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$^{14}CO_2$ Assimilation and Metabolism of ^{14}C-Assimilates in Whole Plants of Spring Barley in Relation to Adult-Plant Resistance to Powdery Mildew

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흰가루病에 대해 成體植物 抵抗性을 지닌 봄보리에서 $^{14}CO_2$ 同化와 ^{14}C-同化産物의 代謝

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ABSTRACT

The effect of powdery mildew infection on the $^{14}CO_2$ assimilation and metabolism of ^{14}C-assimilates was studied with spring barley cultivars, susceptible Peruvian and adult-plant resistant Asse at the four-leaf stage. No consistent differences between Peruvian and Asse were revealed in $^{14}CO_2$ assimilation and metabolism of ^{14}C-assimilates in healthy whole plants. In the two cultivars, $^{14}CO_2$ assimilation and translocation of assimilates decreased as the number of infected leaves increased. Despite the same infection intensity, $^{14}CO_2$ assimilation was less inhibited in Asse than Peruvian. Infection reduced the fixation of $^{14}CO_2$ in noninfected fourth leaves of Peruvian more severely than that of Asse. Infection of the lower 3 leaves also inhibited the incorporation of ^{14}C into carbohydrates such as fructose and glucose in noninfected fourth leaves and their translocation into leaf sheathes, the inhibitions being greater in Peruvian than Asse. In the infected third leaves, there was a reduction of ^{14}C-activity in carbohydrates, more ^{14}C-labeled fructose and glucose being retained in Peruvian. The stimulation of ^{14}C-organic acid synthesis in all plant organs was more pronounced in Peruvian than Asse. Powdery mildew markedly increased the incorporation of ^{14}C into amino acids in infected third and noninfected fourth leaves, but reduced their translocation to the leaf sheathes. A greater rise of ^{14}C-activity in some amino acids in the two leaves was found in Peruvian than Asse.

Key words: adult-plant resistance, barley, powdery mildw, ^{14}C-metabolism.

要 約

흰가루病에 對하여 感受性인 봄보리品種 Peruvian과 成體植物 抵抗性品種 Asse의 4葉期에서 흰가루病에 感

染되었을 때 $^{14}CO_2$ 同化와 ^{14}C-同化産物의 代謝變化를 硏究하였다. 健全植物에서는 Peruvian과 Asse間에 $^{14}CO_2$ 同化와 ^{14}C-同化産物 代謝에서 差異가 없었다. 感染된 葉數가 늘어남에 따라 이들 두 品種에서 $^{14}CO_2$ 同化와 同化産物의 移行量은 減少하였다. 感染정도가 같을 때도 Asse 보다 Peruvian에서 $^{14}CO_2$ 同化가 더 減少되었다. 흰가루病이 感染되지 않은 第4葉에서도 $^{14}CO_2$ 고정이 줄어들었고, Peruvian에서 더 줄었다. 아래 3葉이 感染되었을 때 感染되어 있지 않는 上位 第4葉에서 fructose, glucose 等의 炭水化物로 ^{14}C가 전환되는 것을 억제하였고 Asse보다 Peruvian에서 억제가 더 컸다. 感染된 第3葉에서도 炭水化物內에 ^{14}C이 줄어들었으나 Peruvian에서 ^{14}C로 標識된 fructose, glucose 含量이 더 높았다. 모든 식물기관에 ^{14}C-有機酸合成이 촉진되었고 Asse 보다 Peruvian에서 合成이 더 뚜렷하였다. 感染된 第3葉이나 健全第4葉에서 ^{14}C이 아미노산으로 결합하는 것이 增加하였으나 葉鞘로 移動은 감소되었다. 이들 잎에서 어떤 ^{14}C-아미노산은 Asse 보다 Peruvian에 더 많이 축적되었다.

