Oxygen Supply of Roots by Gas Transport in Alder-Trees

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Z. Naturforsch. **39 c,** 1186–1188 (1984); received August 3/September 6, 1984

Alnus glutinosa, Gas Transport, Oxygen Supply, Root Aeration, Thermo-Osmosis of Gases

It is generally accepted that oxygen diffuses according to the gradient of its partial pressure from the surface of the plants into the heterotrophic tissues through the intercellular spaces. The present experiments show evidence of an additional manifold higher oxygen supply due to a gas transport in leaved as well as leafless trees of *Alnus glutinosa* (L.) Gaertner. This gas transport is directed from the stems to the roots. It is driven by a thermo-osmotic pressurisation within the air space system of the stems, resulting from temperature gradients up to 3.6 K between the stem and the ambient air following the absorption of light energy by the brownish pigments of the bark. This gas phase phenomena appears to enable the alder-trees to survive and grow in wet soil resulting from a high water table or in waterlogged soil.

Introduction

Oxygen is an essential electron acceptor in respiration of plant cells. According to its partial pressure gradient between the atmosphere and the tissue, oxygen arrives at the heterotrophic tissues by diffusion from the surface of the plants through the intercellular spaces [1–4].

In the aquatic vascular plant *Nuphar lutea* the oxygen supply of the rhizomes and the roots buried in the anaerobic sediment of the lake is accelerated by a pressurized ventilation throughout its continuous air space system [5–8] which results from thermo-osmosis of gases [9]. This gase phase phenomena is thought to be mediated by a "porous layer" with pore diameters of about 0.1 μm in the youngest emerged leaves, which forces molecular effusion but prevents mass flow, and is driven by a gradient in temperature some degrees higher inside the leaves than in the surrounding atmosphere.

Trees of *Alnus glutinosa* from the typical European flood-plain woods (Alnion glutinosae) are growing under similar environmental conditions. Our main interest was therefore to study the alder-trees ability to aerate their roots in wet soil and during periods of early spring floodings.

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0341-0382/84/1100-1186 $ 01.30/0

Materials and Methods

Studies were conducted on six- to twelve-month-old alder-trees (*Alnus glutinosa* (L.) Gaertner) cultivated in the tree-nursery and transfered to a greenhouse during the winter.

For the assays the young trees were inserted in an experimental glass chamber (Fig. 1) which is separated into two compartments by a sealing compound (Carlofon, Cologne, W. Germany) and a water trap.

The experiments were carried out either when the plants were equilibrated to room temperature or when the plants obtained a specific temperature gradient between the inside of the stems and the surrounding atmosphere. The experiments were

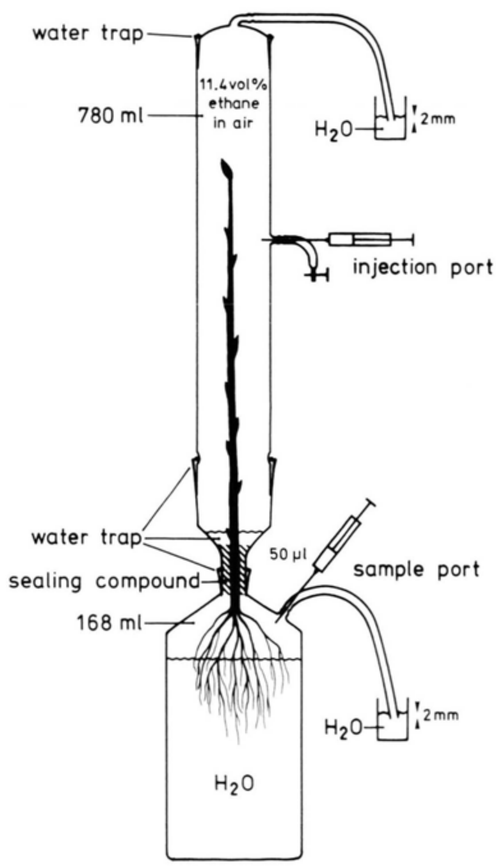

Fig. 1. Experimental glass chamber for determination of gas diffusion and gas transport through young alder-trees.

started by injecting ethane (type 2.0, Linde, W. Germany), a suitable tracer gas [6–8], to the upper compartment (11.4 vol% ethane in air). The stems of the plants were irradiated (up to 200 µE $\text{M}^{-2}\,s^{-1}$) by an 150 Watt incandescent lamp using a water filled cuvette as a thermal trap for lower temperature gradients.

