14CO₂-Assimilation, Translocation of 14C, and 14C-Carbonate Uptake in Different Organs of Spring Barley Plants in Relation to Adult-Plant Resistance to Powdery Mildew

Byung Kook Hwang*, Wolf-Dieter Ibenthal** and Rudolf Heitefuss**

Abstract

The cultivar Peruvian of spring barley, which is susceptible at all growth stages, and Asse, which exhibits adult-plant resistance to powdery mildew, were compared in 14CO₂ assimilation, distribution of 14C, and 14C-carbonate uptake in different organs of healthy and infected plants. The reduction of 14CO₂ assimilation in infected plants at the first and fourth leaf stages was greater in Peruvian than in Asse. In Peruvian, the 14C which was fixed by the infected third leaf of plants with mildew on the lower 3 leaves remained in the third leaves with very little translocation to other parts of the plant. Infection of the lower three leaves at the fourth leaf stage reduced 14CO₂ assimilation in noninfected fourth leaves of Asse less than that of Peruvian, but the flow of 14C from the healthy fourth leaves into other plant parts such as leaf sheaths was markedly stimulated in Peruvian compared to Asse. Infection also reduced the uptake of 14C-carbonate by seedling roots, the reduction being greater in Peruvian than Asse. A greater proportion of the 14C absorbed by roots of Asse was translocated to the infected leaves than that of Peruvian. It was concluded that powdery mildew disrupted the normal pattern of photosynthesis and translocation of metabolites in a susceptible cultivar more markedly than in an adult-plant-resistant cultivar of spring barley.

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Key words: adult plant resistance, barley, powdery mildew, photosynthesis, translocation.

Introduction

As observed with other plant diseases, powdery mildew leads to an altered metabolism in infected and adjacent tissues and organs, i.e., a rise in respiration[1,25], a decrease in photosynthesis[11,14,17,22], and a change in translocation patterns[2-4,16,18,19,21,25].

In contrast to the hypersensitive type of resistance, there is very little information about the processes which retard the development of powdery mildew in compatible host-pathogen relationships. In our previous investigations, the spring barley cultivar Peruvian was susceptible to the isolates of Erysiphe graminis f. sp. hordei used at all plant growth stages, and the cultivar Asse showed adult-plant resistance. These cultivars varied in the infection rates and development of the fungus, especially at later plant growth stages[7,8]. We also demonstrated that carbohydrate metabolism was altered dur-
ing plant development, possibly with some relation to the appearance of adult-plant resis-
tance⁹. The different levels of quantitative resistance in the cultivars Peruvian and
Asse may depend on and affect metabolic processes within infected plants. Therefore,
we examined \(^{14}\text{CO}_2\) assimilation by and translocation from leaves and \(^{14}\text{C}\)-carbonate
uptake and translocation from roots in the two cultivars under conditions of the same
infection intensities.

**Materials and Methods**

*Barley and inoculum.* The spring barley cultivars used were (1) Peruvian, sus-
ceptible to powdery mildew at all plant growth stages and (2) Asse, susceptible at early
growth stages, but resistant at late growth stages. For root uptake and transfer tests,
plants were grown in 7 cm-plastic pots containing artificial clay balls, and were supplied
with Hoagland’s solution every day. Plants were grown in sterilized potting compost for
the photosynthesis tests. Environmental conditions for cultivation of the plants and
mildew fungus were described previously⁷).

The isolate C₁₇Amel of *E. graminis* f. sp. *hordei*, maintained at the Institut für
Pflanzenpathologie und Pflanzenschutz, Univ. Göttingen, was used in all the experiments.
Seven-day-old seedlings and seventeen-day-old plants with third leaves fully expanded
were inoculated with various concentrations of inoculum in order that plants with the
same infection intensity in the two cultivars could be selected. One ml of conidial sus-
pension in FC 43 (Fluorinert Electronic Liquid, Commercial Chemicals Division/3 M, St.
Paul, Minnesota) was sprayed uniformly on 700 cm² of abaxial leaf surface. Prior to
inoculation, the leaves were lined up horizontally next to each other on a galvanized iron
sheet by using small pieces of magnet. A uniform distribution of conidia was obtained
by this method. No colonies were found on fourth leaves expanded 6 days after inocu-
lation. In both cultivars the leaf area infected was approximately 60% for seedlings.
In plants used for \(^{14}\text{CO}_2\) fixation studies, it was approximately 40% for first, 40% for
second and 45% for third leaves. Uninoculated plants were used for control measnre-
ments.

