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## Some effects of exposure to sulphur dioxide on the metabolism of Scots pine in winter. II. Effects on the photosynthetic carbon metabolism\*

### Abstract

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The effect of sulphur dioxide was examined on the uptake of  $^{14}\text{CO}_2$  and the distribution of  $^{14}\text{C}$  among photoassimilates during the winter depression of activity and emergence from it in  $\text{SO}_2$ -tolerant,  $\text{SO}_2$ -relatively tolerant and  $\text{SO}_2$ -susceptible clones of Scots pine (*Pinus sylvestris* L.). Detached twigs were treated with 1.0 ppm  $\text{SO}_2$ , 6 h daily over 3 consecutive days. The fumigated twigs were then exposed to  $^{14}\text{CO}_2$  for 5 min. Low winter temperatures and exposure to  $\text{SO}_2$  inhibited the subsequent total  $^{14}\text{CO}_2$  uptake, decreased the percentage of label in starch, glycolate, glycine and serine. On the other hand there was a marked increase in the percentage of label in sucrose, aspartate, glutamate, alanine and malate. The degree of inhibition or stimulation varied with the susceptibility of trees to  $\text{SO}_2$  and was greatest in the most susceptible one.

*Additional key words:* *Pinus sylvestris*,  $^{14}\text{CO}_2$  uptake, photoassimilates.

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### INTRODUCTION

The inter- and intraspecific variation in resistance to  $\text{SO}_2$  has been widely studied, however the mechanisms responsible for these differences are little understood.

It has been suggested that the variation in  $\text{SO}_2$  resistance which exists between plants could reflect differences in the rate of  $\text{SO}_2$  absorption (Caput et al. 1978), in  $\text{SO}_2$  avoidance (Bressan et al. 1978), in stomatal conductance and in resistance of photosynthesis to  $\text{SO}_2$  (Winner and Mooney 1980), and in biochemical (enzymatic or nonenzymatic) detoxication of  $\text{SO}_2$  incorporated into cells (Kieliszewska-Rockicka 1979).

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Abbreviations: RuDP - ribulose 1,5 biphosphate, PEP - phosphoenolpyruvate.



Studies on the level of variation in the sensitivity of plants to  $\text{SO}_2$  basically concentrate on herbaceous plants (Bressan et al. 1978, Omura et al. 1980). It is rarely that differences in the  $\text{SO}_2$  phytotoxicity are being investigated on trees, particularly coniferous ones (Börtitz 1969, Eckert and Houston 1980). This is most probably caused by differences in the activity of trees during the vegetative season and the related variability in the degree of injury by  $\text{SO}_2$  (Czarnowski 1977). Thus the majority of results concern the effect of  $\text{SO}_2$  on trees during the summer period, i.e. when the photosynthetic activity is at its maximum. There is very little data on the variation in  $\text{SO}_2$  resistance during the winter and after warming up in the spring.

In an earlier study (Lorenc-Plucińska 1986) it has been shown that the action of  $\text{SO}_2$  on Scots pine during the winter and later as the weather warms up causes a much greater depression of photosynthesis ( $P_N$ ) and photorespiration ( $R_L$ ) in the sensitive clones than in the tolerant ones. On the other hand the direction of change in dark respiration ( $R_D$ ) was different depending on the duration of fumigation with  $\text{SO}_2$  and the time of warming up.

In the present study the influence of  $\text{SO}_2$  under controlled conditions was investigated during winter depression of  $\text{CO}_2$  exchange and after its termination due to warming up on the assimilation of  $^{14}\text{CO}_2$  and the distribution of  $^{14}\text{C}$  among the first products of photosynthesis in Scots pines differing in resistance to  $\text{SO}_2$ .

#### MATERIAL AND METHODS

Current year twigs of Scots pine (*Pinus sylvestris* L.), that is grown in the preceding vegetative season, have been used in the study. They were collected from 18 years old clones differing in susceptibility to  $\text{SO}_2$ . They are registered in the Institute of Dendrology under the numbers K-08-02 (tolerant to  $\text{SO}_2$  - T), PSI-6 (relatively tolerant to  $\text{SO}_2$  - I) and K-01-16 (susceptible to  $\text{SO}_2$  - S) (Lorenc-Plucińska 1982).

