Pro Terra
No. 7

Oxygen supply to plant roots in cultivated mineral soils

Asko Simojoki

Department of Applied Chemistry and Microbiology
Agricultural Chemistry and Physics
P.O. Box 27 (Latokartanonkaari 11)
FIN-00014 University of Helsinki, Finland

E-mail: asko.simojoki@helsinki.fi

Academic Dissertation

To be presented, with the permission of
the Faculty of Agriculture and Forestry of the University of Helsinki,
for public criticism in Auditorium XII, Aleksanterinkatu 5, Helsinki,
on May 4th, 2001, at 12 o´clock noon.

DEPARTMENT OF APPLIED CHEMISTRY AND MICROBIOLOGY
UNIVERSITY OF HELSINKI

Helsinki 2001

This thesis belongs to the field of Agricultural Chemistry and Physics.

Supervisor:	Professor Antti Jaakkola Department of Applied Chemistry and Microbiology University of Helsinki, Finland
Reviewers:	Professor Erkki Aura Environmental Research, Soils and Environment MTT Agrifood Research Finland Jokioinen, Finland
	Professor Witold Stępniewski Institute of Environmental Protection Engineering Technical University of Lublin, Poland
Opponent:	Professor Dr. Rainer Horn Institute of Plant Nutrition and Soil Science Christian Albrechts University Kiel, Germany

Cover: A view to soil O_2

ISSN 1457-263X
ISBN 951-45-9926-8
ISBN 951-45-9927-6 (PDF version available at http://ethesis.helsinki.fi)

Yliopistopaino, Helsinki 2001

Simojoki, A. 2001. Oxygen supply to plant roots in cultivated mineral soils. - Doctoral Dissertation, Department of Applied Chemistry and Microbiology, University of Helsinki. Pro Terra No. 7. Helsinki. 59 p. + 6 appendix articles. ISSN 1457-263X, ISBN 951-45-9926-8, ISBN 951-45-9927-6 (PDF).

ABSTRACT

Roots of all plant species need oxygen for growth, and most crops are supplied with oxygen mainly from soil air. Poor aeration is generally a problem only in wet soils. In compacted soils both large mechanical impedance and poor aeration inhibit the growth of roots and may lead to yield reductions.

In this study, the variation in soil air composition, N_2O emission and several environmental variables were monitored in loamy clay and loam fields under various combinations of agricultural management practices including compaction, heavy irrigation or wetting, cropping and N fertilization. The aim was to explore the instances in which poor aeration might be detrimental to plant production or environment. More detailed research into the conditions leading to hypoxia in soil and the effects of hypoxia and compaction on soil respiration and barley growth were carried out in pot experiments with fine sand soil treated with combinations of compaction (loose, compacted), wetting (moist, wet) and forced aeration (0%, 2%, 6%, 10%, 20% O_2 in N_2 gas). Both uncropped and cropped pots were included. In addition, the incidence of wet growing seasons was estimated at five locations in different parts of Finland using long-term weather data to calculate the probability of a precipitation deficit of less than zero at certain times in a growing season.

The weather data indicated that wet weather during the early growing season and during harvesting is not uncommon in Finland. The pot experiments showed that O_2 concentrations as low as 6% in soil air are adequate for respiration and growth of barley roots in soil at moderate moisture contents, but in wet soil plant growth is impaired even if the soil is aerated with a gas stream containing 20% O_2. The observed effects of O_2 concentration on the respiration and growth of barley roots compared fairly well with the critical oxygen concentrations calculated by a simple multicylindrical diffusion model, in which the water-film thickness around the roots was estimated using soil water retention data.

The experiments indicated that, if the soil is wet, in the conditions prevailing in Finland, hypoxia occasionally limits root growth especially below the ploughed layer. In particular, heavy compaction of clay impairs subsoil aeration for several years. Poor aeration can contribute to a low yield and nitrogen uptake in compacted and wet soils. In wet soil, denitrification is obvious and probably contributes to the yield loss. However, if hypoxia lasts only a short time, the risk to yield loss is small. Also well-aerated soil layers near the surface may prevent yield reduction.

The field experiments also showed that leaving land fallow is detrimental to the environment, because it causes N_2O emissions. So do irrigation and N fertilization, but cropping is efficient in diminishing the emissions. Large emissions or concentrations of N_2O in soil air indicate soil hypoxia, but the importance of this on plant growth is confounded by the heterogeneity of field soils.

PREFACE

The work summarized in my thesis was conducted at the Department of Applied Chemistry and Microbiology, University of Helsinki, in collaboration with the Agricultural Research Centre of Finland, Jokioinen, during 1986-2001. The pot experiments and most of the laboratory work were carried out in Viikki, and the field experiments in Hausjärvi and Jokioinen. Many people have been involved in this study. I wish to thank them all.

I am most grateful to my supervisor Professor Antti Jaakkola for his collaboration and for encouraging me to continue studies on soil air. I thank him and Professor Helinä Hartikainen for discussions, criticism and support at various stages of the study. I am also grateful to the late Professor Paavo Elonen, Professor Martti Esala and Dr. Laura Alakukku for their collaboration and help in field experimentation. I thank Dr. Liisa Pietola for help and advice in the root studies. The discussions with Dr. John A. Currie in Uppsala and Harpenden, and with Professor Witold Stępniewski in Lublin and Helsinki, were inspiring. Professors Erkki Aura and Witold Stępniewski are gratefully acknowledged for their pre-examination of the manuscript of my thesis. I also thank Dr. Raina Niskanen for reviewing and commenting on the manuscript.

I am also indebted to numerous people for technical assistance. Special thanks are due to Ms. Susanna Hyvärinen and the staff of our Department for their contribution during all stages of the study, and due to Mr. Timo Simojoki, my brother, for fulfilling various tasks at short notice. I express my warmest thanks also to Mr. Jari Anttila, Mr. Harri Eskelin, Ms. Eeva Kontkanen, Ms. Astrid Kovaljeff, Ms. Heli Kyrönkari, Ms. Leena Laaksonen, Ms. Riitta Lemola, Ms. Päivi Nevalainen, Mr. Harri Pihl, Ms. Riikka Simojoki and Ms. Gerd Tötterman for assistance with the pot experiments and laboratory analyses. The staff of the Agricultural Research Centre, especially Mr. Risto Tanni, Ms. Leena Seppänen, Ms. Airi Kulmala and Ms. Jaana Alihokka, are gratefully acknowledged for help with the field experiments.

I also thank the staff of the Department of Agricultural Engineering and Household Technology and especially Mr. Raimo Kivi for friendly co-operation. The Instrument Centre is acknowledged for help in technical problems. Soils for the pot experiments were provided by Viikki Experimental Farm (University of Helsinki) and by Kotkaniemi Experimental Farm in Vihti (Kemira Agro Oy); I thank especially Mr. Martti Lippo for transporting the soil from Vihti to Viikki. I am grateful to the Finnish Meteorological Institute for help with the weather data. I also express my gratitude to Mr. Donald Smart for the English language revision of my thesis.

This study was financially supported by the University of Helsinki and by the Academy of Finland. Also the grants from the foundations of August Johannes and Aino Tiura, the Finnish Association of Academic Agronomists, Kemira Oyj and the Scientific Agricultural Society of Finland are gratefully acknowledged.

Finally, I thank my parents as well as my friends for their continuing support. Most of all, I am grateful to Meri for being there when I came home late.

To my teachers

Helsinki, April 2001

Asko Simojoki

LIST OF ORIGINAL PUBLICATIONS

The thesis is a summary and discussion of the following articles, which are referred to by their Roman numerals:

I Simojoki A., Jaakkola A. & Alakukku L. 1991. Effect of compaction on soil air in a pot experiment and in the field. *Soil & Tillage Research* 19: 175-186. Reproduced with the permission of Elsevier Science B.V.

II Jaakkola A. & Simojoki A. 1998. Effect of soil wetness on air composition and nitrous oxide emission in a loam soil. *Agricultural and Food Science in Finland* 7: 491-505. Reproduced with the permission of Agricultural and Food Science in Finland.

III Simojoki A. & Jaakkola A. 2000. Effect of nitrogen fertilization, cropping and irrigation on soil air composition and nitrous oxide emission in a loamy clay. *European Journal of Soil Science* 51: 413-424. Reproduced with the permission of Blackwell Science Ltd.

IV Simojoki A. 2000. Responses of soil respiration and barley growth to modified supply of oxygen in the soil. *Agricultural and Food Science in Finland* 9: 303-318. Reproduced with the permission of Agricultural and Food Science in Finland.

V Simojoki A. 2000. Calibration of a desktop scanner and digital image analysis procedure for quantification of root morphology. *Agricultural and Food Science in Finland* 9: 223-230. Reproduced with the permission of Agricultural and Food Science in Finland.

VI Simojoki A. 2001. Morphological responses of barley roots to soil compaction and modified supply of oxygen. *Agricultural and Food Science in Finland* 10: 45-52. Reproduced with the permission of Agricultural and Food Science in Finland.

In addition, some unpublished data are presented.

The author's contribution

Paper I:
Asko Simojoki wrote the paper, is the corresponding author and interpreted the results. He is responsible for the pot experiments and gas analysis.

Paper II:
Asko Simojoki wrote the paper and interpreted the results together with the co-author.

Paper III:
Asko Simojoki designed the experiments. He wrote the paper, is the corresponding author and interpreted the results. He is responsible for all the experimental work.

CONTENTS

ORIGINAL PUBLICATIONS (I-VI)

SYMBOLS AND ABBREVIATIONS

Symbols

C	gas concentration, m^3 m^{-3}
C_a	gas concentration in soil air, m^3 m^{-3}
C_{atm}	gas concentration in the atmosphere, m^3 m^{-3}
C_0	gas concentration at the outer edge of the water-film surrounding the roots, m^3 m^{-3}
C_w	differential water capacity, kPa^{-1}
D	gaseous diffusion coefficient, m^2 s^{-1}
D_i	gaseous diffusion coefficient in phase i, m^2 s^{-1}
D_0	gaseous coefficient in air, m^2 s^{-1}
D_w	gaseous diffusion coefficient in water, m^2 s^{-1}
D/D_0	relative diffusion coefficient of a gas
J	gaseous flux, m^3 m^{-2} s^{-1}
K_m	Michaelis' constant
L	depth, m
Q_{10}	the rate of a process at T + 10 K divided by the rate at T
R	radius, m
R_i	radius of i, m
T	temperature, K
X	random variable

d	thickness of the water-film surrounding the roots, m
$n(\psi_m)$	length density of air-filled pores, m^{-2}
q	respiration rate, m^3 m^{-3} s^{-1}
r	radial distance, m
t	time, s
x	random variable
z	linear distance or depth, m

$\alpha(\varepsilon)$	a term describing the geometry of soil air space
α_B	Bunsen's solubility coefficient
ε	air-filled porosity, m^3 m^{-3}
θ	moisture content, m^3 m^{-3}
σ	surface tension of water, N m^{-1}
ϕ	total porosity, m^3 m^{-3}
ϕ_{film}	porosity in the water-film surrounding the roots, m^3 m^{-3}
ψ_m	matric water suction, kPa

Abbreviations

COC	critical oxygen concentration
FMI	Finnish Meteorological Institute
PET	potential evapotranspiration
n	number of replicates
$\bar{x}$, $\bar{X}$	mean
s, S	standard deviation

1 INTRODUCTION

1.1 Background

The practical background of this thesis lies in the compaction problems of cultivated soils. In general, plant responses to soil compaction are complicated by the fact that the soil structure (the size and distribution of pore space relative to the solid phase) and related soil properties are changed in a spatially and temporally complex manner (see Soane and van Ouwerkerk 1994 for recent reviews). Soil strength is usually increased by compaction, because the number of contacts between soil particles increases. The changes in the hydraulic properties are of special importance, because such soil properties as thermal conductivity, strength and gaseous diffusivity are to a large extent modified by the soil water content.

Insufficient aeration is generally a problem for crop growth only in wet soils (see Stępniewski *et al.* 1994). Soil wetness is controlled by the relative rates of water supply to and removal from the soil. The former is determined mainly by the climate, and cannot be much controlled by agricultural management practices. On the other hand, the removal of water from soil is determined by the structure and topology of the soil and by the rates of drainage and evapotranspiration that are more readily influenced by agricultural practices. Compaction may increase soil wetness by decreasing the number of large pores and the saturated water conductivity in soil.

Although the structural deterioration of soils can certainly reduce root growth in mechanized agriculture, it is often hard to distinguish between the influences of restricted aeration and increased mechanical impedance in soil (see Stępniewski *et al.* 1994). The effects of soil compaction on soil structure and crop growth have been researched extensively both in Finland (Aura 1983, Pietola 1995, Alakukku 1997) and elsewhere (Arvidson and Håkanson 1996, Håkansson and Lipiec 2000, see Soane and van Ouwerkerk 1994 for reviews). On the other hand, despite the extensive research done on soil aeration (see Gliński and Stępniewski 1985, McAfee Graham 1989) and plant physiological responses to oxygen deficiency (reviewed by Drew 1990, Drew 1992, Vartapetian and Jackson 1997), the estimating of soil aeration status in a way that relates to plant growth still remains an important goal (Drew 1992).

A field of active research related to soil aeration studies are the soil-borne emissions of trace gases involved in the global climate change, such as methane (CH_4), carbon dioxide (CO_2), oxides of nitrogen (NO_x, N_2O) (Mosier 1998). In particular, the emissions of nitrous oxide (N_2O) are much researched, as soils account for most (about 65%) of the total global N_2O emission to the atmosphere (see Smith 1997).

1.2 Soil aeration

1.2.1 Conceptual framework

Soil is a natural medium for the growth of plants. It is an open, dynamic system made up of solids, liquids and gases interacting with living organisms (plants, microbes, animals), climate and topology. The main concepts, processes and the features of soil that are considered in this thesis are summarized schematically in Figure 1. These are discussed briefly below and in more detail in later sections.

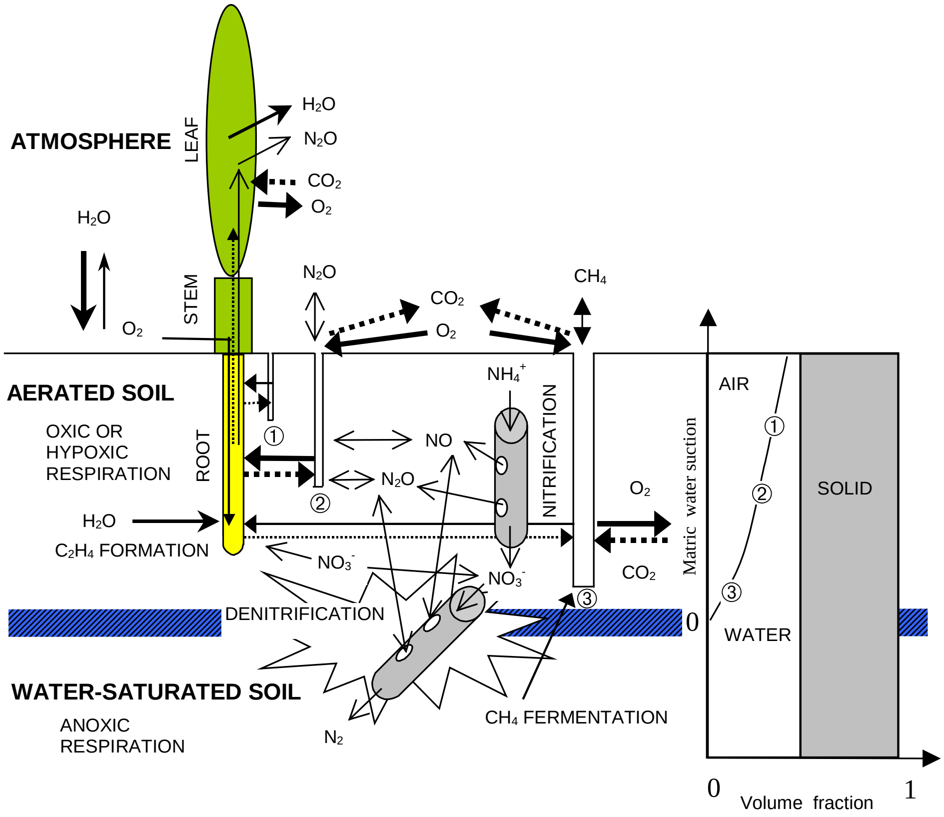

Figure 1 The conceptual framework of the study. Schematic presentation of a plant growing in a hypoxic soil profile. Three examples of air-filled pores nearest to the roots at three depths (①, ②, ③), the distribution of air, water and solid phase, and the “hole-in-the-pipe” model of nitrification and denitrification (Davidson 1991) are shown.

In the aerated part of the soil profile, the pore space is partly filled with air. Soil microbes and plant roots respire O_2 that they receive mainly by diffusion from the nearest air-filled pores through a layer of water-saturated soil (e.g. water films around roots). The minimum flux of O_2 required to keep the respiration of roots oxic, or to keep the O_2 concentration at the root surface above the critical value, is determined by the respiratory and diffusive properties of roots. The maximum rate of oxygen supply to the roots is determined largely by their distance to the nearest air-filled pores and by the O_2 concentration in soil air. At large matric water suctions, e.g. near the soil surface, the distance from the root to the nearest air-filled pores is small enough to maintain oxic respiration in the roots. Deeper in the soil this distance increases as the matric water suction decreases. The decrease in soil air space retards the diffusion of O_2 in soil, which leads to lowering of O_2 concentration in soil air. Eventually, at a certain depth depending on the soil structure, the maximum oxygen flux is inadequate for the requirements of the roots, and the roots become hypoxic, or partly anoxic.

In hypoxic soil, the energy status of roots is impaired, which impedes their growth and active nutrient uptake. Long-lasting anoxia leads to cell death. Plants may respond or adapt to hypoxic stress, for example, by increasing the biosynthesis of ethylene (C_2H_4), thus increasing the formation of air spaces in the root and the rate of internal diffusion of O_2 from shoots to roots. Plants may also grow more roots in favourable parts of the soil to compensate for those in the hypoxic parts, or they may regulate soil aeration by drying the soil through transpiration.

Some of the soil respiration is due to microbial decomposition of organic materials. In contrast to plant roots, many microbes gain energy efficiently by reducing inorganic or organic molecules, if oxygen is lacking. An example of such anoxic respiration is heterotrophic denitrification. In very reduced soil, methane (CH_4) may form.

The rate of denitrification is controlled by the availability of decomposable organic material for active denitrifying microbes and by the competition between the electron acceptors (O_2, NO_3^- and other nitrogen oxides). Denitrification generates gaseous products such as NO, N_2O and N_2. Plant roots may decrease denitrification by taking up nitrate and water from the soil. If the uptake of nitrate is impeded by e.g. hypoxia or if the soil is rich in nitrate, the roots may however increase denitrification in the soil by increasing respiration and degradable organic matter in the soil.

Anoxic respiration does not occur only below ground water level. After heavy rain, even the topsoil may become temporarily water-saturated. Impaired gas transfer and strong respiration may also create anoxic microsites or “hot spots” that may denitrify rapidly even in well-aerated soils. Further, N_2O is produced also aerobically in nitrification, when the oxygen is somewhat deficient. In practice, it is often difficult to separate the proportions of N_2O produced by nitrification and denitrification, because the processes are inter-related due to the heterogeneity of soils. Part of this heterogeneity is determined by the distribution of moisture, but in reality it is affected also by variations of soil structure with depth unlike the homogenous profile shown in Figure 1.

1.2.2 The problem of soil aeration

Soil aeration means gas exchange between the soil and the atmosphere. Respiration is the major process of gas consumption and production in soil, i.e. the consumption of oxygen and production of carbon dioxide by plant roots and microbes. Molecular diffusion is regarded as the most important mechanism of gas transfer in plants and the soil (Romell 1922). Diffusion is a continuous process whose rate depends on the rate of soil respiration. Convection phenomena produced by changes in atmospheric pressure, temperature, soil moisture (rain, irrigation, evaporation, drainage) and wind have only a minor significance on soil aeration, because they do not have such a connection. The rapid fluctuations of atmospheric pressure caused by the wind may however enhance gas transfer through a soil crust (Fukuda 1955, Farrel *et al.* 1966, Scotter *et al.* 1967a, see Currie 1970).

In cultivated soils, aeration should be sufficiently rapid to keep roots and microbes well supplied with oxygen. This research thus aims to predict the spatial and temporal variations of oxygen concentrations, the conditions leading to hypoxia, and the consequences of hypoxia on organisms. Hutchins (1926) was among the first to draw attention to the dynamic nature of the oxygen supplying power of the soil, or to rates at which the soil can deliver oxygen to respiring organisms. Below certain critical oxygen pressures the rate of oxygen supply becomes inadequate for the growth, elongation and active nutrient uptake by roots, as demonstrated with excised (Berry and Norris 1949, Saglio *et al.* 1983, Gibbs *et al.* 1998) and intact (Hutchins 1926, Armstrong and Gaynard 1976, Saglio *et al.* 1984, Armstrong and Webb 1985, Atwell *et al.* 1985) roots in solution cultures, and with intact roots in soil (Scotter *et al.* 1967b).

The mathematics of diffusion has been rigorously applied to study various aspects of soil and plant aeration. These include the supply of oxygen to roots (Wanner 1945, Lemon 1962, Griffin 1968, Luxmoore *et al.* 1970a, Armstrong 1979, de Willigen and van Noordwijk 1984, Armstrong and Beckett 1985, 1987, de Willigen and van Noordwijk 1989, Armstrong *et al.* 1994) and soil crumbs (Currie 1961, Greenwood 1961, Sierra *et al.* 1995, Sierra and Renault 1996), denitrification (Smith 1980, Leffelaar 1987, Arah and Smith 1989, Arah and Vinten 1995), and the gas exchange between the soil and the atmosphere (Romell 1922, van Bavel 1951, Rasmuson *et al.* 1990, Fang and Moncrieff 1999).