INTRODUCTION

Although it is not easy to examine the individual metabolic processes in plant tissues by feeding whole plants with $^{14}CO_2$, the complex of metabolism such as photosynthesis, translocation and their interaction within the plant could be estimated in relation to the effects of disease on energy capture, transfer, development and ultimately yield loss of a crop (15). In particular, the analyses of $^{14}CO_2$ assimilation and metabolism of ^{14}C-labeled assimilates in the whole barley plants will help understand the physiological backgrounds and causes for the higher yields of adult-plant-resistant cultivars.

Our earier results suggested that the differences in levels of adult-plant resistance among all barley cultivars tested may result from changes in gene action during plant development (14) and that the gradual inhibition of mildew development on older barley plants is caused by physiological and biochemical changes in plant tissues with increasing age (12). We also demonstrated that the inhibition of $^{14}CO_2$ assimilation, translocation of ^{14}C and ^{14}C-carbonate uptake in different tissues of spring barley plants due to infection of powdery mildew was more marked in the susceptible cultivar Peruvian than in the adult-plant-resistant cultivar Asse (13) and that carbohydrate metabolism is less altered in infected plants of Asse than in Peruvian (11). However, there has been no direct demonstration of altered metabolism and transport of metabolites in infected whole plants where all matabolic processes may take place concurrently. Obviously the understanding of metabolic and energy-transfer pathways in whole plants may be important if the ultimate goal is to measure the effect of disease on yield of a crop. Lower yields in barley cultivars susceptible to powdery mildew may be attributed to an impaired metabolism of photoassimilates in infected whole plants.

The objective of our investigations was to examine the effect of powdery mildew infection intensities on $^{14}CO_2$ assimilation and metabolism of ^{14}C-assimilates in whole barley plants of susceptible and adult-plant-resistant cultivars.

MATERIALS AND METHODS

Plant and inoculum. The spring barley cultivars used were (1) Peruvian, susceptible to the isolates of *Erysiphe graminis* f. sp. *hordei* used at all plant growth stages and (2) Asse, susceptible at early growth stages, but resistant at late growth stages (10). The plants were grown in 13 cm-plastic pots containing the sterilized potting compost under the controlled environmental conditions as described earier (12). Twenty-day-old plants with third leaves fully expanded were inoculated by uniformly spraying a conidial suspension in FC 43 (Fluorinert Electronic Liquid, Commercial Chemicals Division/3M, St. Paul, Minnesota) of *E. graminis* f. sp. *hordei* (race C_{17} Amsel) on the abaxial surface of individual leaves. The plants that had the same infection intensity in both cultivars after inoculation with various concentrations of inoculum were chosen for these investigations. In both cultivars, the leaf areas infected were approximately 70% on the first, 45% on the second and 35% on the third leaves at four-leaf stage 6 days after inoculation.

$^{14}CO_2$ fixation by plants. Thirty two plants at four-leaf stage of the two cultivars, healthy and infected with the lower 1, 2, or 3 leaves, were placed in a clear plexiglas chamber (70x60x35 cm). Prior to exposure of $^{14}CO_2$, the conidia produced on the sixth day after inoculation were carefully removed by brushing the infected leaves. A solution of $Na_2{}^{14}CO_3$ (500 μCi) was injected into a small vial and $^{14}CO_2$ was released by the subsequent injection of 2 ml of 50% sulphuric acid. Air was circulated in the chamber by a ventilator. The entire apparatus for $^{14}CO_2$ fixation was illuminated by one lamp (220-230 V, 500 W, Nitraphot BR, Osram Inc.) providing 5000 lux on the leaf surface. After an exposure time of 1.5 hr, excess $^{14}CO_2$ was absorbed in 2 N KOH using a vacuum pump.

Separation of ^{14}C-metabolites. After absorbing the excess $^{14}CO_2$, the plants were removed from the chamber, and separated immediately into leaves and leaf sheathes. Organs were placed into small vials containing 80% ethanol and immediately shaken in a water bath (65°C) for 1.5 hr. Aliquots of the ethanol-soluble fraction were placed in 10 ml of the toluene-scintillant (Quiczint 212, Werner Zinsser, Germany) and measured in a liquid scintillation counter.