The twigs were treated with  $\text{SO}_2$  for 3 days, 6 h a day at a concentration of 1.0 ppm according to the method of Karolewski and Białobok (1979). Twigs which were detached at the same time were left in  $\text{SO}_2$  free air to be used as controls. The products of photosynthesis labelled with radioactive carbon were synthesized directly after the third fumigation. Twigs were placed in a photosynthetic chamber with plexiglass integrated with a closed circulation system of 2.67 l capacity. After 20 min of pre-illumination with  $240 \text{ W m}^{-2}$  irradiance at 18-20°C in a normal atmosphere  $^{14}\text{CO}_2$  was introduced into the system. The total radioactivity introduced was 100  $\mu\text{Ci}$  and the initial  $\text{CO}_2$  concentration was 0.04%. The twigs were exposed to  $^{14}\text{CO}_2$  for 5 min. Photosynthesis was stopped by killing the needles in boiling 80% ethanol.

The methods employed for extraction, separation and radioactivity assays of the photosynthetic products have been described by Grishina et al. (1974). The following photosynthetic products were analysed: glucose + fructose, sucrose, raffinose + maltose, starch, glycolate + glycine + serine, alanine, malate, aspartate + glutamate.



The results presented are the mean values obtained from 10  $\text{SO}_2$ -treated twigs and 10 unfumigated controls from each of the three pine clones. The experiment was performed in the winter (January).

## RESULTS

Fig. 1 illustrates the intensity of  $^{14}\text{C}$  assimilation by pine needles after 5 min of exposition in an atmosphere of  $^{14}\text{CO}_2$  in light. The intensity of  $^{14}\text{CO}_2$  assimilation by needles of the tolerant clone and by the relatively tolerant clone after they were

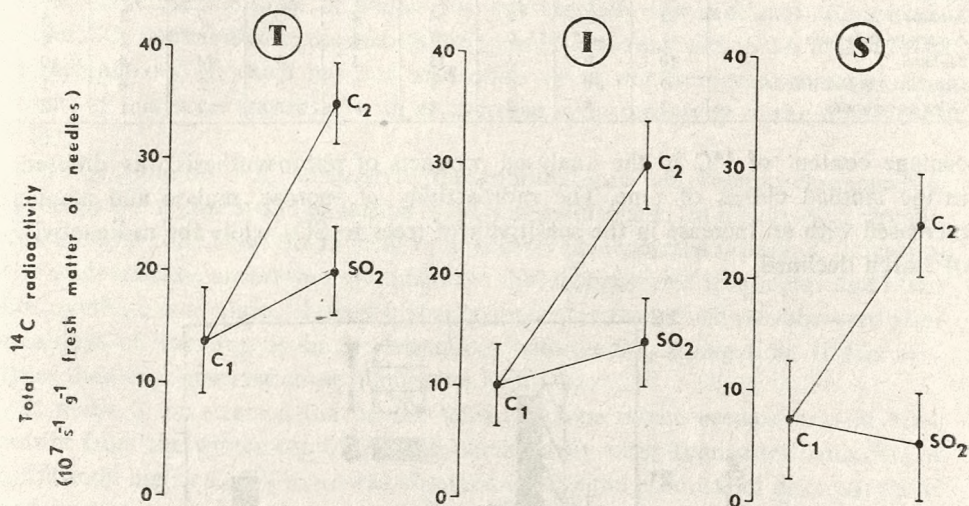


Fig. 1. The effect of  $\text{SO}_2$  action on  $^{14}\text{CO}_2$  uptake after 5 min of photosynthesis of Scots pine twigs (in January)

C<sub>1</sub> - control, 1 h after transferring twigs from natural conditions into the laboratory, C<sub>2</sub> - control (unfumigated twigs) 3 d after transferring twigs from natural conditions into the laboratory, SO<sub>2</sub> - twigs treated with 1.0 ppm  $\text{SO}_2$  for 3 d, 6 h per day. T - clone tolerant to  $\text{SO}_2$ , I - clone relatively tolerant to  $\text{SO}_2$ , S - clone sensitive to  $\text{SO}_2$ . Bars indicate standard errors of the means.

transferred from the cold conditions ( $+5^\circ\text{C}$ ) into the laboratory ( $+20^\circ\text{C}$ ) was much lower compared to that which was noted after three days of maintaining twigs in the conditions of room temperature and after treating the twigs for 3 days 6 h daily with  $\text{SO}_2$ . On the other hand in the sensitive clone the intensity of  $^{14}\text{CO}_2$  assimilation by twigs transferred from the field into the laboratory was similar to that observed after exposition to  $\text{SO}_2$ , but substantially lower than observed after 3 days of maintenance in warm room temperature conditions without  $\text{SO}_2$ .

