Compaction in forest-harvesting operations can cause significant decreases in seedling survival and growth. In extreme cases soil strength may be a limiting factor. In less severe cases soil aeration may be limiting. Detrimental effects of compaction on microbially mediated soil processes of N mineralization and denitrification were hypothesized as one possible mechanism that may reduce survival and growth. Decreased soil oxygen diffusion is one possible mechanism that may limit aerobic microbial processes in compacted soils.

Two sites were studied, a low coastal terrace in southwest Washington (Palix site) and rolling foothills on the east-side of the coastal range in Oregon (Vaughn site). Treatments consisted of four degrees of disturbance, ranging from logged only to primary skid trails. The buried-bag technique was used to assess N mineralization over 30-day periods in the field. The acetylene inhibition method was used for denitrification measurements, incubated \textit{in situ} for one day. Respiration rates were also measured on these samples. Denitrification potentials were measured in the
laboratory. A companion laboratory study used the same soils adjusted to three levels of bulk density and three levels of water content and measured soil respiration and oxygen diffusion rates. Air-filled porosity \((f_a)\) was calculated. Respiration was measured to assess differences in overall microbial activity.

Nitrogen mineralization was 74 and 179 kg-N ha\(^{-1}\) yr\(^{-1}\), nitrification was 48 and 99 kg-N ha\(^{-1}\) yr\(^{-1}\), and denitrification was 0.42 and 3.7 kg-N ha\(^{-1}\) yr\(^{-1}\) for the Vaughn and Palix sites, respectively. No statistically significant differences between treatments were found in N mineralization, nitrification, or respiration. However, potential denitrification increased with increasing severity of compaction, indicating that this microbial population was affected by compaction. Decreases in nitrogen availability from decreases in microbial mineralization or increased denitrification were not significant.

The following physical relationships best fit the gas diffusion data: \(D/D_0 = .86f_a^2\) (Palix) and \(D/D_0 = 1.37f_a^2\) (Vaughn). Respiration rates were linearly correlated to both diffusion coefficients and air-filled porosity. Respiration was found to be more highly correlated with air-filled porosity. An aeration effect on soil respiration was observed as compaction severity increased. Respiration decreased two-fold at Palix and four-fold at Vaughn.
EFFECTS OF FOREST SOIL COMPACtion ON GAS DIFFUSION, DENITRIFICATION, NITROGEN MINERALIZATION, AND SOIL RESPIRATION

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A THESIS submitted to Oregon State University

in partial fulfillment of the requirements for the degree of

Master of Science

Completed September 4, 1992
Commencement June 1993
APPROVED:

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Date thesis is presented September 4, 1992

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# TABLE OF CONTENTS

## INTRODUCTION

- Effects of soil compaction on tree growth 1
- Effects of soil compaction on physical properties 2
- Effects of soil compaction on biological activity 5
  - Microbial activity 5
  - Root growth 8

## PART 1. THE EFFECT OF FOREST-SOIL COMPACTION ON NET N MINERALIZATION, DENITRIFICATION, AND MICROBIAL RESPIRATION 10

## INTRODUCTION 10

## MATERIALS AND METHODS 12

- Site characteristics 12
- Experimental design 12
- Sampling scheme 13
- Measurement methods 13
- Statistics 14

## RESULTS AND DISCUSSION 16

## REFERENCES 32
TABLE OF CONTENTS (CONT'D.)

PART 2. EFFECT OF OXYGEN DIFFUSION ON SOIL RESPIRATION 35

INTRODUCTION 35

MATERIALS AND METHODS 39
- Soil used 39
- Experimental set-up 39
- Diffusion measurement 39
- Respiration measurements 41
- Statistics 42

RESULTS AND DISCUSSION 43

REFERENCES 52

BIBLIOGRAPHY 55
# LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Soil respiration rates for Palix site (a) and for Vaughn site (b)</td>
<td>27</td>
</tr>
<tr>
<td>2.</td>
<td>Net N mineralization rates for the Palix site (a) and for the Vaughn site (b)</td>
<td>28</td>
</tr>
<tr>
<td>3.</td>
<td>Net nitrification rates for the Palix site (a) and the Vaughn site (b)</td>
<td>29</td>
</tr>
<tr>
<td>4.</td>
<td>Denitrification rates for the Palix site (a) and the Vaughn site (b)</td>
<td>30</td>
</tr>
<tr>
<td>5.</td>
<td>Denitrification potential rates for the Palix site (a) and the Vaughn site (b)</td>
<td>31</td>
</tr>
<tr>
<td>6.</td>
<td>Gas diffusion chamber</td>
<td>48</td>
</tr>
<tr>
<td>7.</td>
<td>Air-filled pore space vs. diffusion coefficient for Palix and Vaughn</td>
<td>49</td>
</tr>
<tr>
<td>8.</td>
<td>Air-filled pore space vs. soil respiration for Palix and Vaughn</td>
<td>50</td>
</tr>
<tr>
<td>9.</td>
<td>Diffusion coefficient vs. soil respiration for Palix and Vaughn</td>
<td>51</td>
</tr>
</tbody>
</table>
# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Textural, organic carbon, total nitrogen, and bulk density data for soils at the Vaughn and Palix sites</td>
<td>22</td>
</tr>
<tr>
<td>2. A comparison of the Shapiro-Wilk statistic for the raw data and logarithmically transformed data</td>
<td>23</td>
</tr>
<tr>
<td>3. Average coefficients of variation for soil respiration, net N mineralization, nitrification, denitrification, and denitrification potential</td>
<td>24</td>
</tr>
<tr>
<td>4. Average soil moisture content and soil temperature by sampling period</td>
<td>25</td>
</tr>
<tr>
<td>5. Average rates of field measurements by treatments</td>
<td>26</td>
</tr>
<tr>
<td>6. Summary of treatments</td>
<td>46</td>
</tr>
<tr>
<td>7. Summary of various equations cited in the literature</td>
<td>47</td>
</tr>
</tbody>
</table>
INTRODUCTION

Management of a forest ecosystem must account for its dynamic nature and allow for a wide range of variables and, because a forest ecosystem is a comparatively long-term production cycle, effects of management practices are not always immediately discernable.