The ethanol water fractions extracted from the healthy and lower 3 leaves-infected plants of the two cultivars were evaporated to dryness under vacuum at 36°C and taken up in a known volume of double-distilled water. The water fractions which contained carbohydrates, organic acids and amino acids were applied to ion exchange columns filled with Dowex 50 WX4 (counter ion H^+, 100-200 mesh) and Amberlite IRA 68 (counter ion OH^-). Amino aicds and organic acids were eluted from the Dowex 50 WX4 in 30 ml of 12.5% NH_3 solution and from Amberlite IRA 68 in 30 ml of 1 N HCl, respectively. The eluates from both columns were evaporated to dryness and resuspended in a small volume of 60% ethanol. Aliquots of the samples were used in determining the radioactivities of total ^{14}C-carbohydrates, ^{14}C-organic acids and ^{14}C-amino acids. The remaining ethanol-soluble fractions were stored at −15°C until analyzed.

Gas chromatographic analysis of ^{14}C-carbohydrates. Gas chromatographic analysis of ^{14}C-carbohydrates in the ethanol-soluble fractions was initiated by evaporating to dryness in a small test tube under a stream of nitrogen. Phenyl-ß-D-glucopyranosid was added to the tube as an internal standard. This sample in the tube was lyophilized and dissolved in 0.2 ml of 2.5% hydroxylamine in pyridine. After heating at 80-85°C for 20 min, 0.1 ml of hexamethyldisilazane and 0.1 ml of trimethychlorosilane were added. Each sample was again heated at 80-85°C for 3 min and subsequently centrifuged three times with 1 ml of hexane. The clear supernatant was allowed to stand sealed in the cool room before injection into the gas chromatograph.

The separation of ^{14}C-carbohydrates in the hexane extract was achieved by a Fractovap 2400 V model GC(Carlo Erba, Italy) using a 2 m, 4-mm O.D. glass column containing 3% silicone SE-30 on chromosorb G-AW DMCS (80-100 mesh) (Central Isotope Laboratory, Univ. Göttingen). The ^{14}C-carbohydrates were separated using temperature program of 10°C min^{-1} from 200 to 270°C following a postinjection interval of 2 min. Helium, at a flow rate of 30 ml min^{-1}, was used as the carrier gas. The ^{14}C-labeled sugars were identified by co-chromatography with authentic compounds. Each of the ^{14}C-carbohydrates separated was automatically collected in a small trap filled with quartz sand which was coated with 15% silicone oil in acetone. Subsequently, the bound radioactivity on the small traps was eluted in toluene-scintillant (Quiczint 501, Werner Zinsser, Germany). Triplicates of each sample were chromatographed, but no sample replication was possible.

Analysis of ^{14}C-amino acids. *To identify* ^{14}C-labeled amino acids, 5 μl of amino acid fractions was spotted on a thin-layer plate prepared with cellulose powder (Cell MN-300, 0.5 mm, Macherey Nagel, Germany). The plates were developed in one dimension by electrophoresis (60 mA, 600 V, 45 min, pyridine buffer pH 4.0) and in the second dimension by chromatography with the solvent system 2-butanol-formic acid-water (6:1:2, v/v) (20). The individual ^{14}C-labeled products were detected by autoradiography (X-ray film, Agfa-Gevaert). The ^{14}C-labeled amino acids were identified by co-chromatography with the authentic compounds. The ^{14}C-labeled spots were removed from the plates with a razor blade (the accompanying cellulose powder had no effect on counting efficiency) and placed in a vial containing 1 ml of 60% ethanol.

After shaking for 3 hr, the vials were filled with 10 ml of toluene-scintillant (Quiczint 212). Radioactivity in all samples was counted in a liquid scintillation counter (Philips, Central Isotope Laboratory, Univ. Gottingen). Correction for quenching was made by external standardization.

