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Model calculations on the relative importance of internal longitudinal diffusion for aeration of roots of non-wetland plants

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Abstract

A model is presented with which the contribution of longitudinal oxygen diffusion to total oxygen requirement of a root can be estimated. Oxygen transport in and respiration of the soil are taken into account. Given the air-filled root porosity, root diameter, coefficient of oxygen transfer between root and soil, root and soil respiration rate, and the coefficient for oxygen diffusion in the soil, the maximum length a root can attain with an adequate oxygen supply to the root tip can be calculated. Results show the importance of root porosity for root aeration also in unsaturated soils. For thick roots (radius > 0.03 cm), diffusion along the internal pathway can provide 50–75% of the total oxygen requirement even at modest values of the root porosity.

Introduction

An important condition for proper functioning of root systems is a sufficient supply of oxygen to all root cells. Although roots of some plant species can cope with temporary anaerobic conditions by switching from aerobic to anaerobic forms of metabolism, a sustained supply of molecular oxygen seems to be essential to support active growth and functioning of roots (Armstrong, 1979). The source of oxygen is the atmosphere and for diffusive flow of oxygen from the atmosphere to a certain location in the root two pathways, or combinations thereof, are possible:

a. through the soil to the soil-root interface and then radially through the root tissue (the external pathway);
b. through the aboveground plant parts (leaves, stem), and longitudinally through the root (the internal pathway).

Continuity of gas-filled pores is a prerequisite for longitudinal transport to be of significance. Continuity of air channels exists when aerenchyma (gas spaces) is present. Luxmoore *et al.* (1970) have presented a mathematical treatment of longitudinal transport from shoot to root through such channels. Calculations showed that a considerable part of the oxygen requirement of the root can be provided by the aboveground parts in species adapted to permanently wet soil, *e.g.* rice. For such conditions those properties which limit gaseous exchange between the root and its environment, *i.e.* large root radius and thick water film, improve the supply to the root tip. Aerenchyma is not found in roots of non-wetland species growing under aerated conditions, but usually gas-filled pores form a continuous pathway in longitudinal direction in roots of these species as well (Armstrong, 1979). Even with an effective porosity of no more than 3%, which can be considered a low value for such roots (Armstrong, 1979; see Table 1) there are situations where longitudinal transport of oxygen contributes significantly to the respiratory requirement of the root, as will be shown below. Moreover, when roots of some important non-wetland crops such as maize (Konings, 1983; Yu *et al.*, 1969), wheat, barley (Yu *et al.*, 1969), are growing in a more or less permanently anaerobic environ-

For different soil types in the Netherlands it was found (Bakker, pers. commun.) that the relation between D_s and ε_s can be quite satisfactorily described by

$$D_s(\varepsilon_s) = D_s(1)*(\varepsilon_s)^b. \qquad (16)$$

Table 3 gives values of $D_s(1)$ and b for some Dutch soils; in our calculations the parameters of soil 4 from Table 3 were used.

For a soil at field capacity one can expect ε_s to vary between 0.1 and 0.3 (Boekel, 1962; 1963). We used the range 0.05–0.2.

From the reviews of Brouwer and Wiersum (1977), and Grable (1966), it appears that the range of root respiration rate U_0 can be considerable, viz., 1–60 mg O_2 $cm^{-3}\cdot day^{-1}$, but the majority of the data is in the range 10–20 mg $cm^{-3}\cdot day^{-1}$. In our calculations a value of 10 mg $cm^{-3}\cdot day^{-1}$ was used, considering the fact that soil temperatures in temperate regions are usually lower than the temperatures at which oxygen consumption has been measured.

Luxmoore *et al.* (1970) found that the respiration rate of the apical centimeter of a maize root was about twice as high as that of the remaining part of the root. Accordingly we set $p = 2$, and $\Delta Z = 1$ cm.

Under given environmental conditions, the soil respiration rate depends on amount and decomposition rate of soil organic matter, root respiration, and root density. We used a value of $1.8*10^{-3}$ mg O_2 $cm^{-3}\cdot day^{-1}$. This value has to be augmented by the contribution of root respiration, which was calculated with the above-mentioned value for root respiration U_0, taking into acount root radius and porosity, while root density was assumed to be 1 cm cm^{-3}.