*Feeding with \(^{14}\text{C}.* For \(^{14}\text{CO}_2\) labelling, attached individual whole third, fourth and
seedling leaves, respectively, on the sixth day after inoculation were enclosed in a clear
plexiglas chamber (130×30×6 cm). \(^{14}\text{CO}_2\) was then released from Na₂ \(^{14}\text{CO}_3\) (200 μCi)
by the addition of 50% sulphuric acid. The amount of \(^{14}\text{CO}_2\) added to the chamber was
negligible, thus not altering the normal atmospheric concentration of CO₂. The \(^{14}\text{CO}_2\)
was circulated by a ventilator for 1 hr. The fixation chamber was illuminated with 5000
lux from two lamps (TLD 58 W, Philips). At the end of the feeding period, excess
\(^{14}\text{CO}_2\) was absorbed in 2N KOH.

For \(^{14}\text{C}\) uptake test, 40 seedlings at 4 days after inoculation were placed in 100 ml of
Hoagland’s solution (pH 7.5) in a growth chamber with 70 μCi of Na₂ \(^{14}\text{CO}_3\) for 24 hr.

* Determination of radioactivity. After \(^{14}\text{C}\)-feeding, barley plants were separated
immediately into leaves, leaf sheaths and roots. The soil was washed from the roots
with water. Organs were placed into small vials containing 80% ethanol and immedî-
ately shaken in a water bath (65°C) for 1.5 hr. The plant samples were divided into ethanol-soluble and -insoluble fractions. Aliquots of the ethanol-soluble fraction were added in 10 ml of toluene-scintillant (Quiczint 212, Werner Zinsser, Germany) and measured in a liquid scintillation counter. Correction for quenching was made by external standardization. The remaining radioactivity insoluble in the plant samples was estimated by burning the samples in a “sample-oxidizer” (Central Isotope Laboratory, Univ. Göttingen). The resultant $^{14}$CO$_2$ was absorbed in a solution of oxa-scintillant (phenylethylamine 330 ml, methanol 220 ml, toluol 400 ml, distilled water 75 ml, 2, 5-diphenyl-oxazole 7 g, and p-bis-(o-methystyryl)-benzol 0.7 g) and measured by liquid scintillation counting. $^{14}$CO$_2$ assimilation and distribution of $^{14}$C in plant organs of healthy and diseased barley were expressed as dpm and percentages of total activity of the whole plant.

Results

$^{14}$CO$_2$ assimilation and distribution of $^{14}$C in plant parts

The $^{14}$CO$_2$ fixation and distribution of $^{14}$C among the various parts of healthy and powdery mildewed plants of Peruvian and Asse are presented in Tables 1 and 2. Six days after inoculation, the amount of total $^{14}$C fixed by the diseased leaves was more reduced in Peruvian than in Asse. In particular, infection decreased $^{14}$CO$_2$ assimilation in the third leaves of fourth leaf stage, the reduction being more pronounced in Peruvian than in Asse (Table 2). During $^{14}$CO$_2$ assimilation, $^{14}$C fixed in the leaves is simultaneously translocated to other parts of the plant. The translocation patterns of $^{14}$C fixed in the diseased leaves were different from those of comparable healthy plants. In

Table 1. $^{14}$CO$_2$ assimilation and distribution of $^{14}$C in three plant parts of healthy and powdery mildewed plants of spring barley cultivars (Peruvian-susceptible, Asse-adult-plant-resistant) at the first leaf stage after exposure of the healthy and infected first leaves to $^{14}$CO$_2$