In Table 1 the percentage content of assimilated  $^{14}\text{C}$  in the analysed products of photosynthesis is presented. After transfer of twigs from natural conditions into the laboratory it was found that the labelled carbon is being incorporated primarily into sucrose and glucose + fructose and to a lesser extent into malate, then into starch, aspartate + glutamate, alanine, glycolate + glycine + serine and raffinose, but not maltose (no colour stain for maltose in the raffinose + maltose spot). The per-



Table 1

Effect of SO<sub>2</sub> on the patterns of relative label distribution after 5 min of <sup>14</sup>C fixation by needles in light (in January)

Otherwise: see Fig. 1.

| Compounds                    | % of total <sup>14</sup> C fixed |                |                 |                |                |                 |                |                |                 |
|------------------------------|----------------------------------|----------------|-----------------|----------------|----------------|-----------------|----------------|----------------|-----------------|
|                              | T                                |                |                 | I              |                |                 | S              |                |                 |
|                              | C <sub>1</sub>                   | C <sub>2</sub> | SO <sub>2</sub> | C <sub>1</sub> | C <sub>2</sub> | SO <sub>2</sub> | C <sub>1</sub> | C <sub>2</sub> | SO <sub>2</sub> |
| Glucose + fructose           | 18                               | 10             | 7               | 17             | 11             | 7               | 10             | 12             | 5               |
| Raffinose                    | 5                                |                |                 | 3              |                |                 | 5              |                |                 |
| Raffinose + maltose          |                                  |                | 11              |                |                | 10              |                |                | 18              |
| Sucrose                      | 34                               | 14             | 30              | 39             | 16             | 33              | 44             | 20             | 35              |
| Starch                       | 15                               | 56             | 27              | 12             | 50             | 25              | 10             | 43             | 15              |
| Alanine                      | 5                                | 1              | 5               | 4              | 2              | 5               | 7              | 2              | 4               |
| Aspartate-glutamate          | 7                                | 2              | 7               | 7              | 2              | 5               | 6              | 2              | 8               |
| Malate                       | 10                               | 2              | 5               | 13             | 3              | 7               | 14             | 4              | 10              |
| Glycolate + glycine + serine | 3                                | 10             | 6               | 3              | 8              | 5               | 2              | 6              | 2               |
| Other compounds              | 3                                | 5              | 2               | 2              | 8              | 3               | 2              | 11             | 2               |

centage content of <sup>14</sup>C in the analysed products of photosynthesis was different in the studied clones of pine. The radioactivity of sucrose, malate and alanine increased with an increase in the sensitivity of trees to SO<sub>2</sub> while the radioactivity of starch declined.

