OXYGEN SUPPLY AND CONSUMPTION IN SOILLESS CULTURE: EVALUATION OF AN OXYGEN SIMULATION MODEL FOR CUCUMBER

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Abstract

A soil oxygen simulation model (OXSI) was tested and evaluated for evaluating growing media with respect to aeration. In the model, local oxygen concentrations are calculated from coefficients of diffusion and consumption (respiration), assuming equilibrium conditions.
Apparent oxygen diffusion coefficients (D) were determined under laboratory conditions in 5 cm high samples at different water contents (-3.2, -10 and -20 cm pressure heads). D values were positively related to air-filled porosity (AFP). For fine-graded perlite D ranged from 9.10^{-7} at AFP of 34% to 5.10^{-9} m^2s^{-1} at AFP of 19 %. Possibly due to absence of closed pores in rockwool, the AFP vs. D relation was different for rockwool compared to perlite: D for rockwool ranged from 2.10^{-6} at AFP of 56% to 3.10^{-9} m^2s^{-1} at AFP of 3 %.
A greenhouse experiment with cucumber was carried out to determine respiration and realised oxygen concentrations. The cucumbers were grown in 20 cm high, 3.5 litre containers filled with fine-graded perlite and supplied with high-frequency irrigation. AFP varied between 25 and 45%. At three heights and on four occasions during growth, oxygen concentration (% of volume) in the medium varied between 16.6 and 20% in the perlite.
Root respiration of the cucumbers as determined by two independent methods (*in vivo* and *in vitro*) ranged from 1.4 to 5.4 10^{-6} $ml.ml^{-1}.s^{-1}$. Using these respiration rates, OXSI calculated that no oxygen depletion may occur at D > 1 to 5 10^{-7} m^2s^{-1}, corresponding with an AFP of 30% for both perlite and rockwool. Anoxic condtions were calculated for D values of 10^{-8} m^2s^{-1}, corresponding with AFP below 10% for rockwool and 20% for perlite.

1. Introduction

Oxygen demand in inorganic mineral growing media consists of root and microbial respiration. Root respiration provides plants with energy for root growth, ion uptake and maintenance processes, and is influenced by among others, temperature and relative growth rate (Van der Werf 1993). Microbial respiration is mainly influenced by temperature and – in case of heterotrophic micro-organisms - availability of readily available carbon sources.

Oxygen supply is primarily determined by diffusion, which is governed by the concentration gradient and the apparent diffusion coefficient of oxygen. Since the diffusion in gas-filled pores is three orders of magnitudes higher than in water-filled pores, the apparent diffusion coefficient in agricultural soils has been related to air-filled porosity (Bakker *et al.* 1987).

Oxygen availability to roots grown in soilless culture can become limiting in case oxygen demand exceeds oxygen supply, inducing reduced root growth rate, ion and water uptake, eventually reducing production (e.g. Pezeshki *et al.* 1993). It is therefore

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important to know which criteria/parameters are suitable to judge growing media with respect to oxygen availability.

The program OXSI is a simulation model to calculate oxygen concentrations in a profile under equilibrium conditions, using oxygen diffusion coefficients and respiration as input variables (Stol and Koolen 1997). The present study was set up to determine oxygen diffusion coefficients in fine-graded perlite and rockwool. Furthermore, respiration rates in a system using cucumber grown in fine-graded perlite in pots were determined. Actual oxygen concentrations were compared to model simulations, and situations in which anaerobic conditions occur were calculated.

2. Materials and methods

2.1. Determination of apparent oxygen diffusion coefficients

Oxygen diffusion coefficients were determined according to a method developed by Bakker and Hidding (1970) which is based on the measurement of the oxygen concentration in time with Clark-type membrane electrodes in an initially oxygen-free chamber separated from the atmosphere by a cylinder filled with growing medium. For the measurements, rings (height 5 cm, diameter 7.6 cm) were filled with perlite (fraction 0-1 mm), which were subjected to different pressure heads: -5, -10 and –32 cm. For rockwool, the slab material was cut in order to fill the cylinders. There were three replicates per pressure head. After the measurements, water content of the samples was determined, and air-filled porosity (AFP) was calculated from water content and total porosity.