<table>
<thead>
<tr>
<th>Plant part</th>
<th>Healthy S</th>
<th>I</th>
<th>Total</th>
<th>Diseased S</th>
<th>I</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peruvian</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fed first leaf</td>
<td>35.4±1.7b</td>
<td>7.6±0.4</td>
<td>43.0±1.8</td>
<td>54.2±3.5</td>
<td>9.0±0.5</td>
<td>63.2±3.9</td>
</tr>
<tr>
<td>Remainder of shoot</td>
<td>12.5±0.5</td>
<td>28.1±1.2</td>
<td>40.6±2.1</td>
<td>10.4±0.8</td>
<td>20.1±1.6</td>
<td>30.5±2.3</td>
</tr>
<tr>
<td>Root</td>
<td>5.6±0.2</td>
<td>10.8±0.3</td>
<td>16.4±0.6</td>
<td>3.5±0.5</td>
<td>2.8±0.4</td>
<td>6.3±0.8</td>
</tr>
<tr>
<td>Total $^{14}$C (10$^6$dpm)</td>
<td>15.4±1.3</td>
<td>13.4±0.4</td>
<td>28.8±2.0</td>
<td>9.8±0.5</td>
<td>4.6±0.2</td>
<td>14.4±0.8</td>
</tr>
<tr>
<td>Asse</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fed first leaf</td>
<td>43.1±2.3</td>
<td>6.8±0.7</td>
<td>49.9±2.5</td>
<td>50.6±2.4</td>
<td>9.3±0.7</td>
<td>59.9±3.0</td>
</tr>
<tr>
<td>Remainder of shoot</td>
<td>15.5±0.8</td>
<td>23.2±1.5</td>
<td>38.7±2.9</td>
<td>12.2±0.7</td>
<td>19.1±1.4</td>
<td>31.3±2.2</td>
</tr>
<tr>
<td>Root</td>
<td>4.6±0.5</td>
<td>6.8±0.6</td>
<td>11.4±1.0</td>
<td>5.5±0.4</td>
<td>3.3±0.7</td>
<td>8.8±1.0</td>
</tr>
<tr>
<td>Total $^{14}$C (10$^6$dpm)</td>
<td>23.2±2.5</td>
<td>13.5±0.5</td>
<td>36.7±3.1</td>
<td>14.7±1.1</td>
<td>6.8±0.3</td>
<td>21.5±1.2</td>
</tr>
</tbody>
</table>

a) S and I designate ethanol-soluble and -insoluble fractions, respectively.
b) The values for the plant parts are the percentages of total activity of the whole plant, expressed by means ± standard errors of six replicate plants. Figures in parentheses are the percentage $^{14}$C of the healthy controls.
comparison to the easy mobility from healthy leaves, more of the 14C fixed in the diseased leaves remained there. During exposure of the first leaf in Peruvian to 14CO2, about 63% of the fixed 14C remained in the infected leaves, whereas the comparable

Table 2. 14CO2 assimilation and distribution of 14C in different plant parts of healthy plants and powdery mildewed plants on the lower 3 leaves of spring barley cultivars (Peruvian=susceptible, Asse=adult-plant-resistant) at the fourth leaf stage after exposure of the healthy and infected third leaves to 14CO2

