Microbial respiratory quotient during basal metabolism and after glucose amendment in soils and litter

O. Dilly*

Ökologie-Zentrum, Universität Kiel, Schauenburgerstraße 112, 24118 Kiel, Germany

Received 24 January 2000; received in revised form 11 May 2000; accepted 22 May 2000

Abstract

The microbial respiratory quotient (RQ), defined as the ratio of mol CO₂ evolution per mol O₂ uptake, was estimated in soils in northern and southern Germany under different land use with and without glucose addition in order to: (i) test the degree of corresponding data of the two procedures, and (ii) evaluate discrepancies with reference to the current eco-physiology of the soil microbiota. The RQ was frequently <1 during basal metabolism when no substrate was added. This indicates relatively high O₂ consumption during the current microbial mineralisation of available substrates. Throughout the first 4 h after glucose addition, the RQ values were regularly approximately 1 showing corresponding activity values based on the two procedures. Between 4 and 24 h after glucose addition when microbial growth occurred, the soil RQ was approximately 1.3 or greater but varied significantly depending on land use, soil horizon and soil pre-conditioning. Under such conditions, the RQ value was greater in soils under conventional farming than those under organic farming systems and additionally increased from the L, Of to the Ah horizon in a beech forest. RQ values >1 during the initial period of microbial growth could not be attributed to abiotic soil properties. Thus, the soil microbiota apparently adapt to the degree of complete oxidation and the incorporation of the available substrates. Corresponding measurements of basal and substrate-induced respiration measurements with some litter types also showed RQ values different from 1. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Basal metabolism; CO₂ evolution; Microbial growth; O₂ consumption; O₂ uptake; Respiratory quotient; Substrate-induced respiration

1. Introduction

The soil microbiota perform the complete mineralisation of natural substrates in ecosystems and, thus, ensure that the nutritional requirements of the vegetation are met and facilitate the cycling of elements in higher structures. The microbial mineralisation activity of humic substances is estimated by the rate of CO₂ evolution or O₂ uptake and the two measures have been used commonly as criteria of the microbial activity of soils and have contributed greatly to the study of the soil metabolism (Stotzky, 1960). The rate of CO₂ efflux, under conditions where moisture and temperature are not limiting can provide an indication of organic matter quality and whether the soil environment is conducive to the decomposition process (Sparling, 1997).

Soil respiratory activity is determined either on the basis of the CO₂ evolution or O₂ consumption rate. The measurement of CO₂ evolution appears preferable as it has the advantage of greater sensitivity due to the low background concentration present in the atmosphere and enables measurements for any length of time. However, the two procedures are common and are frequently exchanged depending on laboratory facilities for estimating basal respiration and also microbial biomass based on the substrate-induced respiration method (Stotzky, 1960; Anderson and Domsch, 1978; Bolan et al., 1996; Van de Weter and Verstraete, 1987).

Environmental conditions may, however, control the ratio of mol CO₂ evolution per mol O₂ consumption. For example, when aliphatic organic compounds, amino acids or refractory compounds having low O content are predominantly mineralised, the RQ value is smaller than 1 (Ziegler, 1983). When organic acids derived from root exudates or other organic substances containing more O are extensively decomposed, the ratio should be greater than 1. RQ values greater than 1 may additionally appear under environmental conditions when alternative electron acceptors, such as NO₃⁻, SO₄²⁻ or organic acids, are significantly involved in the current degradation of organic substances. This occurs in soil under anoxic conditions. Only when substrates equivalent to the composition of glucose are completely mineralised according to the equation CₙH₂₀Oₙ₊ₙO₂ → nCO₂ + nH₂O, will the RQ value equal 1. Finally, O₂ may
Table 1  
Characteristics of soils used