According to Fick's first law

(1)

$$J = -D\frac{\partial C}{\partial z}$$

the diffusive flux J of a gas is proportional to the concentration gradient ($\partial C/\partial z$). By combining Fick's law (1) with the conservation law, the general form of the time-dependent uniaxial diffusion equation in an isothermal and isobaric soil profile may be presented according to Gliński and Stępniewski (1985) as

(2)

$$\frac{\partial\{C\,[\varepsilon\,(z,t,\theta)+\alpha_B\theta(z,t)]\}}{\partial t} = \frac{\partial\left[D(z,t,\theta)\frac{\partial C}{\partial z}\right]}{\partial z} \pm q(z,t,\theta,C)$$

which may be solved to calculate the gas concentration (C) in soil air at any depth (z) and time (t), if the values of the other variables are known (D gaseous diffusion coefficient or diffusivity, ε air-filled porosity, θ volumetric moisture content, q respiration rate positive for carbon dioxide production and negative for oxygen consumption, α_B Bunsen's gas solubility coefficient). This equation shows how the variation in soil air composition is determined by a physical process of gaseous diffusion and by a biological process of respiration. In the simplest case, in a homogenous soil with respiration until the depth L and overlying an inactive layer, one obtains the steady-state solution by van Bavel (1951)

(3)

$$C = C_{atm} - \frac{q}{2D}(2Lz - z^2)$$

where q is the rate of O_2 consumption and C_{atm} is the O_2 concentration in the atmosphere. In reality, weather and soil management practices induce variations in soil properties within the profile and with time. For this reason, the spatial and temporal heterogeneities in the values of diffusion coefficient and respiration rate should be taken into account, as shown by the formulation of the differential diffusion equation (2).

Even a complete knowledge of soil air O_2 concentrations does not allow one to assess whether a soil is adequately aerated. In soil, the rates of gaseous diffusion are much restricted by the water surrounding the organisms or organs. Soil aeration status is thus controlled both by O_2 diffusion into such microsites as wet soil crumbs (Currie 1961, Greenwood 1961) and water-film surrounded roots (Wanner 1945, Lemon 1962, Armstrong and Beckett 1985) and by gaseous diffusion through the soil profile. In these microsites, gaseous diffusion is often slower and respiration more rapid as compared to bulk soil. These sites are hence the most likely to become anoxic in wet soils, which in turn, affects the respiration rate in the bulk soil (the term $q(x,t,\theta,C)$ in the diffusion equation (2)).

Lemon (1962) and Armstrong and Beckett (1985) presented radial steady-state models of O_2 diffusion into roots. Armstrong and Beckett (1985) modelled the root and the surrounding water film as n coaxial homogenous shells (i = 1 (stele), 2 (cortex) … n (water film)), in which the distribution of O_2 is governed by a set of ordinary diffusion equations of the form

(4)
$$\frac{D_i}{r}\frac{d}{dr}\left(r\frac{dC_i}{dr}\right)=q_i \qquad i=1,2\ldots n$$

with the general solution

(5)
$$C_i(r)=\frac{1}{4}\frac{q_i}{D_i}r^2+B_i\ln r+A_i$$

applicable to each shell separately (r radial distance, A_i and B_i integration constants).

The O_2 concentration at the outer edge of the water film (C_0) is in equilibrium with that in soil air. If C_0 decreases below a critical level, an anoxic core (radius R_a) develops in the stele. By applying the boundary conditions

(6)
$$\left.\begin{array}{l} C_n(R_n)=C_0 \\ \left.\begin{array}{l} C_i(R_i)=C_{i+1}(R_i) \\ D_i\left(\dfrac{dC_i}{dr}\right)_{r=R_i}=D_{i+1}\left(\dfrac{dC_{i+1}}{dr}\right)_{r=R_i} \end{array}\right\} i=1,2\ldots n-1 \\ C_i(R_a)=0 \\ \left(\dfrac{dC_i}{dr}\right)_{r=R_a}=0 \end{array}\right\}$$

one obtains the following 2n+1 equations with 2n+1 unknowns (A_i, B_i, R_a)

$$\left.\begin{array}{l}\frac{1}{4}\frac{q_n}{D}R_n^2 + B_n \ln R_n + A_n = C_0 \\ \left.\begin{array}{l}\frac{1}{4}\frac{q_i}{D_i}R_i^2 + B_i \ln R_i + A_i = \frac{1}{4}\frac{q_{i+1}}{D_{i+1}}R_i^2 + B_{i+1}\ln R_i + A_{i+1} \\ \frac{1}{2}q_i R_i + \frac{B_i D_i}{R_i} = \frac{1}{2}q_{i+1} R_i + \frac{B_{i+1}D_{i+1}}{R_i}\end{array}\right\} i = 1, 2 \ldots n-1 \\ \frac{1}{4}\frac{q_1}{D_1}R_a^2 + B_1 \ln R_a + A_1 = 0 \\ \frac{1}{2}q_1 R_a + \frac{B_1 D_1}{R_a} = 0\end{array}\right\} \tag{7}$$

from which the relationship between R_a and C_0 can be solved by eliminating A_i and B_i. This enables the calculation of critical oxygen concentrations in soil air, if the radii (R_i), respiration rates (q_i) and diffusion coefficients (D_i) of the coaxial shells are known.

Diffusion equations, such as those shown above, may be solved analytically by making certain simplifying assumptions (Gliński and Stępniewski 1985, Kanwar 1986, Cook 1995) or more generally by numerical simulations (Radford and Greenwood 1970, Leffelaar 1987, Ouyang and Boersma 1992). In practice, incomplete knowledge of the factors affecting the diffusion coefficients and respiration rates in soil restricts the application of the diffusion equations. These factors are discussed in more detail below.

1.2.3 Foundations of gaseous diffusion

According to the kinetic theory of gases, the properties of a dilute gas are completely described by the distribution function given as the solution of the Boltzmann integro-differential equation (Hirschfelder *et al.* 1964). Although the diffusion of gases can be generated by the gradients in pressure (pressure diffusion) and temperature (thermal diffusion), and by external forces, only the gradients in gas concentration (ordinary diffusion) are important under normal circumstances in soil and plant processes (Jaynes and Rogowski 1983).

In multi-component gas mixtures, diffusion does not follow Fick's law accurately, because the gaseous fluxes are not independent (Wood and Greenwood 1971, Jaynes and Rogowski 1983). The comparison of Fick's law to the Stefan-Maxwell diffusion equations based on the kinetic gas theory shows that Fick's law can be applied only for certain special conditions including 1) the diffusion of a trace amount of a gas component in a gas mixture, and 2) the equimolar counter-current diffusion of two gases in a binary gas mixture or 3) that in a ternary mixture with a third gas stagnant (Jaynes and Rogowski 1983). More generally, a simple approach based on Fick's law and on maintaining of isobaric conditions is accurate to within 10%, when the binary diffusion coefficients of the gas components in the mixture do not differ by more than two-fold and when one component is abundantly present, so that the diffusion coefficients can be related to it (Leffelaar 1987, Freijer and Leffelaar 1996).

In very small pores with diameters comparable to the mean free path of the gas molecules (c. 0.1 μm in air), the gas becomes rarefied Knudsen gas, where the ordinary laws of diffusion do not apply (Hirschfelder *et al.* 1964). This mechanism probably operates only in very dry soils, as an effective pore diameter of 0.1 μm represents a soil matric water suction of 3 MPa.

The binary diffusion coefficients of gases as calculated by Leffelaar (1987) using the Chapman-Enskog kinetic gas theory (e.g. Hirschfelder *et al.* 1964) stay mostly within the uncertainty limits of the empirical values (Marrero and Mason 1972, Pritchard and Currie 1982), and the deviations remain less than 10%. The composition dependence of binary diffusion coefficients is usually less than 5% (Marrero and Mason 1972), and was hence disregarded by Leffelaar (1987). Gaseous diffusion coefficients are inversely proportional to the total pressure and directly proportional to the power (n) 1.5-2 of the absolute temperature (Marrero and Mason 1972).

1.2.4 Gaseous diffusion in soil

In porous media such as soils, the gaseous diffusion coefficients are determined both by gases and media. The diffusive properties of soils are often described by the relative diffusion coefficient D/D_0 that expresses the rate of diffusion in the medium relative to that in air without impeding solids. D/D_0 is practically independent of gas (Penman 1940b, Shimamura 1992). Diffusion is 10^4 times faster in air than in water. As a consequence, gaseous diffusion in soil is controlled mainly by the amount and geometry of air space. This can be expressed as

$$D/D_0 = \alpha(\varepsilon)\,\varepsilon \tag{8}$$

where the term $\alpha(\varepsilon)$ depends on the geometry of air space (the tortuosity and constrictions of the flow path) and ε is the air-filled porosity in soil.

Despite recent advances in the modelling of diffusion coefficients by tube or network analogies of soil structure (Freijer 1994, Steele and Nieber 1994), in the image analysis of soil thin sections for more realistic simulations of soil structure (Glasbey *et al.* 1991) and investigation of diffusion through the complex pore space (Horgan and Ball 1994, Horgan 1999), and in the application of fractal geometry to processes in soil (see Baveye *et al.* 1998), the essential features of the pore geometry that would explain the diffusive properties of soils or other complex media are still poorly understood (Horgan 1999). The statement of Troeh *et al.* (1982) that the complex geometries of soils make it necessary to relate D/D_0 empirically to soil structural parameters is still true.

Empirical equations that relate D/D_0 to the air-filled porosity (ε) are often of the form $D/D_0 = a\varepsilon^b$, $D/D_0 = a(\varepsilon\text{-}b)$ or $D/D_0 = [(\varepsilon\text{-}u)/(1\text{-}u)]^v$ (see Troeh *et al.* 1982, Sallam *et al.* 1984, Gliński and Stępniewski 1985, Jin and Jury 1996, Moldrup *et al.* 1997). Perhaps the most well-known one is $D/D_0 = 0.66\,\varepsilon$ by Penman (1940a). Although the empirical parameters determined by fitting the equation to experimental data may sometimes be interpreted physically (de Vries 1950, Currie 1960), the direct measurement of the quantities they represent is impossible.

In a series of recent papers, Moldrup *et al.* (1996, 1999, 2000) have related the gaseous diffusivity to other properties in soil. They compared several earlier soil-independent equations to new equations of the form $D/D_0 = R_p\,(\varepsilon/\phi)^\eta$, where R_p is the relative diffusion coefficient at some reference saturation, ϕ is total porosity, and the soil-dependent parameter η describing the shape of the pores is a function of the water retention properties or soil texture. Moldrup *et al.* (1999) recommend using this model in undisturbed soil with $R_p = \phi^2$ in complete dryness, and $\eta = 2+(3/b)$, where -b is the slope of the water retention curve in a log-log scale.

The most detailed empirical investigations into the factors affecting the diffusion of gases in soils have been carried out by Currie (1960, 1961, 1965, 1970, 1979, 1983, 1984a). Decreasing the air-filled porosity by adding more solid (compaction) or water (wetting) differ radically in the way they change the geometry of soil air-space and gaseous diffusion in soil (Currie 1970, 1984a). Particle shape affects the diffusion in dry soils (Currie 1960), but the effects are much smaller in wet soils, where the pore shapes are modified by the presence of water (Currie 1961). D/D_0 increases very rapidly ($\propto \varepsilon^4$) with increasing air-filled porosity in wet soils (Currie 1961). In soils with a crumb structure, this initial increase is continued until the inter-crumb pores are air-filled; the increase is more gradual and nearly linear as the intra-crumb pores drain. The dissimilarity between the two parts of the D/D_0 - ε relationship becomes less distinct with increased compaction (Currie 1984a).

Within soil crumbs the geometry of the pores is more complex and gaseous diffusivity much less than in the bulk soil even when the crumbs are dry (Currie 1965, 1979). In wet crumbs the diffusivity is decreased by 10^4 orders of magnitude, as shown by direct measurements with microelectrodes in wet model soil aggregates (Zausig *et al.* 1993). The diffusivity is probably decreased similarly in the water films around the roots. However, the thickness of the water films cannot be directly measured.

1.2.5 Gaseous diffusion in plants

Although molecular diffusion is considered to be the main mechanism of gas transfer also within plants (Armstrong 1979), much less is known about the gaseous diffusivity within roots as compared to that in the soil. The diffusion of oxygen inside plant roots has been convincingly demonstrated by experiments with labelled oxygen ($^{15}O_2$) (Evans and Ebert 1960, Barber *et al.* 1962) and by microelectrode measurements (Bowling 1973, Armstrong *et al.* 1994).

The rate of gaseous diffusion is determined mainly by the amount and continuity of air-filled porosity within roots. Differences in the porosity between plant species (Jensen *et al.* 1969, Yu *et al.* 1969, Justin and Armstrong 1987, de Willigen and van Noordwijk 1989) are large. So are the differences between various tissues within plants: the stele, epiderm (rhizoderm), hypoderm and meristems of monocotyledons are usually aporous, whereas large air spaces (aerenchyma) can develop in the middle of the cortex (Armstrong 1979, Armstrong and Beckett 1987, Justin and Armstrong 1987, Erdmann *et al.* 1988). The junctions of the shoot and root and those of root branches do not contain many continuous pores (Armstrong 1979, Erdmann *et al.* 1988).

The most important route of oxygen diffusion from shoots to roots in young plants is probably through the air space between the coleoptile and cotyledon, whereas later the adventitious roots emerging from the lower parts of the stem and growing through this air space become the main routes of internal diffusion (Erdmann *et al.* 1988). According to model calculations with an unbranched vertical root, the internal longitudal diffusion may contribute a major part of the total oxygen requirement of the root when the gas exchange between the root and soil is restricted. For roots of radius thicker than 0.3 mm this is important even at modest root porosities (de Willigen and van Noordwijk 1989). A partial diffusion barrier seems to exist between root branches and the main root (van Noordwijk *et al.* 1993).

Published data on diffusion coefficients in roots are scarce (Gliński and Stępniewski 1985). The estimates of radial diffusion coefficient in aporous tissues adopted by various authors range from 1.4×10^{-10} to 2.1×10^{-9} m^2 s^{-1} (Wanner 1945, Armstrong and Beckett 1985), whereas the longitudal diffusion coefficient is most easily estimated from the air-filled porosity by assuming the diffusivity in the root air-space equals that in air (Armstrong and Beckett 1987). According to Luxmoore *et al.* (1970b), the permeability to radial diffusion in maize and rice roots decreases with increasing distance from the root tip, although the air-filled porosities concurrently increase.

1.2.6 Soil respiration

Soil respiration is biological oxidation of organic compounds that provides the roots and microbes plus other organs and organisms living in soil with energy and metabolites for maintenance, growth and active nutrient uptake. Oxic respiration of roots and microbes is the most important process of gas production and consumption in soil, because mere root growth itself needs much energy and requires oxic conditions (Armstrong 1979, Drew 1990).

Plant growth is a major factor affecting the rate and spatial distribution of soil respiration. The respiration of roots depends on the supply of photosynthates from shoots. The proportion of net fixed C transported into roots of annual plant species is about 30-60% (Lambers 1987, Whipps 1990). On the other hand, microbes decompose the organic material derived from the roots and other plant parts introduced into the soil. Most of the photosynthates transported into roots are consumed by soil respiration before plant maturation (Sauerbeck and Johnen 1976). In mineral soils, respiration is expected to be largest at shallow depths, because the amounts of roots and organic matter decrease deeper in soil (Richter 1974). During the growing season, the daily soil respiration rate in agricultural mineral soils is typically 1-15 dm^3 m^{-2} (Lundegårdh 1927, Brown *et al.* 1965, Richter 1974, de Jong 1981, Parkinson 1981, Rochette *et al.* 1992, Lessard *et al.* 1994, Franzluebbers *et al.* 1995, Akinremi *et al.* 1999). Assuming that a soil contains 20% air space with 20% O_2, a daily respiration rate of 5 dm^3 m^{-2} would consume the oxygen contained in the 20 cm ploughed layer in less than two days, if the gas exchange between the soil and the atmosphere was blocked.

The rates of respiration vary considerably within roots, with time and among plant species (van der Werf *et al.* 1988, 1989, Lambers *et al.* 1991). In field conditions, the course of soil respiration is similar to that of soil temperature (Currie 1975). The proportions of respiration used for active nutrient uptake (up to 40% at the active growth stages) and growth decrease with plant age, whereas that used for maintenance increases (van der Werf *et al.* 1988). The structure and composition of plant tissues and the uptake of nutrients also vary widely among species and with age. Apart from external factors, the variations in the respiration may thus ultimately be determined by the variations in the biochemical composition, maintenance of concentration gradients and cellular proteins and active uptake of nutrients during plant development (Penning de Vries *et al.* 1974, Penning de Vries 1975, Lambers and Rychter 1989). As the organic material introduced into the soil is a substrate for microbial metabolism, the biochemical composition of plants indirectly also controls the rate of microbial respiration in soil.

The rates of respiration in roots may be 1000 times larger than those of microbial respiration in soil. The respiration rates are usually in the range 10-300 mg m^{-3} s^{-1} (7-

210 cm^3 m^{-3} s^{-1}) in roots and 0.1-10 mg m^{-3} s^{-1} (0.07-7 cm^3 m^{-3} s^{-1}) in soil (Gliński and Stępniewski 1985). Moreover, respiration near the apex of primary roots is several times larger than that in more distal tissues (Machlis 1944, Luxmoore *et al.* 1970b). The formation of aerenchyma probably decreases respiration rates in the cortex, except for perhaps near the root apex (Armstrong and Beckett 1987). There is however very little information available on the partitioning of respiratory activity over the entire root system, e.g. in lateral roots (Lambers *et al.* 1991).

1.3 Plant responses to hypoxia in soil

1.3.1 Direct effects of hypoxia on roots

The possible causes of death in anoxic cells and the reasons why some species are able to survive or grow for limited periods even in a totally anoxic environment have been actively researched (Vartapetian and Jackson 1997). The subject has been extensively reviewed (Drew 1990, Armstrong *et al.* 1991, Drew 1992, 1997, Ratcliffe 1997, Vartapetian and Jackson 1997). Plant responses to hypoxia in soil may include changes in growth, biochemical processes and morphology, and in survival.

Plant roots need O_2 as the terminal electron acceptor of the respiratory chain in order to gain energy for ATP synthesis (oxidative phosphorylation) (see e.g. Bryce and Thornton 1996, Vanlerberghe and McIntosh 1997). Very small concentrations of O_2 suffice to sustain oxic respiration in plant mitochondria, as the electrons are transferred to O_2 by a cytochrome oxidase that has a high affinity for O_2 ($K_m \approx 0.02$-0.14 µM, Longmuir 1954, Millar *et al.* 1994). An alternative oxidase that is not linked to ATP synthesis has a lower affinity for O_2 ($K_m \approx 1.7$ µM, Millar *et al.* 1994). Glycolysis does not require oxygen. The roots of higher plants can thus carry out glycolysis and fermentation for several hours even in total anoxia, but as this does not produce enough energy for the metabolism of roots, the energy status of cells declines to a low level in minutes (Roberts *et al.* 1984). As a consequence, the growth (cell division, expansion, and differentiation) and active ion transport of anoxic roots are arrested, and those of hypoxic roots are severely reduced (Amoore 1961a, 1961b, Drew and Sisworo 1979, Gibbs *et al.* 1998). Eventually, after cytoplasmic acidosis and irreversible changes in cell ultrastructure, the anoxic cells die (Roberts *et al.* 1984, Andreev *et al.* 1991). Root tips are especially sensitive to anoxia and die usually within one day of becoming anoxic, whereas more mature root zones may remain viable for several days (see Drew 1997, Vartapetian and Jackson 1997).

1.3.2 Indirect effects of hypoxia on roots

In addition to the direct effects on roots, anoxia or hypoxia can trigger chemical and microbiological changes in soil and plant that may affect plant growth indirectly (reviewed by Drew and Lynch 1980). In contrast to roots, many microbes can gain energy efficiently by reducing inorganic or organic molecules when there is a lack of oxygen. Examples of such anoxic respiration are heterotrophic denitrification, and in very reduced soil methane (CH_4) fermentation. Some of the reduced compounds accumulating in anoxic and hypoxic soils are potentially phytotoxic.

Although reduced forms of manganese (Mn^{2+}) and iron (Fe^{2+}), nitrite (NO_2^-), sulfide (S^{2-}), organic acids and ethanol (C_2H_5OH) may reach toxic concentrations during long-lasting anoxia, the accumulation of these compounds is seldom likely to damage the plants more than anoxia alone (see Drew and Lynch 1980). Similarly, denitrification reduces mineral nitrogen in soil, but this is slow compared to the rapid prevention of nitrogen uptake by plants after the onset of anoxia. On the other hand, after surviving a period of anoxia, the roots may be injured or killed by such toxins as superoxides, other reactive oxygen species and acetaldehyde produced in roots upon re-exposure to oxygen (Monk *et al.* 1987a, 1987b, 1989, Blokhina 2000).

In soil, decreased O_2 concentrations are always accompanied by increased CO_2 concentrations. The responses of plants to CO_2 in soil air are variable and not fully understood (Stolwijk and Thimann 1947, Geisler 1969, Jaakkola *et al.* 1990, Bouma *et al.* 1997). Small CO_2 concentrations (1-2%) are often beneficial, whereas large concentrations (>4-6%) may be detrimental to plants (Geisler 1967, 1969). On the other hand, in several studies CO_2 concentrations less than 10% in soil air produced little, if any, damage to various plant species in well-aerated media (Geisler 1963, Grable and Danielson 1965, Tackett and Pearson 1964, Jaakkola *et al.* 1990). Without being conclusive, these results suggest that large CO_2 concentrations in soil air may have less practical significance in controlling plant growth in hypoxic soil than small O_2 concentrations, because large CO_2 concentrations are rare in soil air.

1.3.3 Plant adaptation to hypoxia in soil

Metabolic and morphological adaptations may help plants to better tolerate or avoid anoxia (see Vartapetian and Jackson 1997). The ability of roots to survive anoxia for longer than a few hours depends on their energy metabolism. In hypoxic or anoxic cells, the energy status may be enhanced by increased synthesis of "anaerobic proteins", many of which are enzymes of glycolysis or fermentation (Sachs *et al.* 1980, Subbaiah *et al.* 1994, Sachs *et al.* 1996). Acclimatization by prior hypoxia improves the energy metabolism of roots and helps them tolerate anoxia (Saglio *et al.* 1988). Anoxia tolerance by metabolic changes is considered to be relevant during short-term flooding, whereas morphological changes of roots, such as the formation of aerenchyma (large air-spaces inside plants) and shallow rooting, may allow the roots to escape anoxia by enabling continued oxic metabolism at least in certain parts of the roots (see Vartapetian and Jackson 1997).

The formation of aerenchyma increases the rate of internal O_2 diffusion from the atmospheric plant parts to the roots (Barber *et al.* 1962, Drew *et al.* 1979a, Benjamin and Greenway 1979, Erdmann *et al.* 1988, Thomson *et al.* 1990, Visser *et al.* 1997), whereas shallow rooting improves the supply of oxygen to roots by shortening the diffusion routes through both soil and plant (Justin and Armstrong 1987, Armstrong *et al.* 1991). Most agricultural crops are non-wetland species in which internal aeration alone cannot sustain the unimpaired activities of extensive root systems (Armstrong 1979, Drew *et al.* 1985, Justin and Armstrong 1987, Thomson and Greenway 1991, Gibbs *et al.* 1995). The adaptations in the shoots of dry-land species include adventitious rooting and physiological responses that serve to minimize nutrient requirements and water loss by the plant. These include slower growth rates, senescence, redistribution of nutrients and stomatal closure (see Drew and Lynch 1980, Vartapetian and Jackson 1997).