Root radius R_0 varies from 0.01 to 0.05 cm and more for roots with secondary thickening. In the calculations we used a range of 0.01–0.03 cm.

The porosity of roots of non-wetland plants varies from 0 to 19% (Armstrong, 1979; Table 1), depending on species and conditions. We used the range 0.1–15%, taking tortuosity into acount.

The conductance L, which is called root permeability by Luxmoore *et al.* (1970) and Armstrong (1979), was estimated by the former at $5*10^{-4}$ cm s^{-1}, or 40 cm day^{-1}. If the gradient of the oxygen concentration in the water film (with thickness d_w cm) adhering to the root can be assumed to be linear, the conductance can be estimated at D_l/d_w. As the diffusion coefficient for oxygen in water is about 0.85 $cm^2 day^{-1}$ and the water film thickness is assumed to be $5*10^{-3}$ to 0.1 cm, L should be in the range of 8.5–170 cm day^{-1}.

Results and discussion

Earlier, two other models on longitudinal transport of oxygen through roots were designed (Luxmoore *et al.*, 1970; Armstrong, 1979). The most important differences from the model presented here are the way in which the boundary conditions were formulated, and the method of solving the differential equation.

Luxmoore *et al.* (1970) developed a numerical model for the steady-state concentration of oxygen within the root. In their model the root of a given length is surrounded by a water film which at its outer boundary is in contact with soil air with a constant oxygen concentration of 18%, or 0% when under wetland conditions.

Armstrong and Wright (1976) presented an electrical analogue model, designed for simulation of oxygen transport in a root growing under anaerobic conditions. At a given distance from the root the oxygen concentration is assumed to be zero. Later their model was adapted in such a way that different soil respiration rates and non-zero oxygen concentration in the soil could be accounted for (Armstrong, 1979).

The model discussed here allows for changes in soil oxygen concentration with depth. The boundary condition at the apical end of the root, together with the requirement of zero concentration at that point, makes calculation of the potential length of the root possible. Figures 1a and b show the effect of root porosity on the maximum length the root can attain, *i.e.* the length where the minimum oxygen concentration in the root is exactly zero. The calculations were made for a moderately and a well-aerated soil ($\varepsilon_s = 0.1$ and 0.2 cm^3/cm^3), a thin and a rather thick root (radius 0.01 and 0.03 cm), and a low and a high conductance (10 and 200 cm day^{-1}). Both roots had the same volumetric respiration rate (10 mg $cm^{-3}\cdot day^{-1}$). The thickness of the aerobic zone of the soil was for the thin root 47 cm ($\varepsilon_s = 0.1$) or 185 cm ($\varepsilon_s = 0.2$); for the thicker root these values were 19 cm and 75 cm. The influence of root porosity is highest when transfer between soil and root is res-