RESULTS

$^{14}CO_2$ assimilation and translocation of ^{14}C in whole plants. To determine possible differences in $^{14}CO_2$ assimilation and distribution of ^{14}C between susceptible and adult-plant-resistant cultivars 6 days after inoculation of *E. graminis* f. sp. *hordei*, the cultivars Peruvian and Asse were compared in the healthy and infected plants after fixation of $^{14}CO_2$ in whole plants at the four-leaf stage.

In healthy leaves and leaf sheathes there was no difference in the activity of ^{14}C in photoassimilates between the two cultivars, but a slightly higher radioactivity in the fourth leaves was found in the adult-plant-resistant cultivar Asse(Fig.1).

Powdery mildew infection markedly decreased the $^{14}CO_2$ assimilation in whole plants, especially in the noninfected fourth leaves and the leaf sheathes

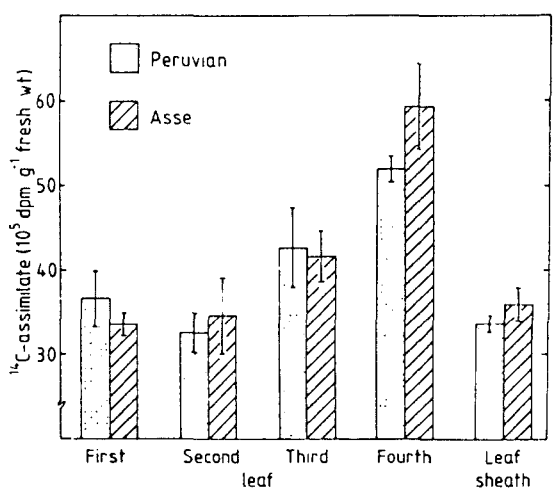

Fig. 1. ^{14}C-activities in photoassimilates in various organs of healthy plants at the four-leaf stage of spring barley cultivars Peruvian(susceptible) and Asse(adult-plant-resistant) after fixation of $^{14}CO_2$ by the whole plants. Each value is the mean of 4 replicates with one standard error.

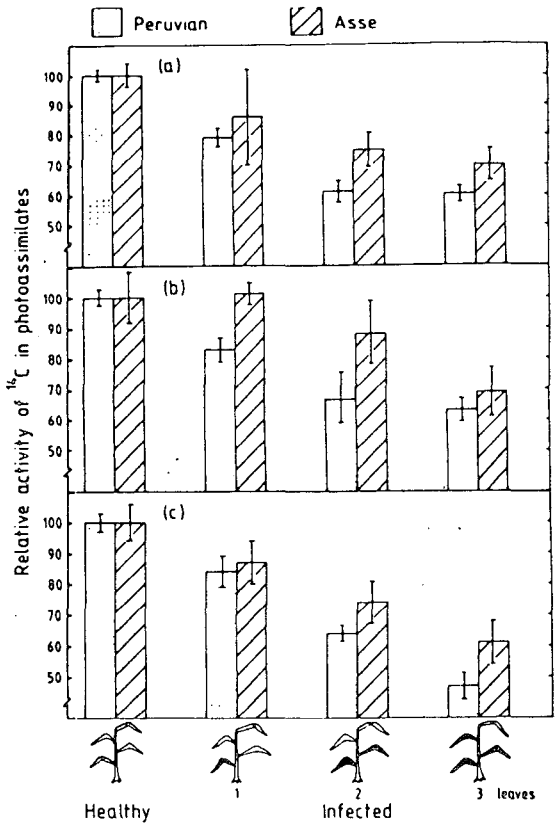

Fig. 2. Relative activities of ^{14}C in photoassimilates in (a) whole plants, (b) healthy fourth leaves and (c) leaf sheathes at the four-leaf stage of spring barley cultivars Peruvian(susceptible) and Asse(adult-plant-resistant) after fixation of $^{14}CO_2$ by the whole plants infected with powdery mildew on the lower leaves. Each value is the mean of 4 replicates with one standard error.