<table>
<thead>
<tr>
<th>Plant part</th>
<th>Healthy S</th>
<th>Healthy I</th>
<th>Healthy Total</th>
<th>Diseased S</th>
<th>Diseased I</th>
<th>Diseased Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peruvian</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fed third leaf</td>
<td>73.9±3.6 b)</td>
<td>17.4±1.6</td>
<td>91.3±3.2</td>
<td>79.5±4.6</td>
<td>19.4±1.4</td>
<td>98.9±3.3</td>
</tr>
<tr>
<td>Leaf sheath</td>
<td>6.8±0.4</td>
<td>1.9±0.3</td>
<td>8.7±0.5</td>
<td>0.8±0.1</td>
<td>0.3±0.1</td>
<td>1.1±0.1</td>
</tr>
<tr>
<td>Other parts</td>
<td>tr</td>
<td>tr</td>
<td>tr</td>
<td>tr</td>
<td>tr</td>
<td>tr</td>
</tr>
<tr>
<td>Total 14C (10^6dpm)</td>
<td>28.5±4.8 (100.0)</td>
<td>6.8±0.3 (100.0)</td>
<td>35.3±4.7 (100.0)</td>
<td>4.3±0.6 (15.1)</td>
<td>1.0±0.2 (14.7)</td>
<td>5.3±0.4 (15.0)</td>
</tr>
<tr>
<td>Asse</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fed third leaf</td>
<td>75.3±5.2</td>
<td>14.8±1.5</td>
<td>90.1±5.0</td>
<td>70.4±3.9</td>
<td>21.2±2.0</td>
<td>91.6±3.8</td>
</tr>
<tr>
<td>Leaf sheath</td>
<td>4.8±1.1</td>
<td>5.1±0.8</td>
<td>9.9±1.3</td>
<td>3.6±0.5</td>
<td>4.8±0.8</td>
<td>8.4±0.7</td>
</tr>
<tr>
<td>Other parts</td>
<td>tr</td>
<td>tr</td>
<td>tr</td>
<td>tr</td>
<td>tr</td>
<td>tr</td>
</tr>
<tr>
<td>Total 14C (10^6dpm)</td>
<td>20.3±1.8 (100.0)</td>
<td>5.1±1.0 (100.0)</td>
<td>25.4±1.7 (100.0)</td>
<td>12.7±1.5 (62.5)</td>
<td>4.5±0.9 (88.2)</td>
<td>17.2±1.4 (67.7)</td>
</tr>
</tbody>
</table>

a) S and I designate ethanol-soluble and -insoluble fractions, respectively.
b) The values for the plant parts are the percentages of total activity of the whole plant, expressed by means±standard errors of four replicate plants. Figures in parentheses are the percentage 14C of the healthy controls.

Table 3. 14CO2 assimilation and distribution of 14C in different plant parts of healthy and powdery mildewed plants on the lower 3 leaves of spring barley cultivars (Peruvian-susceptible, Asse-adult-plant-resistant) at the fourth leaf stage after exposure of the noninfected fourth leaf to 14CO2

<table>
<thead>
<tr>
<th>Plant part</th>
<th>Healthy S</th>
<th>Healthy I</th>
<th>Healthy Total</th>
<th>Diseased S</th>
<th>Diseased I</th>
<th>Diseased Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peruvian</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fed fourth leaf</td>
<td>72.0±2.2 b)</td>
<td>23.9±1.3</td>
<td>95.9±3.1</td>
<td>66.1±1.8</td>
<td>27.0±1.2</td>
<td>93.1±3.3</td>
</tr>
<tr>
<td>Leaf sheath</td>
<td>2.6±0.4</td>
<td>1.4±0.3</td>
<td>4.0±0.5</td>
<td>4.4±0.5</td>
<td>2.5±0.2</td>
<td>6.9±0.6</td>
</tr>
<tr>
<td>Other parts</td>
<td>tr</td>
<td>tr</td>
<td>tr</td>
<td>tr</td>
<td>tr</td>
<td>tr</td>
</tr>
<tr>
<td>Total 14C (10^6dpm)</td>
<td>165.4±7.3 (100.0)</td>
<td>56.2±3.5 (100.0)</td>
<td>221.6±8.5 (100.0)</td>
<td>90.3±5.2 (54.6)</td>
<td>37.9±3.1 (67.4)</td>
<td>138.2±8.0 (62.4)</td>
</tr>
<tr>
<td>Asse</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fed fourth leaf</td>
<td>69.5±2.5</td>
<td>28.3±1.8</td>
<td>97.8±3.9</td>
<td>69.1±2.8</td>
<td>28.2±1.6</td>
<td>97.3±4.5</td>
</tr>
<tr>
<td>Leaf sheath</td>
<td>1.5±0.2</td>
<td>0.7±0.1</td>
<td>2.2±0.4</td>
<td>1.8±0.3</td>
<td>0.8±0.2</td>
<td>2.6±0.5</td>
</tr>
<tr>
<td>Other parts</td>
<td>tr</td>
<td>tr</td>
<td>tr</td>
<td>tr</td>
<td>tr</td>
<td>tr</td>
</tr>
<tr>
<td>Total 14C (10^6dpm)</td>
<td>144.8±7.3 (100.0)</td>
<td>59.2±4.5 (100.0)</td>
<td>204.0±7.6 (100.0)</td>
<td>62.9±4.5 (43.4)</td>
<td>25.8±1.5 (43.6)</td>
<td>88.7±6.1 (43.4)</td>
</tr>
</tbody>
</table>