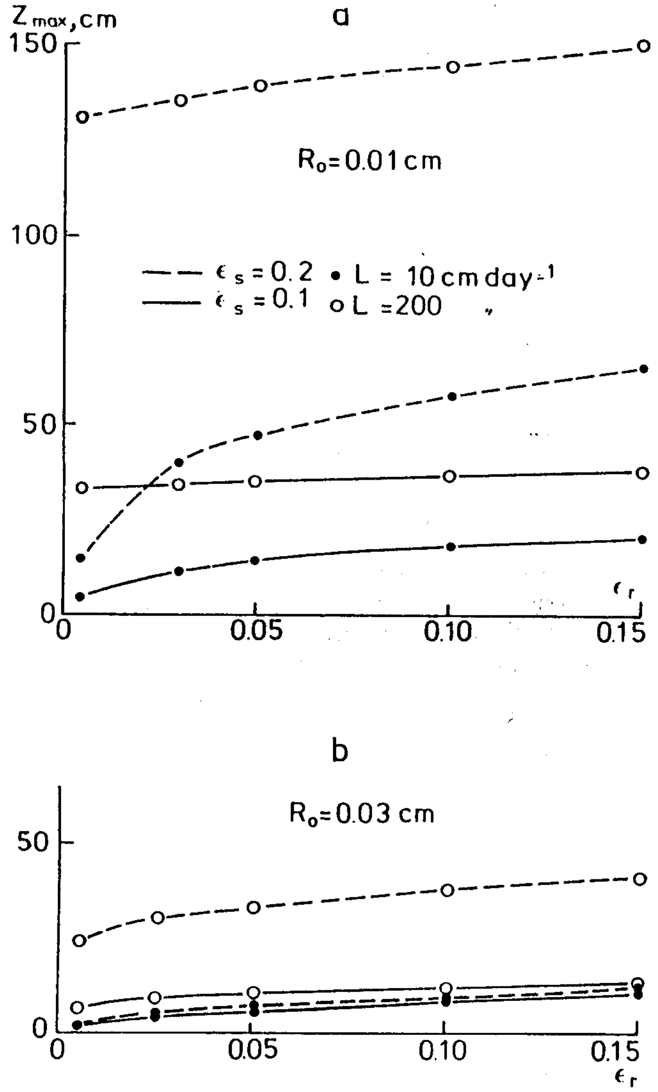

Fig. 1a and b. Maximum attainable root length (Z_{max}) as a function of root porosity (ϵ_r), root thickness (R_0), gas-filled soil porosity (ϵ_s), and conductance (L). Other parameter values: root respiration rate 10 mg $O_2 cm^{-3} \cdot day^{-1}$, soil respiration rate $1.8*10^{-3}$ mg $O_2 cm^{-3} \cdot day^{-1}$.

tricted. For a root radius of 0.01 cm and a soil porosity of 10%, the potential root length increases sevenfold, from 2.8 cm at a root porosity of 0.1% to 20 cm at a root porosity of 15%, when L is only 10 cm day^{-1}. For the higher conductance these lengths are 33 and 39 cm, respectively. For the well-aerated soil these increases are similar. In the case of the thicker root (Figure 1b) a higher rate of exchange between root and soil is more important than a better aeration status of the soil.

The contribution of vertical flow (flow along the internal pathway) to the root respiratory requirement is shown in Figure 2a for the thin root. The highest contribution (up to 30% for a root porosity of 15%) of course occurs when the soil is poorly aerated and exchange between soil and root is limited. In other cases vertical transport contributes less than 10% of the total requirement. Oxygen supply via the internal pathway is much more important for thicker roots, as is shown in Figure 2b. When conductance is low, at least 60% of the requirement is satisfied by vertical transport. In that case the relative contribution of the internal pathway to the oxygen requirement decreases with

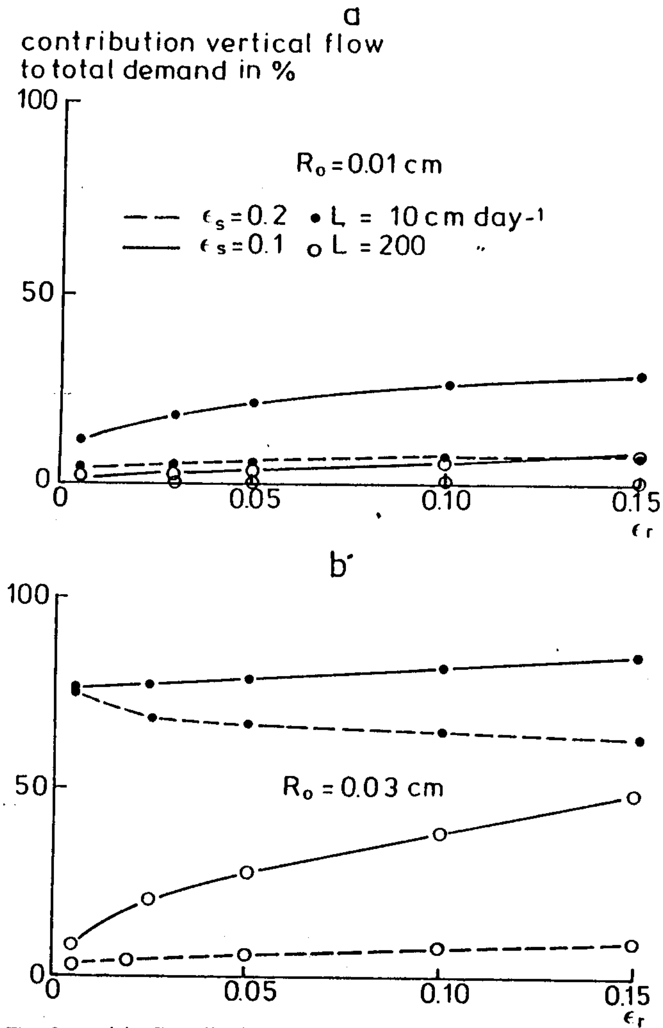

Fig. 2a and b. Contribution of vertical oxygen flow to total oxygen requirement of the root. Respiration parameters as in Figure 1.