(Fig. 2). In the two cultivars, $^{14}CO_2$ assimilation and translocation of assimilates decreased as the number of infected leaves increased. Despite the same infection intensity, $^{14}CO_2$ assimilation was less inhibited in Asse than Peruvian. Infection reduced the fixation of $^{14}CO_2$ in noninfected fourth leaves of Peruvian more severly than that of Asse.

Metabolism of ^{14}C-assimilates in whole plants. ^{14}C incorporation into carbohydrates, organic acids and amino acids in the lower 3 leaves-mildewed and the healthy plants at the four-leaf stage was determined with the cultivars Peruvian and Asse.

Carbohydrates. More activity of ^{14}C in different tissues of barley plants was present per unit fresh weight in

fructose and glucose than in sucrose, but some ^{14}C-labeled carbohydrates were not identified (Fig. 3). In healthy plants, there were no consistent differences between the two cultivars in the activity of ^{14}C in carbohydrates, except a slightly higher activity of ^{14}C in fructose and glucose in the fourth leaves of Asse. In general, powdery mildew infection greatly reduced the activity of ^{14}C in carbohydrates in all plant organs. In the infected third leaves there was a reduction in activity of ^{14}C fixed into carbohydrates, especially glucose and fructose. Infection of the lower 3 leaves also inhibited the incorporation of ^{14}C into carbohydrates in noninfected fourth leaves and their translocation into leaf sheathes. In these two organs ^{14}C-labeled hexoses, especially glucose and fructose, were reduced in Peruvian more conspicuously than in Asse, but the activities of ^{14}C in sucrose and unknown carbohydrates were similar in the two cultivars.

Organic acids. In healthy plants, slightly more ^{14}C was fixed in organic acids in Asse than in Peruvian (Fig. 4). Powdery mildew infection markedly stimulated the incorporation of ^{14}C into organic acids in both cultivars, except for the 37% decrease in the leaf sheathes of Asse. The stimulation of ^{14}C-organic acid synthesis was more pronounced in Peruvian than in Asse. In particular, the increase in labeling of organic acids in the leaf sheathes for infected Peruvian was about 3 times as large as that for the healthy plants.

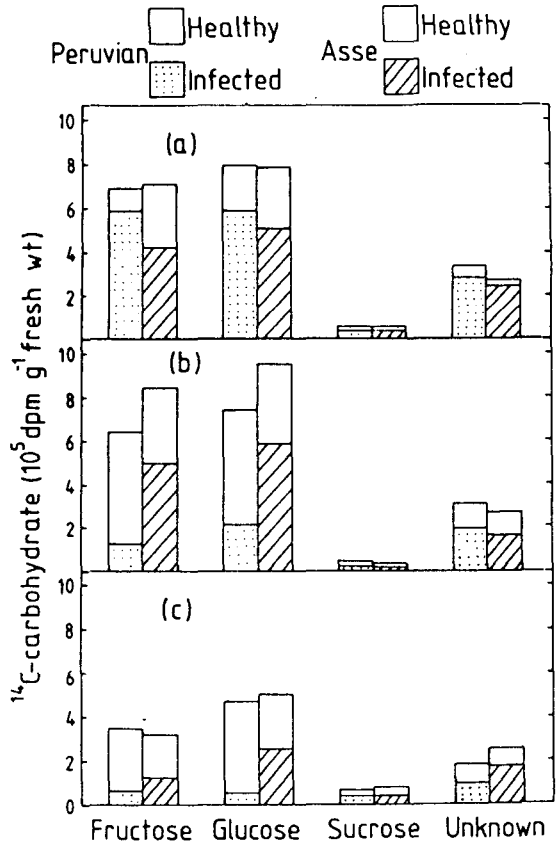

Fig. 3. ^{14}C-activities in carbohydrates in (a) the infected third, (b) healthy fourth leaves and (c) leaf sheathes at the four-leaf stage of spring barley cultivars Peruvian (susceptible) and Asse(adult-plant-resistant) after fixation of $^{14}CO_2$ by the whole plants infected with powdery mildew on the lower 3 leaves. Each value is the mean of 3 measurements for each extract from 4 barley plants.