2.2. Greenhouse experiment

From Jan-May 1999 cucumbers were grown in 3.5 l PVC cylinders (height 20 cm) filled with perlite 0-1 mm. At 5, 10 and 15 cm from the bottom, gas samples were regularly taken from horizontally fitted 3.8 ml gas-sampling cells to determine oxygen concentrations using a Chrompack CP-9003 GC with thermal conductivity detector. More details of the experiment and sampling technique are given by Wever *et al*. (this volume). For the measurements of *in vitro* root respiration (2.3) cucumber plants in the trial were grown in 2.4 l containers filled with perlite (fraction 0-1 mm).

2.3. Respiration analysis

Respiration was determined in two different ways: *in vivo* or *in vitro*. For the *in vivo* measurement the PVC cylinders were closed by using a lid which was sealed airtight around the stems. The cylinders were placed in a layer of nutrient solution to avoid air entrance due to transpiration. Gas samples were taken after 0 and 7 hours at different heights in the cylinder and analysed using GC. For calculation of the respiration, the decrease in oxygen concentration per unit time was divided by the gas volume in the cylinder, using AFP of the perlite.

In the *in vitro* measurement the method of root respiration was based on the oxygen consumption of a root sample in an initially air-saturated solution. The solution in a 125 ml PVC vessel was stirred continuously in order diffusion gradients within the vessel. After decapitating the shoots from pots of 2.4 l, the roots were washed from the growing medium and weighed, and a subsample (2 to 7 g FW) was placed in the vessel. After following the decrease in oxygen concentration for 5 to10 minutes using a membrane electrode, the respiration measurement was terminated, and the root sample was weighed. From the root respiration rate per unit weight (R_w, in mg $O_2.kg^{-1}.min^{-1}$), respiration rate per unit of substrate volume (R_v, in ml $O_2.ml^{-1}.s^{-1}$) was calculated using:

$R_v=(R_w*W_t*22.4)/(M_{O2}*Vp*60*1000)$

where

W_t=total weight of roots in the pot (g)
M_{O2} = molecular weight of oxygen (=32)
V_p=volume of the pot

2.4. Simulation program OXSI

In the model OXSI, oxygen concentrations in a soil profile are calculated from oxygen consumption (R) and the apparent coefficient of diffusion, for the state of equilibrium with constant oxygen flux into the soil (Stol and Koolen 1997). For steady state and vertical diffusion, mass conservation requires for each element in a profile respiration to be equal to diffusion (Bakker *et al* 1987):
$RV = D * \Delta O * A/h$ in which
R = oxygen consumption (respiration) of the element ($m^3.m^{-3}.s^{-1}$)
V = volume of the element (m^3)
A = size of top or bottom surface of the element (m^2)
h = height of element (m)
ΔO = difference in oxygen concentration between upper and lower element surface (-)
D= apparent coefficient of diffusion of oxygen of the element ($m^2.s^{-1}$)

In the calculations, a uniform distribution of D_0 or P in the profile was assumed, and the number of elements chosen was 200 vertically and 10 horizontally.

3. Results and Discussion

3.1. Oxygen diffusion coefficient

The apparent diffusion coefficient of oxygen increased strongly with the air-filled porosity (Fig. 1). However, there were differences between the relations found for rockwool and for perlite. In comparison to the relations found for sand and sandy clays (Bakker *et al* 1987), lower D values at air-filled porosity's around 20% were found for perlite. Possibly the occurrence of closed pores or pores within the perlite particles that do not contribute to gas exchange may explain the difference between perlite and the other growing media. An average of 8 vol.% of closed pores has been found for perlite (Kipp *et al*. 1999).