increasing root porosity, from 75% (ε_r = 0.5%) to 63% (ε_r = 15%). The absolute contribution increases as the root length increases from 1.4 to 4.3 cm, as shown in Fig. 1b.

The influence of soil porosity on attainable root length is shown in Figure 3. Again it is clear that in the case of thick roots a better aeration status of the soil does little to improve the possibilities of deeper penetration, as long as the transfer between soil and root is restricted: when L = 10 cm day^{-1}, the potential root length increases from 6.7 to 9.1 cm as the gas-filled porosity increases from 0 to 20%, whereas the thickness of the aerobic zone in the soil increases from 0 to 180 cm (not shown in the figure).

The relative contribution of the supply via the internal pathway corresponding to the data of Figure 3 is displayed in Figure 4. At low soil porosity values this contribution exceeds 100%, because then oxygen flows from the root to the soil, of course the more so as the permeability of the root is higher. Under anaerobic conditions the combination of a thicker root and restricted exchange of oxygen between soil and root is more favourable; the reverse is true for aerobic conditions.

This is shown more clearly in Figure 5, where the

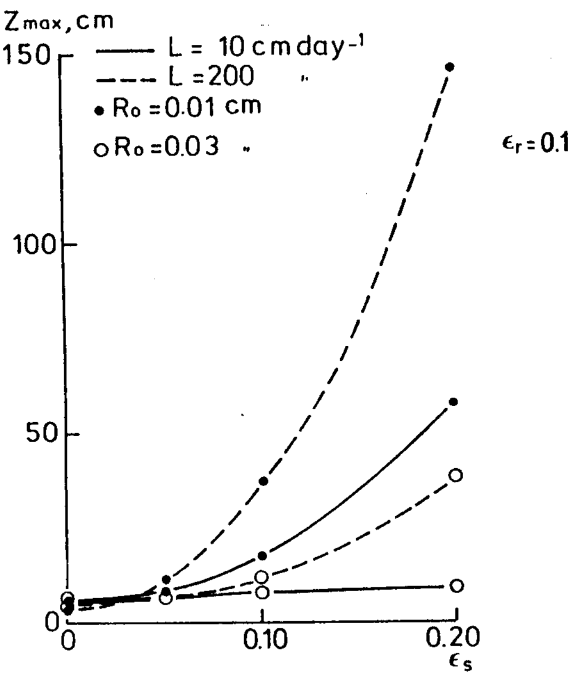

Fig. 3. Maximum attainable root length as a function of gas-filled soil porosity. Respiration parameters as in Figure 1.

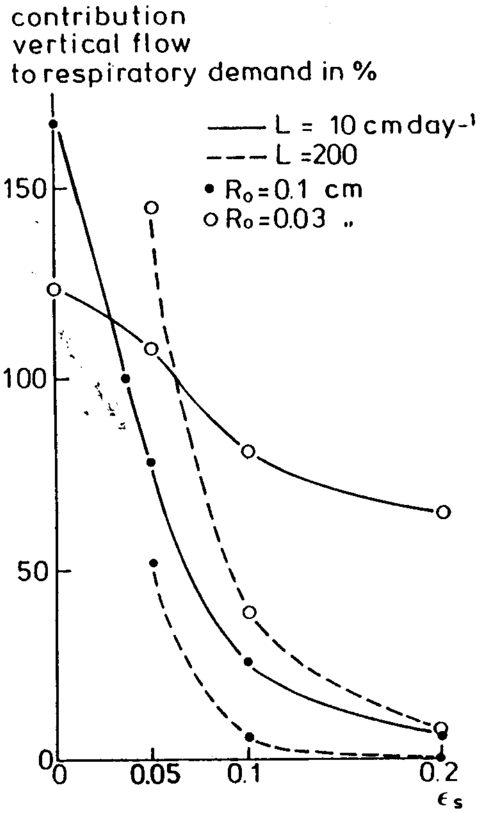

Fig. 4. Relative contribution of vertical flow to total oxygen requirement of roots as a function of gas-filled porosity of the soil. Root porosity 10%, respiration parameters as in Figure 1.