The ability of plants to tolerate post-anoxic oxidative stress is determined partly by their antioxidative defence mechanisms (Monk *et al.* 1989, Blokhina 2000). For example, the ability to avoid post-anoxic injury has been found to correlate positively with the activity of superoxide dismutase (SOD) enzyme in the tissue (Monk *et al.*

1987b, VanToai and Bolles 1991). Plant species differ in the way SOD activity changes during anoxia (Monk *et al.* 1987b, Blokhina 2000).

1.3.4 Interactions of hypoxia with other soil stresses on roots

Plant roots are often simultaneously affected by many interacting soil stresses. For example, any change in soil structure e.g. by compaction also modifies numerous properties and processes, such as water retention, the transfer of mass (water, dissolved chemical species, gases) and heat, and soil strength, that determine whether the plant needs are met or whether stress conditions develop in the soil. In particular, the problems of hypoxia and compactness often coincide, which makes it difficult to separate their effects on roots.

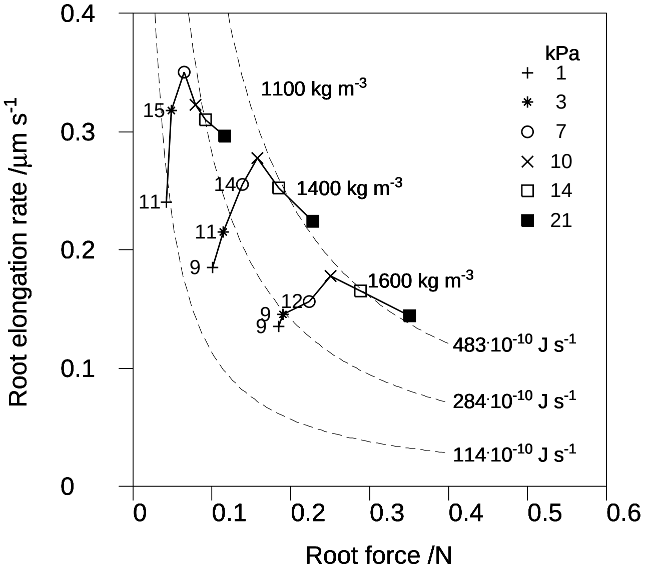

Figure 2 The relationship between the root elongation rate and the force exerted by pea roots in soils at various bulk densities (kg m^{-3}) and matric water suctions (kPa). The curves denote constant rates of working. The numbers beside the plotted points represent oxygen concentrations where these are less than 21% (from Eavis 1972, Currie 1984b).

Soil water retention properties have a key role in relating the effects of soil structure on plant growth, because many physical soil properties are strongly affected by moisture content. Research has been carried out to determine the range of matric water potentials in which the various soil properties are not (or least) limiting plant growth (Stępniewski 1981, Letey 1985, Boone *et al.* 1986, da Silva *et al.* 1994, Lipiec and Håkanson 2000). Typically, penetration resistances above 3 MPa and air-filled porosities below 10% are considered to be limiting for aeration and rootability, respectively. Håkanson and Lipiec (2000) discussed the possible soil-dependencies of these critical limits. In addition, the often-cited critical limit of 10% air-filled porosity is based on scarce (Grable and Siemer 1968) and mostly indirect (Wesseling and van

Wijk 1957, Flühler 1973, Boone *et al.* 1986, Chan and Hodgson 1995) data, and the results in fact show much variation.

The interactions of aeration, mechanical impedance and water stresses in soil are clearly illustrated by the results of Eavis (1972) who studied the effects of soil bulk density and moisture levels on the elongation of pea roots. Compaction and drying of soils increased the mechanical impedance encountered by the roots (Figure 2). Water availability restricted the elongation of roots at matric water suctions above 180-350 kPa. On soil wetting, the elongation of roots was first enhanced at given bulk densities, as the mechanical impedance decreased, but later the growth was restricted by poor aeration at matric water suctions below 10 kPa. Root diameters were increased both by mechanical impedance and poor aeration.

The results (Eavis and Payne 1968, Eavis 1972) show that adequately aerated roots were elongating at a constant rate of working at bulk densities of 1600 and 1400 kg m^{-3}; but in the loosest soil (1100 kg m^{-3}) the rate was less, probably because the elongation was restricted by the cell division rate rather than mechanical impedance (Currie 1984b). In contrast, when the oxygen concentration on the root surface fell below 21%, the rate of working decreased sharply at all bulk densities. Poor aeration restricted root growth at air-filled porosities below 39% in the loose soil but only below 11% in the most compact soil. In the discussion, Eavis (1972) stressed the role of spatial distribution of the gas space around a root in controlling the oxygen movement to roots. He attributed the observation to the greater number of pores per unit area drained at a given matric water suction in a compact soil than in a loose soil.

1.3.5 Whole-plant responses to hypoxia in soil

The yields of non-wetland species are usually reduced by waterlogging or high soil wetness (Yu *et al.* 1969, Drew and Sisworo 1979, Drew et al 1979b, Justin and Armstrong 1987). Yield reductions are largely caused by reductions in nutrient transport to a shoot, as these are among the first and major processes adversely affected when the O_2 supply to roots is low (Drew *et al.* 1979b, Gibbs *et al.* 1998). In wet soils, the root growth of dry-land species is restricted into a small well-aerated volume near the soil surface (Yu *et al.* 1969, Drew and Sisworo 1979). In fields, the rootable soil volume is often restricted further by large mechanical impedance or dryness in certain parts of the profile. Whole plant responses to hypoxia in soil thus depend on the redistribution of nutrients within a plant, and on the ability of well-aerated roots to compensate for the impaired functioning of hypoxic roots.

The relationship between shoots and roots is functional (Brouwer 1983, van Noordwijk and de Willigen 1987). Accordingly, a rather shallow aerated soil layer can alleviate waterlogging damage to shoot growth (Yu *et al.* 1969), if the layer is so rich in nutrients that the roots can supply enough nutrients to the shoots (Drew *et al.* 1979b, Trought and Drew 1981). If the nutrient uptake by roots is reduced, shoot responses are determined by the nutrient status of the shoots (Trought and Drew 1981).

Roots respond flexibly to heterogeneities in soil by growing more roots into favourable parts of the soil. For example, the shoot and root growth of dry bean (*Phaseolus vulgaris* L.) were decreased in total anoxia, but when the roots were split into anoxic and aerated parts the overall plant growth remained usually similar to that in the aerated control, because of the compensatory growth and ion uptake by roots in the aerated part (Schumacher and Smucker 1984, 1987). Another example is that total alleviation of shoot injury to wheat (*Triticum aestivum* L.) in an anoxic solution culture was achieved by compensatory growth and ion uptake of only a single seminal root in an aerated solution containing the full complement of inorganic nutrients (Trought and Drew 1981).

In heterogeneous growing media, such as field soils, the various parts of the plant root system grow in unequally favourable conditions. The mechanisms by which plants react to the heterogeneity of multiple stresses in soil are not well understood. Brouwer (1983) attributes the flexibility of root responses to the large number of growing root tips. The mechanisms probably involve both physical responses of single roots to stresses, multiple signalling of the stresses e.g. in the form of plant hormones, and source-sink relationships of carbon compounds in the plant (see Tardieu 1994). Many experimental results can however be explained simply by assuming that shoots and roots are competing for photosynthates and mineral nutrients, and that the organ nearest to the source is the most successful in meeting the requirements (Brouwer 1983).

Plant hormones are a part of the biochemical and genetic system that regulates plant development (see Morgan 1990, Kende and Zeevaart 1997). The changes in plant hormones induced by various physiological stresses have been reviewed (Jackson 1990, Morgan 1990, Wang *et al.* 1990, Lynch and Brown 1997, Morgan and Drew 1997). In hypoxia, the amounts of abscisic acid, auxins and ethylene usually increase, but those of gibberellins and cytokinin decrease. Ethylene is thought to have a central role in mediating plant responses to several stresses that increase the biosynthesis of ethylene or the sensitivity of tissues to ethylene (see Lynch and Brown 1997, Morgan and Drew 1997).

Root responses to hypoxia and mechanical impedance in soil are probably much regulated by ethylene, as both of these stresses increase the biosynthesis of ethylene in roots (Jackson *et al.* 1985, Sarquis *et al.* 1991, He *et al.* 1996). The biosynthesis of ethylene ceases in anoxia (Drew *et al.* 1979a, Jackson *et al.* 1985). The formation of aerenchyma is increased by ethylene (Drew *et al.* 1979a, Kawase 1979), but only in roots that are not severely oxygen-deficient (Jackson *et al.* 1985). Large concentrations of ethylene (>1 $\mu l\ l^{-1}$) decrease root elongation and increase root widths (Smith and Robertson 1971, Crossett and Campbell 1975, see Jackson 1991). Small concentrations of ethylene increase the elongation of roots in some species, but not those of barley that is more sensitive to ethylene than the other cereals (Smith and Robertson 1971, see Jackson 1991). In wet soil, the effects of small oxygen concentrations and large ethylene concentrations on the elongation of roots are difficult to separate, because they both depend similarly on the rate of gaseous diffusion through the root. Ethylene may also promote adventitious rooting, but the mechanisms involved are not always clear (see Vartapetian and Jackson 1997).

1.4 Emissions of nitrous oxide from soil

The emissions of nitrous oxide (N_2O) from soil have been much researched during the last few decades, because N_2O is involved in global climate change and destruction of stratospheric ozone (see the reviews by Granli and Bøckman 1994, Bremner 1997, Smith 1997, Mosier 1998). Nitrous oxide has a global warming potential of 320 relative to CO_2 and is responsible for about 5% of the anticipated global warming (Mosier 1998). The N_2O concentration in the atmosphere was about 311 ppb at the beginning of 1993, and is increasing at a rate of about 0.25% yr^{-1} (Smith 1997). It is estimated that soils account for about two-thirds (9.5 Tg N) of the total N_2O emissions of all identified sources (15 Tg N), with about one-third of this coming from cultivated soils (Smith 1997). However, the global budget for N_2O is not well balanced, and the sources may be underestimated (Smith 1997). According to Smith (1997), global warming is likely to increase N_2O emissions from soils.

In cultivated soils, N_2O is produced mainly by a wide range of heterotrophic denitrifiers involving bacteria of such genera as *Pseudomonas* and *Alcaligenes*, or by autotrophic nitrifiers involving bacteria of such genera as *Nitrosomonas and Nitrobacter*, whereas other biological and chemical sources are unlikely to be significant (Tiedje 1988, Bremner 1997). Only denitrification is recognized as a significant biological consumptive fate for N_2O (Firestone and Davidson 1989). The relative contributions of nitrification and denitrification are often difficult to separate from each other, because of the proximity of anoxic and oxic sites in soil (see Focht 1992). Moreover, most data on the production of N_2O by denitrification has been obtained using the acetylene inhibition technique that may underestimate denitrification rates in oxic conditions (Bollman and Conrad 1997, McKenney *et al.* 1997).

According to the “hole-in-the-pipe” concept of Firestone and Davidson (1989, Davidson 1991), the processes of nitrification and denitrification can be visualized as leaky pipes through which N is flowing (see Figure 1). Nitrous oxide emissions from soils are thus controlled by factors that affect 1) the rates of denitrification and nitrification (or N cycling), 2) the relative proportions of end products produced (or the size of the holes in the pipe wall), and 3) the gaseous diffusion through the soil to the atmosphere (Davidson 1991).

At the cellular level, the production of N_2O during denitrification is controlled by the availability of electron donors to active denitrifying microorganisms and by the competition between electron acceptors (O_2, NO_3^- and other N oxides) (Tiedje 1988, Cho *et al.* 1997). Nitrifiers form N_2O during oxidation of ammonium when the oxygen is somewhat deficient (Arnold 1954, Bremner and Blackmer 1979, see Bremner 1997). The reactions producing N_2O in soil are controlled by processes such as diffusion of the reactive components, respiration, mineralization and immobilization of N, evaporation and drainage of water, and changes in soil structure (see Granli and Bøckman 1994). These processes are themselves controlled by such factors as the soil, plants, climate, and management practices (Tiedje 1988).

Anoxic microsites may develop even in rather well-aerated soils (Currie 1961, Flessa and Beese 1995) and denitrify rapidly (Christensen *et al.* 1990, Højberg *et al.* 1994). Their formation is enhanced, for example, when soil aeration is impaired by wetting or compaction, and when respiration is increased by the incorporation of degradable organic material into the soil. Moreover, even moderate temperature-induced increases in respiration rate, for example with values of Q_{10} factor (the rate of a process at T + 10 K divided by the rate at T) of two, can result in large increases in anoxic volume and denitrification rates in soil, with apparent Q_{10} factors for the N_2O emission exceeding 10 (Dowdell and Smith 1974, Smith 1997). Patchy distribution of anoxic microsites is responsible for the large spatial variability of N_2O emissions in the field (Folorunso and Rolston 1984, Parkin 1987, Ball *et al.* 2000).

The ratio between the products of nitrification (N_2O/NO_3^-) increases with increasing soil moisture, whereas that of denitrification (N_2O/N_2) decreases. Consequently, the N_2O emissions are most rapid at intermediate soil moisture contents (Linn and Doran 1984, Smith *et al.* 1998, see Granli and Bøckman 1994). The little information available about the effect of soil types on N_2O emissions suggests that heavy textured mineral soils have larger emissions than lighter soils, and that drained organic soils have larger emissions than mineral soils (Bouwman 1996, Kulmala and Esala 2000). Nitrogen fertilization generally increases N_2O emissions from soil (Bouwman 1996). Plant roots can affect N_2O production in various ways. Respiration and the introduction of degradable organic material by roots into soil tend to increase denitrification and N_2O production. On the other hand, the uptake of water and nitrate by roots may reduce denitrification. Thus, although plant roots generally stimulate denitrification from wet soils containing much nitrate (Woldendorp 1962, Mahmood *et al.* 1997), they may reduce denitrification and N_2O emissions from soils with less nitrate and moisture (Smith and Tiedje 1979, Aulakh *et al.* 1984, Bakken 1988, Mahmood *et al.* 1997). The N_2O emissions from leguminous crops may be considerable (Bouwman 1996).

In an analysis of previously published measurements on N_2O emissions from soils, Bouwman (1996) concluded that although the factors that control N_2O production are known, it is impossible to predict their interaction in field conditions on the basis of the available information. More data on N_2O emissions is thus needed from a wider range of sites and environmental conditions.

1.5 Objectives of the study

In the field, the aim was to observe the variations in soil air composition, N_2O emissions and several environmental variables, as modified by various agricultural management practices, in order to explore the instances in which poor soil aeration might be detrimental to plant production or environment. Management practices which differed greatly in their impacts on the processes regulating soil air composition and N_2O emissions (i.e. respiration, denitrification, nitrification, gaseous diffusion) were chosen for the study. In the pot experiments, the aim was to characterize in more detail the conditions likely to cause hypoxia in soil, and the effects of compaction and modified oxygen supply on plant growth. In addition, the incidence of wet growing seasons was estimated at five locations in different parts of Finland based on a long time series of previously published weather data (1900-1999, Finnish Meteorological Institute).

The specific objectives were to:

1. Estimate the incidence of the wet growing seasons in Finland.
2. Determine the range of variation in soil air composition (CO_2, O_2, N_2O, C_2H_4, CH_4) and N_2O emission likely to occur in the field at various depths in cultivated mineral soils during a growing season (Papers I, II, III).
3. Establish the effects of soil compaction, wetting, cropping and N fertilization on soil air composition and N_2O emissions in the field at various depths in cultivated mineral soils during a growing season (Papers I, II, III).
4. Relate the variations in soil air composition and N_2O emission to soil variables and to the growth and nutrient uptake of plants (Papers I, II, III).
5. Determine the plant responses (growth, root respiration, root morphology) to compaction and modified oxygen supply to roots (Papers I, IV, V, VI).
6. Relate the soil water retention properties to the supply of oxygen to roots (Paper IV).

2 MATERIAL AND METHODS

2.1 Experiments

The pot and field experiments included in this thesis were carried out on fine sand, loam and clay soils subjected to various combinations of compaction, wetting, cropping, N fertilization and aeration as shown in Table 1. The soil, plant and environmental variables measured, and the methods used, are summarized in Table 2 and in Table 3, respectively. Soil air composition, gas emissions, temperature and moisture content were measured repeatedly during the experiments (at the time intervals of 1-2 weeks and 2-3 days in the field and pot experiments, respectively) to explore their temporal variation. Mineral N content in the soil was determined more infrequently. Plant variables were measured at harvest.

The effect of compaction on soil air composition was investigated in clay soils in which barley was grown (I). In a pot experiment (Viikki 1986), the effects of compaction on soil air composition in a humic clay soil were investigated at two levels of soil moisture (moist, wet). In the field, the effect of compaction was studied at several depths in a loamy clay soil (Jokioinen 1988). Heavy compaction with a 19 Mg tandem axle unit had been performed 7 years earlier.

The field experiments on loam and clay soils (Hausjärvi 1993-94, Jokioinen 1993) were designed to allow exploration of natural variations in N_2O emission and air composition in the soil profile, and how these are modified by irrigation, cropping and N fertilization (II, III). Soil air composition and N_2O emissions were related to the contents of soil moisture and mineral nitrogen.

In the pot experiments (Viikki 1994-95), the responses of barley growth and soil respiration to modified oxygen supply were determined in fine sand soil at two levels of compaction and moisture (IV). The design of the respirometer pots built for this purpose allowed the packing, watering and easy sampling of soil. The oxygen supply was modified independently of soil compactness and wetness by flushing the soil (forced aeration) with gas streams containing known concentrations of O_2. The wetting and aeration treatments were started 11-12 days after sowing, and continued until the harvest of barley seedlings at the end of the experiment at about 2 months age.

In pot experiments Nos. 1-3 (IV), the O_2 concentrations in soil air were kept constant at 0, 2, 10 or 20% during the experiment. Besides plant growth and soil respiration, the cumulative N_2O losses and N balances were determined (this thesis). Each experiment included an additional 2-4 pots that were harvested before initiation of the wetting and aeration treatments, and four open pots that received no gas flow. In pot experiment No. 4 (IV), barley growing in a loose moist soil was subjected to varying time patterns of O_2 concentration (0, 2, 6, 10 or 20%) in soil air. The 20-day treatment period was started 26 days after sowing. The O_2 concentration was either A) increased at 4-day intervals, B) decreased at 4-day intervals, C) alternated at 2-day intervals (= decreasing similarly to B but returned to 20% O_2 after two days) or D) kept constant at 20%. At other times the O_2 concentration in soil air was maintained at 20%.

Table 1 Characteristics of the soils and experimental treatments in the experiments

	Pot experiments		Field experiments		
	Viikki 1986	Viikki 1994-95	Jokioinen 1988	Hausjärvi 1993-94	Jokioinen 1993
Soil textural class[a]	Humic clay (clay)	Fine sand (sandy loam)	Loamy clay (clay)	Loam (silt loam)	Loamy clay (clay)
Soil name (Soil Taxonomy)	ND	Typic Cryochrept, Ap	Aquic Cryumbrept	Aquic Cryochrept	Aquic Cryumbrept
Soil name (FAO)	ND	Eutric Cambisol	Eutric Cambisol	Eutric Cambisol	Eutric Cambisol
Topsoil					
Clay (0-2 µm), %	44	10	48	17	39
Silt (2-20 µm), %	19	9	26	47	25
Fine sand (20-200 (20-60) µm), %	33 (25)	59 (18)	17	34 (24)	20 (10)
Organic C, g 100 g^{-1}	10	2.5	2.8	2.4	2.5
Particle density, Mg m^{-3}	2.42	2.59	ND	2.66	2.66
pH (0.01 M $CaCl_2$)	5.5	6.5	ND	7.2	5.8
Subsoil textural class[a]	-	-	Heavy clay (clay)	Clayey loam (Silty clay loam)	Heavy clay (clay)
Experimental factors					
Soil compaction	No; Yes	No; Yes	No; Yes	No	No
Irrigation or wetting	No; Yes	No; Yes	No	No; Yes	No; Yes
Cropping	Barley[b]	No; Barley	Barley	Fallow; Ley[c]	Fallow; Barley
N fertilization	200 g m^{-3}	200 g m^{-3}	90 kg N ha^{-1}	0; 100 kg N ha^{-1}	0; 103 kg N ha^{-1}
Forced aeration	No	No; 0-20% O_2	No	No	No
Reference	Paper I	Paper IV, V, VI	Paper I	Paper II	Paper III

[a] Names used in this study (UK system); [b] Spring barley *Hordeum vulgare* cv. Arra (Viikki 1986), cv. Kymppi (Viikki 1994-95), cv. Pomo (Jokioinen 1988), cv. Kustaa (Jokioinen 1993), [c] mixture of winter rye (*Secale cereale*), Italian rye grass (*Lolium multiflorum*), Persian clover (*Trifolium resupinatum*), timothy (*Phleum pratense*) and meadow fescue (*Festuca pratense*); ND not determined

Table 2 Summary of plant, soil and environmental variables measured in the experiments[a]

	Pot experiments		Field experiments		
	Viikki 1986	Viikki 1994-95	Jokioinen 1988	Hausjärvi 1993-94	Jokioinen 1993
Plant					
Shoot dry mass	Grain, Straw	Grain, Straw	Grain, Straw	Crop	Grain, Straw
Shoot uptake of N	Grain, Straw	Grain, Straw	Grain, Straw	Crop	Grain, Straw
Root dry mass	ND	0-5, 5-10, 10-15 cm	ND	ND	ND
Root morphology	ND	0-5, 5-10, 10-15 cm	ND	ND	ND
Soil					
Moisture content	Controlled	Controlled	12.5-17.5, 45-50 cm	0-20 cm	0-15, 15-30 cm
Air composition	10 cm	7.5 cm	5, 15, 25, 50 cm	15, 30 cm	15, 30 cm
Gas emissions	ND	N_2O, CO_2	ND	N_2O	N_2O, CO_2
Mineral N content	ND	0-5, 5-10, 10-15 cm	ND	0-15, 15-30 cm	0-20 cm
Temperature	ND	ND	ND	15, 30 cm	2, 15, 30 cm
Environment	Greenhouse	Phytotron	Natural	Natural	Natural
Day/night cycle (h)	Natural	Controlled (16/8)	Natural	Natural	Natural
Temperature (day/night, °C)	Natural	Controlled (20/15)	ND	FMI Hyvinkää	FMI Jokioinen
Precipitation	Zero	Zero	FMI Jokioinen	FMI Hausjärvi	FMI Jokioinen
Water additions to soil	Controlled	Controlled	Rain	Rain + Irrigation	Rain + Irrigation
Reference	Paper I	Paper IV, V, VI	Paper I	Paper II	Paper III

[a] Information about plant parts, soil depths (cm), gas species, measurement sites and the controlling of the variables is given; FMI Finnish Meteorological Institute, ND not determined

Table 3 Analytical methods used in the experiments

Variable	Method	Reference
Dry mass	Oven drying, gravimetry	
Gas analysis	Gas chromatography	Smith and Arah (1991), Paper II
Gas emissions in field	Closed chamber, gas chromatography (N_2O, CO_2)	Findlay and McKenney (1979)
Gas emissions from pots	Flow-through approach, gas chromatography (N_2O, CO_2) Alkali traps, titrimetry (CO_2)	
Plant N content	Dumas, Kjeldahl	Bremner and Mulvaney 1982
Root morphology	Cleaning of roots by hydropneumatic elutriation and manual removal of organic debris, image analysis	Smucker *et al.* 1982, V
Soil mineral N content	Extraction of NH_4^+ and NO_3^- with 2 M KCl, colorimetry	Esala (1991), QuicChem® methods 12-107-06-2-A, 12-107-04-1-E
Soil moisture content	Time domain reflectometry, gravimetry	Topp *et al.* (1980)
Soil organic C content	Dry combustion, IR spectroscopy	
Soil particle density	Pycnometer method with water as the displaced fluid	Blake and Hartge (1986)
Soil particle size distribution	Pipette method	Elonen (1971)
Soil temperature	Platinum resistance (Pt100 probes)	
Soil water retention	Suction plate (hanging water column at matric water suction $\psi_m \leq 10$ kPa, pressure plate at $\psi_m > 10$ kPa)	Klute (1986)

2.2 Estimation of the incidence of wet growing seasons

The occurrence of wet growing seasons (May-October) at five locations in Finland was assessed based on monthly data published in the reports of the Finnish Meteorological Institute. Following Elonen and Pietola (1991), small precipitation deficits at certain times of growing seasons were considered to indicate wet growing seasons. In particular, cumulative precipitation deficits equal or less than zero in June and in May-July were considered important, because many crops are sensitive to hypoxia at early growth stages.