a) S and I designate ethanol-soluble and -insoluble fractions, respectively.
b) The values for the plants are the percentages of total activity of the whole plant, expressed by means±standard errors of four replicate plants. Figures in parentheses are the percentage 14C of the healthy controls.
Table 4. Effect of powdery mildew infection on the uptake and distribution of Na₂\(^{14}\)CO₃ into different plant parts of spring barley cultivars (Peruvian=susceptible, Asse=adult-plant-resistant) at the first leaf stage\(^{a)}\)

<table>
<thead>
<tr>
<th>Plant part</th>
<th>Healthy</th>
<th>Diseased</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>S(^b))</td>
<td>I</td>
</tr>
<tr>
<td>Peruvian</td>
<td></td>
<td></td>
</tr>
<tr>
<td>First leaf</td>
<td>17.1±1.1(^c))</td>
<td>7.3±0.5</td>
</tr>
<tr>
<td>Remainder of shoot</td>
<td>17.6±0.8</td>
<td>23.4±1.2</td>
</tr>
<tr>
<td>Root</td>
<td>12.3±0.9</td>
<td>22.3±1.6</td>
</tr>
<tr>
<td>Total (^{14})C (10⁶dpm)</td>
<td>44.6±5.7 (100.0)</td>
<td>50.4±5.9 (100.0)</td>
</tr>
<tr>
<td>Asse</td>
<td></td>
<td></td>
</tr>
<tr>
<td>First leaf</td>
<td>19.1±1.8</td>
<td>4.7±0.4</td>
</tr>
<tr>
<td>Remainder of shoot</td>
<td>14.9±1.0</td>
<td>26.5±2.0</td>
</tr>
<tr>
<td>Root</td>
<td>16.1±1.4</td>
<td>18.7±1.1</td>
</tr>
<tr>
<td>Total (^{14})C (10⁶dpm)</td>
<td>70.0±7.6 (100.0)</td>
<td>70.0±6.4 (100.0)</td>
</tr>
</tbody>
</table>

\(^{a)}\) The 40 healthy and diseased plants were placed in Hoagland’s solution with 70 μCi of Na₂\(^{14}\)CO₃ for 24 hr.
\(^{b)}\) S and I designate ethanol-soluble and -insoluble fractions, respectively.
\(^{c)}\) The values for the plants are the percentages of total activity of the whole plant, expressed by means±standard errors of six replicate plants. Figures in parentheses are the percentage \(^{14}\)C of the healthy controls.

Healthy plants had only 43% of the radioactivity in these leaves (Table 1). The \(^{14}\)C which was fixed by the third leaf of either plants mildewed on the lower three leaves or healthy plants also remained in the third leaf, with very little translocation to other parts of the plant (Table 2). Slight reduction in translocation of the fixed \(^{14}\)C by infection in susceptible cultivar Peruvian was not shown in the adult-plant-resistant cultivar Asse.

Infection of the lower three leaves of barley plants at the fourth leaf stage severely reduced \(^{14}\)CO₂ assimilation in noninfected fourth leaves, the reduction being slightly greater in Asse than in Peruvian (Table 3). Although infection had little effect on translocation, the translocation of \(^{14}\)C fixed by the noninfected fourth leaves in Peruvian was apparently different from that of Asse. In Peruvian, more \(^{14}\)C was transported from the noninfected fourth leaves into the leaf sheaths of infected plants than was translocated in healthy controls. In Asse, an activity of \(^{14}\)C similar to the level in the healthy control was present in leaf sheaths, indicating that infection had no effect on translocation in this cultivar.