<table>
<thead>
<tr>
<th>Horizon</th>
<th>pH (0.01 mol CaCl₂)</th>
<th>Corg (mg g⁻¹ dry soil)</th>
<th>Corg/Nt</th>
<th>Water content (mg g⁻¹ fresh soil)</th>
<th>Basal respiration (µg CO₂-C g⁻¹ soil h⁻¹)</th>
<th>SIR (4–24 h)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bornhöved</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crop rotation field, Oat (CR)</td>
<td>Ap 5.4</td>
<td>13.9</td>
<td>9</td>
<td>125</td>
<td>0.33 ± 0.02</td>
<td>2.86 ± 0.10⁴</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ex maize monoculture field, Wheat (MM ex.)</td>
<td>Ap 4.9</td>
<td>10.6</td>
<td>10</td>
<td>113</td>
<td>0.39 ± 0.02</td>
<td>2.18 ± 0.11⁴</td>
</tr>
<tr>
<td>Dry grassland</td>
<td>Ah 5.4</td>
<td>12.5</td>
<td>10</td>
<td>100</td>
<td>0.47 ± 0.03</td>
<td>4.37 ± 0.21⁴</td>
</tr>
<tr>
<td>Wet grassland</td>
<td>Aa 4.9</td>
<td>82.2</td>
<td>12</td>
<td>460</td>
<td>3.20 ± 0.61</td>
<td>17.93 ± 2.09⁴</td>
</tr>
<tr>
<td>Beech forest</td>
<td>L 4.9</td>
<td>484.0</td>
<td>19</td>
<td>633</td>
<td>112.68 ± 18.45</td>
<td>343.86 ± 49.52</td>
</tr>
<tr>
<td></td>
<td>Of 3.8</td>
<td>374.6</td>
<td>20</td>
<td>610</td>
<td>18.31 ± 5.31</td>
<td>71.72 ± 14.22</td>
</tr>
<tr>
<td></td>
<td>Ah 3.5</td>
<td>26.2</td>
<td>17</td>
<td>143</td>
<td>0.40 ± 0.07</td>
<td>2.71 ± 0.08⁴</td>
</tr>
<tr>
<td>Alder forest, dystric</td>
<td>nH 3.9</td>
<td>283.6</td>
<td>16</td>
<td>722</td>
<td>4.68 ± 1.08</td>
<td>21.38 ± 2.87⁴</td>
</tr>
<tr>
<td>Alder forest, eutric</td>
<td>nH 5.5</td>
<td>280.4</td>
<td>16</td>
<td>821</td>
<td>6.67 ± 0.18</td>
<td>17.76 ± 3.29⁴</td>
</tr>
<tr>
<td>Scheyern</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HP³, Maize, high N supply</td>
<td>Ap 6.1</td>
<td>15.3</td>
<td>11</td>
<td>182</td>
<td>0.25 ± 0.02</td>
<td>5.53 ± 0.03³</td>
</tr>
<tr>
<td>HC, Maize, medium N supply</td>
<td>Ap 5.9</td>
<td>14.5</td>
<td>10</td>
<td>184</td>
<td>0.26 ± 0.05</td>
<td>5.24 ± 0.17³</td>
</tr>
<tr>
<td>LC, Maize, medium N supply</td>
<td>Ap 6.2</td>
<td>12.7</td>
<td>11</td>
<td>163</td>
<td>0.34 ± 0.02</td>
<td>5.39 ± 0.01³</td>
</tr>
<tr>
<td>LP, Maize, low N supply</td>
<td>Ap 6.2</td>
<td>12.4</td>
<td>11</td>
<td>154</td>
<td>0.30 ± 0.07</td>
<td>4.48 ± 0.38⁵</td>
</tr>
<tr>
<td>LO1, Clover-lucerne-grass</td>
<td>Ap 6.5</td>
<td>15.4</td>
<td>11</td>
<td>150</td>
<td>0.56 ± 0.02</td>
<td>6.91 ± 0.18⁶</td>
</tr>
<tr>
<td>HO1, Clover-lucerne-grass</td>
<td>Ap 5.6</td>
<td>14.7</td>
<td>11</td>
<td>146</td>
<td>0.51 ± 0.02</td>
<td>6.57 ± 0.06⁶</td>
</tr>
<tr>
<td>LO2, Clover-lucerne-grass</td>
<td>Ap 5.6</td>
<td>18.3</td>
<td>11</td>
<td>147</td>
<td>0.55 ± 0.02</td>
<td>5.91 ± 0.45⁵</td>
</tr>
<tr>
<td>MO2, Clover-lucerne-grass</td>
<td>Ap 5.8</td>
<td>12.9</td>
<td>12</td>
<td>144</td>
<td>0.55 ± 0.01</td>
<td>6.21 ± 0.12⁵</td>
</tr>
<tr>
<td>HO2, Clover-lucerne-grass</td>
<td>Ap 6.1</td>
<td>15.2</td>
<td>11</td>
<td>153</td>
<td>0.68 ± 0.05</td>
<td>7.21 ± 0.46⁴</td>
</tr>
</tbody>
</table>