The precipitation deficit was calculated as the difference between potential evapotranspiration (PET) and precipitation. PET was calculated in accordance with the definition of Penman (1956): "… the amount of water transpired in unit time by a short green crop, completely shading the ground, of uniform height and not short of water". PET in 1961-1999 was calculated by the Finnish Meteorological Institute using 3-hourly synoptic weather observations and the Penman-Monteith approach in which a surface resistance term was included to match the calculated PET with the results from lysimeter experiments (see Vakkilainen 1982, Ansalehto *et al.* 1985, Venäläinen and Nordlund 1988, Elomaa 1993). In a longer time series 1900-1999, monthly PETs in May-October were calculated by using the monthly averages of air temperature and relative humidity in the empirical Ivanov equation (see Vakkilainen 1982, Elomaa 1993) that was corrected for time and location by analysis of covariance to match the PET in 1961-1999 given by the Penman-Monteith approach ($R^2 = 0.99$, residual standard deviation 4.3 mm).

2.3 Statistical analysis

The treatment effects were analysed by analysis of variance, and treatment means were examined with multiple comparison methods as explained in Papers I-IV. Logarithmic transformations of variables and non-parametric procedures were used where necessary. Due to unequal group variances non-parametric tests based on the ranks of data (see IV) were applied for cumulative N_2O emission and N balance reported in this thesis. The precipitation deficit data for 1900-1999 were approximately normally distributed. The incidence of wet growing seasons was estimated by fitting normal distributions to the data and estimating the probability of years with precipitation deficits less than or equal to zero. The temporal variations in the gas concentrations and N_2O emissions were summarized by drawing box-and-whisker plots of treatment means observed during the experiment. Treatment effects were summarized by calculating the overall direction of the effects during the experiment. The numbers of positive and negative effects observed during the experiment were calculated, and the sign test was applied to test the significance ($P < 0.05$).

3 RESULTS AND DISCUSSION

3.1 Incidence of wet growing seasons in Finland

The occurrence of wet weather in Finland shows large temporal and spatial variability as indicated by the data from five locations representing various agricultural and climatic zones (Figure 3, Figure 4, Table 4). Jokioinen and Helsinki, Vaasa and Jyväskylä, and Kajaani, represent the cereal cultivation zones of the Southern and Western Finland and the Southern coast, the feed grain cultivation zones of Ostrobothnia and the Northern Lake district of Finland, and the grassland farming zone of Kainuu in North-Eastern Finland, respectively (see Venäläinen and Nordlund 1988).

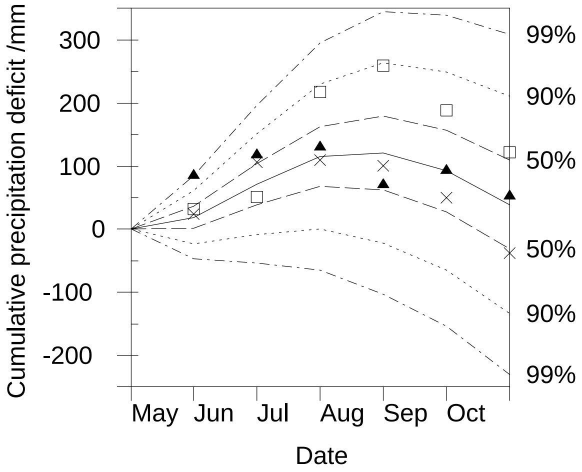

Figure 3 Cumulative precipitation deficit in Jokioinen during the growing season: the mean and the 50%, 90% and 99% probability limits (in 1929-1999), and the values in 1988 (×), 1993 (▲) and 1994 (□).

Precipitation deficits are smallest in May and October, and largest in the middle of the summer (Table 4). On adopting the view that precipitation deficits of smaller than or equal to zero are indicative of wet weather, May is wet every third or fourth year in all of the locations studied. June is wet only once in 10 or more years in the cities of Helsinki and Vaasa on the coast of the Baltic but more often than once in 5 years in the inland cities of Jyväskylä and Kajaani. In this respect, Jokioinen resembles the coastal rather than the inland areas despite its inland location. The early growing period from the beginning of May to the end of July is wet more seldom than once in 20 years in Helsinki, Vaasa and Jokioinen, but more often than once in 10 years in Jyväskylä and Kajaani.

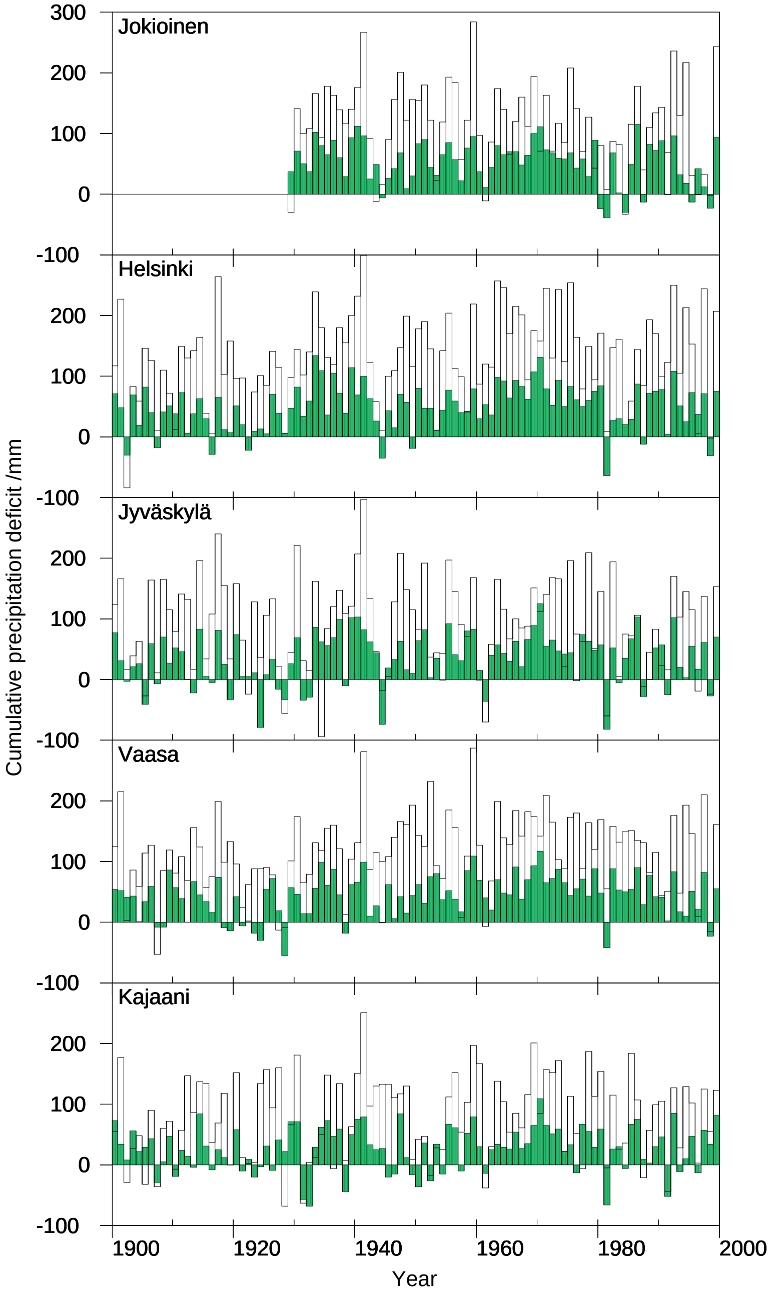

Figure 4 Cumulative precipitation deficit in May-July (transparent) and in June (shaded) during the 20th century at several stations of the Finnish Meteorological Institute.

Table 4 The amounts of monthly potential evapotranspiration (PET), rain, precipitation deficit[a], and the cumulative precipitation deficit in May-October, during the 20th century at several stations of the Finnish Meteorological Institute, mm

Location (Years)	Month	PET	Rain	Precipitation deficit[b]		Cumulative precipitation deficit[b]	
				$\bar{x} \pm s$	$P(x \le 0)$	$\bar{X} \pm S$	$P(X \le 0)$
Jokioinen	May	56	37	19 ± 26	0.23	19 ± 26	0.23
(1929-1999)	Jun	100	47	52 ± 37	0.08	71 ± 48	0.07
	Jul	119	75	44 ± 52	0.20	115 ± 70	0.05
	Aug	83	78	6 ± 44	0.45	121 ± 87	0.08
	Sep	33	62	-29 ± 30	0.83	92 ± 96	0.17
	Oct	8	61	-53 ± 30	0.96	39 ± 105	0.35
Helsinki	May	55	40	16 ± 31	0.31	16 ± 31	0.31
(1900-1999)	Jun	98	48	50 ± 38	0.10	65 ± 56	0.12
	Jul	124	59	66 ± 45	0.07	131 ± 73	0.04
	Aug	87	75	12 ± 47	0.40	143 ± 97	0.07
	Sep	37	68	-31 ± 35	0.81	112 ± 107	0.15
	Oct	12	70	-58 ± 39	0.93	54 ± 117	0.32
Jyväskylä	May	53	40	12 ± 27	0.32	12 ± 27	0.32
(1900-1999)	Jun	96	61	34 ± 43	0.21	47 ± 55	0.20
	Jul	118	72	46 ± 55	0.20	93 ± 75	0.11
	Aug	75	83	-9 ± 51	0.57	85 ± 100	0.20
	Sep	27	67	-40 ± 34	0.88	44 ± 103	0.33
	Oct	6	61	-55 ± 31	0.96	-10 ± 115	0.54
Vaasa	May	50	33	16 ± 25	0.26	16 ± 25	0.26
(1900-1999)	Jun	91	47	44 ± 35	0.10	60 ± 47	0.10
	Jul	115	58	57 ± 44	0.10	117 ± 62	0.03
	Aug	78	64	14 ± 44	0.38	131 ± 83	0.06
	Sep	32	60	-28 ± 33	0.81	103 ± 85	0.11
	Oct	11	55	-44 ± 26	0.95	59 ± 89	0.26
Kajaani	May	45	38	6 ± 25	0.40	6 ± 25	0.40
(1900-1999)[c]	Jun	90	62	28 ± 37	0.23	34 ± 47	0.24
	Jul	117	70	47 ± 52	0.18	81 ± 68	0.12
	Aug	73	78	-5 ± 45	0.54	76 ± 89	0.20
	Sep	24	60	-35 ± 31	0.88	40 ± 96	0.34
	Oct	3	51	-48 ± 27	0.96	-8 ± 105	0.53

[a] Precipitation deficit = potential evapotranspiration (PET) – precipitation; PET was calculated from monthly data with a time-corrected Ivanov method; PET calculated from daily data by the Penman-Monteith approach (Venäläinen and Nordlund, 1988) was used to calibrate the method.

[b] Mean ± standard deviation. Incidence of wet years with precipitation deficit (x) and cumulative precipitation (X) less than or equal to 0.

[c] Data for 1919 and Sep and Oct 1918 in Kajaani are missing.

In reality, the precipitation deficits are smaller than those calculated here, because the calculation is based on potential rather than actual evaporation rates. According to Venäläinen and Nordlund (1988), the potential evaporation rates are by about 10-20% or by even 30% greater than the actual evaporation rates estimated by a regional water balance method in Southern and Central Finland or Northern Finland, respectively.

The years of the field experiments of this study differed from each other with respect to the course of the precipitation deficit during the growing season, as shown by the data in Jokioinen in Figure 3. It can be seen that 1988 was nearly normal during the whole growing season. In 1993, May was extremely dry, but from June onwards the situation normalized. In 1994, the growing season was nearly normal, except for July and August, which were notably dry.

Plants are sensitive to excess wetness in the early development stages (Stępniewski and Łabuda 1989). Wetness also increases the risk of structural deterioration of soils by field traffic. The data in Figure 4 and Table 4 show that wet weather during the early development stages of spring crops in May-July, and during sowing and harvesting in May and September-October, are not uncommon in Finland. The risk of wet growing seasons is somewhat greater in the inland than on the coast. During the field experiments of this study, the weather was not exceptionally wet (Figure 3).

3.2 Plant responses to compaction and modified oxygen supply to roots

In a pot experiment with a humic clay (I), wetness and compaction decreased the uptake of nitrogen by barley. The yields were not affected by wetness, but compaction reduced plant growth in the wet soil. The decreases in the concentrations of O_2 and increases in those of CO_2 in soil air by both compaction and excess watering were explained by the decreased rate of gaseous diffusion due to smaller air-filled porosities. The large amounts of N_2O and C_2H_4 detected in the compacted soils during the first month indicated that the soils were hypoxic rather than totally oxic, although the O_2 concentration in the soil air only rarely dropped below 10%. The results thus show that poor aeration can contribute to a low yield and nitrogen uptake of plants in compacted and wet soils.

In a series of pot experiments with fine sand soil (IV), the growth of shoots and roots of barley in a loose soil was reduced by both wetting of soil and lowering of O_2 concentration in the soil air. Plant growth decreased only at 0-2% O_2 in the moist soil (13-19% air-space) but as early as at 20% O_2 in the wet soil (0-5% air-space). Compaction reduced the growth of shoots and roots in both moist and wet soils, regardless of whether the soil air contained 10% or 20% O_2.

The growth of barley was decreased in wet soils and at small O_2 concentrations in soil air, because the O_2 supply from soil air was probably inadequate to sustain oxic respiration. This is supported by the fact that respiration in moist loose soil cropped with barley decreased clearly when, by varying the O_2 concentration in soil air at 2- or 4-day intervals, the concentration fell to 2% or below (IV). The CO_2 emission (q_s) from the soil versus the O_2 concentration (C) followed Michaelis-Menten equation $q_s = q_{max} C / (K_m + C)$ with a K_m value of 1.4%. The respiration of uncropped soil was not affected by the O_2 concentrations in soil air between 0% and 20%.

Besides reducing root growth, wetness and compaction also modified the distribution of roots at various depths in soil (IV). If adequately supplied with O_2 from soil air, most roots grew in the deepest soil layer, whereas in wet soils the roots preferred the well-aerated volumes near or even partly on the surface. In compact soils, all root growth was restricted to the uppermost soil layer.

Compaction and hypoxia were expected to induce root morphological changes similar to those induced by large concentrations of ethylene (V), because both of them promote the production of ethylene in roots (see Morgan and Drew 1997). Such changes include increased width, decreased specific length, and increased porosity (or specific volume). Root morphological properties were determined by image analysis (V). Root widths were increased by compaction, obviously as a reaction of barley roots to increased mechanical impedance in soil (VI). Further, the roots near the surface in well-aerated loose soils were thinner, and of higher specific length or lower specific volume, than those in the deepest soil layer. Also these changes were probably reactions to increased mechanical impedance in the soil. However, such changes were not observed in roots under severe hypoxia (VI). The results suggest that severe hypoxia lessens the possibilities of roots to adapt to the hypoxic soil by reducing root growth and impeding the formation of aerenchyma (VI).

The results (IV) show that concentrations as low as 6% in soil air are adequate for respiration and the growth of barley roots in soils at moderate moisture contents. Conversely, in wet soils plant growth is impaired even if the soil is aerated with a gas stream containing 20% O_2. The results also indicate that heavy compaction can impair plant growth by increasing the mechanical impedance deeper in the soil and thus restricting the growth of roots to a small volume near the surface.

Accurate comparison of the results with earlier studies on the effects of soil aeration on plant performance (see Gliński and Stępniewski 1985) is impossible because of methodological differences. The results however compare well with the finding that the dry matter yields of barley were reduced by hypoxia in a loose moist sandy soil only when the O_2 concentrations in soil air were below 5% (Jaakkola *et al.* 1990). Also Geisler (1969) reported that O_2 concentrations below 4% limited the shoot and root growth of barley. Scotter *et al.* (1967b) reported that the O_2 uptake by pea roots in a sand soil at matric water suctions of 1.6-1.9 kPa was decreased at O_2 concentrations in soil air below 15%. The larger critical O_2 concentration in their experiment may be partly due to a larger diameter of pea roots (about 0.5 mm) compared to that of barley roots in the present study.

3.3 Critical O_2 concentrations in soil air

The empirical results on the effects of O_2 concentrations in soil air on the growth and respiration of barley roots compared fairly well with the critical O_2 concentrations (COC) calculated with simple multicylindrical steady-state models (Lemon 1962, Armstrong and Beckett 1985) on oxygen diffusion from soil air to roots, when the water-film thickness around the roots was estimated using soil water retention data (IV). The calculations required the values of radii, respiration rates and diffusion coefficients for the coaxial shells of stele, cortex and water-film (IV, see p. 13).

In the calculation of COC, the respiration rate and root radius used were based on the measurements in study (IV, VI). The stele radius equalled half of the root radius. Assuming a regular array of air-filled pores in the soil, the thickness of the water-film (the distance from the root surface to nearest air-filled pores), was approximated by

$$\textbf{(9)} \qquad d = 2\left(\sqrt{\frac{1}{\pi\, n(\psi_m)}} - R\,(\psi_m)\right)$$

with

(10)

$$n(\psi_m) = \int_0^{\psi_m} \frac{C_w(\psi_m)}{\pi R^2(\psi_m)} d\psi_m$$

where $C_w = d\theta/d\psi_m$ and $R(\psi_m) = 2\,\sigma / \psi_m$ (σ the surface tension of water, and ψ_m the matric water suction) (IV).

The diffusion coefficients of O_2 in the root were based on the values in the literature (Wanner 1945, Armstrong and Beckett 1985). The diffusion coefficient in the water film D_{film} was estimated by

(11)

$$D_{film} = (D/D_0)D_w = f(\phi_{film})D_w = f\left(\frac{\phi - \varepsilon}{1 - \varepsilon}\right)D_w$$

using empirical expressions for the relative diffusion coefficient D/D_0 (Penman 1940a, Millington and Quirk 1960) as a function of the porosity inside the water film ϕ_{film} (ϕ total porosity, ε air-filled porosity, see Currie 1965). The O_2 concentrations at the outer edge of the water film (C_0) and in the soil air (C_a) were considered to be in equilibrium so that $C_0 = \alpha_B\ C_a$ (α_B Bunsen's solubility coefficient). The range of COCs in soil air was estimated by calculating the smallest concentration at which all of the root is oxic, and the largest at which all the stele is anoxic.

The approach used to calculate the COCs in soil air seems to give reasonable estimates for the minimum requirements of soil air O_2 concentrations for root growth and respiration at various moisture contents in coarse-textured soils (IV). In the field, it may also be applicable more generally to e.g. wet clays as discussed in IV. This problem deserves further study.

3.4 Effects of compaction and modified oxygen supply on the cumulative N_2O emissions and N balance in soil

In experiments Nos. 1-3 reported in IV, the cumulative emission of N_2O from the soil was increased by wetness ($P < 0.001$) and soil anoxia (0% O_2) ($P < 0.05$) in the loose soil (Table 5). The largest emissions from anoxic soil corresponded to about 10% of the fertilizer nitrogen applied. The effects of cropping depended on soil compaction (the interaction of cropping and compaction significant at $P < 0.05$): cropping tended to decrease the emissions from the compact soil, but increase those from the loose soil. In the compact soil, wetness did not increase the emissions significantly.

The amounts of mineral nitrogen recovered in plants, soil and N_2O emissions were occasionally much less than the amount of nitrogen in the unfertilized soil plus that added at fertilization (Figure 5). In the cropped wet soil, on average more than 35% of the nitrogen remained unaccounted for. Soil anoxia (0% O_2) ($P < 0.01$), wetness ($P < 0.05$) and cropping ($P < 0.05$) increased the difference, whereas compaction tended to make it smaller ($P = 0.06$). The results suggest that the difference probably mainly represents the production of N_2 by denitrification, as there were practically no leaching losses in this experiment.

Table 5 Cumulative emission of N_2O-N from soil[a], mg pot^{-1}

	O_2 %	n	Cropped soil	n	Uncropped soil
Loose soil					
Wet	0	1	41	1	54
	2	2	15 ± 0	3	24 ± 1
	10	4	20 ± 7	3	13 ± 4
	20	2	33 ± 10	3	7 ± 3
Moist	0	3	27 ± 8	1	47
	2	4	7 ± 3	3	3 ± 1
	10	6	2 ± 1	3	0 ± 0
	20	8	1 ± 1	3	0 ± 0
Compact soil					
Wet	10	2	3 ± 1	2	17 ± 9
	20	2	3 ± 0	2	5 ± 1
Moist	10	2	3 ± 1	2	7 ± 1
	20	2	2 ± 0	2	8 ± 2

[a]Cumulative emission ± standard error

During long-term oxygen deficiency, the losses of nitrogen from soil by e.g. denitrification and emissions of N_2O may eventually lead to nitrogen deficiency in plants. The roots may increase these losses by increasing respiration and adding decomposable organic material in soil, or decrease them by the uptake of nitrogen (Woldendorp 1962, Smith and Tiedje 1979, Mahmood *et al.* 1997, III). When subjected to inadequate oxygen supply, plant roots cannot compete efficiently with denitrifiers for the uptake of nitrate (see Bakken 1988). Accordingly, most mineral nitrogen in the present study was lost from anoxic and wet soils that were cropped.

