How Tree Roots Gather Oxygen from Soil for Energy Supply by Respiration

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The gas exchange between the root system of the European alder (*Alnus glutinosa* (L.) Gaertn.) and the surrounding soil is studied using four-year-old trees. For the experiments the root system connected to its stump is exposed to gases of different molar mass. The stump is cut above the soil surface and in contact with the external atmosphere. A net convective volume flow of gas from the soil into the roots and out of the stump is observed if the mean molar mass of the gas present in the soil is lower than that present in the intercellular space of the roots. The direction of the convective gas flow can be reversed by increasing the molar mass of the gas present in the soil. These phenomena are governed by Graham's law of diffusion. They demonstrate the importance of gas convection for the gas exchange in tree roots.

Introduction

In trees the leaves and chlorenchyma of stems and branches are those tissues which are able to self-support with oxygen by day. But at night, all tree tissues permanently depend on a sufficiently high oxygen supply from the ambient to cover the energy demand of the plant cells by respiratory ATP production (Brändle, 1980). Otherwise the plant cells would be endangered by depletion of storage compounds, lactic acid fermentation and proton release from leaky vacuoles (Pfister-Sieber and Brändle, 1994). This especially accounts for roots which are in competition with the oxygen consuming microorganisms. It is commonly assumed that roots which are growing in well-aerated soil, gather oxygen from gas-filled pores according to Fick's law of diffusion along concentration gradients generated by oxygen consumption of respiring root cells. But, oxygen supply to root tissues by diffusive gas transport is only effective over distances no longer than 20 cm (Armstrong, 1997) and is strongly limited in dense-packed tissues. Therefore, it is not surprizing that wetland trees which are unable to gather oxygen from the water-saturated anoxic soil, have developed a pressurized ventilation mechanism to improve internal aeration by oxygen transport from shoots through the aerenchymatous tissues in the roots as recently reviewed by Grosse (1997). Evidence is accumulating that Graham's law of diffusion plays a role in plant aeration by generating gas convection through the intercellular spaces of plant organs (Schiwinsky *et al.*, 1996).

Graham's law of diffusion (Graham, 1833) refers to a system in which two gases (or mixtures of gases) of different (mean) molar mass are separated by a porous membrane under isothermal and isobaric conditions (Fig. 1). Under these conditions it is found that the ratio of the molar flow densities of the two gaseous components across a porous membrane is equal to the inverse of the square root of the ratio of the molar masses of the components

$$-\left(j_1 / j_2 \right) = \left(M_2 / M_1 \right)^{1/2} \tag{1}$$

with j_1 and j_2 as the molar flow density of the two gaseous species 1 and 2 across the membrane in units of [mol cm^{-2} s^{-1}]. The negative sign indicates that the j_1 and j_2 have opposite directions.

If the bulk phases are maintained at constant pressure, a volume flow across the membrane takes place. The volume of the external phase formed by the higher molar mass component

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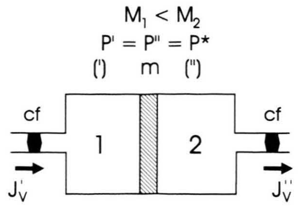

Fig. 1. Isothermal membrane system in which a porous membrane (m) separates two gaseous phases ('), ('') at atmospheric pressure (P' = P'' = P*). The number 1 and 2 are the indices of the gaseous particle species (i), filling the chamber (') and ('') respectively. M_i is the molar mass of the component (i). The letter cf marks the positions of the confining fluid plug in the horizontally positioned capillaries. If the molecular mass M_i of species 2 is greater than the molecular mass of species 1 ($M_1 < M_2$) the volume of the bulk phases changes and the droplets of the confining fluid move in the direction indicated by the arrows (J_V volume flow; $J_V' + J_V'' = 0$, $J_V(a) = dV/dt$ with a = (') or ('')).

(component 2) increases, while that of the lower molar mass (component 1) decreases.

This has been shown in experiments with detached leaves of the White Waterlily (*Nymphaea alba* L.) (Schiwinsky *et al.,* 1996). In that plant species and other floating-leaved aquatic plants from the Nymphaeacean, Nelumbonacean and Menyanthacean families in which the rhizomes and roots are burried in an anoxic sediment of freshwater lakes a gas flow from young to older leaves through the whole plant is observed (Dacey, 1980, 1981). The basic processes involved in the gas uptake by young influx leaves and pressurization in their aerenchyma are: differences in external and internal temperature (thermal transpiration), in partial vapour pressure of water (humidity-induced pressurization), and gas convection governed by Graham's law of diffusion (Grosse *et al.,* 1991; Grosse, 1996a,b). This internal aeration procedure gives these plant species an advantage to settle in anoxic habitats such as lake sediments. In the present studies with tree roots it is demonstrated that gas convection governed by Graham's law of diffusion contributes significantly to the aeration of tree roots.

