Plant-induced changes in the redox potentials of rice rhizospheres

H. FLESSA¹ and W.R. FISCHER

Lehrstuhl für Bodenkunde, Technische Universität München-Weihenstephan, DW-8050 Freising, Germany and Institut für Bodenkunde und Standortslehre, Universität Hohenheim, DW-7000 Stuttgart, Germany. ¹Present address: Institut für Bodenökologie, GSF, DW-8042, Neuherberg, Germany

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Abstract

Redox potentials in microsites of the rhizosphere of flooded rice were continuously measured for several days. Close to the root tips redox potential markedly increased. The highest increase was measured in the rhizosphere of the tips of short lateral roots. Aerobic redox conditions were reached there, except in a very strongly reduced soil. Both the extension of the oxidation zone around the root tips and the maximum redox potential reached were influenced by the reducing capacity of the soil. The radius of the redox rhizosphere varied from less than 1 mm in a strongly reduced soil up to 4 mm in a weakly reduced one. The root-induced oxidation processes in the rhizosphere depended on the atmospheric oxygen supply to the roots.

Introduction

The roots of marsh plants such as lowland rice (Oryza sativa L.) grow in submerged soils. In this environment, oxygen supply to the roots through the soil is impossible. The rate of oxygen diffusion through water-filled pores is only about one-ten thousandth of that through airfilled pores of aerated soils, and oxygen slowly diffusing into the submerged soil is consumed by microbial respiration and the oxidation of mobile and nonmobile reductants (Howeler and Bouldin, 1971; Reddy et al., 1980). The roots of marsh plants obtain their essential oxygen through a system of air-filled intercellular spaces (aerenchyma) streaking the whole plant, through which oxygen moves from the foliar parts down to the roots (Armstrong, 1971; Luxmoore et al., 1970). Some oxygen diffuses into the rhizosphere, oxidizing various reducing substances in the close vicinity of the roots (Ando et al., 1983). The oxidizing power of the roots protects the plant against reducing substances like ferrous iron or hydrogen sulfide, which may reach phytotoxic concentrations in waterlogged soils (Van Breemen and Moormann, 1978; Tadano and Yoshida, 1978).

The oxidizing power of rice roots is of great interest, because the productivity of rice is influenced by the oxidizing power of its roots (Armstrong, 1969; Joshi et al., 1975).

Different techniques have been described to study the oxidizing power of rice roots. In a deoxygenated liquid medium the oxygen release of rice roots was shown by polarographic analysis of oxygen diffusion (Armstrong, 1967; Luxmoore et al., 1970). In agar culture media, redox indicators like leuco methylene blue were used for characterizing the redox status of the rhizosphere (Trolldenier, 1988). Unfortunately, experiments in nutrient solutions and agar do not reflect the actual processes which occur in soils, because buffering and transport reactions in soils differ markedly from those in the above described culture media.

In the natural soil environment, the oxidizing power can often be detected through the enrichment of red brown ferric oxides/hydroxides around the roots. Measurements of redox potential with poor spatial resolution showed that rice roots can increase the redox potential in a reduced soil (Reddy and Patrick, 1986; Yu Tian-Ren, 1985). However, the redox status reached directly in the rhizosphere and the radial extension of this oxidized soil compartment are still unknown.

The objective of the present research was to investigate the changes in redox potential of microsites in the rhizosphere of single rice roots and to show the influence of the soil's reducing capacity on the extension of the oxidized rhizosphere. following the technique described by Fischer and Schaller (1980) and Fischer et al. (1989). Thirty electrodes were inserted side by side at an equal distance of 0.5 mm into a plexiglass plate. Such plates were fixed in an inclined position in transparent plant containers. The tips of the electrodes projected 1 mm into the containers. The experimental setup used is presented schematically in Figure 1.

Homogenized wet soil was placed into the plant containers and then flooded. After twenty to thirty days, when the electrodes showed constant potentials, five-week-old rice plants were planted into the containers. Roots growing along the inclined plexiglas plate and passing the electrodes were observed, and the potentials of the electrodes were continuously measured against a calomel reference electrode. The experiments were done in three soils showing different reducing capacities (Table 1).

Materials and methods

Redox potentials in the rhizosphere were measured using platinum microelectrodes, which were prepared from Pt wire (diameter 0.5 mm),

Results and discussion

In all soils the rice roots caused marked increases in the redox potential (Figs. 2–4). As long as the root grew above the row of electrodes, constant



Fig. 1. Experimental setup for the measurement of Eh values in the rhizosphere.

	Soil		
	Constantly submerged river sediment	Weathered soil	Unweathered soil
$\overline{\mathrm{C}_{\mathrm{arg}}(\%)}$	6.9	0.7	0.1
$\mathbf{N}_{t}(\%)$	0.49	0.08	
Grain size fraction (%):			
63-2000 μm	18	9	21
$2-63 \ \mu m$	51	52	77
$>2 \mu m$	31	39	2
Eh (mV)	-250	-120	100
PH	6.8	6.7	7.2
$Fe^{2+}(\mu g g^{-1})$	14	0.6	-
$Mn^{2+}(\mu g g^{-1})$	4.5	13.2	1.4
Sulfides	+ ^a	_ ^b	-

Table 1. Some properties of the soils used in the experiment

^adectectable; ^bnot detectable.