Gas diffusion and gas transport through the plant were calculated from the increase of ethane-content in the air space of the lower compartment after detection of ethane by a Hewlett Packard 5700 A gas chromatograph (Column: Porapak R, 80–100 mesh, 3 ft. × 1/8″, Col. temp.: 40 °C, Flow rate: 30 ml min^{-1}, nitrogen, Det.: FID).

Differences in temperature ($T_i - T_0$) between the inside of the stems (T_i) and the surrounding atmosphere (T_0) were determined using temperature probes NiCr–Ni for the instant action thermometer model 9400-9411 (Technoterm, Lenzkirch, W. Germany). One probe was inserted into the stem and one placed near the plant in the shade of the stem.

Differences in pressure ($p_i - p_0$) between the inside of the stems (p_i) and the atmosphere (p_0) were determined by a micrometer manometer (Gilmont Instruments, Great Neck, N.Y., USA) in pascal (1 Pa = 10^{-5} bar). Iso-octane (density 0.7 g ml^{-1}) was used as the manometric fluid.

Light intensities were determined by a Quantum/Radiometer/Photometer, model LI-185A (Lambda Instruments Corp., Lincoln, Nebraska, USA).

Results and Discussions

When stems of young, leafless alder-trees are exposed to a gas mixture of 11.4 vol% ethane in air in the darkened upper compartment of the experimental glass chamber (Fig. 1), an increasing amount of ethane becomes detectable (Fig. 2) in the air space of the roots-containing compartment. Since the two compartments are sealed by a water trap, the ethane detected must reach the lower compartment by passing through the plant and escaping from the roots. After a lag phase of about 30 min the emanation of ethane from the roots becomes constant at a rate of 0.16 ± 0.06 µl ethane min^{-1}.

Trees which are exposed to air without the tracer gas do not release ethane from their roots (Fig. 2). Therefore the detectable ethane does not result from stress, but is based upon the normal gas diffusion in the intercellular spaces of these trees and represents an influx of approximately 1.41 µl air min^{-1} to the roots.

The release of ethane increases immediately when the stems are irradiated by incandescent light (Fig. 2, arrow). After an equilibration period of 20 min a constant rate of 0.66 ± 0.25 µl ethane min^{-1} representing an influx to the roots of approximately 5.82 µl air min^{-1} is obtained. During this period a constant temperature difference of 1.9 K between the stem and ambient air is developed.

This increased release of ethane does not result from a thermal acceleration of gas diffusion. When the ambient air is heated from 293 K to 303 K by an electric heater the release of ethane is elevated by a neglectable amount only.

On the other hand the rate of ethane emission decreases immediately to the former value after darkening the irradiated plants. Therefore we suggest that the gas emission in the dark represents the normal influx of air to the roots by diffusion of gas through the intercellular spaces. The temperature difference between the stem and the ambient air,