Soil compaction is one common disturbance with distinct effects on site productivity. It is a complex phenomenon. In extreme cases strictly physical effects of compaction may explain decreases in productivity. More commonly, a site is shifted from its current equilibrium point and reductions in growth may or may not occur depending on the capability of a site to rebound or establish a new equilibrium point (Childs et al. 1989). The mechanisms through which changes occur are not clearly understood. This introduction is a brief review of the effects of compaction on tree growth, soil physical properties, soil microbiological activity, and root growth.

Effects of soil compaction on tree growth

Many studies have found detrimental effects of compaction on seedling survival, tree height, and volume. This work has been reviewed recently (Lousier and Smith 1988, Froehlich and McNabb...
1984, Greacen and Sands 1980). Decreases in height and volume growth have been described after 32 years (Wert and Thomas 1981), others have documented effects up to 40 years later (Froehlich and McNabb 1984).

With data from various sources Froehlich and McNabb (1984) found a positive curvilinear relationship with percent decrease in height growth and percent increase in bulk density. A significant (p = 0.07) negative relationship was found for total growth of ponderosa pine (Pinus ponderosa) and percent increase of bulk density on skid trails when compared to adjacent undisturbed soil. No significant relationship was found for lodgepole pine (Pinus contorta), however (Froehlich et al. 1986). Although direct comparison of the lodgepole and ponderosa pine sites is not reasonable, this contrast does further highlight the complexity of the forest ecosystem and the site dependent nature of compaction effects.

Effects of soil compaction on physical properties

Compaction directly affects several physical soil properties. Bulk density increases because of a decrease in macroporosity. Compaction also results in the conversion of macropores to micropores, which alters aeration, infiltration, and hydraulic conductivity (Greacen and Sands 1980). Soil strength also increases. Although these changes in soil physical properties have direct and indirect impacts on seedling survival and growth, the mechanisms are not well understood.

It has been shown that growth-limiting bulk densities occur and vary with soil texture. Daddow and Warrington (1983) developed
an empirical relationship that correlated growth-limiting bulk densities with average pore radii. By determining percent sand, silt, and clay, and calculating average pore radii, a limiting bulk density could be found. High silt or clay soil had growth-limiting bulk densities ranging from 1.45-1.40 Mg m\(^{-3}\), whereas values for sandy soils were as high as 1.65-1.75 Mg m\(^{-3}\) (Daddow and Warrington 1983). Bulk densities of this magnitude may reflect a limiting soil strength that cannot be penetrated by roots. Before soil reaches this point of severe compaction, seedlings already show significant growth reduction. Thus, other factors likely play a significant role in reducing tree growth (Froehlich and McNabb 1984).

Taylor (1949) found that gas diffusion rates decreased with increasing bulk density and water content. When relative diffusivity (the diffusion rate in a given medium relative to the diffusion rate in air) was plotted against air-filled porosity, a positive, linear relationship was observed. Others (Grable and Siemer 1968, Lai et al. 1976) have found that curvilinear representations better describe this relationship. Upon further investigation, Currie (1983) found that this relationship consisted of two parts. At lower air-filled porosities, the relationship was curvilinear and represented diffusion through aggregates, whereas at higher air-filled porosities, diffusion occurred through macropores between aggregates and was more linear in nature. One soil even exhibited a three-step relationship. Currie and Rose (1985) have shown that a three-step relationship can be produced with stone chip packings. The third step is related to the diffusion occurring within the stone chips, which is analogous to diffusion within the micro-pedal
structure in soil crumbs. Currie (1984) found that compaction affected gas diffusion as a function of air-filled porosity. The effect was different than when moisture content alone was varied and was suggested to be the result of two factors. First, compaction changed crumb structure so that, as the soil was dried, the observed increase in diffusion was not as great as that for noncompacted soil. Thus the first pores to empty were no longer as efficient at transporting gases due to distortion from the compaction. Second, an increase in the bulk density reflected increased amounts of crumbs. Therefore, intra-crumb pore space increased; resulting in lower diffusion rates. Simply wetting a sample did not reflect the permanent increase in intra-crumb diffusion, although some changes were noted with wetting and drying.

When samples are compared at the same water potential, compacted soils will have higher volumetric water content (Grable and Siemer 1968, Reicosky et al. 1981) and lower diffusion rates (Currie 1984, Pritchard 1985). The greatest changes in diffusion rates per unit change in water content were seen at the point when inter-aggregate pore space was drained and water was held only within the intra-aggregate space, i.e., about field capacity. These results illustrate the dependency of soil aeration on both total porosity and pore size distribution, with gas diffusion effectively halted when total air-filled porosity drops below about 10% in soils (Cannell 1977).
Effects of soil compaction on biological activity

**Microbial activity**

It should be noted that very few studies have directly examined the effect of soil compaction on microbial activity. However, the most likely effect of soil compaction on microbial activity is through its effect on gas transport in soils.

Fungal populations are sensitive to soil structure and thus affected by soil compaction. A study of compaction on forest soils found significant differences in fungal populations between control and compacted plots (Smeltzer *et al.* 1986). Total fungal populations were lower on the compacted plots. Interestingly, *Fusarium sp.*, which are often pathogenic to young plants, reacted in the opposite manner. These differences were significant for at least two years following compaction, but after five years differences could no longer be detected. This same study found no significant differences in total bacterial populations as a result of compaction at any time during the study period.

Skinner and Bowen (1974) found strong trends showing that compaction reduced mycorrhizal strand penetration by 73% in unsterilized forest soil. However, they found increased mycorrhizal penetration in the compacted soils that had been sterilized. This could suggest that microbial activity, together with poorer gas transport of the compacted soil, further decreased oxygen concentration, thereby reducing mycorrhizal growth.

Measurements of total microbial populations may be indicative of overall status of a system. However, activity measurements are a more direct measure of the impact of a given perturbation to the
system. For example, Dick et al. (1988) found that soil enzymes were more sensitive than total microbial biomass to soil compaction, although both measurements were significantly lower in compacted soil. Most other studies that are relevant to the effects of soil compaction have examined the effect of aeration on biological activity using two different measures of aeration: oxygen concentration of the gas phase or some measure of air-filled porosity.