a Substrate-induced respiration.  
b In 1999.  
c The substrate rate was 5 mg glucose-monohydrate g⁻¹ dry soil (the glucose was mixed with talcum in the ratio 3:5).  
d In 1999; the field was previously a long-term maize monoculture plot (Dilly and Munch, 1998).  
e The substrate rate was 12.5 mg glucose-monohydrate g⁻¹ dry soil.  
f The substrate rate was 60 mg glucose-monohydrate g⁻¹ dry soil.  
g The substrate rate was 30 mg glucose-monohydrate g⁻¹ dry soil.  
h The substrate rate was 25 mg glucose-monohydrate g⁻¹ dry soil.  
i High yield site, H; precision farming, P; conventional fertilisation, C; low-yield site, L; organic farming, O; sequence 1; sequence 2.
be consumed with poor CO₂-liberation under conditions of extensive nitrification. Studies of Hooijmans et al. (1990) with *Thiosphaera pantotropha* showed that the amount of oxygen necessary for nitrification was 11% of the total oxygen uptake. This demonstrates that the RQ refers to the quality and composition of organic matter and the current environmental conditions.

Thus, the RQ value may vary depending on the composition of available substrates, the current physiology of the soil microbial communities and microbial adjustment to the nutritional conditions although this is generally considered weak. Therefore, this ratio was determined in soils under various land use, in contrasting soil horizons of single systems and under different nutritional conditions. The RQ was compared for: (i) the basal metabolism, (ii) the first 4 h after the addition of the readily available substrate which refers to the maximal initial respiratory response, MIRR, without significant microbial growth, and (iii) the subsequent 20 h reflecting an initial period of microbial growth. This approach considers soils in northern Germany belonging to the interdisciplinary program ‘Ecosystem Research in the Bornhöved Lake District’ and long-term agricultural plots, with the main objective of studying the effects of sustainable land use, as well as soils from southern Germany with site-specific management practices of the research network ‘Agricultural Ecosystems, Munich’.

Finally, one soil amended with straw and three types of fresh litter from typical ecosystems in northern Germany were analysed.

### 2. Material and methods

#### 2.1. Sites and soils

The soils investigated belong essentially to the interdisciplinary programs ‘Ecosystem Research in the Bornhöved Lake District’ (close to Kiel) and the research network ‘Agricultural Ecosystems, Munich’ (FAM, at the ‘Hofgut Scheyern’ close to Munich). Both represent typical regions for northern and southern Germany, respectively.

The Bornhöved Lake District has a moderate oceanic climate with a long-term annual temperature of 8.3°C and 757 mm precipitation and was formed during the Pleistocene. Dystric and eutric Cambisols, Luvisols and Arenosols have been developed at the top of the Kames Hill, Kolluviosols on its slopes and Gleysols and Histosols at its base (FAO, 1988). Cambisols that have been developed from sediments containing more clay and calcareous material of the Molasse and that were mixed with some loess dominated in Scheyern. The more continental climate of Scheyern has a long-term mean annual temperature of 7.4°C and 833 mm precipitation. The soil characteristics are given in Table 1.

Soils from the Bornhöved Lake District were selected as a typical (range) of collective arable land, grassland and forest systems in northern Germany, whereas the Scheyern soils represent diverse field management practices in southern Germany. In Scheyern, the conventionally managed soils were fertilised with inorganic N according to the conservative regional-typical amounts, whereas the ‘precision farming’ system supplies N according to the expected harvest.

#### 2.2. Sampling and respiration measurements

Multiple soil cores (0–20 cm) were taken from each site. After removal of living plant residue, fresh soil was sieved (<2 mm) and mixed. Material from the Of horizon in the beech forest was sieved at <5 mm. Litter samples were taken freshly from fallen material and thoroughly mixed. Samples were stored at 4°C for no longer than 1 month until analysis. The samples were generally pre-conditioned for about 3 days at the laboratory temperature (approximately 22°C) before analyses. The soils were analysed at approximately 40–70% WHC except those from the wet grassland and the alder forest. The latter soils were investigated at the naturally occurring high moisture level (see also Table 1).

The oxygen uptake by the soil was continuously monitored in a Sapromat respirometer (Fa. Voith Sulzer, Ravensburg, Germany). Sodium hydroxide (1 mol) was used to absorb CO₂. The total volume of CO₂ produced during the course of the experiments was determined from the volume of 0.1 mol HCl required to titrate the alkali absorbent until phenolphthalein became colourless.