3.2. Oxygen profiles

Oxygen concentrations in gas-sampling cells were followed at three heights in the perlite-filled cylinders (Fig 2). On average, the lowest oxygen concentrations were 16.6 %, although individual measurements went as low as 14%. Highest oxygen concentrations were generally found in the highest position in the profile. Concentrations were higher than found in rockwool slabs (Wever *et al*., this volume) and in rockwool blocks used for seedling growth of cucumbers (Baas, unpublished results) where concentrations as low as 10% were found. It is not clear whether these concentrations have negative effects on plant functioning. In water culture, where mass flow of oxygen to the roots can be realised to minimise boundary layer effects around roots, a critical oxygen pressure - defined as the lowest partial pressure for a physiological process such as root extension to have its maximum activity - as low as 0.8% have been found for maize roots (Armstrong and Webb 1985). However, for roots grown in media, diffusion is the only significant process involved to reach the root surface, and boundary layer effects are therefore significant. Greenwood (1968) reached the conclusion that root extension in different systems and species was on average reduced to 70% at an oxygen concentration of 6%. For chrysanthemum grown in separate layers in pots, growth in the lower layers was poorest, in which higher (10-20%) oxygen concentrations were found (Strojny *et al* 1998)

3.3. Growth and respiration

Root weight increased six-fold during the experiment (Table 1). Root respiration *in vitro* as determined from subsamples was relatively constant, with the exception of day 41. On the day previous to day 41, accumulated light, and probably photosynthesis was far less than on the other sampling dates (Table 1), which may provide an explanation for the lower root respiration at the moment of sampling. The respiration data per unit FW are comparable to results obtained with young cucumber plants (Daum and Schenk 1995), chrysanthemum and carnation grown in nutrient solution, and rose plants grown in perlite (Baas, unpublished results).

The *in vitro* respiration method is destructive, and errors are possible since only a very small subsample (on average 3%) was taken. Besides, microbial respiration in the growing medium is not determined which may underestimate the respiration per unit volume of growing medium. On the other hand, an overestimation of *in vitro* respiration could be expected since in this method roots are subjected to air-saturated nutrient solution, which may have increased respiration rate compared to possible *in situ* hypoxic conditions. Therefore, an *in vivo* method was also used to estimate respiration by sealing the cylinders airtight and measure the decrease in oxygen during a period of time (Table 2). Similar respiration rates were reached with both methods. Perhaps the somewhat lower respiration rates indicate that the contribution of microbial respiration was – for the inert perlite – not very significant.

When compared to agricultural systems, the respiration rates from Table 1 and 2 are higher than the 0.7 to 4.10^{-7} $ml.ml^{-1}s^{-1}$ as found for sport turfs (Van Wijk 1980) and 5.10^{-7} $ml.ml^{-1}s^{-1}$ as found for *Plantago* in climate chambers (Baas *et al*. 1989).

3.4. Simulation

With the OXSI model, oxygen profiles were simulated for different D and respiration values (Table 3a). Uniformly distributed D and respiration were assumed. Certainly these assumptions are grossly simplified, but may provide an indication over which range of oxygen diffusion coefficients oxygen depletion may occur.

Under these assumptions, a positive effect of decreasing the height (Table 3c and 3d) of the growing medium was found on oxygen concentrations. The explanation is that consumption in the higher layers decreased the concentration gradient and diffusion to the layers lower in the profile. In reality however, D decreases with height due to the higher water content, and - if rooting density is not different - respiration per unit volume will be higher if a lower medium height is used. When this is taken into account in the model, the positive effect of decreasing medium height can be overcome completely. Such a situation of lower D in the lower half of the profile is given in Table 3e and 3f, which resulted in lower oxygen concentrations in the profile.

From the results it was calculated that no oxygen depletion is expected in the range of respiration values of 1 to 5 10^{-6} $ml.ml^{-1}.s^{-1}$ if D values are above 5 10^{-7} $m^2.s^{-1}$, corresponding with AFP of 31% for perlite and 29% for rockwool (Fig. 1). The simulation results were therefore in accordance with the high O_2 concentrations found in th cylinders (Fig. 2) at realized AFP of 22 to 47% in the cylinders (Table 2) and 31 to 37% in the pots filled with perlite (Table 1).