Parr and Reuszer (1962) studied the effect of oxygen concentration on organic matter decomposition. They found that CO$_2$ evolution at 5% oxygen was about half that at atmospheric oxygen concentrations, however, decomposition at 0.5% oxygen was still almost three times the anaerobic rate. The work of Greenwood (1961) also illustrates the ability of aerobic heterotrophs to actively metabolize at low oxygen concentrations. He found that $K_m$ values for oxygen uptake (the oxygen concentration at which oxygen uptake is half the maximum rate) were approximately 4 mM, which corresponds to about 0.3% oxygen in the gas phase. Similarly, Greenwood (1962) found little change in nitrate and nitrite concentrations at oxygen concentrations as low as 2%, suggesting that autotrophic nitrifiers were not inhibited at this oxygen concentration.

Linn and Doran (1984) worked on tilled and nontilled soils with bulk densities of 1.4 and 1.14 Mg m$^{-3}$, respectively. They found that aerobic microbial activity increased until the water-filled pore space reached 60% (water volume/total pore volume), which corresponds to 25% air-filled porosity (air-filled pore volume/total...
soil volume). At this point of maximum aerobic activity, anaerobic processes were still negligible. Aerobic processes decreased and anaerobic processes increased at higher levels of water-filled pore space, indicating that oxygen diffusion was becoming limiting. Although the data of Linn and Doran suggested that 25% air-filled porosity was optimal for aerobic microbial activity in soils, other data suggest that this optimum value may be soil dependent. For example, Bridge and Rixon (1976) found maximum oxygen uptake rates varied between 15 to 30% air-filled porosity for soils of three different textures. Skopp et al. (1990) have shown that aerobic microbial activity peaks at a water content where the limiting effects of substrate diffusion (through water) and oxygen supply are offset.

Smith and Cook (1946) found significant differences in nitrate production between compacted (air-filled porosities of 7.1% and lower) and noncompacted treatments. Similar results were obtained by Whisler et al. (1965), who looked at aeration effects on microbial activity and found a highly significant correlation between air-filled porosity and nitrate production for two of the three soils. These were soils with low (6.7% and lower) air-filled porosity. Oxygen diffusion at this level of air-filled porosity probably represents a limiting value for nitrification in these soils.

Nitrogen fixation rates in soil have been shown to be affected by compaction. Landina and Klevenskaya (1985) observed lower rates in compacted soils (bulk densities of 1.3 to 1.4 Mg m\(^{-3}\), 7 to 16% air-filled porosities) than in noncompacted (1.1 to 1.2 Mg m\(^{-3}\), 10 to 19% air-filled porosities).
These data illustrate the effect of oxygen concentration or air-filled porosity on aerobic microbial activity. Generally, optimum aerobic activity occurs at about 25% air-filled porosity and aerobic activity becomes greatly depressed at less than 10% air-filled porosity. Alternatively, aerobic activity decreases at oxygen concentrations less than about 2-5%. However, neither oxygen concentration or air-filled porosity alone completely describes the supply of oxygen to microorganisms in soil. It seems reasonable that a measurement of oxygen diffusion would account for both concentration and porosity and may be a more valid measurement.

**Root growth**

Soil aeration effects on plant root growth were examined by Leyton and Rousseau (1958). They found that oxygen concentration less than 6-10% greatly reduced root growth expressed as a percentage of growth under normal aeration conditions. A compilation of data from 11 studies for various crop species showed critical oxygen concentrations for roots to be around 10-15% (Glinsky and Stepniewski 1985). Greenwood (1971), reviewing aeration and its effect on plant growth, noted that root elongation was decreased to 70% of maximum with oxygen concentrations of 6%, although some studies had shown little effect at oxygen concentrations as low as 2%. Asady and Smucker (1989) found that soil oxygen diffusion rates became limiting to root growth below compacted layer (BD of 1.7 Mg m$^{-3}$), partially due to root accumulation immediately above the compacted area.
Fewer studies on the effect of compaction on root growth have used porosity changes as an index. Foil and Ralston (1967) found inversely proportional linear relationships between bulk density and root length or root weights. They also presented data for non-capillary pore space (air-filled porosity at -6 kPa) that suggested that root growth was decreased approximately 50% when non-capillary pore space was less than about 10%.

Although both root growth and microbial activity exhibit a wide variation in responses, the data do seem to indicate a higher sensitivity to oxygen deficit for roots, perhaps because of the higher respiration rates of roots compared to that of microbial populations in bulk soil (Glinski and Stepniewki 1985). Aeration and gas diffusion affect both microbial activity and root activity, but there is also an interaction between the two. Conceivably, under given conditions of air-filled porosity, soil conditions could be aerobic or anaerobic depending on the activity of the roots and microbes.

My studies attempt to describe the interaction of compaction and microbial activity, more specifically, denitrification, nitrification, net N mineralization, and respiration. A companion study relates compaction, moisture content, and gas diffusion rate to microbial respiration.
PART 1. THE EFFECT OF FOREST-SOIL COMPACTION ON NET N MINERALIZATION, DENITRIFICATION, AND MICROBIAL RESPIRATION

INTRODUCTION

Compaction directly affects several physical soil properties. Bulk density increases because of a decrease in macroporosity. Compaction also results in the conversion of macropores to micropores, which alters aeration, infiltration, and hydraulic conductivity (Greaten and Sands 1980). Soil strength also increases. Growth-limiting bulk densities occur and vary with soil texture (Daddow and Warrington 1983). High silt or clay soils were found to have growth-limiting bulk densities ranging from 1.45 to 1.40 Mg m⁻³; values for sandy soils were as high as 1.65 to 1.75 Mg m⁻³. Bulk densities of this magnitude may reflect a limiting soil strength that cannot be penetrated by roots.

Before soil reaches severe compaction, seedlings already show a significant growth reduction. Other factors likely play a significant role in reducing tree growth (Froehlich and McNabb 1984). One possible mechanism through which these growth reductions occur would be a decrease in nutrient availability as the result of a decline in microbial activity. Smith and Cook (1946), working with a clay loam, found significant differences in nitrate production between compacted (1.43 Mg-N m⁻³) and noncompacted (1.0 Mg-N m⁻³) soils. Whisler et al. (1965) found a highly significant positive correlation between air-filled porosity and
Nitrate production. Nitrogen fixation rates in soil have been shown to be decreased by compaction (Landina and Klevenskaya 1985). Denitrification rates increased two to six times in compacted versus uncompacted agricultural loam soil (Bakken et al. 1987). Significant decreases in biomass C and various enzyme activities associated with nitrogen, phosphorus, and sulfur cycling were found at 10-20cm depths (Dick et al. 1988). The ameliorative treatments used (subsoiled, subsoiled and disked) successfully returned these values to uncompacted control levels.