Materials and Methods

Plant material

Specimens of the European alder (*Alnus glutinosa* (L.) Gaertn.) were cultivated from seeds in well aerated soil consisting of a mixture of gardenmould and sand (ratio 1 : 1); they were potted into plastic containers (170 mm x 170 mm x 170 mm) at normal outdoor conditions in the Experimental garden of the Botanical Institute of the University of Cologne. The root system of about 4-year-old trees was used for the experiments after cutting the shoot at a hight of about 1 cm above the soil surface.

Experimental method

A cylindrical acryl glass chamber (diameter 150 mm, hight 150 mm) with a central bore in its top plate was used to separate the tree's root system from the shoot. The stump of the root system is sealed within the bore using the sealing wax Terostate IX (Teroson, Heidelberg, Germany). The chamber with the root system attached was placed in a bowl containing water (water level, about 1 cm at the bottom, see Fig. 2) to maintain a constant humidity of the atmosphere surrounding the roots. The wall of the chamber had one gas inlet

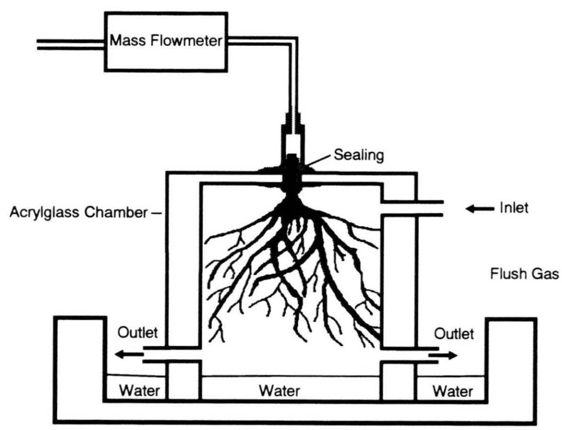

Fig. 2. Experimental set up for gas exchange studies on Alder tree (*Alnus glutinosa* (L.) Gaertn.) roots. The arrows indicate the flow direction of the flush gas.

and two gas outlets to change the composition of the gaseous atmosphere in the chamber at atmospheric pressure. A constant flow rate of the gas of 300 cm^3 min^{-1} was applied using a manostate (Wallace & Tiernan, Type Fa-149, Guenzburg, Germany). To record the flow rate of gas into and out of the stump of the tree, it was connected to a gas flow meter (Mass Flowmeter, FMA 1802, Omega Engineering, INC, Stanford CT, USA; sensitivity: 0–10 cm^3 min^{-1}) and a datalogger (Typ

Squirrel, Grant Instruments (Cambridge) Ltd, Barrington Cambridge, UK) with a narrow tube (diameter $\approx$ 3 mm). The experiments were carried out at room temperature ($T \approx 293$ K).

The following gases supplied by Linde AG, Höllriegelskreuth, Germany, were used for the experiments : Helium (He, molar mass M = 4.00 g mol^{-1}), nitrogen (N_2, molar mass M = 28.01 g mol^{-1}) and methane (CH_4, molar mass M = 16.04 g mol^{-1}). Air has a mean molar mass of M = 28.96 g mol^{-1}. Care was taken that the surface of the cut stump was not blocked by bleeding sap.

Table I. Direction of gasflow at the surface of the cut tree stump (outflow + ; inflow –). The cross area of the stem is 0.9 cm^2.

Gases		$(M_2/M_1)^{1/2}$	Composition of the external phase of root system change from	J_{Vmax}* cm^3 min^{-1}
He	N_2	2.6	N_2 to He	+ 1.2
			He to N_2	– 1.2
He	CH_4	2.0	He to CH_4	+ 1.0
			CH_4 to He	– 0.9
CH_4	N_2	1.3	N_2 to He	+ 0.4
			He to N_2	– 0.6

* Data are calculated from Fig. 3A.

Results

A transient efflux of gas across the surface of the cut stem into the outer atmosphere is observed when the root stock of a tree free of soil and fixed inside the acryl glass chamber is exposed to a gas having a molar mass smaller than that in the intercellular space of the roots. A transient influx of gas across the same surface is found when the root system is exposed to a gas having a molar mass larger than that in the intercellular space of the roots. This is shown by the curves given in Fig. 3A. At the beginning of each experiment the net gas flow across the surface of the cut stem is zero i.e. the composition of the external gas phase and that of the intercellular space of the root system relevant to the observed effect has the same composition. Qualitatively the same phenomena – although on different time scale and with a smaller amplitude – are observed if the same experiments are carried out with the root system covered by the potting soil (see Fig. 3B).