The results also show that the emissions of N_2O and denitrification start to increase at O_2 concentrations that are smaller than the critical O_2 concentrations for root growth and functioning, as at 2% O_2, plant growth was clearly impaired in the moist soil (IV), whereas the gaseous losses were not increased (Table 5, Figure 5). This can be expected, because denitrification is an anoxic process and very small partial pressures of O_2 suffice to inhibit it (see Tiedje 1988). However, in soils N_2O is also produced when chemoautotrophic nitrifiers use nitrate as an electron acceptor when oxygen is somewhat deficient during ammonium oxidation (Arnold 1954, Bremner and Blackmer 1979, see Granli and Bøckman 1994, Bremner 1997). This nitrifier denitrification probably operates mostly at the oxic-anoxic interface (see Focht 1992). Thus, the N_2O produced by this mechanism could also be taken to indicate at least slight hypoxia in soils, although it is unknown whether this affects root growth. It may however be safely concluded that large accumulation of N_2O in wet soils indicate conditions that impair root growth and respiration in soil.

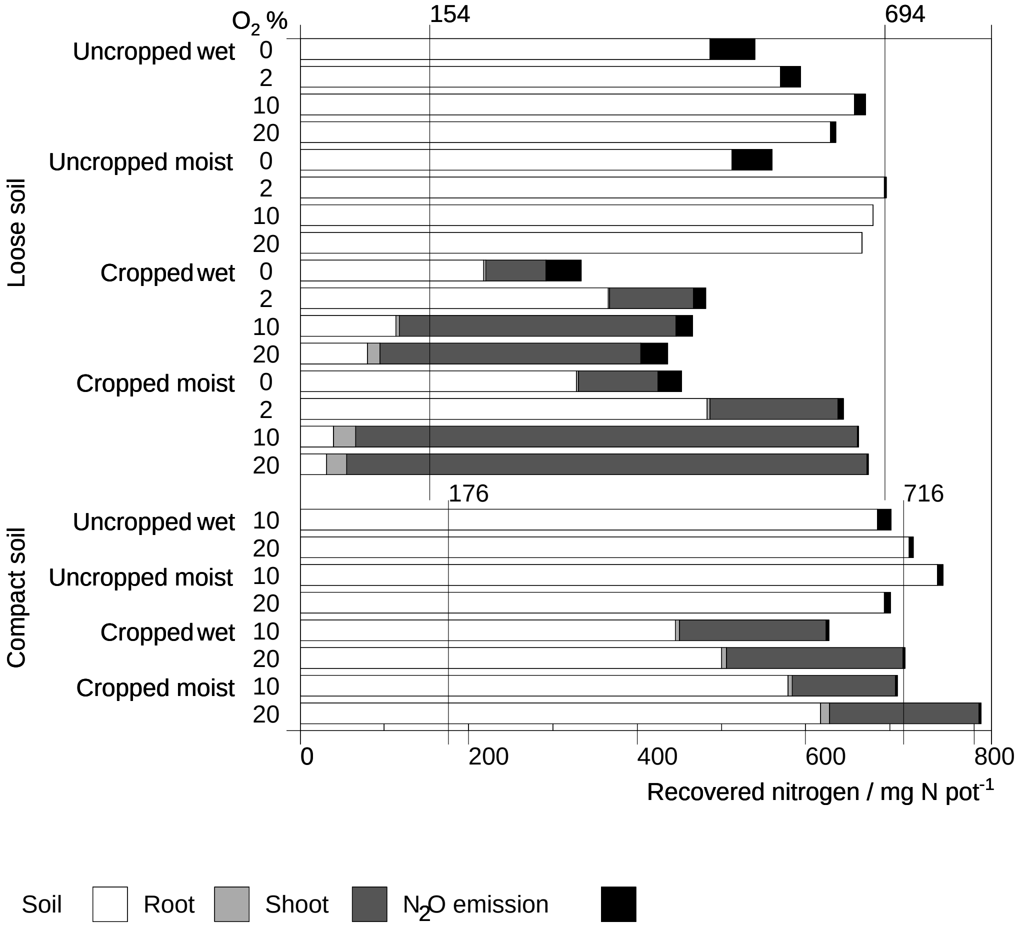

Figure 5 The amount of N recovered in soil (NH_4^+, NO_3^-), roots and shoots at the end of the experiments, and in N_2O emissions during the experiment. The N content of roots was assumed to be 2%. The vertical lines show the amount of mineral N in soil before fertilization (left) and after fertilization (right).

Although nitrogen deficiency thus probably aggravated the yield reductions in wet soils, the primary reason for the reduced yields was however the inadequate supply of oxygen to the roots, which prevented the growth and active nutrient uptake of roots. This conclusion is supported by the fact that there was usually plenty of N left in the soil after the experiments in those treatments where plants grew poorly, and in no case was the amount less than that in the well-aerated soils (Figure 5). Compaction decreased the losses of nitrogen from the cropped soil probably by restricting the growth of roots to the well-aerated surface layer. In the uncropped soil, denitrification was probably retarded by slow respiration and the lack of decomposable organic material.

3.5 Variation in soil air composition and N_2O emission in the field

3.5.1 O_2 and CO_2 in soil air

In loamy clay fields (Jokioinen 1988 and 1993), the typical ranges of O_2 and CO_2 concentrations in the air of uncompacted soil under various combinations of irrigation, cropping and N fertilization were 16-21% O_2 and 0.1-4% CO_2 at depths of 15-30 cm in the ploughed layer, and 11-20% O_2 and 1-4% CO_2 deeper in the soil (at a depth of 50 cm), respectively (Figure 6, Figure 7). The smallest O_2 concentration (4%) and largest CO_2 concentration (6%) were observed at a depth of 30 cm in the irrigated unfertilized soil under barley on 29 June 1993. Near the surface (at a depth of 5 cm) the concentrations were almost atmospheric (20-21% O_2, 0.05-0.3% CO_2).

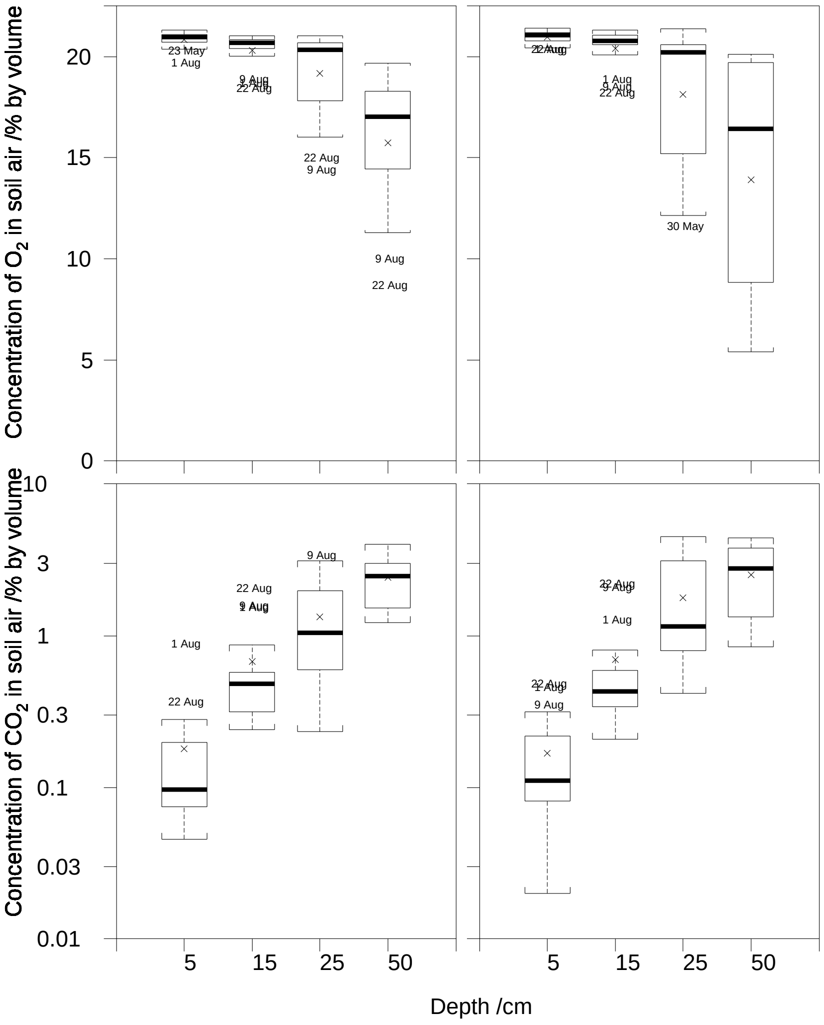

Figure 6 Box-and-whisker plots of O_2, CO_2 and N_2O concentrations in soil air at various depths in a loamy clay field in the uncompacted (left) and in the compacted (right) treatments in Jokioinen in 1988 (I). The box is drawn between the lower (Q1) and upper (Q3) quartiles, the median is the thick line inside the box, × denotes the mean, and the whiskers are drawn to the nearest values not beyond the standard span (1.5 × (Q3-Q1)) from the quartiles (typical range). Outliers are indicated by the date of measurement. Treatments: 1-4: fallow, 5-8: cropped; 1, 2, 5, 6: unirrigated, 3, 4, 7, 8: irrigated; 1, 3, 5, 7: unfertilized; 2, 4, 6, 8: N applied.

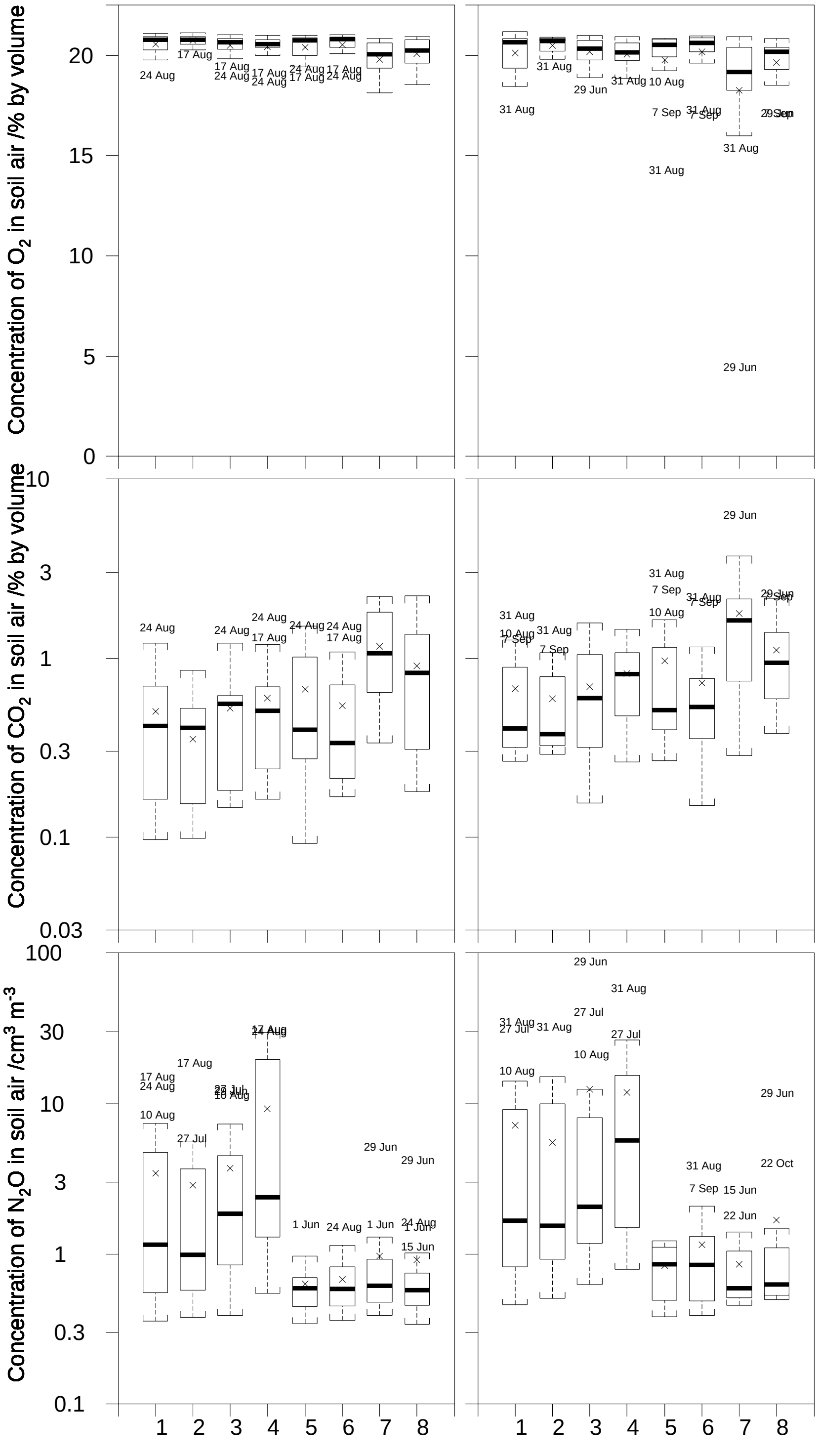

Figure 7 Box-and-whisker plot of O_2, CO_2 and N_2O concentrations in soil air at depths of 15 cm (left) and 30 cm (right) in a loamy clay field (III) in Jokioinen in 1993. The box is drawn between the lower (Q1) and upper (Q3) quartiles, the median is the thick line inside the box, × denotes the mean, and the whiskers are drawn to the nearest values not beyond the standard span ($1.5 \times (Q3-Q1)$) from the quartiles (typical range). Outliers are indicated by the date of measurement. Treatments: 1-4: fallow, 5-8: cropped; 1, 2, 5, 6: unirrigated, 3, 4, 7, 8: irrigated; 1, 3, 5, 7: unfertilized; 2, 4, 6, 8: N applied.

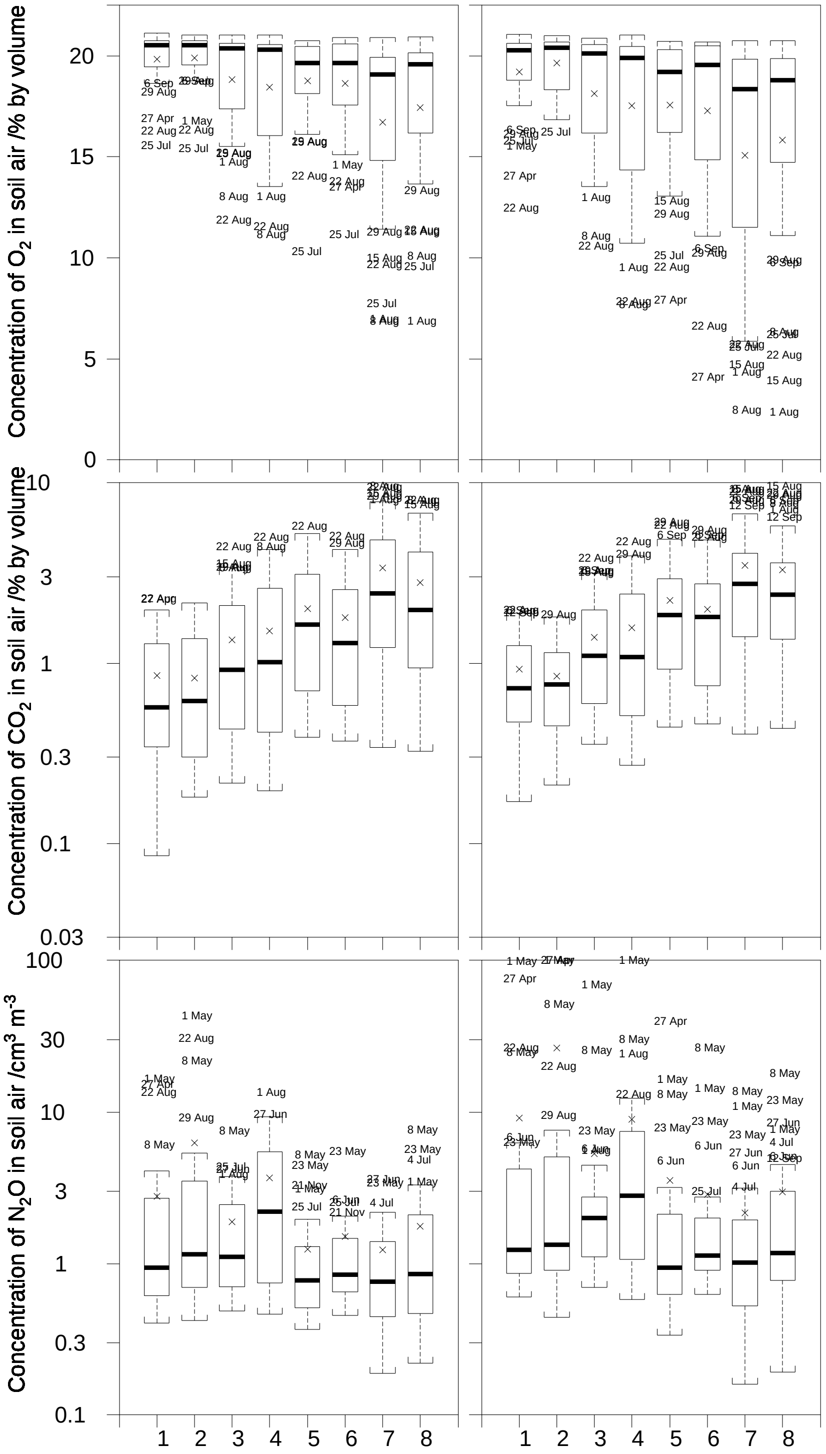

Figure 8 Box-and-whisker plots of O_2, CO_2 and N_2O concentrations in soil air at depths of 15 cm (left) and 30 cm (right) in a loam field (II) in Hausjärvi in 1993-94. The box is drawn between the lower (Q1) and upper (Q3) quartiles, the median is the thick line inside the box, × denotes the mean, and the whiskers are drawn to the nearest values not beyond the standard span (1.5 × (Q3-Q1)) from the quartiles (typical range). Outliers are indicated by the date of measurement. Treatments: 1-4: fallow, 5-8: cropped; 1, 2, 5, 6: unirrigated, 3, 4, 7, 8: irrigated; 1, 3, 5, 7: unfertilized; 2, 4, 6, 8: N applied.

Table 6 Typical effects of irrigation, cropping and N fertilization on soil air composition and soil moisture content in the field

Variable		Irrigation	Cropping		N fertilization			
Experiment	Depth		Unirrigated soil	Irrigated soil	Unirrigated soil		Irrigated soil	
	cm				Fallow	Crop	Fallow	Crop
O_2 concentration in soil air								
1993 Jokioinen	15	-	-	-	+	+	0	+
	30	0	0	-	0	+	-	+
1993-94 Hausjärvi	15	(-)	-	-	0	0	0	+
	30	(-)	-	-	+	0	-	+
CO_2 concentration in soil air								
1993 Jokioinen	15	+	+	+	-	-	0	-
	30	0	+	+	0	-	+	-
1993-94 Hausjärvi	15	(+)	+	+	0	-	0	-
	30	+	+	+	0	-	0	-
N_2O concentration in soil air								
1993 Jokioinen	15	+	-	-	0	0	+	0
	30	0	-	-	0	0	+	0
1993-94 Hausjärvi	15	0	0	(-)	+	0	+	+
	30	0	0	-	0	0	(+)	+
N_2O emission from soil								
1993 Jokioinen	0	+	-	-	+	+	+	0
Soil moisture content								
1993 Jokioinen	0-15	+	0	0	0	0	-	-
	15-30	+	-	0	0	-	+	-
1993-94 Hausjärvi	0-20	+	0	0	-	-	-	-

Symbols: + increase and - decrease ($P < 0.05$ according to the sign test; if paranthesized $P < 0.10$), 0 no effect

In a loam soil (Hausjärvi 1993-94), especially if irrigated and cropped, the variation in the gas concentrations was larger than that in the loamy clay (Figure 8). The concentration of O_2 in the ploughed layer ranged typically between 6% and 21%, and that of CO_2 between 0.1% and 8%. The smallest O_2 concentrations (minimum 2%) and the largest CO_2 concentrations (maximum 10%) were observed in the N fertilized irrigated soil at a depth of 30 cm under a vigorously growing ley in August 1993.

Heavy compaction performed seven years earlier in the loamy clay did not have any observable effects on soil air composition at shallow depths (5-15 cm) or in subsoil (at a depth of 50 cm) but decreased the concentration of O_2 and increased that of CO_2 at the bottom of the ploughed layer (at a depth of 25 cm, $P < 0.05$ according to the sign test) (I, Figure 6). Compaction also increased the variation of the gas concentrations in the soil profile compared to the uncompacted soil (Figure 6). The smallest O_2 concentrations were decreased by compaction to 12% and 5% in the ploughed layer and subsoil, respectively. In contrast, the largest CO_2 concentrations were similar in the compacted and uncompacted soils.

Irrigation and cropping generally decreased the concentrations of O_2 and increased those of CO_2 in soil air in both loamy clay and loam soils, although less pronouncedly deeper in the loamy clay (Table 6, II, III). These changes were obviously due to the smaller air-filled porosities and increased soil respiration rates in the irrigated and cropped soils, respectively. In the loam, the effects were generally larger than in the loamy clay. In the ploughed layer, irrigation and cropping of the loam decreased the average O_2 concentration by up to 7-10% and 4-5%, respectively, during a two-week period in August 1993. The effects of irrigation on the concentration of CO_2 (up to 3-4%) were only about a half of that on O_2. The effects of N fertilization on O_2 and CO_2 in soil air were rather small and variable. The fertilizer-induced increased the O_2 concentration and decreased the CO_2 concentration, especially in the cropped soil. This could be attributed to improved aeration brought about by enhanced transpiration and consequent soil drying.