After determining basal respiration for about 24 h, the alkali trap was exchanged and glucose added at the rate to induce maximal initial respiratory response, MIRR (doses are given in Table 1). Thereafter, the alkali trap was

<table>
<thead>
<tr>
<th>Table 2</th>
<th>Spearman rank order correlation coefficients (r) between soil O₂ consumption and CO₂ evolution rate during basal metabolism and substrate-induced respiration separating maximal initial respiratory response (MIRR) and microbial growth of soils and litter sampled in the Bornhöved Lake District and Scheyern (P &lt; 0.05)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
</tr>
<tr>
<td>Bornhöved</td>
<td>27</td>
</tr>
<tr>
<td>Scheyern</td>
<td>27</td>
</tr>
<tr>
<td>B. &amp; S.</td>
<td>54</td>
</tr>
<tr>
<td>Litter, B.</td>
<td>9</td>
</tr>
</tbody>
</table>

<sup>a</sup> P = 0.056.
exchanged again and the respiration measured for an additional 20 h.

2.3. Data handling and statistics

Three independent samples were analysed for each soil. The values after ‘±’ refer to the confidence intervals at $P < 0.05$. Statistical analyses were performed using Microsoft Excel 2000 and SigmaStat (Jandel Scientific, Erkrath, Germany).

3. Results and discussion

3.1. Correlation between $O_2$ consumption and $CO_2$ evolution rate

Generally, high correlation coefficients were determined between the soil $O_2$ consumption and $CO_2$ evolution rate (Table 2). While the broader data set gathered from arable, grassland and forest soils from the Bornhöved Lake District produced high correlation coefficients between the two estimates, the agricultural Scheyern soils, representing a range of agricultural management practices, showed weaker correlations, particularly for basal respiration and maximal initial respiratory response. Despite the fact that significant correlations between the two approaches were detected, microbial RQ values, that is the ratio between the two correlated activities, varied significantly in the different biotopes as will be discussed later.

3.2. Basal respiration

The RQ value was frequently smaller than 1 when estimating basal respiration (Fig. 1). On average, the RQ value was approximately $0.77 \pm 0.03$ (confidence limit, $P < 0.05$, $n = 27$) for the Bornhöved soils. Thus, $CO_2$ data were 23% lower than $O_2$ values. The pre-incubation with an alkali trap additionally reduced the RQ of non-amended
soils (data not shown), which is in accordance with the findings of Theenhaus et al. (1997). Thus, the microbial eco-physiology showed a relatively high oxygen requirement for basal metabolism.

Surprisingly, abiotic soil properties as specified in Table 1 had apparently no significant effect on the RQ value. For example, the soils of the wet grassland and the alder forest contained much water, organic matter and microbial biomass but exhibited RQ values lower than 1 despite the anaerobic conditions, which had been initially assumed, would promote high values.

The Scheyern soils showed RQ values smaller than 1 in three out of four soils under conventional farming but around 1 or greater in soils under organic management. The RQ value varied in conventional systems between 0.5 and 1.1. The low values in the maize field suggest that aliphatic organic compounds, amino acids or refractory compounds containing relatively little O were predominantly mineralised. After Schulten (1993), the elemental composition of humic acids may be approximated as $C_{308}H_{328}O_{90}N_5$. This corresponds to a C/O-ratio (mol mol$^{-1}$) of approximately 3.42. Applying Eq. (1), in which the C/O-ratio of the decomposed compound corresponds to the RQ, and Eq. (2) as displayed in Fig. 8, their oxidation concurs with RQ values lower than 1 being 0.29 and 0.906, respectively. In diesel-oil-contaminated soil, the RQ values averaged 0.40, which reflected the current eco-physiological activity of the microbiota in the environment dominated by O-poor substrates (Moller et al., 1996). Nitriﬁcation may have also lowered the RQ values considerably as the C/N mineralisation rate estimated at 22°C after 12 days for the Scheyern soils ranged between 7 and 29 (mg CO$_2$–C (mg δNH$_4$–N + mg δNO$_3$–N$^{-1}$) presumably dependent on the C- and N-use strategy of the soil microbiota (unpublished data) and the N mineralisation was essentially based on NO$_3$-liberation. The higher RQ values of the organic-managed soils may result from beneficial

---

**Fig. 2.** Respiratory quotient during the first 4 h after glucose addition (substrate-induced respiration) in Bornhöved and Scheyern soils; different letters indicate significant differences when applying the Student–Newman–Keuls Method, $p < 0.05.$
root exudates by the clover-grass that was growing in the soil before sampling.