This study measured microbial activity through respiration, net N mineralization, nitrification, and denitrification. Two forest soils with varying degrees of compaction were used. The purpose was to see if measurable differences of these biological processes could be found in the field.
MATERIALS AND METHODS

Site characteristics

Two experimental sites were chosen. One was on Weyerhaeuser Company property, adjacent to the mouth of the Palix River, on the southwestern coast of Washington state (lat. 46° N 04', long. 123° W 57'). The other was on International Paper Company property near Vaughn, Oregon (lat. 44° N 10', long. 123° W 05'). These will be referred to as the Palix and Vaughn sites.

The Palix site is on a low coastal terrace (25 m elevation) with an average annual rainfall of 2060 mm and an average annual temperature of 11°C. The soil series is Willapa silt loam, a medial, mesic, Andic Haplumbrept, (Fisher et al. 1984). It has notably low bulk density and high organic matter content (Table 1). The site was clearcut and planted with two-year-old Douglas-fir (Pseudotsuga menziesii Franco) seedlings in 1975.

The Vaughn site is on the eastern side of rolling foothills (230 m elevation) of the Coast Range. Average annual precipitation is 1300 mm, with an average annual temperature of 12°C. The soil series is a Bellpine silty clay loam, a Xeric Haplohumult (Table 1). This site was clearcut and planted with two year old Douglas-fir seedlings in 1982.

Experimental design

Four sampling periods were used, August 1985, November 1985, March 1986, and September 1986 representing summer, winter, spring, and fall. At the Palix site, four treatments were
replicated four times. The treatments were primary skidtrail, secondary skidtrail, rehabilitated skidtrail, and logged only. The difference between primary skidtrail and secondary skidtrail is the number of passes by heavy equipment. The number of passes has been shown to be correlated to percent increases in bulk density (Froehlich et al. 1980). At the Vaughn site, four treatments were replicated three times. The treatments were skidtrail, subsoiled skidtrail, subsoiled and disked skidtrail, and logged only.

Sampling scheme

Three subsamples were taken for denitrification, respiration, and net N mineralization measurements on each plot every sampling period. The plots (4 X 33m) were arranged in a block design on skidder trails (except for the logged-only treatments) and were established shortly after logging operations (Froehlich and Miles 1984). Actual sample points within the plots were determined randomly with grid coordinates supplied by a random-function computer program.

Measurement methods

Denitrification was measured by the acetylene block technique (Yoshinari et al. 1977, Robertson and Tiedje 1984). An impact coring device was used to extract soil cores encased in 2.5-cm diameter by 20-cm acrylic tubes. Cores were incubated for about 24 hours in the actual sample holes on site. Gas samples were placed in evacuated containers and later analyzed for N\textsubscript{2}O using a gas chromatograph equipped with an electron-capture detector.
dioxide accumulation was measured simultaneously for soil respiration measurements.

Net N mineralization measurements were made using the buried-bag technique (Matson and Vitousek 1981). Sampling depth was 20 cm. The bags were incubated on site for one month. Beginning and ending KCl extracts (10 g soil:100 ml 2M KCl) of the sampled soil were analyzed for NH$_4^+$ (salicyclate/nitroprusside) and NO$_3^-$ (cadmium reduction followed by diazotization) content by colorimetric methods using an autoanalyzer.

Denitrification potential of soil collected during the spring sampling period was measured in the laboratory by the anaerobic denitrification potential method (Smith and Tiedje 1979). A core was taken from each plot and split into two depths (1-10 cm, 10-20 cm). Corresponding depths within each treatment were then combined, mixed thoroughly, and two subsamples were taken. Gas samples were analyzed for N$_2$O accumulation over time using gas chromatography.

Organic carbon was determined by total combustion in a Leco carbon analyzer.

Bulk density measurements were taken from previous research done (Miller et al. 1988, Froehlich and Miles 1984) on these sites.

Statistics

Visual inspection of frequency distributions for each data set revealed a decided skewness with many small values and few larger values. Consequently the data was tested for normality using the Shapiro-Wilk Statistic, W. This statistic is the ratio of the best
linear unbiased estimator of the variance to the corrected sum of squares estimator of variance (Shapiro and Wilk 1965). In the case of a normal distribution this ratio would be one. As data strays from normality, the ratio decreases. Table 2 shows the comparison of W values calculated for each set of measurements made on both sites. On the basis of these calculations, all further statistical analysis was done using logarithmically transformed data.

The experimental design was a completely random design with a split-plot in time. Analysis of variance was done with the Statistical Analysis System (SAS 1985).
RESULTS AND DISCUSSION

There were no statistically significant differences between treatments, on either site, for any of the microbial activity measurements at $p \leq 0.1$ level of probability. Significant seasonal differences ($p \leq 0.01$) were only found for the net N mineralization rate on the Palix site and for the nitrification rate on the Vaughn site.

Table 3 lists average coefficients of variation (CV) for each of the soil microbial processes measured at each site. Reported CV, from Pacific Northwest sites, often exhibit fairly wide ranges. For example, soil respiration CV range from 7-60, for denitrification from 10-1,803, for denitrification potential from 10-100 (Myrold 1988, Myrold et al. 1989, Vermes and Myrold 1992). Unfortunately, this high variability and relatively low treatment replication (four replications at Palix, three replications at Vaughn) resulted in insensitivity for determining statistical differences. It should be noted that the Palix site has also shown no treatment effects on Douglas-fir seedling growth (Miller et al. 1988). Thus, on this site, treatment differences in microbial activities may not be pronounced.

Although this experiment was not designed to draw statistical comparisons between the two sites, we can see, qualitatively, that they are very different in soil characteristics (Table 1), climate, and vegetation. Thus one would expect the soil microbial processes to vary markedly between them. The Palix site had higher levels of microbial activity than the Vaughn site for all measurements taken. This would be expected given the higher
productivity and much higher soil organic matter content present at the Palix site.