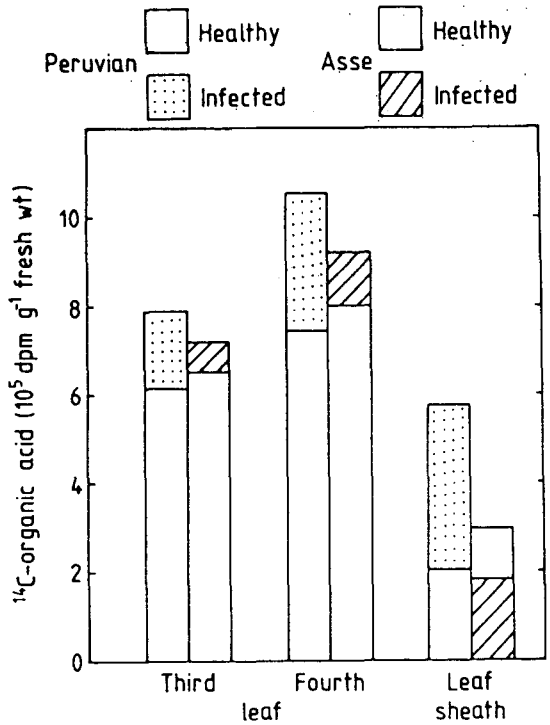

Fig. 4. ^{14}C-activities in organic acids in the infected third, healthy fourth leaves and leaf sheathes at the four-leaf stage of spring barley cultivars (susceptible) and Asse(adult-plant-resistant) after fixation of $^{14}CO_2$ by the whole plants infected with powdery mildew on the lower 3 leaves. Each value is the mean of 3 measurements for each extract from 4 barley plants. barley leaf extract. Asn=asparagine, Gly=glycine, Ser=serine, Gln=glutamine, Thr=threonine,

Amino acids. The effects of powdery mildew infection on the incorporation of ^{14}C into amino acids in different tissues of barley plants were examined determining ^{14}C-labeled amino acids in the plant tissue extracts (Fig. 5). Infection markedly increased the incorporation of ^{14}C into amino acids in infected third and noninfected fourth leaves, but reduced their translocation to the leaf sheathes (Fig. 6). The increase was greater in Peruvian than in Asse. Nevertheless, a considerable proportion of ^{14}C-amino acids were transported from the leaves into the leaf sheathes of infected plants, but there was no difference in translocation patterns between the two cultivars. Higher radioactivities (3.10^4-10.10^4 dpm g^{-1} fresh weight) were detected in glycine, serine, glutamine, alanine, glutamic acid and aspartic acid (Figs. 5 and 6). The levels of radioactivity in amino acids, with the exception of threonine, glutamic acid and aspartic acid, were higher in infected third than healthy leaves. In spite of the same infection intensity in the two cultivars, the increases in labeled asparagine, glycine, serine, glutamine, alanine, tyrosine, valine and methionine in infected third leaves were more pronounced in Peruvian than in Asse. In Peruvian there was a striking increase in labeling alanine and γ-aminobutyric acid, but Asse showed increased activities of ^{14}C in glycine, serine and glutamine. ^{14}C-tyrosine, -valine and -methionine slightly decreased in both cultivars. Infection also reduced ^{14}C-amino acids, with the