It is necessary to recognise that the respiratory quotients were here determined at 22°C. According to Chapman and Thurlow (1998), lower temperature increases the RQ and may favour conditions for the mineralisation of cellulose rather than for lignin.

3.3. Substrate-induced respiration during the first 4 h

Shortly after glucose addition, the RQ value was 0.95 ± 0.08 and 1.00 ± 0.05, for the Bornhöved (excluding the beech forest topsoil) and Scheyern soils, respectively. The results indicate that the two gases can be reliably used to estimate the maximal initial respiratory response that is a physiological estimate for the soil microbial biomass (Anderson and Domsch, 1978). This conclusion confirms previous investigations by Theenhaus et al. (1997). Interestingly, the RQ value was significantly greater in the organic management, being 1.06 vs. 0.95, when combining the Scheyern data according to the two farming systems (data not shown). This concurs with the respective CO₂ evolution rates as indicated in Table 1.

For the Bornhöved and the Scheyern soils, RQ values did not significantly differ between the soils (Fig. 2). The only exception was the topsoil of the beech forest with an average value of about 1.4 ± 0.2. In this soil horizon, the metabolically active soil microbiota seemed to mineralise glucose incompletely during the first 4 h after amendment under the environmental conditions present. Soils having high water and microbial biomass content, i.e. in the wet grassland and the black alder forest, showed RQ values around 1 or even lower. In the latter case, glucose mineralisation seemed, therefore, to coincide with the degradation of O-poor substrates or with the nitrification. The glucose addition may also have stimulated the decomposition of compounds with fair O accessibility.

RQ > 1 are frequently discussed as being the result of
anaerobic processes (Stotzky, 1960; Beck and Bengel, 1992; Theenhaus et al., 1997). RQ values >1 will be found in anaerobic soils or in partially anaerobic soils if the oxygen supply does not meet the demand. However, in aerobic soils with good oxygen supply anaerobic microsites will exist. Locally, the RQ will again be >1 but as fermentation products such as ethanol, acetate or hydrogen diffuse out into the surrounding soil they will be oxidised giving a net RQ = 1. Only if fermentation products accumulate, will RQ be >1, which certainly occurred during the 24 h incubation.

However, Leffelaar (1993) found RQ values of approximately 1 in partially anaerobic soil compartments. Therefore, the RQ may not be a sensitive enough measure to decide whether a soil is partially anaerobic. In any case, a high RQ indicates that more CO2 is evolved per unit of consumed O2. The soil microbial populations may have performed: (i) to a larger extent glycolysis, the hexose monophosphate shunt, and Entner-Doudoroff pathway for biosynthetic purpose, the pyruvate decarboxylation and tricarboxylic acid cycle to obtain precursor metabolites (Stryer, 1995; Perry and Stanley, 1997) and (ii) to a lower degree oxidative phosphorylation via the respiration chain for ATP production as indicated with equations of O-demanding processes in Fig. 8.

3.4. Substrate-induced respiration between 4 and 24 h

Adding glucose increased the RQ value to 1.37 ± 0.02 (confidence limit, P < 0.05, n = 54) between 4 and 24 h (Fig. 3). The effect significantly differed between the soils investigated. The varying RQ values could not be attributed to soil properties favouring anaerobic conditions. Again, the highest RQ value was determined in the topsoil of the beech forest, which is an acid sandy soil with a moderate content of organic matter and microbial biomass (Table 1). In this soil the RQ significantly increased with soil depth from L, O to Ah. This suggests that the eco-physiological strategy of the microbial communities with reference to the C-use became less complete in deeper biotopes in this system; a higher portion of the substrate-C may have been incorporated because microbial growth certainly occurred during this period. In contrast to the first 4 h, the RQ value was now significantly higher in the conventional farming system when compared with the organic farming system in the Scheyern soils. Thus, less-complete mineralisation and probably the short-term accumulation of metabolites and additionally an enlarged glucose-C incorporation occurred in conventional farming. Since the soil CO2 production rate was higher in the high-yield conventionally managed soils than in the other Scheyern soils (Table 1), less C was immobilised by the soil microbiota in the conventionally managed soils during this period. The predominant biochemical pathways of the soil microbiota seemed to vary in soils under different land use and farming systems and also changed considerably depending on the substrate input during the season as detected by Andersen and Scagel (1997) for higher plants.