Soil respiration rates were higher at Palix than at Vaughn (Fig. 1a and 1b). Since the Palix site has over three times more organic carbon and more than five times the amount of total nitrogen (Table 1), this difference between the respiration rates is expected. The annual estimates averaged over all treatments were 12.6 kg-C kg\(^{-1}\) yr\(^{-1}\) at Palix and 4.3 kg-C kg\(^{-1}\) yr\(^{-1}\) at Vaughn. Myrold et al. (1989) reported values of 5.5 and 6.9 kg-C kg\(^{-1}\) yr\(^{-1}\) on sites similar to the Vaughn site. On another site with high organic matter content, somewhat similar to the Palix site, they measured 17.8 kg-C kg\(^{-1}\) yr\(^{-1}\).

Although not statistically significant, the Palix logged only treatment (Fig 2a) consistently had the lowest N mineralization rates for this site, whereas, on average, the logged only treatment at Vaughn was at least 50% greater than the other treatments (Fig. 2b). The logged only treatment had the least amount of soil disturbance. It appears that in a soil of very low initial bulk density, such as the Palix site (0.64 Mg m\(^{-3}\), Miller et al. 1988), increased disturbance beyond simply logging stimulated N mineralization, possibly by mixing the soil and litter layers. In contrast, disturbance of the Vaughn soil, with its lower organic matter content (Table 1) and higher bulk density (1.30 Mg m\(^{-3}\), Froehlich unpublished data), may have depressed N mineralization.

Significant seasonal differences (p < .01) were found for net N mineralization rates at the Palix site. During the winter sampling period net N mineralization dropped to almost zero. Our lowest soil
temperature (Table 4) was recorded during this period and probably contributed to this low rate. At the Vaughn site, the highest net N mineralization value (averaged across treatments) was found during the winter period; the lowest during the summer period. These differences were not statistically significant, however they may reflect the low soil water content in the summer (Table 4).

Annual net N mineralization rates were 74 and 179 kg-N ha\(^{-1}\) yr\(^{-1}\) for Vaughn and Palix. These values were calculated by adjusting the measured values to represent a 30-day incubation, averaging the four seasonal values and then extrapolating to a full year. Net N mineralization rates ranging from 26-94 kg-N ha\(^{-1}\) yr\(^{-1}\) have been reported for north central forests (Lennon et al. 1985). Powers (1990) reported 58.5 kg-N ha\(^{-1}\) yr\(^{-1}\) for mixed coniferous forest in northern California, which agrees well with the Vaughn site. The Palix site had greater N mineralization than what is generally reported for coniferous sites. This is probably because of its favorable moisture and temperature regime (it is located on a low coastal terrace) and its relatively high N content (Table 1).

Figures 3a and 3b show the nitrification rates for the Palix and Vaughn sites. At the Vaughn site, significant seasonal differences (p ≤ .01) were found for nitrification rates. As with the net N mineralization data, the highest values were found during the winter period and the lowest during the summer. The Palix nitrification measurements showed no significant seasonal patterns, however they also mirrored the N mineralization data. This would indicate that on these sites nitrifying bacteria respond
similarly to overall conditions as does the general heterotrophic microbial population that is involved in net N mineralization.

The percent net N mineralization accounted for by nitrification on an annual basis was similar for both sites: 65% and 55% for Vaughn and Palix. Ecologically the sites are very different, yet on each site these differences do not alter the relative contribution by nitrification to net N mineralization. Apparently, nitrification is not limited by substrate on these two sites. The relative importance of nitrification at the Vaughn and Palix sites is intermediate between the values of 40% found by Powers (1990) in a northern California mixed conifer stand and about 80% found by Vitousek et al. (1982) for mature western hemlock and Douglas-fir stands in Washington.

Because of the high variability of field denitrification rates, no statistically significant seasonal or treatment differences were observed. Denitrification was, however, about ten-times greater at the Palix than the Vaughn site (Fig. 4a and 4b). When extrapolated to an annual basis these represent denitrification losses of 3.7 kg ha\(^{-1}\) yr\(^{-1}\) for Palix and 0.4 kg ha\(^{-1}\)yr\(^{-1}\) for Vaughn. These are higher than those reported by Myrold et al. (1989) for mature conifer forests, but similar to those found for recently clear-cut sites or sites occupied by red alder (Alnus rubra Bong., Vermes and Myrold, 1992).

Unlike field denitrification rates, denitrification potential measurements showed distinct treatment trends; the undisturbed treatments showed the lowest potentials and the most severely compacted treatments, the highest potentials (Fig. 5a and 5b). Because denitrification is an anaerobic process, higher potential
activities would be expected in more compacted treatments. Besides being limited by the presence of oxygen, denitrification is also dependent on the presence of nitrate and available carbon. The surface 10 cm consistently exhibited a higher denitrification potential than the lower, 10-20 cm layer. Aeration conditions in the deeper layer are likely to be at least as anaerobic as the surface layer, so some other factor, such as nitrate, is likely to become limiting. Nitrate is often the limiting factor for denitrification in forest soils (Robertson and Tiedje 1984) and this has been shown for other similar forest soils in the Pacific Northwest (Vermes and Myrold, 1992).

Denitrification potentials were greater in Palix than in Vaughn soils. Averaged across treatments, denitrification potentials at Palix were 166 ng-N g⁻¹ h⁻¹ for the surface and 115 ng-N g⁻¹ h⁻¹ for the 10-20 cm layers, whereas at Vaughn they were 70 and 8 ng-N g⁻¹ h⁻¹ for the upper and lower layers. These values are comparable to those found for similar mature and disturbed forest soils in Oregon (Vermes and Myrold, 1992) and typical of forest soils in general (Davidson et al., 1990).