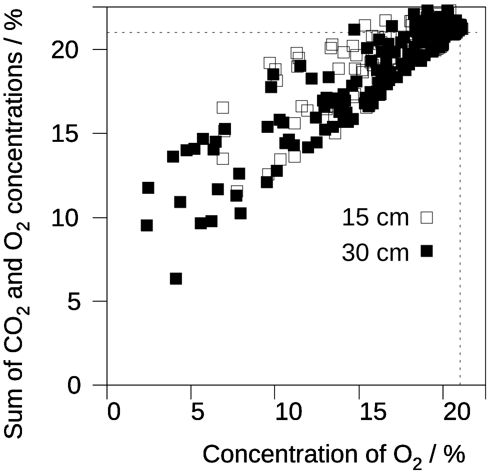

Figure 9 The sum of O_2 and CO_2 concentrations in soil air as related to O_2 concentration in a loam soil (II). The dotted lines denote the ambient atmospheric O_2 concentration. Points are treatment means on various measurement days

The concentrations of O_2 and CO_2 in soil air deviated strongly from those in the ambient air only when the soil moisture exceeded 30-35% (by volume) corresponding to air-filled porosities of about 15% in the ploughed layer (II, III). This limit was remarkably similar in the loamy clay and loam soils.

The sum of O_2 and CO_2 concentrations in soil air was never much larger than 21%, which provides evidence that the anoxic production of CO_2 was small (see Gliński and Stępniewski 1985). In both soils, the sum of O_2 and CO_2 concentrations in fact decreased as O_2 concentration decreased in wet soil (I, II, III). The magnitude of the decrease was roughly similar in both soils, although the scatter was larger in the loam than in the loamy clay: the sum was about 21% near the ambient O_2 concentration, but only about 10% when the O_2 concentration in soil air was 5% (III, Figure 9). As a consequence, the O_2 concentration decreased more steeply with depth than the CO_2 concentration increased. Similar observations have been made in many other studies (e.g. Russell and Appleyard 1915, Pietola 1995, see Gliński and Stępniewski 1985) and can be attributed to the larger solubility in water of CO_2 than O_2.

From the small difference between the diffusion coefficients of O_2 and CO_2 in the gaseous phase (the ratio between them is 1.25 at 25°C) it follows that under steady-state oxic conditions with equal rates of CO_2 production and O_2 consumption the sum of CO_2 and O_2 should slightly exceed the O_2 concentration in the atmosphere (see Gliński and Stępniewski 1985). The results however suggest that in wet soils the steady-state assumption may not be valid. The large amounts of CO_2 dissolved in water apparently buffer the changes in CO_2 concentration in soil air, so that the diffusion of CO_2 approaches steady state more slowly than that of O_2. This probably explains why the sum of O_2 and CO_2 concentrations decreases with decreasing O_2 concentration in wet soils, why the effects of irrigation are much smaller on CO_2 concentration than on O_2 concentration, and why the maximum CO_2 concentrations sometimes occur later than the minimum O_2 concentrations (II, III, Russell and Appleyard 1915, Pietola 1995). Dissolved CO_2 is lost from the soil also by mechanisms other than gaseous diffusion, such as by percolation and plant uptake of water.

These considerations have some notable consequences. Firstly, the results show that the instances where the fluxes of CO_2 and O_2 are not equal and opposite are common in cultivated soils. As a consequence, the limitations of Fick’s law in describing diffusion in multinary gas mixtures (Leffelaar 1987, Freijer and Leffelaar 1996) and the various mechanisms affecting the fluxes of CO_2 should be taken into account when modelling soil aeration. Secondly, the measurement of respiration rates in wet soils is likely to be confounded by the time-dependency of gaseous diffusion, which is different for CO_2 and O_2 gases. Thirdly, the dissolution of CO_2 into water generally decreases the likelihood of large CO_2 concentrations in wet soils. Although several studies indicate that plant growth is impaired by CO_2 only at concentrations above 10% (Tackett and Pearson 1964, Grable and Danielson 1965, Jaakkola *et al.* 1990), other studies suggest that much smaller CO_2 concentrations (>4-6%) may be detrimental to plants at small O_2 concentrations in soil air (Geisler 1967, 1969). The results of the present study suggest that in the field CO_2 concentrations do not generally rise above 5% even at small O_2 concentrations in soil air. In the irrigated loam field, however, this limit was occasionally exceeded.

3.5.2 N_2O in soil air and N_2O emissions from soil

The concentrations of N_2O in soil air ranged typically from 0.36 to 30 $cm^3\ m^{-3}$ and from 0.16 to 12 $cm^3\ m^{-3}$ in the ploughed layers of loamy clay (Figure 7) and loam (Figure 8) soils, respectively, but occasionally concentrations approaching 100 $cm^3\ m^{-3}$ were found in wet uncropped soils. The largest concentrations in the loam (May 1994) were probably caused by the spring thaw (see Nyborg *et al.* 1997). Cropping efficiently reduced the concentrations of N_2O in both soils, when the soil was wet, except for during the early growth stages (Table 6). In the cropped soils, the concentrations were usually below 5 $cm^3\ m^{-3}$. Irrigation or soil wetness raised the N_2O concentration, if nitrate was present abundantly (II, III). As a consequence, N fertilization increased N_2O concentrations especially under irrigated fallow (Table 6).

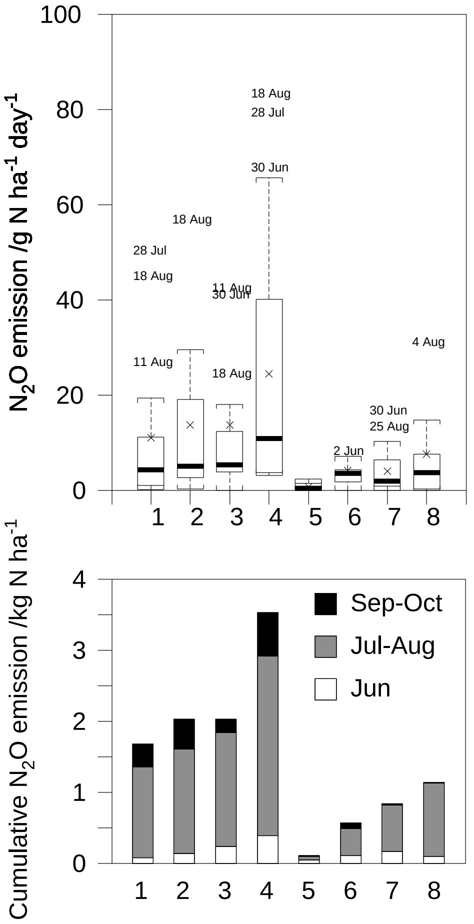

Figure 10 Box-and-whisker plots of daily N_2O emissions from a loamy clay, and the cumulative N_2O emissions during the period 1 June – 22 October 1993 in Jokioinen (see the statistical tests in III). The box is drawn between the lower (Q1) and upper (Q3) quartiles, the median is the thick line inside the box, × denotes the mean, and the whiskers are drawn to the nearest values not beyond the standard span (1.5 × (Q3-Q1)) from the quartiles (typical range). Outliers are indicated by the date of measurement. Treatments: 1-4: fallow, 5-8: cropped; 1, 2, 5, 6: unirrigated, 3, 4, 7, 8: irrigated; 1, 3, 5, 7: unfertilized; 2, 4, 6, 8: N applied.

The emissions of N_2O from the loamy clay, similarly to the N_2O concentrations in soil air, were much larger and more variable when the soil was fallowed (0.1-66 g N ha^{-1} day^{-1}) than when it was cropped (0.0-15 g N ha^{-1} day^{-1}) (Figure 7). The cumulative

N_2O emissions were roughly doubled by irrigation and N fertilization, but cropping reduced them by a factor of 3-7 (Figure 10, III). Most N_2O was thus emitted from the irrigated fertilized soil under fallow (3.5 kg N ha^{-1}), and least from the unirrigated unfertilized soil under barley (0.1 kg N ha^{-1}). These results agree with the findings in earlier field experiments that plant growth can efficiently reduce N_2O emission from soils (Aulakh *et al.* 1984, Hénault *et al.* 1998, Mahmood *et al.* 1997).

The largest N_2O emissions from the loamy clay were found when 60-90% of the soil pore space was filled with water (III). This supports the view that N_2O is emitted most rapidly at intermediate soil moisture contents (Linn and Doran 1984, Smith *et al.* 1998). The emission rates seemed to be limited mainly by slow respiration and dryness in the uncropped soil, and by slow respiration and a small content of mineral N in the cropped soil (III).

In the loam soil, the average N_2O emission (7 g N ha^{-1} day^{-1}) was about half of that in the loamy clay (15 g N ha^{-1} day^{-1}) during the experiments (II, III). Although the differences could not be tested, the effects of treatments on N_2O emission were probably roughly similar to those on the N_2O concentration in soil air, because the positive correlation between the two variables was strong in both soils (II, III).

The magnitude of N_2O emissions (II, III) agree rather well with those found from cultivated mineral soils in earlier studies in Finland (Jaakkola 1985, 1994) and elsewhere (see Bouwman 1996). The emissions for the loamy clay under barley were somewhat smaller than those from a slightly heavier clay soil under barley (2.2-2.3 kg N ha^{-1} during May-October 1983) reported by Jaakkola (1985). Several times larger emissions have been measured from cultivated organic soils (see Bouwman 1996, Kasimir-Klemedtsson *et al.* 1997, Kulmala and Esala 2000).

3.5.3 C_2H_4 and CH_4 in soil air

C_2H_4 and CH_4 did not accumulate in soil air in the field experiments (II, III) of this study. C_2H_4 concentration in soil air did not rise above the detection limit of 0.5 cm^3 m^{-3} in any sample. Also the CH_4 concentrations were small (0-43 cm^3 m^{-3}) with no apparent response to the treatments or sampling dates.

The lack of CH_4 accumulation in soil air can be explained by the fact that the field soils were hypoxic rather than anoxic. No great CH_4 accumulation was to be expected, as extremely anoxic conditions are required for CH_4 production (Ponnamperuma 1972). In the case of C_2H_4 the situation is less clear. In earlier field experiments (Smith and Dowdell 1974, Campbell and Moreau 1979) and in the first pot experiment of this study (I), concentrations of several cm^3 m^{-3} were observed in relatively wet soils. Anoxia may stimulate microbial C_2H_4 production in soil (Zechmeister-Boltenstern and Nikodim 1999), whereas oxic conditions favour decomposition of both CH_4 and C_2H_4 (Cornforth 1975, Zechmeister-Boltenstern and Smith 1998, Zechmeister-Boltenstern and Nikodim 1999). On the other hand, soil hypoxia, but not anoxia, enhances C_2H_4 production by plant roots (see Morgan and Drew 1997), and microbes produce C_2H_4 even in oxic soil, if amended with organic substances (see Zechmeister-Boltenstern and Smith 1998). Thus, in the present experiment the accumulation of CH_4 and C_2H_4 was probably prevented by decomposition in the oxic parts of the soil.

3.6 Magnitude and timing of hypoxia in the pot experiments and in the field

In contrast to the pot experiments (I, IV), the dry matter yields and N uptake of plants were not adversely affected by compaction and wetting in the field experiments, even if the effects on soil air composition were clearly established (I, II, III). In fact, irrigation occasionally increased the yields (II, III). In this sense, the range of variation in soil air composition observed in this study does not seem to be of great concern for plant growth. The lack of plant response to the impaired soil aeration is discussed below in terms of the magnitude and timing of hypoxic stress in soil.

The magnitude of the hypoxic stress in soil may be assessed by the difference between the measured and critical O_2 concentrations in soil air, and the extent of the hypoxia in the soil profile. The discussion is complicated by the facts that soil air composition is temporally and spatially variable and that the parameters needed to estimate the critical O_2 concentrations (COC) in soil air have not been determined in field conditions.

The sensitivity of plants to hypoxic stress in soil varies during the development. Cereal crops are particularly sensitive to excessively large soil moisture contents during stem elongation, whereas such grass species as timothy are more tolerant to flooding (Saukko 1950/51, Stępniewski and Łabuda 1989, see van't Woudt and Hagan 1957). In Finland, cereal crops and timothy are probably in the most sensitive growth stages in late June - early July and August-September, respectively (Saukko 1950/51). Differences in the sensitivity of plants to soil hypoxia were demonstrated also in this study (IV, No. 4). Shoot yield was more clearly decreased by an 8-day period of severe hypoxia (0-2% O_2 in soil air) at about 3.5 week after sowing than one week later. Short hypoxic stresses (2 days of hypoxia followed by aeration with 20% O_2) at the later growth stage did not however decrease the yield significantly (IV).

Table 7 Water-film thicknesses for different soils[a] and critical O_2 concentrations in soil air[b]

Soil	Matric water suction kPa	Air-filled porosity $m^3 m^{-3}$	Thickness of water film mm	Critical O_2 concentration in soil air %
Sand	1	0.06	0.71	8-10
	10	0.23	0.05	2-3
Sandy loam	1	0.04	1.03	9-11
	10	0.14	0.06	2-3
Clay	1	0.04	1.54	10-13
	10	0.07	0.15	4-5
Humic clay, loose	1	0.13	1.95	10-14
	10	0.21	0.19	4-6
Humic clay, compacted	1	0.06	3.18	12-16
	10	0.10	0.32	5-7

[a] Calculated as described in IV using data in I and in Andersson and Wiklert (1972)

[b] Computed with a multicylindrical radial diffusion model (Armstrong and Beckett 1985) using the values given in IV (see Table 4 in IV, percentage root respiration 50%) for the parameters other than the water-film thickness

The empirical results and modelling from the pot experiments suggest that the COC in soil air for root growth and respiration may be 4-5% O_2 in moist soils (water-film thickness <0.2 mm) and 11-15% O_2 in wet soils (water-film thickness >2 mm), and even larger in compact soils (IV). In order to get a somewhat more general view of the water-film thickness in different soils, values of water-film thickness at various matric water suctions are calculated in Table 7 using the water retention data given by Andersson and Wiklert (1972) for various field soils and the data for the humic clay in the first pot experiment of this study (I). The selection of soils is not comprehensive, or even very representative of the given soils, but rather demonstrates the differences between various soils and the orders of magnitude involved.

According to Table 7 the water-film thicknesses in various soils at 10 kPa matric water suction are of the same order of magnitude as those in the moist soils in IV. As a consequence, COCs are also rather similar, about 5% O_2 or slightly less for the coarse-textured soils. Small O_2 concentrations in soil air are thus generally adequate for root growth in moist soils, despite large differences in the air-filled porosities. In wet soils at 10 kPa matric water suction, the water-film thicknesses of field soils are slightly less, and the COCs correspondingly smaller than those calculated in IV. It can be concluded that in the field O_2 concentrations smaller than 8-13% in soil air impair root growth and respiration in wet soils containing about 5% air-filled pores, whereas concentrations as small as 2-5% may be adequate in moist soils containing more than 10% air-filled pores. COCs seem to increase slightly with the fineness of soil texture.

At shallow depths in the ploughed layer of the uncompacted loamy clay, the O_2 concentrations in soil air always remained above 18% (I, III). The air-filled porosities probably dropped below 5% only at around harvest time (III). Also in the lower part of the ploughed layer the O_2 concentrations were large, usually above 16%. Only on 29 June 1993 did the O_2 concentrations in the irrigated unfertilized soil drop to a small value (4%), coinciding with an air-filled porosity of less than 5%. It seems thus certain that the ploughed layer of the uncompacted loamy clay was nearly always well aerated during the growing season. Hypoxia probably limited the root growth of barley only in the unfertilized irrigated soil at the end of the irrigation period.

In the compacted loamy clay, the O_2 concentration dropped to 12% in late May 1988, when the soil was wet (I). Considering that COC was probably slightly increased by compaction, concentrations of O_2 as low as this, and especially the smaller concentrations (down to 5% O_2) deeper in the soil, were probably limiting root growth. Poor aeration of the subsoil was almost certainly responsible for the reduced yields and N uptake of annual crops in the compacted soil in the wetness of 1987 (Alakukku and Elonen 1995).

The loam soil was extremely wet during August-September 1993, especially when it was irrigated (II). In contrast to the upper part of the ploughed layer, where the O_2 concentration only rarely dropped below 10%, the O_2 concentration deeper in the soil was below 10% probably limiting root growth during all of August 1993 in the irrigated soil. Small O_2 concentrations in wet soil were also found under the ley after snow melt in spring 1994.

In contrast to the field experiment, the O_2 concentrations in the wet compacted soil of the first pot experiment (I) were for several weeks in the range that probably limited root growth. This no doubt contributed to a low yield and nitrogen uptake besides the gaseous losses of N by denitrification.

The presence of large N_2O concentrations in soil air can be taken to indicate hypoxic soil conditions (I, II, III). The results from the pot experiments described in IV indicated that root growth and respiration is impaired by a less severe hypoxia than that needed to evoke denitrification (IV). This seems to disagree with the results from the other experiments, in which N_2O emissions from soil and N_2O concentrations in soil air were frequently large, although plant growth was not reduced by hypoxic stress (I, II, III). The discrepancy can be attributed to the spatial heterogeneity in soil.

The production of N_2O was largest in uncropped soils (II, III). It is possible that the large N_2O emissions and concentrations in the soil air of uncropped soils indicated the presence of hypoxia deeper in the soil as compared to the well-aerated layers affecting plant growth. There were indeed some signs that N_2O originated from deeper layers in the uncropped soil than in the cropped soils (II). It is also generally accepted that anoxic microsites may be present even in rather well aerated soils and denitrify rapidly (Currie 1961, Flessa and Beese 1995). This probably explains the occasionally large N_2O emissions originating from very shallow depths in the cropped soil (III). Compaction can be expected to increase the occurrence of such sites, and this leads to enhanced denitrification in soils rich in nitrate and degradable organic matter (Bakken *et al.* 1987). This may explain the large N_2O concentrations observed in the compacted moist soil where O_2 concentration in soil air was apparently larger than COC (I). The model for calculating the COCs (IV) probably cannot be used for predicting denitrification, because the underlying assumption of regularly distributed air-filled pores is not equally valid for root growth and denitrification.

To sum up, the data on the O_2 concentrations in soil air and soil moisture contents suggest that although shallow soil depths are usually well-aerated, hypoxia may limit root growth occasionally at greater depths in loamy clay and clay fields under normal management practices, if the soil is wet (I, II, III). The short duration of hypoxic stress in the most sensitive growth stages and the presence of well-aerated soil at shallow depths explain why the plant yields were not decreased in the field experiments. Large N_2O emissions and N_2O concentrations in soil air indicate that part of the soil is hypoxic, but the importance of this on plant growth is confounded by the spatial heterogeneity of field soils.

4 CONCLUSIONS

1. Wet weather during the early development stages of spring crops, and during sowing and harvesting, is not uncommon in Finland. The risk of wet growing seasons is somewhat greater in inland than on the coast.
2. O_2 concentrations as low as 6% in soil air are adequate for respiration and growth of barley roots in soils at moderate moisture contents. In loose soil, the CO_2 emission (q_s) versus the O_2 concentration (C) follows the Michaelis-Menten equation $q_s = q_{max}\, C / (K_m + C)$ with a K_m value of 1.4%. Conversely, in wet soils with less than 5% air space plant growth is impaired even if the soil is aerated with a gas stream containing 20% O_2.
3. The observed effects of O_2 concentrations on the respiration and growth of barley roots compare fairly well with the COCs calculated by a simple multicylindrical diffusion model, in which the water-film thickness around the roots is estimated using soil water retention data.
4. In the conditions prevailing in Finland, hypoxia occasionally limits root growth especially below the ploughed layer in loamy clay and loam fields under normal management practices, if the soil is wet. However, if hypoxia, even if it occurs at the most sensitive growth stages, lasts for only a short time, the risk for yield loss is small. Also well-aerated soil layers near the surface may prevent yield reduction.
5. The increases of CO_2 concentration in soil air, although occasionally large, probably do not reach levels that are detrimental to roots.
6. Marked increases of CH_4 and C_2H_4 in soil air do not seem to be probable in the field soils studied.
7. Heavy compaction of clay impairs subsoil aeration for several years.
8. Poor aeration can contribute to a low yield and nitrogen uptake of plants in compacted and wet soils. In wet soils, denitrification causing losses of nitrate N and increasing N_2O emission is obvious, and this probably contributes to the low yields.
9. Leaving land fallow causes N_2O emission and is therefore detrimental to the environment, whereas cropping is efficient in diminishing N_2O emission. Also irrigation and N fertilization increase N_2O emission.
10. Large N_2O emissions and N_2O concentrations in soil air indicate soil hypoxia, but the importance of this on plant growth is confounded by the spatial heterogeneity of field soils.
11. The approach used for calculating COCs in this study seems to give reasonable estimates of the minimum requirements of O_2 concentrations in soil air for the respiration and growth of plant roots. In future studies, the applicability of the approach may be further specified by more accurate determination of the variables in field conditions and by incorporating the model obtained into larger models of plant growth and soil aeration.

REFERENCES

Akinremi, O.O., McGinn, S.M. & McLean, H.D.J. 1999. Effects of soil temperature and moisture on soil respiration in barley and fallow plots. *Canadian Journal of Soil Science* 79: 5-13.

Alakukku, L. 1997. *Long-term soil compaction due to high axle load traffic.* Jokioinen: Agricultural Research Centre of Finland. 55 p.

Alakukku, L. & Elonen, P. 1995. Long-term effects of a single compaction by heavy field traffic on yield and nitrogen uptake of annual crops. Soil & Tillage Research 36: 141-152.

Amoore, J.E. 1961a. Arrest of mitosis in roots by oxygen-lack or cyanide. *Proceedings of the Royal Society of London. Series B. Biological Sciences.* 154: 95-108.

Amoore, J. E. 1961b. Dependence of mitosis and respiration in roots upon oxygen tension. *Proceedings of the Royal Society of London. Series B. Biological Sciences.* 154: 109-129.

Andersson, S. & Wiklert P. 1972. Markfysikaliska undersökningar i odlad jord. XXIII. Om de vattenhållande egenskaperna hos svenska jordarter (Water-holding properties of Swedish soils. In Swedish. Summary in English.). *Grundförbättring* 25: 53-143.

Andreev, V.Y., Generozova, I.P. & Vartapetian, B.B. 1991. Energy status and mitochondrial ultrastructure of excised pea root at anoxia and postanoxia. *Plant Physiology and Biochemistry* 29: 171-176.

Ansalehto, A., Elomaa, E., Esala, M., Nordlund, A. & Pilli-Sihvola, Y. 1985. Maatalouden sääpalvelukokeilu kesällä 1984 (The experiment of farm weather service in Finland during the summer 1984. In Finnish.). *Maatalouden tutkimuskeskus, Tiedote* 2/85. Jokioinen: Maatalouden tutkimuskeskus. 127 p.

Arah, J.R.M. & Smith, K.A. 1989. Steady-state denitrification in aggregated soils: a mathematical model. *Journal of Soil Science* 40: 139-149.