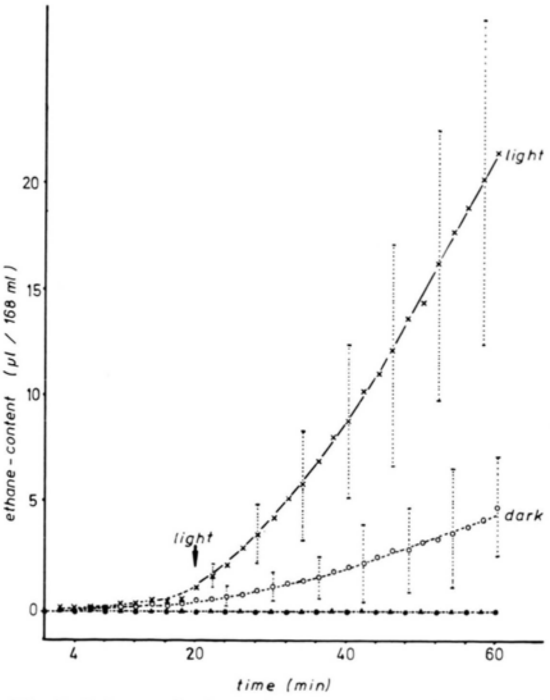

Fig. 2. Release of ethane from the roots of young leafless alder-trees with stems exposed to an ethane containing air mixture (11.4 vol% ethane in air): ○- - - -○ dark; ×——× irradiation; ●-·-·-● without plant; ▲-·-·-▲ without ethane; ↓ light on.

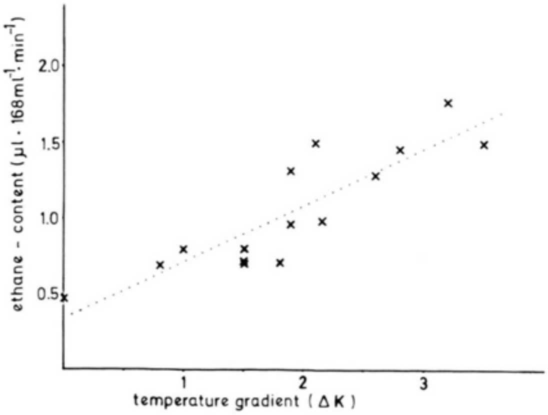

Fig. 3. Correlation between light induced temperature gradients ($T_i - T_0$) and gas transport from the stems to the roots by 12-month-old leaf covered alder-trees (i = inside the stems; ○ = surrounding atmosphere).

Table I. Temperature gradients ($T_i - T_0$) and pressure gradients ($p_i - p_0$) between the inside of the stems (T_i; p_i) and the surrounding atmosphere (T_0; p_0) induced by irradiation of 12-month-old leaf covered alder-trees.

Light intensity [µE m^{-2} s^{-1}]	Temperature gradients ($T_i - T_0$) [ΔK]	Pressure gradients ($p_i - p_0$) [Pa]
50	0.6 ± 0.3	5.0 ± 1.8
75	1.3 ± 0.3	8.4 ± 2.2
100	1.9 ± 0.3	10.8 ± 1.0
125	2.0 ± 0.5	13.4 ± 5.0
150	2.4 ± 0.3	15.9 ± 4.0
200	3.6 ± 0.3	16.9 ± 1.2

resulting from the absorption of light energy by the brownish pigments of the bark, generates an increased flow of air through the alder-trees to their roots by which more oxygen is transported to the heterotrophic part of these plants.

Such an aeration mechanism has also been determined in alder-trees, which are covered with leaves. When the stems of 12-month-old alder-trees are subjected to increasing light intensities, temperature gradients up to Δ 3.6 ± 0.3 K are detectable, accompanied by an increase in pressure within the stems up to a difference of 16.9 ± 1.2 Pa (Table I).

These temperature gradients accelerate the transport rates to a value of 1.7 µl ethane min^{-1} (Fig. 3). From this value we can calculate that 14.7 µl air min^{-1} and 2.7 µl oxygen are transported by this mechanism.

Such an oxygen transport may also occur in the natural habitat. Absorption of the sunlight will create the gradient in temperature necessary to produce the ventilation, which will guarantee a sufficient oxygen supply for the roots of the alder-trees that are often submerged for a long period during that season.

Acknowledgements

This work was supported by the Deutsche Forschungsgemeinschaft. The authors wish to thank Mrs. J. Mevi-Schütz for reading the manuscript.

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