Despite the lack of statistically significant treatment effects, there are a few consistent patterns when the data is averaged by treatments over the whole experiment (Table 5). At Vaughn, the logged only treatment had higher soil respiration, net N mineralization, and nitrification rates than skid trail treatments. This may indicate that compaction affected microbial activity at this site in such a way as to be detrimental to N availability. On the other hand, no consistent treatment effects were seen at the Palix
site. This may indicate the resiliency of this low bulk density, high organic matter soil to compaction. Indeed, the lack of microbial response to treatments at Palix is consistent with the lack of tree response (Miller et al., 1988).
Table 1. Textural, organic carbon, total nitrogen, and bulk density data for soils at the Vaughn and Palix sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>Palix</th>
<th>Vaughn</th>
</tr>
</thead>
<tbody>
<tr>
<td>%Sand</td>
<td>32.7</td>
<td>6.7</td>
</tr>
<tr>
<td>%Silt</td>
<td>44.2</td>
<td>63.4</td>
</tr>
<tr>
<td>%Clay</td>
<td>23.0</td>
<td>30.0</td>
</tr>
<tr>
<td>Textural Class</td>
<td>loam</td>
<td>silty clay loam</td>
</tr>
<tr>
<td>%Organic Carbon</td>
<td>13.9</td>
<td>4.4</td>
</tr>
<tr>
<td>%Total N</td>
<td>.42</td>
<td>.08</td>
</tr>
<tr>
<td>Bulk Density (Mg m(^{-3}))</td>
<td>0.64</td>
<td>1.30</td>
</tr>
</tbody>
</table>
Table 2. A comparison of the Shapiro-Wilk statistic for the raw data and logarithmically transformed data.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>W Values</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Vaughn</td>
</tr>
<tr>
<td></td>
<td>raw</td>
</tr>
<tr>
<td>Denitrification</td>
<td>0.491</td>
</tr>
<tr>
<td>Net N Mineralization</td>
<td>0.541</td>
</tr>
<tr>
<td>Nitrification</td>
<td>0.729</td>
</tr>
<tr>
<td>Respiration</td>
<td>0.848</td>
</tr>
</tbody>
</table>

* .001 probability of value less than W
Table 3. Average coefficients of variation for soil respiration, net N mineralization, nitrification, denitrification, and denitrification potential.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Vaughn</th>
<th>Palix</th>
</tr>
</thead>
<tbody>
<tr>
<td>soil respiration</td>
<td>76</td>
<td>126</td>
</tr>
<tr>
<td>net N mineralization</td>
<td>128</td>
<td>109</td>
</tr>
<tr>
<td>nitrification</td>
<td>138</td>
<td>75</td>
</tr>
<tr>
<td>denitrification</td>
<td>131</td>
<td>194</td>
</tr>
<tr>
<td>denitrification potential</td>
<td>140</td>
<td>71</td>
</tr>
</tbody>
</table>
Table 4. Average soil moisture content and soil temperature by sampling period.

<table>
<thead>
<tr>
<th></th>
<th>Palix moist. cont. (%)</th>
<th>Palix temp.(°C)</th>
<th>Vaughn moist. cont. (%)</th>
<th>Vaughn temp.(°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>summer</td>
<td>76</td>
<td>15</td>
<td>17</td>
<td>20</td>
</tr>
<tr>
<td>(8/85)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>autumn</td>
<td>119</td>
<td>16</td>
<td>58</td>
<td>13</td>
</tr>
<tr>
<td>(9/86)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>winter</td>
<td>110</td>
<td>9</td>
<td>38</td>
<td>11</td>
</tr>
<tr>
<td>(11/85)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>spring</td>
<td>78</td>
<td>10</td>
<td>36</td>
<td>15</td>
</tr>
<tr>
<td>(3/86)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 5.  Average rates of field measurements by treatments.

<table>
<thead>
<tr>
<th>Site/Treatment</th>
<th>Palix Resp.</th>
<th>Palix N min.</th>
<th>Palix Nit.</th>
<th>Palix Denit.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary skid trail</td>
<td>35.1</td>
<td>9.2</td>
<td>4.8</td>
<td>3.9</td>
</tr>
<tr>
<td>Secondary skid trail</td>
<td>40.1</td>
<td>9.0</td>
<td>4.7</td>
<td>11.7</td>
</tr>
<tr>
<td>Rehabilitated skid trail</td>
<td>29.9</td>
<td>9.2</td>
<td>4.1</td>
<td>2.2</td>
</tr>
<tr>
<td>Logged only</td>
<td>33.4</td>
<td>5.7</td>
<td>3.8</td>
<td>2.6</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Skid trail</td>
<td>11.6</td>
<td>3.1</td>
<td>1.6</td>
</tr>
<tr>
<td>Subsoiled</td>
<td>10.9</td>
<td>3.1</td>
<td>2.2</td>
</tr>
<tr>
<td>Subsoiled and disked</td>
<td>11.9</td>
<td>2.5</td>
<td>2.2</td>
</tr>
<tr>
<td>Logged only</td>
<td>13.7</td>
<td>4.6</td>
<td>2.8</td>
</tr>
</tbody>
</table>
Fig. 1  Soil respiration rates for Palix site (a) and for Vaughn site (b).
Fig. 2 Net N mineralization rates for the Palix site (a) and for the Vaughn site (b).
Fig. 3  Net nitrification rates for the Palix site (a) and the Vaughn site (b).
Fig. 4  Denitrification rates for the Palix site (a) and the Vaughn site (b).
Fig. 5 Denitrification potential rates for the Palix site (a) and the Vaughn site (b).
REFERENCES


PART 2. EFFECT OF OXYGEN DIFFUSION ON SOIL RESPIRATION

INTRODUCTION

Soil aeration is an important factor in soil productivity. Most plants cannot adequately meet the demands for oxygen at the roots through internal transfer from above-ground parts. In order for maximum growth to occur there must then be sufficient gas exchange between the soil air and the atmosphere (Hillel 1982).

Gas exchange occurs through the process of mass flow and diffusion. If the driving gradient is a difference in total pressure, mass flow occurs. If the driving gradient is a difference in partial pressures, diffusion occurs. Under certain circumstances mass flow has been shown to be of importance (Vomocil and Flocker 1961, Kimball and Lemon 1971), however, diffusion is generally the dominant process. For example, it has been shown that only 3-4% interconnected air-filled pores are needed to allow sufficient diffusion to occur for high rates of respiration (Grable and Siemer 1968). Thus, the assumption can be made that diffusion is the major process for aerating soils in undisturbed conditions (Russell 1952, Wesseling 1962, Wilson et al. 1985).

Diffusion occurs through liquids as well as gases, but diffusion rates are considerably lower through liquids. Soil aeration is largely dependent on diffusion through the volume fraction of air-filled pores (Hillel 1982).
The effects of reduced soil aeration on plant root growth was conceptually analyzed by Froehlich and McNabb (1984). They expect the relative importance of a strength effect to be dominant at lower moisture contents. With increasing percent saturation, however, aeration plays an increasingly important role until at about 70% saturation it becomes the dominant factor attributing to root growth reduction.