Anoxic conditions were calculated for D values of 10^{-8} $m^2.s^{-1}$ corresponding with AFP below 10% for rockwool and 20% for perlite. Since water contents in rockwool can sometimes be higher than 80% under commercial growing conditions, oxygen depletion may occur under these conditions with concomitant adverse effects. Indeed, for roses in rockwool propagation, it was shown that an AFP of 8 to 22% used in commercial propagation decreased growth compared to 39% AFP (Baas *et al*. 1995). In rockwool, a positive effect of decreasing water content from 70 to 50% during the first months of cultivation was obtained for tomato (Blok 1997).

A requirement of AFP of 30% agrees also with results obtained with

chrysanthemum, where the activity of the enzyme alcohol dehydrogenase – which is induced under hypoxic conditions - was increased below an AFP of 30% (Baas and Warmenhoven 1995).

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Tables

1. Air-filled porosity, growth parameters and root respiration *in vitro* of cucumber grown in 2.4 l perlite pots. (n=4-8)

days after plan-ting	AFP perlite (%)	no. leaves main stem	root weight (gFW)	root respiration ($mg.kg^{-1}$ $FW.min^{-1}$)	root respiration ($10^{-6}ml.ml^{-1}.s^{-1}$)	light sum day before sampling ($J.cm^{-2}.day^{-1}$)
13	37	12	45	5.4	1.5	1083
21	32	19	179	5.5	4.9	1182
41	36	25	172	2.8	2.3	651
53	31	29	281	4.2	5.4	2385

2. Results of oxygen decrease in 7 h at different heights in closed cylinders and calculation of respiration *in vivo* 53 days after planting in the cucumber experiment (n=2).

sample height (cm)	AFP perlite (%)	oxygen decrease ($\%.h^{-1}$)	root respiration (10^{-6} $ml.ml^{-1}.s^{-1}$)
23	100	0.30	1.4
15	47	0.45	
10	45	0.30	
5	22	0.33	

3. a-f. Calculated minimum oxygen concentrations (% v/v) in a profile as a function of respiration ($ml.ml^{-1}.s^{-1}$) and oxygen diffusion coefficient D (m^2s^{-1}); the grey area represents the range of respiration as found in the cucumber greenhouse experiment.

	a. Profile height = 0.2 m					
Respiration\D	1.10^{-8}	5.10^{-8}	1.10^{-7}	5.10^{-7}	1.10^{-6}	5.10^{-6}
1.10^{-5}	0	0	0	0	14	21
5.10^{-6}	0	0	0	14	21	21
1.10^{-6}	0	0	14	21	21	21
5.10^{-7}	0	14	21	21	21	21

	b. Profile height = 0.2 m; respiration only in lower = 0.1 m					
Respiration\D	1.10^{-8}	5.10^{-8}	1.10^{-7}	5.10^{-7}	1.10^{-6}	5.10^{-6}
1.10^{-5}	0	0	0	4	21	21
5.10^{-6}	0	0	0	21	21	21
1.10^{-6}	0	4	21	21	21	21
5.10^{-7}	0	21	21	21	21	21