When \(^{14}\)CO₂ was fixed by the third or fourth leaves at the fourth leaf stage (Tables 2 and 3), very little translocation occurred to other leaves or roots in either healthy or diseased plants.

**Uptake of \(^{14}\)C-carbonate by roots**

The activities of \(^{14}\)C translocated into various tissues of healthy and mildewed plants after feeding roots of seedlings with Na₂\(^{14}\)CO₃ in the nutrient solution for 24 hr are presented in Table 4. The roots of diseased Asse plants were more active than those.
of Peruvian in absorbing $^{14}$C-carbonate. The infected leaves were the major area of accumulation of $^{14}$C taken up by the roots. As a consequence of the rapid transport into infected leaves, only a small percentage of radiolabel remained in the stems and roots of infected plants compared to the healthy controls. In particular, more $^{14}$C taken up by the roots was accumulated in the infected leaves of Asse than in those of Peruvian.

**Discussion**

Our previous studies demonstrated that when using precise inoculation methods, adult plant resistance of spring barley to powdery mildew can be detected already on the seedlings and estimated more precisely at the third or fifth leaf stage, without examination of disease reactions at the later growth stages of plants. In contrast to a gradual change in colony production in susceptible cultivar Peruvian, adult-plant-resistant cultivar Asse showed an abrupt reduction of colony number as the plants became increasingly older. The experiments were done using juvenile plants of spring barley at first and fourth leaf stages, because mature plants at later growth stages could not be uniformly infected by artificial inoculation with *E. graminis f. sp. hordei*.

Previously it has been shown that powdery mildew markedly disrupts the normal pattern of photosynthesis and translocation within its host plant. The data obtained in this investigation indicate that the reduction in $^{14}$CO$_2$ fixation and translocation of fixed $^{14}$C by powdery mildew infection was greater in the susceptible cultivar than in the adult-plant-resistant cultivar, in spite of the same infection intensity. These findings raise two questions: what is the importance of photosynthesis and translocation in determining the quantitative difference of susceptibility to powdery mildew in Peruvian and Asse, and what are the underlying mechanisms bringing about the more pronounced decrease in photosynthesis and carbon translocation in the susceptible cultivar?

The percentages of germination and appressorium formation of *E. graminis f. sp. hordei* were similar for all leaf stages in the susceptible cultivar and the adult-plant-resistant cultivar. In Asse, however, the production of elongating secondary hyphae and colonies was strongly inhibited, and the trend was consistent at all growth stages of plants. Thus, the observed differences in reduction of photosynthesis and translocation between Peruvian and Asse may be associated with the different potentials of the two cultivars to retard hyphal development of powdery mildew. It is not known if this hypothesis is applicable to other host-pathogen relationships with quantitative differences in compatibility.

An interesting fact is that the reduction of $^{14}$CO$_2$ assimilation in the noninfected fourth leaves of infected barley plants was quite distinct. This may imply that possibly harmful metabolites transported from the infected into the healthy leaves would affect the photosynthetic machinery and the related biochemical processes in the healthy leaves. This phenomenon is in disagreement with the findings that photosynthesis was stimulated in healthy leaves of rust-infected bean and wheat and powdery mildew-infected barley. Recently, Walters and Ayres found a stimulation of net photosynthe-
sis in noninfected third leaves when the lower two leaves of barley plants were infected by *E. graminis*. The difference in results of the two investigations may be due to the different experimental methods for measurement of CO₂ fixation and different leaf stages of barley plants and cultivars tested. The causes for slightly greater decline of ¹⁴CO₂ assimilation in the adult-plant-resistant cultivar Asse than in the susceptible cultivar Peruvian could not be well explained, but it seems obvious that there were different translocation patterns. An increased flow of ¹⁴C from the noninfected fourth leaves into the leaf sheaths in Peruvian indicates that this susceptible cultivar requires more metabolites for the stimulation of metabolic activity with high rates of respiration and/or biosynthesis in the infected tissues. The "sink" effect of infected leaves in Peruvian seems to be much more intensive compared to Asse. Consequently, the greater mobilization of energy sources to the sites of infection in Peruvian relative to Asse can be an advantage to the invading powdery mildew fungus which may need an abundant supply of energy during its multiplication and sporulation¹². In contrast, less metabolites may be utilized for mildew development from the normal metabolic processes in Asse, thereby retaining high yielding capacity even under mildew infection.

