and other changes in sunflower (*Helianthus annuus* L.). *Planta*, 127, 263, 1975.
272. Wample R. L., Reid D. M.: The role of endogenous auxins and ethylene in the formation of adventitious roots and hypocotyl hypertrophy in flooded sunflower plants (*Helianthus annuus*). *Physiol. Plant.*, 45, 219, 1979.
273. Wanner H.: Oxygen diffusion as a limiting factor of plant root respiration. *Vierteljahrsschr. Naturforsch. Ges. Zuerich*, 90, 98, 1945.
274. Watson E. R., Lapins P., Barron R. J. W.: Effect of waterlogging on the growth, grain and straw yield of wheat, barley and oats. *Aust. J. Exp. Agric. Anim. Husb.*, 16, 116, 1976.
275. Wiedenroth E. M.: Relations between photosynthesis and root metabolism of cereal seedlings influenced by root anaerobiosis. *Phytosynthetica*. 15, 575, 1981.
276. Wiegand C. L., Lemon E. R.: A field study of some plant-soil relation in aeration. *Soil Sci. Soc. Am. Proc.*, 22, 216, 1958.
277. Wiersma D., Mortland M. M.: Response of sugar beets to peroxide fertilization and its relationship to oxygen diffusion. *Soil Sci.*, 75, 355, 1953.
278. Wiersum L. K.: Presumed aerotropic growth of roots of certain species. *Naturwissenschaften*, 54, 203, 1967.
279. Wiersum L. K.: Potential subsoil utilization by roots. *Plant Soil*, 27, 383, 1967.
280. Wiersum L. K.: Tulip root behaviour and aeration requirements. *Acta Hortic.*, 23, 318, 1971.
281. Wiersum L. K.: A comparison of the behaviour of some root systems under restricted aeration. *Neth. J. Agric. Sci.*, 27, 92, 1979.
282. Willey C. R.: Effect of short periods of anaerobic and near-aerobic conditions on water uptake by tobacco roots. *Agron. J.*, 62, 224, 1970.
283. Williams W. T., Barber D. A.: The functional significance of aerenchyma in plant. 15th Symposium Soc. Expt. Biol., 1961, 132.
284. Williamson R. E.: Effect of soil gas composition and flooding on growth of *Nicotiana tabacum* L. *Agron. J.*, 62, 80, 1970.
285. Williamson R. E., Splinter W. E.: Effects on light intensity temperature, and root gaseous environment on growth of *Nicotiana tabacum* L. *Agron. J.*, 61, 285, 1969.
286. Yamasaki T.: Studies on the "excess moisture injury" of upland crops in over-moist soil from the viewpoint of soil chemistry and plant physiology (Japanese, English summary). *Bul. Nat. Inst. Agr. Sci.*, (Japan), 8, 1, 1, 1952.
287. Yu P. T., Stolzy L. H., Letey J.: Survival of plants under prolonged flooded conditions. *Agron. J.*, 61, 844, 1969.
288. Zimmerman J. F., Berry L. J.: Studies of onion root respiration. III. Amperometric titration as a method for the measurement of respiratory overshoot. *Biochem. Acta*, 3, 615, 1949.

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INFLUENCE DES CONDITIONS D'OXYGÈNE DANS LE SOL SUR LA CROISSANCE ET LE FONCTIONNEMENT DES RACINES (LA REVUE DES PUBLICATIONS)

R é s u m é

L'état d'aération du sol est un des plus importants facteurs qui influencent les racines des plants. L'oxygène du sol exerce sur les racines l'influence directe et indirecte. Les racines des plusieurs plantes ne sont approvisionnées en oxygène que par la diffusion radiale d'oxygène de la surface de la racine vers

son intérieur. Avec la présence de l'oxygène est étroitement liée la respiration des racines (respiration de croissance, de maintien et d'adsorption).

La respiration des racines, outre l'oxygène, est influencée par d'autres facteurs extérieurs (bioxyde de carbone, éthylène, température, résistance mécanique du sol, potential rédox et acidité du sol, fumure minérale et salinité du sol) et par des facteurs intérieurs liés avec la respiration des tissus et l'action des parties aériennes des racines. La respiration des nodosités a été peu étudiée.

Sous l'effet du manque d'oxygène dans les racines apparaissent le bioxyde de carbone et les métabolites fermentatifs (éthanol, éthylène et son précurseur ACC et aussi certains acides organiques). De même, la réserve d'énergie est limitée, ce qui entraîne le freinage du processus d'adsorption et du transfert de l'eau et des éléments nutritifs dans les racines. Le déficit d'oxygène dans le sol influence la croissance des racines, le prélèvement des éléments nutritifs leur teneur dans les racines.

Les racines des certaines plantes ont la faculté d'adaptation au stress d'oxygène dans le sol par le changement de leur structure anatomique et morphologique, l'enracinement peu profond et les changements métaboliques et physiologiques.

Dans ce travail sont présentées les questions énumérées ci-dessus, fondées sur la littérature et les résultats des recherches effectuées par les auteurs.

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#### W PŁYW WARUNKÓW TLENOWYCH GLEBY NA WZROST I FUNKCJE KORZENI (PRZEGLĄD LITERATURY)

#### S t r e s z c z e n i e

Stan natlenienia gleby jest jednym z najważniejszych czynników wpływających na korzenie roślin. Tlen glebowy wywiera na korzenie wpływ zarówno bezpośredni, jak i pośredni. Korzenie wielu roślin zaopatrywane są w tlen jedynie na drodze radialnej dyfuzji tlenu od powierzchni korzenia do jego środka. Z obecnością tlenu ściśle jest związana respiracja korzeni (wzrostowa, zachowawcza i adsorpcyjna).

Oprócz tlenu na respirację korzeni wpływają inne czynniki zewnętrzne (dwutlenek węgla, etylen, temperatura, opór mechaniczny gleby, potencjał redoks i kwasowość gleby), jak i wewnętrzne związane z oddychaniem tkanek i wpływem części nadziemnych korzeni. Charakterystyczna jest respiracja brodawek korzeniowych.

Pod wpływem niedotlenienia pojawia się w korzeniach dwutlenek węgla i fermentacyjne metabolity (etanol, etylen i jego prekursor ACC oraz niektóre kwasy organiczne). Również ograniczany jest zasób energii powodujący spowolnienie procesu adsorpcji i przemieszczania wody i składników pokarmowych w korzeniach. Niedobór tlenu w glebie wpływa na wzrost korzeni oraz pobieranie składników pokarmowych i ich zawartość w korzeniach.

Korzenie niektórych roślin mają zdolność adaptacji do stresów tlenowych w glebie poprzez zmianę ich budowy anatomicznej i morfologicznej, płytkie korzenienie oraz zmiany metaboliczne i fizjologiczne.

W opracowaniu omówiono szczegółowo wymienione wyżej zagadnienia na podstawie obszernej literatury oraz wyników badań własnych.