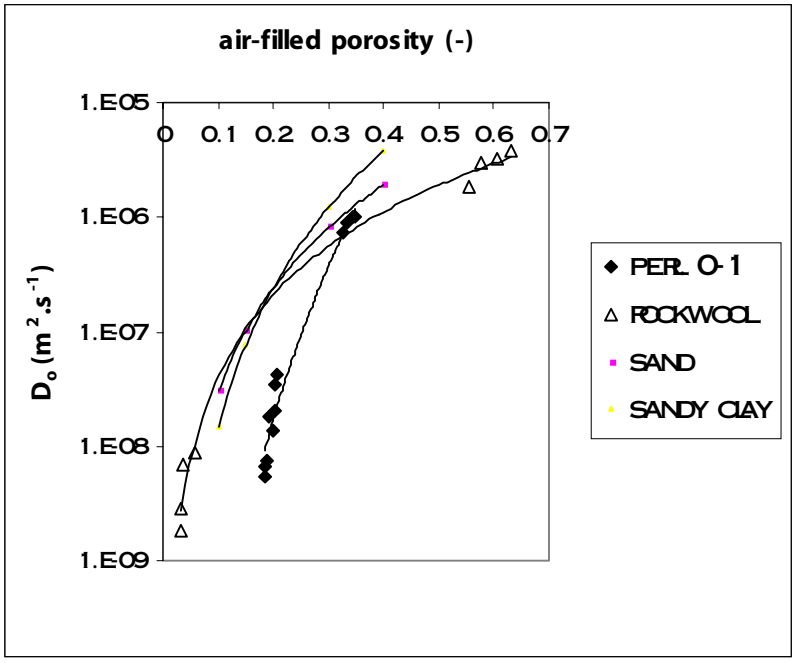
	c. Profile height = 0.10 m					
Respiration\D	1.10^{-8}	5.10^{-8}	1.10^{-7}	5.10^{-7}	1.10^{-6}	5.10^{-6}
1.10^{-5}	0	0	0	21	21	21
5.10^{-6}	0	0	8	21	21	21
1.10^{-6}	0	21	21	21	21	21
5.10^{-7}	8	21	21	21	21	21

	d. Profile height = 0.07 m					
Respiration\D	1.10^{-8}	5.10^{-8}	1.10^{-7}	5.10^{-7}	1.10^{-6}	5.10^{-6}
1.10^{-5}	0	0	9	21	21	21
5.10^{-6}	0	9	21	21	21	21
1.10^{-6}	9	21	21	21	21	21
5.10^{-7}	21	21	21	21	21	21

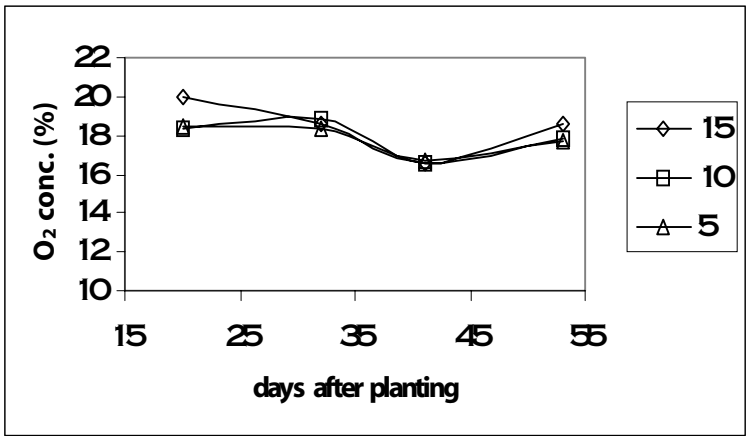
	e. Profile height = 0.2 m; top 10 cm D = 1.10^{-7}					
Respiration\D	1.10^{-8}	5.10^{-8}	1.10^{-7}	5.10^{-7}	1.10^{-6}	5.10^{-6}
1.10^{-5}	0	0	0			
5.10^{-6}	0	0	0			
1.10^{-6}	0	5	14			
5.10^{-7}	0	18	21			

	f. Profile height 0.2 m; top 10 cm D 1 E^{-6}					
Respiration\D	1.10^{-8}	5.10^{-8}	1.10^{-7}	5.10^{-7}	1.10^{-6}	5.10^{-6}
1.10^{-5}	0	0	0	5	14	
5.10^{-6}	0	0	0	18	21	
1.10^{-6}	0	16	21	21	21	
5.10^{-7}	2	21	21	21	21	

Figures



1. Oxygen diffusion coefficients in fine graded perlite and rockwool of 5 cm high samples at -3.2, -10 and –20 cm pressure head in relation to air-filled porosity. Relations as found by Bakker *et al.* (1987) for agricultural soils are also given.



2. Realised oxygen concentrations in fine perlite containers with cucumber at different heights.