The data indicate that the reduction in uptake of ¹⁴C-carbonate by roots was greater in infected seedlings of Peruvian than in those of Asse. The differences between Peruvian and Asse may appear distinct in reduced uptake of ¹⁴C-carbonate in infected plants, possibly as a result of the differences in reduced absorptive capacity, reduced root growth, utilization by the fungus, impaired translocation, accumulation in nutrient sinks around infection sites, or loss from exudation and respiration⁶,²⁰. This is consistent with the difference between Peruvian and Asse in reduction of ¹⁴CO₂ assimilation (Tables 1, 2 and 3). The nutrients accumulated at infection sites in the two cultivars may not only be valuable for mildew growth; the accumulation of mineral nutrients around the infection court may also constitute a mechanism of host defence⁶). The excess accumulation of metabolites in the infected leaves of Asse compared to Peruvian may also be associated with the delay of mildew development⁷,⁸). Martin and Ellingboe¹³ demonstrated that during the early stage of infection the powdery mildew fungus on the infected wheat in incompatible interactions absorbed more ³²P than in compatible interactions. Our results agree with those of Frič⁴¹, which indicated that roots of mildewed barley plants showed reduced rates of phosphate uptake 5 to 8 days after inoculation. In contrast, Walters and Ayres²¹ reported that powdery mildew infection stimulated ³²P-phosphate uptake by roots of barley plants, in spite of reducing growth.

In all our experiments of ¹⁴CO₂ assimilation and uptake of ¹⁴C-carbonate by roots, the differences in incorporation of radioactivity into structural elements and insoluble substances in the cultivars Peruvian and Asse were similar to those in soluble metabolites.

**Literature cited**


和文摘要

黄炳國・Ibenthal, W.-D・Heitefuss, R.: 春まきオウムギのうどん病に対するadult-plant resistance
と各部器官における$^{14}$CO$_2$同化, $^{14}$C移行および$^{14}$C-carbonate吸収との関係

全生育期間を通じてうどん病に感受性である品種 Peruvian と生育後期抵抗性を示す品種 Asse を供試
して、健全および罹病植物の異なる器官における$^{14}$CO$_2$同化, $^{14}$C分布および$^{14}$C-carbonate吸収を比較した。
第1および第4本葉期の罹病植物における$^{14}$CO$_2$同化の低下は、同程度に罹病しているにもかかわらず、
AsseにおいてよりもPeruvianで大きかった。Peruvianでは下位葉3枚がうどん病に罹病している第3
本葉によって固定された$^{14}$Cは同葉にとどまり、他部位への移行はほとんど認められなかった。
第4本葉期の下位3葉が罹病したAsseの健全な第4葉における$^{14}$CO$_2$同化の低下はPeruvianよりも少なかった。しかし、
同葉から葉鞘などの他の部位への$^{14}$Cの移行はAsseに比べてPeruvianにおいて顕著であった。うどん病
に罹病すると、実生苗の根による$^{14}$C-carbonate吸収が低下したが、その減少はAsseよりもPeruvian
においてより大きかった。Asseの根から吸収された$^{14}$Cの罹病葉への移行割合はPeruvianの場合に比べ、
より大きかった。これらの結果から、春まきオウムギではうどん病罹病により光合成産物および代謝産物の
移行の正常なパターンが阻害され、その程度は生育後期抵抗性をもつ品種に比べて感受性品種においてより顕
著であると結論された。