Not many studies have examined the effects of limited aeration on microbial activity. Parr and Reuszer (1962) found that microbial organic matter decay at 5% oxygen was about half that at atmospheric oxygen concentrations. At 0.5% oxygen decomposition was still, however, almost three times higher than the anaerobic rate. Greenwood (1962) found little change in nitrate and nitrite concentrations at oxygen concentrations as low as 2%, suggesting that autotrophic nitrifiers were not inhibited at this oxygen concentration.

Linn and Doran (1984) found that aerobic microbial activity increased until the water-filled pore space reached 60% (water volume/total pore volume) which corresponds to 25% air-filled porosity (air-filled pore volume/total soil volume). At this point of maximum aerobic activity, anaerobic processes were negligible. Aerobic processes decreased and anaerobic processes increased at higher levels of water-filled pore space, indicating that oxygen diffusion was becoming limiting. Skopp et al. (1990) showed that a maximum in aerobic microbial activity occurs at the water content where the limiting effects of substrate diffusion (through liquid) and oxygen supply are equal. Although the data of Linn and Doran
suggested that 25% air-filled porosity was optimal for aerobic microbial activity in soils, other data suggest that this optimum value may be soil dependent. For example, Bridge and Rixon (1976) found maximum oxygen uptake rates varied between 15-30% air-filled porosity for soils of three different textures. Whisler et al. (1965) found a highly significant correlation between air-filled porosity and nitrate production. These were soils of low (6.7% and lower) air-filled porosity. Oxygen diffusion at this low level of air-filled porosity probably represents a limiting value for nitrification in these soils. Landina and Klevenskaya (1985) observed lower rates of nitrogen fixation in compacted soils (7-16% air-filled porosity) than in noncompacted soils (10-19% air-filled porosities).

Generally, optimum aerobic activity occurs at about 25% air-filled porosity and aerobic activity becomes greatly depressed at less than 10% air-filled porosity. Alternatively, aerobic activity decreases at oxygen concentrations less than about 2-5%. However, neither oxygen concentration or air-filled porosity alone completely describes the supply of oxygen to microorganisms in soil. Oxygen diffusion rate data through soil would presumably account for physical characteristics of the soil pore structure such as continuity and tortuosity.

In this experiment we measured oxygen diffusion coefficients (D/Do, where D= measured diffusion rate and Do= diffusion rate of oxygen in air) at various water contents and bulk densities. This data was then related to soil respiration. The purpose was to determine whether soil respiration is better correlated to oxygen diffusion rate than percent air-filled porosity. Comparisons of
various relationships found in the literature, relating diffusion coefficient \((D/D_0)\) to air-filled porosity and total porosity \((f = \text{volume of air and water}/\text{volume of soil, air, and water})\) were made.
MATERIALS AND METHODS

Soil Used

Soil was collected from two sites: a medial, mesic Andic Haplumbrept, hereafter referred to as the Palix soil, and a xeric Haplohumult, hereafter referred to as the Vaughn soil. The Palix soil is characterized by a low bulk density (0.64 Mg m\(^{-3}\)), high % organic matter content (13.9), and a high water holding capacity typical of its andic classification. The Vaughn soil has a higher bulk density (1.30 Mg m\(^{-3}\)) and a low % organic matter content (4.4).

Experimental Set-Up

Dry soil was sieved and placed in cores (2.5\(\times\)4 cm) in small increments, each increment being compacted uniformly. Moisture contents were adjusted with each increment. Using this procedure each tube was brought to one of three bulk densities. For each bulk density, soil was adjusted to three different water contents. Each of the nine water content and bulk density combinations was replicated three times. Table 6 is a summary of the treatments.

Diffusion Measurement

These soil cores were placed on a gas diffusion apparatus (Fig. 6), which allows one side of the core to be open to the atmosphere while the other side is open to a chamber that has been flushed with nitrogen. As air diffuses through the soil the oxygen concentration in the chamber increases. This system was first described by Taylor (1949). Oxygen concentration was measured
with a Beckman Oxygen Analyzer, Model D. The internal atmosphere of the chamber was mixed with a peristaltic pump for one minute prior to each measurement. Previous experimentation with the apparatus has shown this mixing time to be adequate in establishing a uniform gas mixture. During this mixing time the sliding trap door to the sample was closed because the decrease in internal pressure due to movement of gas was enough to significantly alter the determination of the diffusion coefficient. A damp sponge was placed over the top of the cores to delay drying of the soil. The diffusion rate of oxygen through the sponge was determined experimentally to be fast enough such that it did not interfere with determining diffusion coefficients through soil cores. The experiment was conducted at room temperature (22° ± 2°C). To test the gas tightness of the system, the chamber was left in a low-oxygen condition (the system could only reach low levels of 4-4.25% oxygen) for three days and no change in concentration was observed.

Diffusion results from a difference in partial pressure of the gas involved. Therefore the rate of diffusion can be described by Fick's Law of Diffusion: \( F = -D \frac{dC}{dx} \). This is for a steady-state, one dimensional flow model, where \( D \) is the apparent diffusion coefficient of gas, \( C \) is the gas concentration, \( x \) is distance, and \( F \) is the gaseous flux. For the purposes of this experiment, we are assuming the microbial oxygen consumption in the soil core has a negligible effect on the determination of the diffusion coefficient.

The solution to Fick's Law using the experimental system described is: \[ \ln \left( \frac{C_0 - C}{C_0} \right) = -\frac{DA}{VL}t \]
where:

C = O₂ concentration in the diffusion chamber (%)
C₀ = O₂ concentration at the upper boundary of the soil core (20.95%)
D = diffusion coefficient, mm² sec⁻¹
A = cross-sectional area of soil, mm²
L = soil depth, mm
V = volume of chamber and tubing
t = time, sec.

For convenience we algebraically manipulated this equation to render the following: \[ \ln\left(\frac{C₀}{C₀-C}\right)VL/A = Dt. \]
Graphical representation of this equation is linear with D being the slope of the line.

Our preliminary data was linear further verifying the effectiveness of the system. If, for example, the cores were drying out excessively, temperature fluctuations were occurring, or microbes within the cores were consuming significant amounts of oxygen, curvilinear results would be expected.

Percent air-filled pores (AFP= volume air/ total pore volume) and air-filled pore space (fₐ=volume air/ (total soil volume), also called air-filled porosity) were calculated from bulk density, percent water content, and an estimated particle density of 2.5 g cm⁻³. The total volume of each core was 29 cm³.