Fig. 2. Time course of Eh in the rhizosphere of rice at two different electrode positions. Electrode El came into contact with the root tip after 41 hours. The minimum distance of electrode E2 to the root surface was 1 mm. After 193 hours formation of a lateral root. Soil: River sediment.

Eh values were measured. After the root tip had reached this row the potentials reflected the actual Eh profile through the rhizosphere. The largest Eh differences were measured at the electrodes closest to the root, whereas the electrodes far from the root displayed the Eh of the bulk soil. Due to the single root movement along one electrode, the Eh changes with time reflected the redox status of the rhizosphere of different root zones. The oxidizing power of the root was concentrated at the root tip. In the most strongly reduced soil (river sediment with high content of organic matter), the redox poten-



Fig. 3. Time course of Eh in the rhizosphere of rice at three different electrode positions. Electrode El came into contact with the root tip after 70 hours. The distances of electrodes E2 and E3 to the root surface were 1 mm and 2 mm, respectively. After 175 hours formation of lateral roots. Soil: Weathered soil.

tial in the rhizosphere of the primary root tip increased from -250 mV up to 100 mV (Fig. 2). Only the electrode which was in contact with the root (El) showed this marked and very rapid Eh increase. At a 1-mm distance from the root surface (E2), the redox potential remained nearly constant. One centimeter behind the root tip the potential decreased and reached the level of the bulk soil. The second Eh increase (after 193 hours) was caused by the oxidizing power of a small lateral root tip, which arose from the primary root and enlarged the extension of oxidation processes around the primary root. In the



Fig. 4. Time course of Eh in the rhizosphere of rice at thirteen different electrode positions. After 22 hours the root reached the elec rode row. After 115 hours formation of lateral roots. Soil: Unweathered soil.

other soils, the time course of the redox potential along the rice root showed similar characteristics, with a first Eh increase at the tip of the prinary root and a second increase which was caused by the oxidizing power of the lateral roots (Figs. 3-4). Compared to the primary root, the Eh increase was higher near the tip of the laterals. This was probably due to the slow growth of the short lateral roots. Their oxidizing power could influence a distinct soil zone for a longer period. The primary roots grew faster and were therefore continuously exposed to the reduced soil. In the unweathered and weathered soils, close to the lateral roots redox potentials were characteristic of those prevailing under aerated conditions assuming constant pH values (Ponnamperuma, 1972). The results are in accordance with observations made by Armstrong (1971, 1979) in deoxygenated liquid media. Using the technique of polarographic oxygen measurement he found that the oxygen release of rice roots was highest at the root tips and diminished rapidly towards older root zones.

The extension of the oxidation zone around the root tips and the maximum redox potential reached were influenced by the reducing capacity of the soil (Fig. 5). The reducing capacity of



Fig. 5. Eh profiles through the rhizosphere of the primary root tip of rice in three soils differing in reducing capacity.

submerged soils depends on the concentration of mobile and nonmobile reducing substances and on microbial respiration (Howeler and Bouldin, 1971; Reddy et al., 1980). Consequently, oxygen diffusing into the rhizosphere is consumed by respiration and chemical reactions, and the extension of the Eh increase is restricted. The maximum extension of the Eh increase around the tip of the primary root varied from less than 1 mm in a strongly reduced soil (river sediment) up to 4 mm in a weakly reduced one (unweathered soil). Armstrong (1970) predicted the probable dimension of the oxidized rhizosphere of rice on the basis of oxygen diffusion measurements in distilled water. Assuming constant rates of oxygen consumption, his mathematical model predicted an extension of about 4 mm in weakly reduced soils and 1 mm in strongly reduced ones and showed an excellent correspondence with measured redox potential profiles.

The oxidizing power of rice roots depends on the continuous supply of atmospheric oxygen through the intercellular spaces. Changing the atmosphere from air to nitrogen gas caused a rapid decrease in redox potential of the rhizosphere (Fig. 6). The gassing with nitrogen gas stopped the internal oxygen supply to the roots. Furthermore, the oxygen as well as the previously oxidized compounds in the rhizosphere were reduced by microbial respiration and reductants. The experiments done by Ando et al. (1983) in water showed similar results. They reported that the oxygen release of rice roots decreased with a decreasing oxygen concentration in the atmosphere.



Fig. 6. Effect of atmospheric oxygen supply on redox potentials of the rhizosphere at four different electrode positions. After 40 hours Eh increase (El) caused by the oxidizing power of a lateral root. The distances of E2, E3 and E4 to the primary root were 1 mm, 2 mm and 3 mm, respectively. After 164 hours the atmosphere was changed to nitrogen gas. Soil: River sediment.

Plant-induced changes in redox potential 59

The results show that lowland rice is capable of markedly increasing the redox potential in the rhizosphere of its root tips even in strongly reduced soils. This ability is an essential part of its adaptation to the ecological properties of its natural habitat because it is an effective protection against phytotoxic concentrations of reducing substances.

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60 Plant-induced changes in redox potential

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