Discussion

The data shown in Fig. 3 demonstrate that the observed gas transport processes are governed by Graham's law of diffusion. From redox measure-

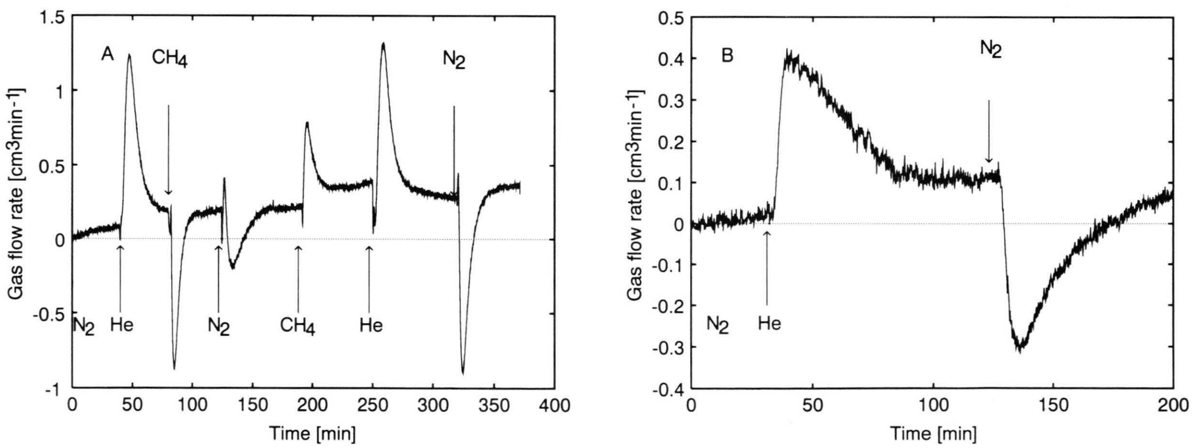

Fig. 3. Records of the direction and the value of the volume flow J_V of gas as function of time at the stump of the cut tree after changing the composition of the gas phase in the acrylglass chamber. Positive and negative values represent efflux and influx of gas, respectively. The composition of the gaseous atmosphere at the tree roots, freed from soil (Fig. 3A) and covered with potting soil (Fig. 3B), respectively, was Helium (He, molar mass M = 4.00 g mol^{-1}), methane (CH_4, molar mass M = 16.04 g mol^{-1}) or nitrogen (N_2, molar mass M = 28.01 g mol^{-1}). The external atmosphere (pressure P: about 1 bar) changed in certain time intervals as indicated by arrows. 'System peaks' result from the interruption of gas supply when flush gas is changed. The presented records are selected from more than 20 replications.

ments with willow roots (*Salix viminalis* (L.)) (Grosse *et al.*, 1996) and oxygen leakage from roots of the European alder (Lattermann, 1994) it is concluded that the relevant porous partition is located at the root tips and those areas where the lateral roots break through the exodermis. Therefore it is expected that local pressure differences will develop across these porous partitions within the root system. It has to be assumed that the hydrodynamic resistance of these porous partitions to the gas flow is higher than that of the conducting porous structures leading to the stump. In this case a short circuiting of the gas flow is avoided. The driving force of the volume flow out of the stump (efflux) is a pressure gradient between the internal phase of the root system near the porous partition (higher pressure) and the outer atmosphere (lower pressure). The opposite is expected to be true in the situation in which a gas influx is observed at the surface of the stump.

In the natural habitat, the mean molar mass of the gas mixture in the intercellular space of the root tissue is expected to be higher than that in the pores of the soil caused by respiratory CO_2 gas (CO_2, molar mass M = 44.01 g mol^{-1}). Consequently a net flow of air (oxygen) enters the root system. The flow of air takes place as long as a difference in the mean molar mass of the gas phases is be maintained by the metabolic CO_2 production. The net flow of air (mean molar mass M = 28.96 g mol^{-1}) into the roots will be increased when methane (CH_4, molar mass M = 16.04 g mol^{-1} from neighboring anoxic aggregates will decrease the mean molar mass of soil gas.

Studies of gas flow through the root system show, that the supply of root tissues with oxygen in well aerated soil, and gas exchange between roots and soil organisms is not governed by diffusive transport alone as generally assumed, to date. From the present results it is concluded, that the aeration of roots and the gas exchange between roots and soil can be significantly enhanced by gas flow processes governed by Graham's law of diffusion.

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