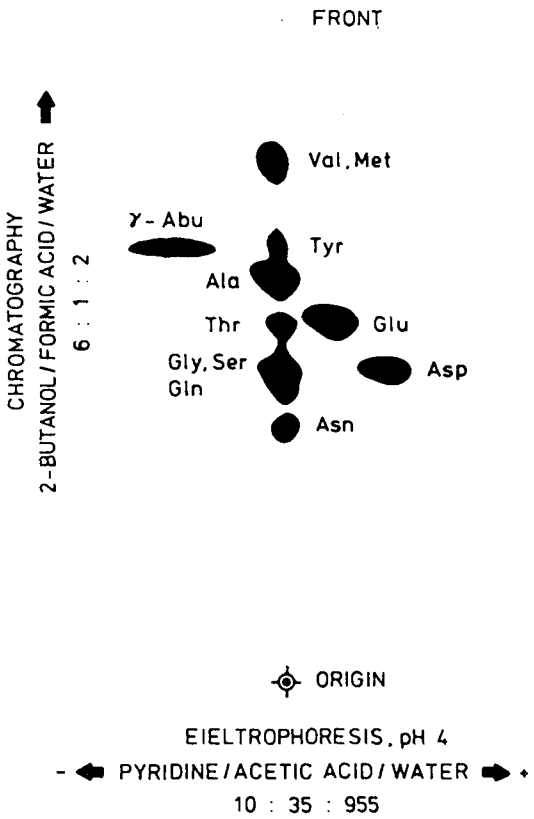

Fig. 5. A radioautogram of ^{14}C-labeled amino acids after two-dimentional separation of a spring barley leaf extract. Asn=asparagine, Gly=glycine, Ser=serine, Gln=glutamine, Thr=threonine, Ala=alanine, Tyr=tyrosine, Val=valine, Met=methionine, Glu=glutamic acid, Asp=aspartic acid, γ-Abu=γ-aminobutyric acid.

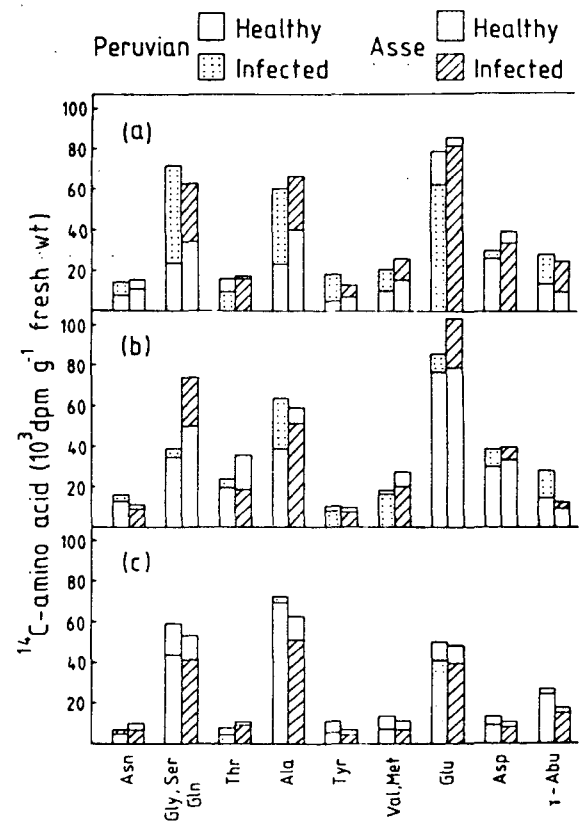

Fig. 6. ^{14}C-activities in amino acids in (a) the infected third, (b) healthy fourth leaves and (c) leaf sheathes at the four-leaf stage of spring barley cultivars Peruvian(susceptible) and Asse(adult-plant-resistant) after fixation of $^{14}CO_2$ by the whole plants infected with powdery mildew on the lower 3 leaves. Each value is the mean of 3 measurements for each extract from 4 barley plants. For abbreviations see Fig. 5.

exception of aspartic acid, in the leaf sheathes without significant differences between the two cultivars.