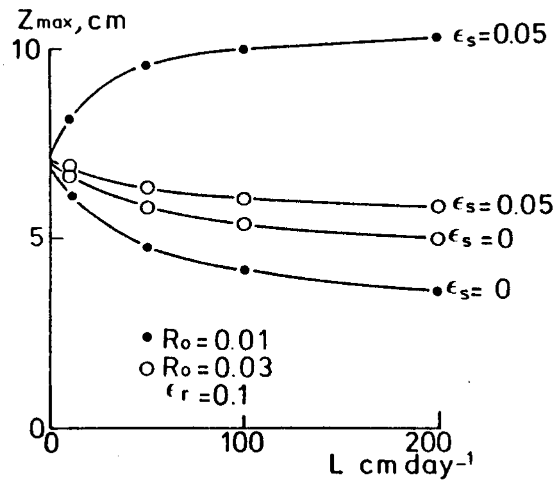

Fig. 5. Maximum attainable root length as a function of conductance of the root wall.

potential maximum root length is given as a function of the conductance. Qualitatively, an increase in root radius and a decrease in conductance have the same effect, as both increase the resistance between the soil air and the location in the root where the minimum concentration will occur.

This can be observed once more in Figure 6, giving Z_{max} as a function of root radius.

In the model treated here it has been assumed that the porosity is distributed evenly over the root tissue. This is obviously a simplification of the actual root structure. Armstrong and Beckett (1985) reported that porosity is often mainly concentrated in the cortex. They discuss the case of radial diffusion of oxygen into a cylindrical root, where the diffusion coefficient in the cortex, which has a thickness of about half the radius of the root, was assumed to be 30 times as large as that in the stele. Because of the high diffusion coefficients, calculated radial gradients in the cortex were found to be practically zero. This implies that, as far as diffusion of oxygen is concerned, the cortex may be neglected, *i.e.* it may be assumed that the effective root radius is the real radius less the thickness of the cortex. With Figure 6 the effect of high diffusion in the cortex can be estimated. For thick roots ($R_0 > 0.04$ cm) with low conductance (thick water film) the maximum length that can be attained is only slightly increased when it is assumed that the effective root radius is half the real root radius. When root conductance is high, the effect of high transport rate in the cortex is considerable.

Our model considers an unbranched vertical root. For a root growing under a known angle β with the normal to the soil surface, $Z \cos \beta$ instead of Z should be used in (8a, b). For branched roots details of the "plumbing" system and continuity of air channels between main axes and branch roots have to be known (Van Noordwijk and Brouwer, in press).

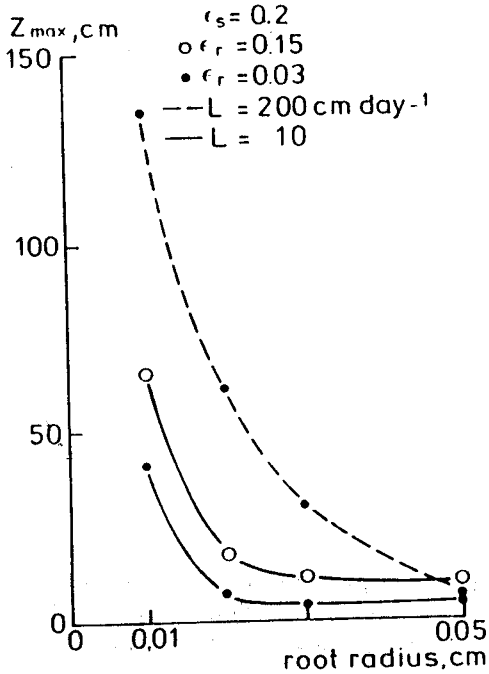

Fig. 6. Maximum attainable root length as a function of root radius. Respiration rate as in Figure 1.

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