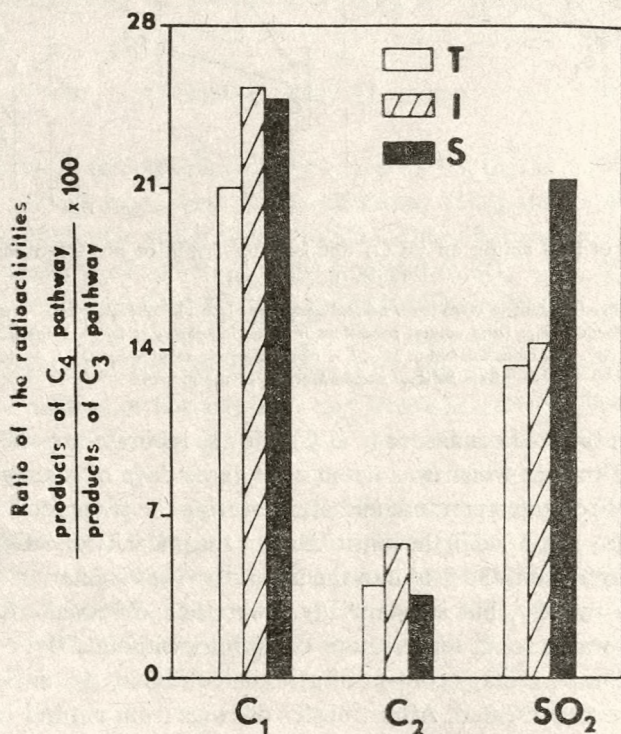


Fig. 2. Effect of SO<sub>2</sub> on the radioactivity ratio  $\frac{\text{products of C}_4 \text{ pathway}}{\text{products of C}_3 \text{ pathway}}$  in pine needles after 5 min of <sup>14</sup>C-fixation in light

Otherwise: see Fig. 1



After three days of holding twigs at room temperature a percentage change was observed in the content of assimilated  $^{14}\text{C}$  in individual products. It was manifest by a substantial, almost three-fold increase in the incorporation of labelled carbon into starch and glycolate+glycine+serine, particularly in the tolerant clone. At the same time the participation of assimilated  $^{14}\text{C}$  declined in all other products of photosynthesis.

On the other hand as a result of the action of  $\text{SO}_2$  the percentage content of labelled products of photosynthesis was similar to that observed in the needles immediately after transfer from the natural low temperature conditions except for glucose+fructose the label of which was substantially lowered after fumigation. Besides,  $\text{SO}_2$  contributed to the incorporation of  $^{14}\text{C}$  into maltose, that is to a product the radioactivity of which has not been observed in non-fumigated material. The content of this sugar increased with an increase in the sensitivity of the pine clones to  $\text{SO}_2$ .

In Fig. 2 the ratio of radioactivity incorporated into the products characteristic for the  $\text{C}_4$  and  $\text{C}_3$  pathways of carbon reduction is illustrated. In the material straight from the cold conditions the ratio of radioactivity incorporated into the  $\text{C}_4$  dicarboxylic acids (malate, aspartate+glutamate) to that incorporated into sugars and other photosynthates was almost 4 times higher compared to that which was observed after three days of warming up in the laboratory without  $\text{SO}_2$  fumigation. It was also higher than that observed after fumigation with  $\text{SO}_2$ .

It needs to be stressed that in the sensitive clone in the needles straight after transfer from the winter conditions and particularly after fumigation with  $\text{SO}_2$  a significantly higher  $\text{C}_4/\text{C}_3$  ratio was observed among the products of photosynthesis compared to the tolerant and relatively tolerant clone.

## DISCUSSION

The presented results indicate that  $\text{SO}_2$  changes the intensity of  $^{14}\text{CO}_2$  assimilation and the metabolism of carbon in a similar manner as low temperature does, and the similarities in the inhibition of photosynthesis by these two stress agents increase with an increase in the sensitivity of the studied trees to  $\text{SO}_2$  (Fig. 1).

Literature reports indicate that the winter depression in photosynthesis in coniferous trees is caused by the inactivation of chloroplasts, a decline in the transport of electrons from water to NADP, a lower permeability of the cuticle to  $\text{CO}_2$  and an increase in the resistance of mesophyll to  $\text{CO}_2$  penetration (Hashimoto and Suzuki 1978, Martin et al. 1978). A reduction in the photosynthetic assimilation of  $\text{CO}_2$  under the influence of  $\text{SO}_2$  is also usually explained by injuries to chloroplasts (Malhotra 1976), by changes in resistance of leaves (Sisson et al. 1981) or by an inhibition of carboxylation (Gezelius and Hällgren 1980).

Similarly as low temperature  $\text{SO}_2$  resulted in a reduced incorporation of  $^{14}\text{C}$  into starch and glycolate+glycine+serine while at the same time an increase in label is



observed in sucrose, malate and aspartate + glutamate. On the other hand low temperature caused an increase in the incorporation of  $^{14}\text{C}$ -glucose + fructose while  $\text{SO}_2$  into maltose which was not observed in non-fumigated material (Tab. 1).