Respiration Measurements

Soil respiration measurements were made, after the diffusion measurements, by incubating the sealed tubes in a incubator at 25°C
for approximately 24 hours. Gas samples were then analyzed in a gas chromatograph equipped with a thermal conductivity detector and the accumulation of CO$_2$ calculated.

Statistics

Regression analysis was done relating the various measured and calculated values. Goodness of fit was based on comparing regression coefficients.
RESULTS AND DISCUSSION

Many models have been proposed to explain the relationship between gas diffusion coefficients and air-filled pore space. Buckingham (1904) used a non-linear model: \( \frac{D}{D_0} = K f_a^2 \). Pennman (1940) and others (Blake and Page, 1948; Van Bavel, 1952) found a linear relationship: \( \frac{D}{D_0} = K f_a \), where values for \( K \) ranged between 0.62 to 0.8. Millington (1959) reported the relationship \( \frac{D}{D_0} = (f_a/f)^2 f_a^{4/3} \), where \( f \) is total porosity (\( f = \) volume of air and water/volume of soil, air, and water).

The soils used in our experiment were sieved and packed to densities realistically found in the field. Figure 7 shows the relationship between \( \frac{D}{D_0} \) and \( f_a \). We tested the various models proposed above (Table 7). The Buckingham relationship with \( \frac{D}{D_0} \) being a function of \( f_a^2 \) fit best for both soils.

Currie (1962) found the relationship to be cuspatc. He suggested that the point of discontinuity was due to the changeover of diffusion occurring primarily through the intra-aggregate spaces to inter-aggregate (within crumb) spaces. Pritchard (1985) noted that for aggregate collections the pore size distribution is bimodal such that a discontinuous relationship would be expected. Further research by Currie and Rose (1985) found a trimodal relationship was even possible. At high moisture contents, diffusion was forced to occur primarily through pores within micro-aggregates (crumblets).

Our results do not show any definite two or three part curve. Peds tended to be closely packed in the soil cores minimizing inter-
aggregate space. Possibly pore variability (with respect to size and tortuosity) within natural micro-aggregates (Currie used artificial aggregates) is such that diffusion at this level is negligible. Also, the moisture contents in this experiment were probably not high enough for diffusion to occur within the micro-aggregates.

Figure 8 shows the relationship between the soil respiration rate and air-filled pore space; Fig. 9 compares soil respiration to D/D₀. For both soils, air-filled pore space was the better predictor of soil respiration. This does not confirm what we expected. Because air-filled pore space is directly related to bulk density and water content we were assured of having a wide spread of air-filled pore space values but this was not the case for the diffusion coefficient values. In fact we had a preponderance of low values (< 0.1). It is possible that the packing technique used in making the cores favored dead-end pores. Possibly using a vibration technique would allow a wider range of oxygen diffusion coefficients. There was also, a high variability of diffusion coefficients within replications. Apparently diffusion is responding to an uncontrolled factor in our method. These factors could explain the poorer fit (Fig. 9).

It is not surprising that soil respiration would be higher for the Palix soil given its higher organic matter content (over three times higher). It is interesting, however, that the slope of the air-filled pore space and soil respiration relationship (Fig. 8) is similar for both the Vaughn and Palix soils. This means that despite the differences in the properties of these two soils, respiration rates respond similarly to air-filled pore space.
Linn and Doran (1984) found a maxima for soil respiration at 60% water-filled pore space (25% air-filled pore space). Data for the Vaughn soil reach 40% air-filled pore space and that for the Palix soil reaches 58% air-filled pore space. Neither set of data shows any sign of reaching a maxima. Other work (Bridge and Rixon, 1976, Whisler et al. 1965, Landina and Klevenskaya, 1985) have demonstrated that soil microbial activity maxima are soil dependent.

Increasing bulk density has potential to detrimentally affect gas diffusion rates through soil. However, air-filled pore space seems to be a better predictor of aeration status with respect to soil microbial respiration. This experiment did not compare effect of compaction occuring on wet soil versus compacted soil that is then wetted. We can see, however, that a compacted forest soil would suffer from impeded aeration all year around and not just during winter and spring months when the combined effects are observed.
Table 6. Summary of treatments

<table>
<thead>
<tr>
<th></th>
<th>PALIX</th>
<th>VAUGHN</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bulk Density (Mg m(^{-3}))</td>
<td>Moisture Content (%)</td>
<td>Moisture Content (%)</td>
</tr>
<tr>
<td>0.57</td>
<td>35</td>
<td>0.98</td>
</tr>
<tr>
<td>0.83</td>
<td>40</td>
<td>1.11</td>
</tr>
<tr>
<td>1.00</td>
<td>45</td>
<td>1.27</td>
</tr>
</tbody>
</table>
Table 7. Summary of various equations cited in the literature.

<table>
<thead>
<tr>
<th>Palix:</th>
<th>( \frac{D}{D_0} = 0.64f_a + 0.11 )</th>
<th>( R^2 = 0.73 )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( \frac{D}{D_0} = 0.93f_a^2 - 0.01 )</td>
<td>( R^2 = 0.82 )</td>
</tr>
<tr>
<td></td>
<td>( \frac{D}{D_0} = 1.05(f_a/f)^2f_a^{4/3} - 0.02 )</td>
<td>( R^2 = 0.80 )</td>
</tr>
<tr>
<td>Vaughn:</td>
<td>( \frac{D}{D_0} = 0.55f_a - 0.03 )</td>
<td>( R^2 = 0.64 )</td>
</tr>
<tr>
<td></td>
<td>( \frac{D}{D_0} = 1.22f_a^2 + 0.01 )</td>
<td>( R^2 = 0.68 )</td>
</tr>
<tr>
<td></td>
<td>( \frac{D}{D_0} = 1.70(f_a/f)^2f_a^{4/3} + 0.01 )</td>
<td>( R^2 = 0.57 )</td>
</tr>
</tbody>
</table>
Fig. 6  Gas diffusion chamber.
Fig. 7  Air-filled pore space vs. diffusion coefficient for Palix and Vaughn
Fig. 8  Air-filled pore space vs. soil respiration for Palix and Vaughn
Fig. 9   Diffusion coefficient vs. soil respiration for Palix and Vaughn
REFERENCES


BIBLIOGRAPHY