Arah, J.R.M. & Vinten A.J.A. 1995. Simplified models of anoxia and denitrification in aggregated and simple-structured soils. *European Journal of Soil Science* 46: 507-517.

Armstrong, W. 1979. Aeration in higher plants. *Advances in Botanical Research* 7: 225-332.

Armstrong, W. & Beckett, P.M. 1985. Root aeration in unsaturated soil: a multi-shelled mathematical model of oxygen diffusion and distribution with and without sectoral wet-soil blocking of the diffusion path. *New Phytologist* 100: 293-311.

Armstrong, W. & Beckett, P.M. 1987. Internal aeration and the development of stelar anoxia in submerged roots. A multishelled mathematical model combining axial diffusion of oxygen in the cortex with radial losses to the stele, the wall layers and the rhizosphere. *New Phytologist* 105: 221-245.

Armstrong, W. & Gaynard, T.J. 1976. The critical oxygen pressures for respiration in intact plants. *Physiologia Plantarum* 37: 200-206.

Armstrong, W., Justin, S.H.F.W., Beckett, P.M. & Lythe, S. 1991. Root adaptation to soil waterlogging. *Aquatic Botany* 39: 57-73.

Armstrong, W., Strange, M.E., Cringle, S. & Beckett, P.M. 1994. Microelectrode and modelling study of oxygen distribution in roots. *Annals of Botany* 74: 287-299.

Armstrong, W. & Webb, T. 1985. A critical oxygen pressure for root extension in rice. *Journal of Experimental Botany* 36: 1573-1582.

Arnold, P.W. 1954. Losses of nitrous oxide from soil. *Journal of Soil Science* 5: 116-128.

Arvidson, J. & Håkanson, I. 1996. Do effects of soil compaction persist after ploughing ? Results from 21 long-term field experiments in Sweden. *Soil & Tillage Research* 39: 175-197.

Atwell, B.J., Thomson, C.J., Greenway H., Ward G. & Waters, I. 1985. A study of the impaired growth of roots of *Zea mays* seedling at low oxygen concentrations. *Plant, Cell and Environment* 8: 179-188.

Aulakh, M.S., Rennie D.A. & Paul, E.A. 1984. Gaseous nitrogen losses from soils under zero-till as compared with conventional-till management systems. *Journal of Environmental Quality* 13: 130-136.

Aura, E. 1983. Soil compaction by the tractor in spring and its effect on soil porosity. *Journal of the Scientific Agricultural Society of Finland* 55: 91-107.

Bakken L.R. 1988. Denitrification under different cultivated plants: effects of soil moisture tension, nitrate concentration, and photosynthetic activity. *Biology and Fertility of Soils* 6: 271-278.

Bakken, L.R., Børresen, T. & Njøs, A. 1987. Effect of soil compaction by tractor traffic on soil structure, denitrification, and yield of wheat (*Triticum aestivum* L.). *Journal of Soil Science* 38: 541-552.

Ball, B.C., Horgan, G.W. & Parker, J.P. 2000. Short-range spatial variation of nitrous oxide fluxes in relation to compaction and straw residues. *European Journal of Soil Science* 51: 607-616.

Barber, D.A., Ebert, M. & Evans, N.T.S. 1962. The movement of ^{15}O through barley and rice plants. *Journal of Experimental Botany* 13: 397-403.

Baveye, P., Parlange, J.-Y. & Stewart, B.A. (eds.) 1998. *Fractals in Soil Science.* Advances in Soil Science. Boca Raton, Florida.: CRC Press. 377 p.

Benjamin, L.R. & Greenway, H. 1979. Effects of a range of O_2 concentrations on porosity of barley roots and on their sugar and protein concentrations. *Annals of Botany* 43: 383-391.

Berry, L. Joe & Norris Jr., W.E. 1949. Studies of onion root respiration. I. Velocity of oxygen consumption in different segments of root at different temperatures as a function of partial pressure of oxygen. *Biochimica et Biophysica Acta* 3: 593-606.

Blake, G.R. & Hartge, K.H. 1986. Particle density. In: Klute A. (ed.). *Methods of Soil Analysis. Part 1. Physical and Mineralogical Methods.* Agronomy 9. Madison, Wisconsin: ASA, SSSA. p. 377-382.

Blokhina, O. 2000. *Anoxia and oxidative stress: lipid peroxidation, antioxidant status and mitochondrial functions in plants.* Dissertationes Biocentri Viikki Universitatis Helsingiensis 26. Helsinki: Yliopistopaino. 79 p.

Bollman, A. & Conrad, R. 1997. Acetylene blockage technique leads to underestimation of denitrification rates in oxic soils due to scavenging of intermediate nitric oxide. *Soil Biology and Biochemistry* 29: 1067-1077.

Boone, F.R., van der Werf, H.M.G., Kroesbergen, B., ten Hag, B. A. & Boers, A. 1986. The effect of compaction of the arable layer in sandy soils on the growth of maize for silage. 1. Critical matric water potentials in relation to soil aeration and mechanical impedance. *Netherlands Journal of Agricultural Science* 34: 155-171.

Bouma, T.J., Nielsen, K.L., Eissenstat, D.M. & Lynch, J.P. 1997. Soil CO_2 concentration does not affect growth or root respiration in bean or citrus. *Plant, Cell and Environment* 20: 1495-1505.

Bouwman, A.F. 1996. Direct emission of nitrous oxide from agricultural soils. *Nutrient Cycling in Agroecosystems* 46: 53-70.

Bowling, D.J.F. 1973. Measurement of a gradient of oxygen partial pressure across the intact root. *Planta* 111: 323-328.

Bremner, J.M. 1997. Sources of nitrous oxide in soils. *Nutrient Cycling in Agroecosystems* 49: 7-16.

Bremner, J.M. & Blackmer, A.M. 1979. Effects of acetylene and soil water content on emission of nitrous oxide from soils. *Nature, London* 280: 380-381.

Bremner, J.M. & Mulvaney, C.S. 1982. Nitrogen - Total. In: Page A.L. (ed.). *Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties.* Agronomy 9. Madison, Wisconsin: ASA, SSSA. p. 595-624.

Brouwer, R. 1983. Functional equilibrium: sense or nonsense? *Netherlands Journal of Agricultural Science* 31: 335-348.

Brown, N.J., the late Fountaine, E.R. & Holden, M.R. 1965. The oxygen requirement of crop roots and soils under near field conditions. *Journal of Agricultural Science* 64: 195-203.

Bryce, J.H. & Thornton, J.M. 1996. Respiration and growth metabolism. In: Zamski, E. & Schaffer, A.A. (eds.). *Photoassimilate Distribution in Plants and Crops: Source-Sink Relationships.* New York: Marcel Dekker. p. 43-61.

Campbell, R.B. & Moreau, R.A. 1979. Ethylene in a compacted field soil and its effect on growth, tuber quality, and yield of potatoes. *American Potato Journal* 56: 199-210.

Chan, K.Y. & Hodgson, A.S. 1995. Subsoil structure changes of a typic Pellustert under dryland cropping. *Soil Science* 160: 376-838.

Cho, C.M., Burton, D.L. & Chang, C. 1997. Kinetic formulation of oxygen consumption and denitrification processes in soil. *Canadian Journal of Soil Science* 77: 253-260.

Christensen, S., Simkins, S. & Tiedje J.M., 1990. Spatial variation in denitrification: Dependency of activity centers on the soil environment. *Soil Science Society of America Journal* 54: 1608-1613.

Cook, F.J. 1995. One-dimensional oxygen diffusion into soil with exponential respiration: analytical and numerical solutions. *Ecological Modeling* 78: 277-283.

Cornforth, I.S. 1975. The persistence of ethylene in aerobic soils. *Plant and Soil* 42: 85-96.

Crossett, R.J. & Campbell, D.J. 1975. The effects of ethylene in the root environment upon the development of barley. *Plant and Soil* 42: 453-463.

Currie, J.A. 1960. Gaseous diffusion in porous media. Part 2. Dry granular materials. *British Journal of Applied Physics* 11: 318-324.

Currie, J.A. 1961. Gaseous diffusion in porous media. Part 3. Wet granular materials. *British Journal of Applied Physics* 12: 275-281.

Currie, J.A. 1965. Diffusion within soil microstructure. A structural parameter for soils. *Journal of Soil Science* 16: 279-289.

Currie, J.A. 1970. Movement of gases in soil respiration. In: *Sorption and Transport Processes in Soils. S.C.I. Monograph* 37: 152-171.

Currie, J.A. 1975. Soil respiration. In: Soil physical conditions and crop growth. Ministry of Agriculture, Fisheries and Food, Technical Bulletin 29: 461-468.

Currie, J.A. 1979. Rothamsted studies of soil structure IV. Porosity, gas diffusion and pore complexity in dry soil crumbs. *Journal of Soil Science* 30: 441-452.

Currie, J.A. 1983. Gas diffusion through soil crumbs: the effects of wetting and swelling. *Journal of Soil Science* 34: 217-232.

Currie, J.A. 1984a. Gas diffusion through soil crumbs: the effects of compaction and wetting. *Journal of Soil Science* 35: 1-10.

Currie, J.A. 1984b. The physical environment in the seed-bed. *Aspects of Applied Biology* 7: 33-54.

da Silva, A.P., Kay, B.D. & Perfect, E. 1994. Characterization of the least limiting water range of soils. *Soil Science Society of America Journal* 58: 1775-1781.

Davidson, E.A. 1991. Fluxes of nitrous oxide and nitric oxide from terrestrial ecosystems. In: Rogers, J.E. & Whitman, W.B. (eds.). *Microbial Production and Consumption of Greenhouse Gases: Methane, Nitrogen Oxides and Halomethanes.* Washington D.C.: American Society for Microbiology. p.219-235.

de Jong, E. 1981. Soil aeration as affected by slope position and vegetative cover. *Soil Science* 131: 34-43.

de Vries, D.A. 1950. Some remarks on gaseous diffusion in soils. *Transactions of the International Congress Soil Science 4th, Amsterdam* 2b: 41-43.

de Willigen, P. & van Noordwijk, M. 1984. Mathematical models on diffusion of oxygen to and within plant roots, with special emphasis on effects of soil-root contact. I. Derivation of the models. *Plant and Soil* 77: 215-231.

de Willigen, P. & van Noordwijk, M. 1989. Model calculations on the relative importance of internal longitudal diffusion for aeration of roots of non-wetland plants. *Plant and Soil* 113: 111-119.

Dowdell, R.J. & Smith, K.A. 1974. Field studies of the soil atmosphere. II. Occurrence of nitrous oxide. *Journal of Soil Science* 25: 231-238.

Drew, M.C. 1990. Sensing soil oxygen. *Plant, Cell and Environment* 13: 681-693.

Drew, M.C. 1992. Soil aeration and plant root metabolism. *Soil Science* 154: 259-268.

Drew, M.C. 1997. Oxygen deficiency and root metabolism: injury and acclimation under hypoxia and anoxia. *Annual Reviews in Plant Physiology and Plant Molecular Biology* 48: 223-250.

Drew, M.C., Jackson, M.B. & Giffard, S. 1979a. Ethylene-promoted adventitious rooting and development of cortical air spaces (aerenchyma) in roots may be adaptive responses to flooding in *Zea mays* L. *Planta* 147: 83-88.

Drew, M.C. & Lynch, J.M. 1980. Soil anaerobiosis, microorganisms, and root function. *Annual Reviews in Phytopathology* 18: 37-66.

Drew, M.C., Saglio, P.H. & Pradet, A. 1985. Larger adenylate energy charge and ATP/ADP ratios in aerenchymatous roots of *Zea mays* in anaerobic media as a consequence of improved internal oxygen transport. *Planta* 165: 51-58.

Drew, M.C. & Sisworo, E.J. 1979. The development of waterlogging damage in young barley plants in relation to plant nutrient status and changes in soil properties. *New Phytologist* 82: 301-314.

Drew, M.C., Sisworo, E.J. & Saker, L.R. 1979b. Alleviation of waterlogging damage to young barley plants by application of nitrate and a synthetic cytokinin, and comparison between the effects of waterlogging, nitrogen deficiency and root excision. *New Phytologist* 82: 315-329.

Eavis, B.W. 1972. Soil physical conditions affecting seedling root growth. I. Mechanical impedance, aeration and moisture availability as influenced by bulk density and moisture levels in a sandy loam soil. *Plant and Soil* 36: 613-622.

Eavis, B.W. & Payne, D. 1968. Soil physical conditions and root growth. In: W. J. Whittington (ed.). *Root Growth.* London: Butterworths. p. 315-338.

Elomaa, E. 1993. Estimating potential evapotranspiration and precipitation deficit. In: Sevruk, B. & Lapin, M. (eds.). *Proceedings of the Symposium on Precipitation and Evaporation*, Bratislava, Slovakia 20-24 September 1993. 3: 82-86.

Elonen, P. 1971. Particle-size analysis of soil. *Acta Agralia Fennica* 122: 1-122.

Elonen, P. & Pietola, L. 1991. Sprinkler irrigation of field crops during rainy growing seasons. *Annales Agriculturae Fenniae* 30: 359-373.

Erdmann, B., Wiedenroth, E.M. & Ostareck, D. 1988. Anatomy of the root-shoot junction in wheat seedlings with respect to internal oxygen transport and root growth retardation by external oxygen shortage. *Annals of Botany* 62: 521-529.

Esala, M. 1991. Split application of nitrogen: effects on the protein in spring wheat and fate of ^{15}N-labelled nitrogen in the soil-plant system. *Annales Agriculturae Fenniae* 30: 219-309.

Evans, N.T. & Ebert, M. 1960. Radioactive oxygen in the study of gas transport down the root of *Vicia faba*. *Journal of Experimental Botany* 11: 246-257.

Fang, C. & Moncrieff, J.B. 1999. A model for soil CO_2 production and transport 1: Model development. *Agricultural and Forest Meteorology* 95: 225-236.

Farrell, D.A., Greacen, E.L. & Gurr, C.G. 1966. Vapor transfer in soil due to air turbulence. *Soil Science* 102: 305-313.

Findlay, W.I. & McKenney, D.J. 1979. Direct measurement of nitrous oxide flux from soil. *Canadian Journal of Soil Science* 59: 413-421.

Firestone, M.K. & Davidson, E.A. 1989. Microbiological basis of NO and N_2O production and consumption in soil. In: Andreae, M.O. & Schimel, D.S. (eds.). *Exchange of Trace Gases between Terrestrial Ecosystems and the Atmosphere.* New York: John Wiley & Sons. p. 7-21.

Flessa, H. & Beese, F. 1995. Effects of sugarbeet residues on soil redox potential and nitrous oxide emission. *Soil Science Society of America Journal* 59: 1044-1051.

Flühler, J. 1973. Sauerstoffdiffusion im Böden (Oxygen diffusion in soils. In German. Summary in English). Mitteilungen der Schweizerische Anstalt für das forstliche Versuchswesen 49: 125-250.

Focht, D.D. 1992. Diffusional constraints on microbial processes in soil. *Soil Science* 154: 300-307.

Folorunso, O.A. & Rolston, D.E. 1984. Spatial variability of field-measured denitrification gas fluxes. *Soil Science Society of America Journal* 48: 1214-1219.

Franzluebbers, A.J., Hons, F.M. & Zuberer, D.A. 1995. Tillage-induced seasonal changes in soil physical properties affecting soil CO_2 evolution under intensive cropping. *Soil & Tillage Research* 34: 41-60.

Freijer, J.I. 1994. Calibration of jointed tube model for the gas diffusion coefficient in soils. *Soil Science Society of America Journal* 58: 1067-1076.

Freijer, J.I. & Leffelaar, P.A. 1996. Adapted Fick's law applied to soil respiration. *Water Resources Research* 32: 791-800.

Fukuda, H. 1955. Air and vapor movement in soil due to wind gustiness. *Soil Science* 79: 249-256.

Geisler, G. 1963. Morphogenetic influence of (CO_2 + HCO_3^-) on roots. *Plant Physiology* 38: 77-80.

Geisler, G. 1967. Interactive effects of CO_2 and O_2 in soil on root and top growth of barley and peas. *Plant Physiology* 42: 305-307.

Geisler, G. 1969. Die Wirkung der Kohlensäurekonzentration (CO_2 + HCO_3^-) im Bereich niedriger Sauerstoffkonzentrationen (O_2) in der Bodenluft auf das Spross- und Wurzelwachstum von Kulturpflanzen (The effect of carbonic acid (CO_2 + HCO_3^-) in the range of low oxygen concentrations (O_2) in soil air on shoot and root growth of cultivated plants. In German. Summary in English.). *Zeitschrift für Acker- und Pflanzenbau* 130: 1-15.

Gibbs, J., de Bruxelle, G., Armstrong, W. & Greenway, H. 1995. Evidence for anoxic zones in 2-3 mm tips of aerenchymatous maize roots under low O_2 supply. *Australian Journal of Plant Physiology* 22: 723-730.

Gibbs, J., Turner, D.W., Armstrong, W., Darwent, M.J. & Greenway, H. 1998. Response to oxygen deficiency in primary maize roots. I. Development of oxygen deficiency in the stele reduces radial solute transport to the xylem. *Australian Journal of Plant Physiology* 25: 745-758.

Glasbey, C.A., Horgan, G.W. & Darbyshire, J.F. 1991. Image analysis and three-dimensional modelling of pores in soil aggregates. *Journal of Soil Science* 42: 479-486.

Gliński, J. & Stępniewski, W. 1985. *Soil Aeration and Its Role for Plants.* Boca Raton, Florida: CRC Press. 229 p.

Grable, A.R. & Danielson, R.E. 1965. Influence of CO_2 on growth of corn and soybean seedlings. *Soil Science Society of America Proceedings* 29: 233-238.

Grable, A.R. & Siemer, E.G. 1968. Effects of bulk density, aggregate size and soil-water suction on oxygen diffusion, redox potentials and on elongation of corn roots. *Soil Science Society of America Journal* 32: 180-186.

Granli, T. & Bøckman, O.C. 1994. Nitrous oxide from agriculture. *Norwegian Journal of Agricultural Sciences* (Supplement 12): 1-128.

Greenwood, D.J. 1961. The effect of oxygen concentration on the decomposition of organic materials in soil. *Plant and Soil* 14: 360-376.

Griffin, D.M. 1968. A theoretical study relating the concentration and diffusion of oxygen to the biology of organisms in soil. *New Phytologist* 67: 561-577.

He, C.-J., Finlayson, S.A., Drew, M.C., Jordan, W.R. & Morgan, P.W. 1996. Ethylene biosynthesis during aerenchyma formation in roots of maize subjected to mechanical impedance and hypoxia. *Plant Physiology* 112: 1679-1685.

Henault, C., Devis, X., Page, S., Justes, E., Reau, R. & Germon, J.C. 1998. Nitrous oxide emissions under different soil and land management conditions. *Biology and Fertility of Soils*, 26: 199-207.

Hirschfelder, J.O., Curtiss, C.F. & Bird, R.B. 1964. *Molecular Theory of Gases and Liquids.* 2nd ed. New York, John Wiley & Sons. 1249 p.

Horgan, G.W. 1999. An investigation of the geometric influences on pore space diffusion. *Geoderma* 88: 55-71.

Horgan, G.W. & Ball, B.C. 1994. Simulating diffusion in a Boolean model of soil pores. *European Journal of Soil Science* 45: 483-491.

Hutchins, L.M. 1926. Studies on the oxygen-supplying power of the soil together with quantitative observations on the oxygen-supplying power requisite for seed germination. *Plant Physiology* 1: 95-150.

Håkansson, I. & Lipiec, J. 2000. A review of the usefulness of relative bulk density values in studies of soil structure and compaction. *Soil & Tillage Research* 53: 71-85.

Højberg, O., Revsbech N.P. & Tiedje J.M. 1994. Denitrification in soil aggregates analyzed with microsensors for nitrous oxide and oxygen. *Soil Science Society of America Journal* 58: 1691-1698.

Jaakkola, A. 1985. Denitrifikaatio viljapellosta ja nurmesta mitattuna asetyleeni-inhibitiomenetelmällä (Denitrification in cornfield and grass ley as determined by the acetylene inhibition method. In Finnish. Abstract in English.). In: *Lannoite- ja kasviainestypen hyväksikäyttö ja typen häviö. Biologisen typensidonnan ja ravinnetypen hyväksikäytön projekti. Julkaisu 13.* Helsinki: SITRA. p. 75-108.

Jaakkola, A. 1994. Soil air composition and nitrous oxide emission in freezing and thawing soils. *Transactions of 15th World Congress of Soil Science*, Acapulco, Mexico. 3b: 252-253.

Jaakkola, A., Auramo, J. & Simojoki, A. 1990. Effect of soil air composition on plant growth and nutrient uptake. *Transactions of 14th International Congress of Soil Science*, Kyoto, Japan. IV: 62-65.

Jackson, M.B. 1990. Hormone and developmental change in plants subjected to submergence or soil waterlogging. *Aquatic Botany* 38: 49-72.

Jackson, M.B. 1991. Ethylene in root growth and development. In: Mattoo, A. K. & Suttle, J. C. (eds.). *The Plant Hormone Ethylene.* Boca Raton, Florida: CRC Press. p. 159-181.

Jackson, M.B., Fenning, T.M., Drew, M.C. & Saker, L.R. 1985. Stimulation of ethylene production and gas-space (aerenchyma) formation in adventitious roots of *Zea mays* L. by small partial pressures of oxygen. *Planta* 165: 486-492.

Jaynes, D.B. & Rogowski, A.S. 1983. Applicability of Fick's law to diffusion. *Soil Science Society of America Journal* 47: 425-430.

Jensen, C.R., Luxmoore, R.J., Gundy, S.D. & Stolzy, L.H. 1969. Root air space measurements by a pycnometer method. *Agronomy Journal* 61: 474-475.

Jin, Y. & Jury, W.A. 1996. Characterizing the dependence of gas diffusion coefficient on soil properties. *Soil Science Society of America Journal* 60: 66-71.

Justin, S.H.F.W. & Armstrong, W. 1987. The anatomical characteristics of roots and plant response to soil flooding. *New Phytologist* 106: 465-495.

Kanwar, R.S. 1986. Analytical solutions of the transient state oxygen diffusion equation in soils with a production term. *Journal of Agronomy & Crop Science* 156: 101-109.

Kasimir-Klemedtsson, Å., Klemedtsson, L., Berglund, K., Martikainen, P., Silvola, J. & Oenema, O. 1997. Greenhouse gas emissions from farmed organic soils: a review. *Soil Use and Management* 13: 245-250.

Kawase, M. J. 1979. Role of cellulase in aerenchyma development in sunflower. *American Journal of Botany* 66: 183-190.