Glucose application has led to the induction and de-repression of metabolic processes and to the stimulation of microbial growth during this period (Johansson et al., 1998; Stenstrom et al., 1991, 1998). Carbon should be fixed by synthesising microbial tissue with a mean C/O-ratio of 3.33 on a molar basis (Perry and Stanley, 1997). Accordingly, relatively more oxygen should be liberated from the glucose and, thus, RQ values >1 were expected (Herbert, 1976). In agreement, values significantly >1 were detected indicating either C assimilation or incomplete degradation of the available glucose. As already described by Stotzky (1960), the RQ may provide an indicator of the types of metabolic intermediates being utilised at a specific time and the type of
populations involved in the decomposition process. Govind et al. (1997) found RQ values close to 1 until a plateau of oxygen uptake was reached and, thereafter, RQ values >1 due to degradation of metabolite products.

Adding glucose generally increased continuously the respiratory activity after approximately 4 h (Dilly, 1999). Maximal respiration rates were often observed after around 24 h. Since the RQ value was frequently 1.3 or higher, the slope of the increasing respiration rate certainly differed depending on the gas being analysed and was higher for CO$_2$ than for O$_2$. With a factor of 1.3, the active microbiota or the growing populations may be overestimated by 30% when determining CO$_2$ rather than O$_2$ (Van de Werf and Verstraete, 1987; Panikov and Sizova, 1996; Stenstrom et al., 1998).

Soils of long-term agricultural plots, analysed with the main objective of studying the effects of sustainable land use in Schleswig-Holstein, also showed distinctly high RQ values varying between 1.4 and 2.4 during the initial period of microbial growth (Fig. 4) which can be attributed, as previously discussed, to the varying degree of glucose oxidation and incorporation. More information about the metabolism of the soil microbiota is presented by Menzel and Dilly (1999). During our sampling in spring, the RQ values of the soils under sugar beet were smaller than those under winter wheat. Extensive root development in the soils under wheat at this sampling date may have favoured organisms that are adjusted to degrade readily available organic compounds such as glucose and to metabolise organic acids derived from exudates and, thus, produce comparatively more CO$_2$ (Fig. 8). The highest value of 2.4 was determined in a soil with high organic matter and microbial biomass content under winter wheat in which anoxic conditions prevailed may additionally have played a role. However, high RQ values cannot directly be linked to anoxic...
conditions. As previously discussed, the seasonal waterlogged dystric and eutric soil of the alder forest in the Bornhöved region should have favoured organisms susceptible to such conditions. Thus, the effect of readily degradable compounds seems to be a key role for the RQ value and was therefore subsequently considered in more detail.

3.5. Effect of plant residues

Soil amended with 0.2 and 1.5% (w w\(^{-1}\)) oat straw significantly increased the RQ during basal respiration after 46 days of incubation at 22°C (Fig. 5). In addition, the RQ value was significantly larger in the amended soils during the first 4 h after glucose addition, but RQ values of the amended soils were only slightly higher than 1. Thus, the supply with plant residues significantly modified the respiratory metabolism. The RQ during microbial growth decreased with an increasing amount of straw. Thus, a more balanced mineralisation activity seems to occur when the soil microbiota with its community structure (i.e. proportion of fungi and bacteria) are adjusted to the presence of fresh plant residues. This, however, contradicts the fact that straw amendment and its readily available substrates may have favoured anaerobic prerequisites by the preceding stimulation of the microbial growth and activity.

3.6. Leaf litter and straw

The comparison of three types of fresh litter, coming from different ecosystem types in the Bornhöved Lake District, showed that the RQ varied significantly between the kinds of fresh substrate (Fig. 6). The two leaf litter types did not differ during the basal respiration but greater values occurred in fresh oat straw. The high RQ value of the oat straw suggests that organic acids with high O content may predominantly be mineralised. The RQ value was, however, considerably lower than 1 during the first 4 h after glucose addition for all litter types. Thus, glucose mineralisation in litter coincided, probably co-metabolically, with the degradation of compounds low in O content. The fact that glucose addition increased the respiratory activity by a maximum of 2.4 times, and a mean of 1.8 times (data not shown), suggests a high C availability (Cheng et al., 1996) and supports, in addition, the fact that the microbial metabolism may have changed considerably in the presence of high amounts of glucose. During microbial growth, the values were about 1.17 ± 0.06 showing an incomplete mineralisation that was lower than in the above considered mineral soils. This value additionally indicates a relative smaller glucose-C incorporation.