DISCUSSION

Since the artificial infection was not desirably obtained after the development of fifth leaves in the cultivar Asse, the plants of four-leaf stage were used for powdery mildew infection in these investigations. The more number of mildewed leaves reduced more severely $^{14}CO_2$ assimilation and translocation of ^{14}C-assimilates, the decline being more distinct with the susceptible cultivar Peruvian. As previously shown by Hwang *et al.* (13), these observations provide very strong evidence that powdery mildew infection greatly disrupts various metabolic processes in the non-infected parts of susceptible plants. It has been known that powdery mildew infection decreases photosynthesis in noninfected leaves (source site) of susceptible cultivars, but stimulates translocation of ^{14}C-assimilates from noninfected into infected leaves, as a result of the sink-effect of infected tissues (4, 8, 11, 13, 22, 24). Our earier results demonstrate that powdery mildew infection of lower leaves protected the leaf above from challenger infection, the protection being more effective in the adult-plant-resistant cultivar (9). This phenomenon could be due partly to the disordered photosynthesis and translocation by powdery mildew in noninfected upper leaves of diseased plants. In particular, the less impairmant of photosynthesis and translocation patterns by powdery mildew in adult-plant-resistant cultivars may lead to the utilization of more assimilates for the development of plants and ultimately high yields. It has been shown that powdery mildew infection on wheat plants after anthesis caused loss of grain yields due to decreased photosynthesis and translocation of assimilates into grains (1). In interpreting our results it must be considered that the data for $^{14}CO_2$ assimilation were obtained from the cultivars Peruvian and Asse under conditions of the same infection intensity. Since the adult-plant-resistant cultivars are less infected in fields, especially on the upper leaves (18), the reduction in photosynthesis and translocation may be smaller, thereby being favorable for high yields in such cultivars.

Powdery mildew infection greatly reduced the activity of ^{14}C in carbohydrates in noninfected leaves and leaf sheathes, the reduction being greater in Peruvian than Asse. An interesting fact is that in the infected third leaves there was a greater reduction in $^{14}CO_2$ assimilation in Peruvian (13), but more ^{14}C-labeled carbohydrates, organic acids and amino acids were retained in Peruvian in comparison to Asse. This phenomenon could well explain a greater mobilization of metabolites to the sites of infection and an increased host metabolic activity favoring infection on susceptible cultivars compared to adult-plant-resistant cultivars (11).

As previously reported by Daly *et al.* (3), and Edwards and Allen (5), the ^{14}C-organic acids associated with the tricarboxylic acid cycle were accumulated in mildewed and noninfected leaves during $^{14}CO_2$ assimilation. In contrast, Magyarosy *et al.* (16) reported a relative decrease of organic acids in chloroplasts isolated from powdery mildew-infected sugar beet leaves. The fact that ^{14}C-organic acid in infected plants increased in Peruvian more than in Asse may be a reflection of drastically increased respiratory activity which provides a favorable environment for fungal development, consequently leading to the starvation for energy in suceptible cultivars (19, 23). The development of a an increased rate of respiration may be accompanied by marked physiological and biochemical changes involving the synthesis of enzymes (6, 7, 11, 21).

The findings that a rise in biosynthesis of ^{14}C-amino acids, in spite of same infection intensity, was more marked in Peruvian than in Asse suggest that in susceptible cultivars the metabolic activity in infected plants is markedly promoted in the direction favorable for powdery mildew development by the increased activity of enzymes in comparison with adult-plant-resistant cultivars.

The carbon skeletons of the common amino acids are derived from a very few metabolic intermediates, each of which is associated with a central metabolic pathway, out of reactions of carbon fixation, glycolysis, and the tricarboxylic acid cycle (2). Our results show that ^{14}C-incorporation into the most amino acids in infected leaves was remarkably great in the susceptible cultivar Peruvian. As many organic acids are strongly compartmentalized in plant cells (17), a greater in-

crease of ^{14}C-alanine content in infected leaves of Peruvian could be associated with the availability of pyruvate, which acts as amino acceptor in the direct synthesis of alanine by transamination. Glycine and serine are known to be metabolized in the peroxisomes from gycolate, a substrate for photorespiration (25). Edwards and Allen (5) have reported an increase in labeled serine in barley leaves infected with powdery mildew. Recently, Walters and Ayres (26) have shown a stimulated photorespiration in barley leaves after inoculation with an incompatible race of *E. graminis* f. sp. *hordei*. The great ^{14}C-incorporation in glycine and serine in Peruvian suggests that in susceptible barley cultivars there would be an increased photorespiration in infected leaves based on stimulated activity of peroxisomes.

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