Kende, H. & Zeevaart, J.A.D. 1997. The five "classical" plant hormones. *Plant Cell* 9: 1197-1210.

Klute, A. 1986. Water retention: laboratory methods. In: Klute A. (ed.). *Methods of Soil Analysis. Part 1. Physical and Mineralogical Methods.* Agronomy 9. Madison, Wisconsin: ASA, SSSA. p. 635-662.

Kulmala, A. & Esala, M. 2000. Agriculture and greenhouse gas emissions. Literature review. *Publications of Agricultural Research Centre of Finland. Serie A 76.* Jokioinen: Agricultural Research Centre of Finland. 67 p.

Lambers, H. 1987. Growth, respiration, exudation and symbiotic associations: the fate of carbon translocated to the roots. In: Gregory, P. J., Lake, J. V. & Rose, D. A. (eds.). *Root Development and Function.* Cambridge: Cambridge University Press. p. 125-145.

Lambers, H. & Rychter, A.M. 1989. The biochemical background of variation in respiration rate: respiratory pathways and chemical composition. In: Lambers, H. (ed.). *Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants.* The Hague: SPB Academic Publishing. p. 199-225.

Lambers, H., van der Werf, A. & Konings, H. 1991. Respiratory patterns in roots in relation to their functioning. In: Waisel, Y., Eshel, A. & Kafkafi, U. (ed.). *Plant Roots. The Hidden Half.* New York: Marcel Dekker. p. 229-263.

Leffelaar, P. A. 1987. Dynamic simulation of multinary diffusion problems related to soil. *Soil Science* 143: 79-91.

Lemon, E. R. 1962. Soil aeration and plant root relations. I. Theory. *Agronomy Journal* 54: 167-170.

Lessard, R., Rochette, P., Topp, E., Pattey, E., Desjardins, R.L. & Beaumont G. 1994. Methane and carbon dioxide fluxes from poorly drained adjacent cultivated and forest sites. *Canadian Journal of Soil Science* 74: 139-146.

Letey, J. 1985. Relationships between soil physical properties and crop production. In: Stewart, B. A. (ed.). *Advances in Soil Science* 1: 277-294.

Linn, D.M. & Doran, J.W. 1984. Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and nontilled soils. *Soil Science Society of America Journal* 48: 1267-1272.

Lipiec, J. & Håkanson, I. 2000. Influences of degree of compactness and matric water tension on some important plant growth factors. *Soil & Tillage Research* 53: 87-94.

Longmuir, I. S. 1954. Respiration rate of bacteria as a function of oxygen concentration. *Biochemical Journal* 57: 81-87.

Lundegårdh, H. 1927. Carbon dioxide evolution of soil and crop growth. *Soil Science* 23: 417-453.

Luxmoore, R.J., Stolzy, L.H. & Letey, J. 1970a. Oxygen diffusion in the soil-plant system. I. A model. *Agronomy Journal* 62: 322-324.

Luxmoore, R.J., Stolzy, L.H. & Letey, J. 1970b. Oxygen diffusion in the soil-plant system. II. Respiration rate, permeability and porosity of consecutive excised segments of maize and rice roots. *Agronomy Journal* 62: 322-324.

Lynch, J. & Brown, K.M. 1997. Ethylene and plant responses to nutritional stress. *Physiologia Plantarum* 100: 613-619.

Machlis, L. 1944. The respiratory gradient in barley roots. *American Journal of Botany* 31: 281-282.

Mahmood, T., Ali, R., Malik, K.A. & Shamsi, S.R.A. 1997. Denitrification with and without maize plants (*Zea mays* L.) under irrigated field conditions. *Biology and Fertility of Soils*, 24: 323-328.

Marrero, T.R. & Mason, E.A. 1972. Gaseous diffusion coefficients. *Journal of Physical and Chemical Reference Data* 1: 3-118.

McAfee Graham, M. 1989. *The effects of agricultural practices on soil aeration*. Department of Soil Science. Reports and Dissertations 1. Uppsala: Swedish University of Agricultural Sciences. 59 p.

McKenney, D.J., Drury, C.F. & Wang, S.W. 1997. Reaction of nitric oxide with acetylene and oxygen: implications for denitrification assays. *Soil Science Society of America Journal* 61: 1370-1375.

Millar, A.H., Bergersen, F.J. & Day, D.A. 1994. Oxygen affinity of terminal oxidases in soybean mitochondria. *Plant Physiology and Biochemistry* 32: 847-852.

Millington, R.J. & Quirk, J.P. 1960. Transport in porous media. *Transactions of 7th International Congress of Soil Science*, Madison, Wisconsin. I: 97-106.

Moldrup, P., Kruse, C.W., Rolston, D.E. & Yamaguchi, T. 1996. Modeling diffusion and reaction in soils: III. Predicting gas diffusivity from the Campbell soil-water retention model. *Soil Science* 161: 366-375.

Moldrup, P., Olesen, T., Rolston, D.E. & Yamaguchi, T. 1997. Modeling diffusion and reaction in soils: VII. Predicting gas and ion diffusivity in undisturbed and sieved soils. *Soil Science* 162: 632-640.

Moldrup, P., Olesen, T., Schjønning, P., Yamaguchi, T. & Rolston, D.E. 2000. Predicting gas diffusion coefficient in undisturbed soil from soil water characteristics. *Soil Science Society of America Journal* 64: 94-100.

Moldrup, P., Olesen, T., Yamaguchi, T., Schjønning, P. & Rolston, D.E. 1999. Modeling diffusion and reaction in soils: IX.The Buckingham-Burdine-Campbell equation for gas diffusivity in undisturbed soil. *Soil Science* 164: 542-551.

Monk, L.S., Braendle, R. & Crawford, R.M.M. 1987a. Catalase activity and post-anoxic injury in monocotyledonous species. *Journal of Experimental Botany* 38: 233-246.

Monk, L.S., Fagerstedt, K.V. & Crawford, R.M.M. 1987b. Superoxide dismutase as an anaerobic polypeptide. A key factor in recovery from oxygen deprivation in *Iris pseudacorus*? *Plant Physiology* 85: 1016-1020.

Monk, L.S., Fagerstedt, K.V. & Crawford, R.M.M. 1989. Oxygen toxicity and superoxide dismutase as an antioxidant in physiological stress. *Physiologia Plantarum* 76: 456-459.

Morgan, P.W. 1990. Effects of abiotic stresses on plant hormone systems. In: Alscher, R.G. & Cumming, J.R (eds.). *Stress Responses in Plants: Adaptation and Acclimation Mechanisms.* New York: Wiley-Liss. p. 113-146.

Morgan, P.W. & Drew, M.C. 1997. Ethylene and plant responses to stress. *Physiologia Plantarum* 100: 620-630.

Mosier, A.R. 1998. Soil processes and global change. *Biology and Fertility of Soils* 27: 221-229.

Nyborg, M., Laidlaw, J.W., Solberg, E.D. & Malhi, S.S. 1997. Denitrification and nitrous oxide emissions from a Black Chernozemic soil during spring thaw in Alberta. *Canadian Journal of Soil Science* 77: 153-160.

Ouyang, Y. & Boersma, L. 1992. Dynamic oxygen and carbon dioxide exchange between soil and atmosphere: I. Model development. *Soil Science Society of America Journal* 56: 1695-1702.

Parkin, T.B. 1987. Soil microsites as a source of denitrification variability. *Soil Science Society of America Journal* 51: 1194-1199.

Parkinson, K.J. 1981. An improved method for measuring soil respiration in the field. *Journal of Applied Ecology* 18: 221-228.

Penman, H.L. 1940a. Gas and vapour movements in the soil. I. The diffusion of vapours through porous solids. *Journal of Agricultural Science, London* 30: 437-462.

Penman, H.L. 1940b. Gas and vapour movements in the soil. II. The diffusion of carbon dioxide through porous solids. *Journal of Agricultural Science, London* 30: 570-581.

Penman, H.L. 1956. Evaporation: an introductory survey. *Netherlands Journal of Agricultural Science* 4: 9-29.

Penning de Vries, F.W.T. 1975. The cost of maintenance processes in plant cells. *Annals of Botany* 39: 77-92.

Penning de Vries, F.W.T., Brunsting, A.H.M. & van Laar, H.H. 1974. Products, requirements and efficiency of biosynthesis: a quantitative approach. *Journal of Theoretical Biology* 45: 339-377.

Pietola, L. 1995. Effect of soil compactness on the growth and quality of carrot. *Agricultural Science in Finland* 4: 139-237.

Ponnamperuma, F.N. 1972. The chemistry of submerged soils. *Advances in Agronomy* 24: 29-96.

Pritchard, D.T. & Currie, J.A. 1982. Diffusion coefficients of carbon dioxide, nitrous oxide, ethylene and ethane in air and their measurement. *Journal of Soil Science* 33: 175-184.

Radford, P.J. & Greenwood, D.J. 1970. The simulation of gaseous diffusion in soils. *Journal of Soil Science* 21: 304-313.

Rasmuson, A., Gimmi, T. & Flühler, H. 1990. Modeling reactive gas uptake, transport, and transformation in aggregated soils. *Soil Science Society of America Journal* 54: 1206-1213.

Ratcliffe, R. G. 1997. In vivo NMR studies of the metabolic response of plant tissue to anoxia. *Annals of Botany* 79 (Supplement A): 39-48.

Richter, J. 1974. Untersuchungen zum Bodenlufthaushalt in einem Bodenbearbeitungsversuch (A comparative study of soil gas regimes in a soil tillage experiment with different soils: I. Field measurements. In German. Summary and captions in English.). *Zeitschrift für Planzenernährung und Bodenkunde* 137: 135-147.

Roberts, J.K., Callis, J., Jardetsky, O., Walbot, V. & Freeling, M. 1984. Cytoplasmic acidosis as a determinant of flooding intolerance in plants. *Proceedings of the National Academy of Sciences of the United States of America* 81: 6029-6033.

Rochette, P., Desjardins, R.L., Gregorich, E.G., Pattey, E. & Lessard, R. 1992. Soil respiration of barley (*Hordeum vulgare* L.) and fallow fields. *Canadian Journal of Soil Science* 72: 591-603.

Romell, L.-G. 1922. Luftväxling i marken som ekologisk factor. Die Bodenventilation als ökologischer Faktor (In Swedish and German). *Meddelande från Statens Skogsförsöksanstalt* 19: 125-359.

Russell, E.J. & Appleyard, A. 1915. The atmosphere of the soil. *Journal of Agricultural Science* 7: 1-48.

Sachs, M.M., Freeling, M. & Okimoto, R. 1980. The anaerobic proteins of maize. *Cell* 20: 761-767.

Sachs, M.M., Subbaiah, C.C. & Saab, I.N. 1996. Anaerobic gene expression and flooding tolerance in maize. *Journal of Experimental Botany* 47: 1-15.

Saglio, P.H., Drew, M.C. & Pradet, A. 1988. Metabolic acclimation to anoxia induced by low (2-4 kPa partial pressure) oxygen pretreatment (hypoxia) in root tips of *Zea mays*. *Plant Physiology* 86: 61-66.

Saglio, P.H., Rancillac, M., Bruzan, F. & Pradet, A. 1984. Critical oxygen pressure for growth and respiration of excised and intact roots. *Plant Physiology* 76: 151-154.

Saglio, P.H., Raymond, P. & Pradet, A. 1983. Oxygen transport and root respiration of maize seedlings. A quantitative approach using the correlation between ATP/ADP and the respiration rate controlled by oxygen tension. *Plant Physiology* 72: 1035-1039.

Sallam, A., Jury, W.A. & Letey, J. 1984. Measurement of gas diffusion coefficient under relatively low air-filled porosity. *Soil Science Society of America Journal* 48: 3-6.

Sarquis, J.I., Jordan, W.R. & Morgan, P.W. 1991. Ethylene evolution from maize (*Zea mays* L.) seedling roots and shoots in response to mechanical impedance. *Plant Physiology* 96: 1171-1177.

Sauerbeck, D. & Johnen, B. 1976. Der Umsatz von Pflanzenwurzeln im Laufe der Vegetationsperiode und dessen Beitrag zur "Bodenatmung" (The turnover of plant roots during the growth period and its influence on “soil respiration”. In German. Summary and captions in English.). *Zeitschrift für Pflanzenernährung und Bodenkunde* 3: 315-328.

Saukko, P. 1950/51. Om översvämningsskador å kulturväxter (Flood damge to crops. In Swedish.). *Grundförbättring* 4: 26-34.

Schumacher, T.E. & Smucker, A.J.M. 1984. Effect of localized anoxia on *Phaseolus vulgaris* L. root growth. *Journal of Experimental Botany* 35: 1039-1047.

Schumacher, T.E. & Smucker, A.J.M. 1987. Ion uptake and respiration of dry bean roots subjected to localized anoxia. *Plant and Soil* 99: 411-422.

Scotter, D.R., Thurtell, G.W. & Raats, P.A.C. 1967a. Note. Dispersion resulting from sinusoidal gas flow in porous materials. *Soil Science* 104: 306-308.

Scotter, D.R., Thurtell, G.W. & Tanner, C.B. 1967b. Measuring oxygen uptake by the roots of intact plants under controlled conditions. *Soil Science* 104: 374-378.

Shimamura, K. 1992. Gas diffusion through compacted sands. *Soil Science* 153: 274-279.

Sierra, J. & Renault, P. 1996. Respiratory activity and oxygen distribution in natural aggregates in relation to anaerobiosis. *Soil Science Society of America Journal* 60: 1428-1438.

Sierra, J., Renault, P. & Valles, V. 1995. Anaerobiosis in saturated soil aggregates: modelling and experiment. *European Journal of Soil Science* 46: 519-531.

Smith, K.A. 1980. A model of the extent of anaerobic zones in aggregated soils, and its potential application to estimates of denitrification. *Journal of Soil Science* 31: 263-277.

Smith, K.A. 1997. The potential for feedback effects induced by global warming on emissions of nitrous oxide by soils. *Global Change Biology* 3: 327-338.

Smith, K.A. & Arah, J.R.M. 1991. Gas chromatographic analysis of the soil atmosphere. In: Smith, K. A. (ed.). *Soil Analysis. Modern Instrumental Techniques.* 2nd ed. New York: Marcel Dekker. p. 505-546.

Smith, K. & Dowdell, R.J. 1974. Field studies of the soil atmosphere. I. Relationships between ethylene, oxygen, soil moisture content and temperature. *Journal of Soil Science* 25: 217-230.

Smith, K.A. & Robertson, P.D. 1971. Effect of ethylene on root extension of cereals. *Nature* 234: 148-149.

Smith, K.A., Thomson, P.E., Clayton, H., McTaggart, I.P. & Conen, F. 1998. Effects of temperature, water content and nitrogen fertilisation on emissions of nitrous oxide by soils. *Atmospheric Environment* 32: 3301-3309.

Smith, M.S. & Tiedje, J.M. 1979. The effect of roots on soil denitrification. *Soil Science Society of America Journal* 43: 951-955.

Smucker, A.J.M., McBurney, S.L. & Srivastava, A.K. 1982. Quantitative separation of roots from compacted soil profiles by the hydropneumatic elutration system. *Agronomy Journal* 74: 500-503.

Soane, B.D. & van Ouwerkerk, C. (eds.). 1994. *Soil Compaction in Crop Production.* Developments in Agricultural Engineering 11. Amsterdam: Elsevier. 662 p.

Steele, D.D. & Nieber, J. L. 1994. Network modeling of diffusion coefficients for porous media: I. Theory and model development. *Soil Science Society of America Journal* 58: 1337-1345.

Stępniewski, W. 1981. Oxygen diffusion and strength as related to soil compaction. IV. Choice of optimum parameters. *Polish Journal of Soil Science* 14: 89-95.

Stępniewski, W., Gliński, J. & Ball, B.C. 1994. Effects of compaction on soil aeration properties. In: Soane, B.D. & van Ouwerkerk, C. (eds.). *Soil Compaction in Crop Production.* Developments in Agricultural Engineering 11. Amsterdam: Elsevier. p. 167-189.

Stępniewski, W. & Łabuda, S. 1989. The influence of 10 days' flooding in seven development stages of spring barley on its growth, yield, and N, P, K content and uptake. Part I. Growth and yield. *Polish Journal of Soil Science* 22: 93-99.

Stolwijk, J.A.J. & Thimann, K.V. 1947. On the uptake of carbon dioxide and bicarbonate by roots, and its influence on growth. *Plant Physiology* 35: 513-520.

Subbaiah, C.C., Zhang, J.K. & Sachs, M.M. 1994. Involvement of intracellular calcium in anaerobic gene expression and survival of maize seedlings. *Plant Physiology* 105: 369-376.

Tackett, J.L. & Pearson, R.W. 1964. Effect of carbon dioxide on cotton seedling root penetration of compacted soil cores. *Soil Science Society of America Proceedings* 28: 741-743.

Tardieu, F. 1994. Growth and functioning of roots and root systems subjected to soil compaction. Toward a system with multiple signalling? *Soil & Tillage Research* 30: 217-243.

Thomson, C.J., Armstrong, W., Waters, I. & Greenway, H. 1990. Aerenchyma formation and associated oxygen movement in seminal and nodal roots of wheat. *Plant, Cell and Environment* 13: 395-403.

Thomson, C.J. & Greenway, H. 1991. Metabolic evidence for stelar anoxia in maize roots exposed to low O_2 concentrations. *Plant Physiology* 96: 1294-1301.

Tiedje, J. M. 1988. Ecology of denitrification and dissimilatory nitrate reduction to ammonium. In: Zehnder, A. J. B. (ed.). *Biology of Anaerobic Microorganisms.* New York: John Wiley & Sons. p. 179-244.

Topp, G.C., Davies, J.L. & Annan, A.P. 1980. Electromagnetic determination of soil water content: Measurements in coaxial transmission lines. *Water Resources Research* 16: 574-582.

Troeh, F.R., Jabro, J.D. & Kirkham, D. 1982. Gaseous diffusion equations for porous materials. *Geoderma* 27: 239-253.

Trought, M.C.T. & Drew, M.C. 1981. Alleviation of injury to young wheat plants in anaerobic solution cultures in relation to the supply of nitrate and other inorganic nutrients. *Journal of Experimental Botany* 32: 509-522.

Vakkilainen, P. 1982. *Maa-alueelta tapahtuvan haihdunnan arvioinnista* (*On the estimation of evapotranspiration.* In Finnish. Summary and captions in English). Acta Universitatis Ouluensis. Series C Technica No. 20. Artes Constructionum No. 6. 146 p.

van Bavel, C.H.M. 1951. A soil aeration theory based on diffusion. *Soil Science* 72: 33-46.

van der Werf, A., Hirose, T. & Lambers, H. 1989. Variation in root respiration; causes and consequences for growth. In: Lambers, H. (ed.). *Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants.* The Hague: SPB Academic Publishing. p. 227-240.

van der Werf, A., Kooijman, A., Welschen, R. & Lambers, H. 1988. Respiratory energy costs for the maintenance of biomass, for growth and for ion uptake in root of *Carex diandra* and *Carex acutiformis*. *Physiologia Plantarum* 72: 483-491.

van Noordwijk, M. & de Willigen, P. 1987. Agricultural concepts of roots: from morphogenetic to functional equilibrium between root and shoot growth. *Netherlands Journal of Agricultural Science* 35: 487-496.

van Noordwijk, M., Brouwer, G. & Harmanny, K. 1993. Concepts and methods for studying interactions of roots and soil structure. *Geoderma* 56: 351-375.

van't Woudt, B.D. & Hagan, R.M. 1957. Crop responses at excessively high soil moisture levels. In: Luthin, J.N. (ed.). *Drainage of Agricultural Lands.* Agronomy 7. Madison, Wisconsin: ASA. p. 514-578.

Vanlerberghe, G.C. & McIntosh, L. 1997. Alternative oxidase: from gene to function. *Annual Reviews in Plant Physiology and Plant Molecular Biology* 48: 703-734.

VanToai, T. & Bolles, C. 1991. Postanoxic injury in soybean (*Glycine max*) seedlings. *Plant Physiology* 97: 588-592.

Vartapetian, B.B. & Jackson, M.B. 1997. Plant adaptations to anaerobic stress. *Annals of Botany* 79 (Supplement A): 3-20.

Venäläinen, A. & Nordlund, A. 1988. Kasvukauden ilmastotiedotteen sisältö ja käyttö (Contents and use of the climatological report of a growing season. In Finnish.). *Finnish Meteorological Institute. Reports* N:o 1988:6. Helsinki: Finnish Meteorological Institute. 63 p.

Visser, E.J.W., Nabben, R.H.M., Blom, C.W.P.M. & Voesenek, L.A.C.J. 1997. Elongation by primary lateral roots and adventitious roots during conditions of hypoxia and high ethylene concentrations. *Plant, Cell and Environment* 20: 647-653.

Wang, S.Y., Wang, C.Y. & Wellburn, A.R. 1990. Role of ethylene under stress conditions. In: Alscher, R.G. & Cumming, J.R. (eds.). *Stress Responses in Plants: Adaptation and Acclimation Mechanisms.* New York: Wiley-Liss. p. 143-173.

Wanner, H. 1945. Sauerstoffdiffusion als begrenzender Faktor der Atmung von Pflanzenwurzeln. *Vierteljahrschrift der Naturforschende Gesellschaft in Zürich* 90: 98-119.

Wesseling, J. & van Wijk, W.R. 1957. Soil physical conditions in relation to drain depth. In: Luthin, J.N. (ed.). *Drainage of Agricultural Lands.* Agronomy 7. Madison, Wisconsin: ASA. p. 461-504.

Whipps, J. M. 1990. Carbon economy. In: Lynch, J.M. (ed.). *The Rhizosphere.* New York: John Wiley & Sons. p. 59-97.

Woldendorp, J.W. 1962. The quantitative influence of the rhizosphere on denitrification. *Plant and Soil* 17: 267-270.

Wood, J.T. & Greenwood, D.J. 1971. Distribution of carbon dioxide and oxygen in the gas phase of aerobic soils. *Journal of Soil Science* 22: 281-288.

Yu, P.T., Stolzy, L.H. & Letey, J. 1969. Survival of plants under prolonged flooded conditions. *Agronomy Journal* 61: 844-847.

Zausig, J., Stępniewski, W. & Horn, R. 1993. Oxygen concentration and redox potential gradients in unsaturated model soil aggregates. *Soil Science Society of America Journal* 57: 908-916.

Zechmeister-Boltenstern, S. & Nikodim, L. 1999. Effect of water tension on ethylene production and consumption in montane and lowland soils in Austria. *European Journal of Soil Science* 50: 425-432.

Zechmeister-Boltenstern, S. & Smith, K.A. 1998. Ethylene production and decomposition in soils. *Biology and Fertility of Soils* 26: 354-361.