When the material was subjected for 35 days to laboratory conditions, the respiration rate estimated either on the basis of CO\(_2\) evolution or O\(_2\) consumption continuously decreased and the RQ values were moderately modified (results not shown). However, the differences between basal and substrate-induced respiration were the most prominent. The RQ was again drastically reduced during maximal initial respiratory response and enhanced during the subsequent 20 h by the substrate addition (Fig. 7). During the course of the next 7 days, the RQ value continuously decreased for all litter types. As detected for the soils, high correlation coefficients were also achieved between CO\(_2\) evolution and the O\(_2\) uptake rate for the litter (Table 2). Generally, the normality test (Kolmogorov-Smirnov) for

\[
\begin{align*}
(1) & \quad \text{RQ} = 1.0 \\
& \quad C_nH_{2n}O_n + n O_2 \quad \rightarrow n CO_2 + n H_2O \\
(2) & \quad \text{RQ} = 0.909 \\
& \quad C_{308}H_{120}O_{96}N_8 + 338.75 O_2 + 5 OH^- \quad \rightarrow 308 CO_2 + 156.5 H_2O + 5 NH_4^+ \\
(3) & \quad \text{RQ} = \infty \\
& \quad C_nH_{12}O_6 \quad \rightarrow 2 CH_3COH + 2 CO_2 + 2 H_2 \\
(4) & \quad \text{RQ} = 4.0 \text{ and } 1.2 \\
& \quad C_2H_2O_4 + 0.5 O_2 \quad \rightarrow 2 CO_2 + H_2O \\
& \quad C_6H_12O_6 + 5 O_2 \quad \rightarrow 6 CO_2 + 4 H_2O
\end{align*}
\]

Fig. 8. Formulae for the degradation of: (1) sugars, (2) humic acids, (3) glucose without oxygen demand, and (4) oxalic and citric acids.

Fig. 7. Respiratory quotient of beech and alder leaf litter and also oat straw during basal and substrate-induced respiration after 35 days of pre-incubation at laboratory conditions; glucose was added at time zero; bars indicate standard errors.
the collective of litter data failed for basal respiration but not for SIR. This indicates that linear regression is acceptable for SIR but not for basal respiration. Furthermore, microbial CO$_2$ evolution and O$_2$ uptake seems not to be linearly coupled under native environmental conditions, which can be explained by varying microbial metabolism in different soils (Fig. 8).

3.7. Conclusions

1. The experiments showed that the O$_2$ consumption and CO$_2$ evolution rate in soil and litter were generally highly correlated.
2. RQ values <1 were frequently estimated during soil basal metabolism.
3. The RQ values were approximately 1 in soil during maximal initial respiratory response indicating that both CO$_2$ evolution and O$_2$ uptake may be reliably used for the microbial biomass using substrate-induced respiration method. However, a few significant differences in RQ values between the soils occurred.
4. During the initial period of glucose-stimulated microbial growth, the RQ value was generally >1, which suggests unbalanced glucose degradation and enhanced incorporation of available substances. RQ values significantly differed between soils under different management, being higher in the soils under the conventional than under the organic farming system.
5. The soil RQ value during basal metabolism and after glucose addition was significantly modified when plant residues were previously added to the soil. This demonstrates that available substrates modified the RQ.
6. Different types of plant residues, decomposing apart from the soil, showed varying RQ values during basal metabolism and the initial period of glucose-induced microbial growth. High RQ values during the initial period of glucose-induced microbial growth decreased successively over time.

Acknowledgements

The author is grateful for the excellent technical assistance from Nicole Lodders and Imke Meyer, for valuable comments on the manuscript by an anonymous reviewer, and for financial support by the German Research Foundation (DFG; project no. BL 91/35-1) and the state of Schleswig-Holstein. I would like to thank, on behalf of all other co-researchers, Dr Margit von Lützow from the GSF — National Research Center for Environment and Health, Institute of Soil Ecology, in Neuherberg involving me in this delightful collaboration.

References