It is reported that a winter accumulation of sucrose and monosaccharides as a result of starch hydrolysis lowers the freezing temperature of water in the tissues, stabilizes lipoprotein membranes of chloroplasts and mitochondria and constitutes the main source of energy for oxidation (Heber 1968, Santarius and Heber 1972).

On the other hand Koziol and Jordan (1978) and Koziol and Cowling (1980) suggest that increased amounts of free carbohydrates and decreased starch after exposure to  $\text{SO}_2$  might serve as readily accessible substrates for respiratory/repair metabolism. Energy utilisation of these substrates is reflected in increased respiration. As injury to plants by  $\text{SO}_2$  increases a greater amount of energy is needed for its repair, as a result of which the level of sugars will become lower as respiration increases (Koziol and Jordan 1978).

In our study an inhibition of the rate of  $^{14}\text{CO}_2$  assimilation as well as an accumulation of soluble sugars due to the action of  $\text{SO}_2$  was greatest in the clone most sensitive to this gas. On the other hand an increase in respiration after exposition to  $\text{SO}_2$  was noted only in the tolerant clone (Lorenc-Plucińska 1982), in which the reduction of photosynthesis and the accumulation of sucrose and raffinose + maltose was lower than in the other trees (Fig. 1 and Tab. 1). Thus the commonly accepted hypothesis of Koziol and Jordan (1978) is only partially capable of explaining the results. It needs to be remembered however that the increased level of soluble sugars may have an inhibitory effect on the activity of RuDP carboxylase, the consequence of which is a lowering of photosynthesis.

Exposition to  $\text{SO}_2$  and the low winter temperature (winter stress) have lowered the level of labelled glycolate + glycine + serine (Tab. 1). Incorporation of  $^{14}\text{C}$  into these products declined proportionately with an increase in the sensitivity of the trees to  $\text{SO}_2$ . This inhibition is reflected also in the inhibition of photorespiration (Lorenc-Plucińska 1982). Decrease in the accumulation of the glycolic acid pathway intermediates and of the rate of photorespiration cannot be regarded simply as a consequence of glycolate oxidase inhibition or glycolate synthesis caused by  $\text{SO}_2$  as it is commonly assumed (Libera et al. 1975).

It has already been shown that the action of  $\text{SO}_2$  changes the content of individual amino acids and organic acids (Jäger and Grill 1975, Malhotra and Sarkar 1979, Sarkar and Malhotra 1979). In the present investigation both the action of  $\text{SO}_2$  and the low temperatures (winter stress) have contributed to an increase in the labelling with radioactive carbon of malate, aspartate + glutamate and alanine (Tab. 1). Particularly the labelling of malate increased significantly together with an increase in the sensitivity of the studied pines to  $\text{SO}_2$ .

The high radioactivity of malate was the decisive factor in the increase of the ratio of radioactivity in the  $\text{C}_4/\text{C}_3$  products in the material under winter conditions compared to the control after 3 days of maintenance under room temperature (Fig. 2). This result might indicate that during the winter PEP carboxylation is injured less than RuDP.



A lowering of the level of activity of carboxylase RuBP during winter stress has been observed by Öquist et al. (1980) and Gezelius and Hallen (1980). The latter authors have established that in the middle of the winter RuBP carboxylase extracted from needles of Scots pine demonstrated only 50% activity of the summer period.

Changes in the level of glutamate, aspartate, alanine or malate under the influence of SO<sub>2</sub> and the reasons for them and consequences have been already well documented (Jäger 1977, Hällgren 1978).

However in the present study it needs to be stressed that the increase in the radioactivity of malate was differentiated depending on the degree of sensitivity of the studied trees to SO<sub>2</sub>. In the sensitive clone the labelling of malate was twice as high as in the tolerant one (Tab. 1). This difference was one of the main reasons why the proportion of radioactivity passing through the C<sub>4</sub>/C<sub>3</sub> pathways after the action of SO<sub>2</sub> was 60% higher in the sensitive clone compared to the other ones (Fig. 2). This result may indicate that in the sensitive clone after fumigation with SO<sub>2</sub> there is a greater need for compounds which could be carriers of a reductive potential (malate), and therefore an accumulation of NADPH and inhibition of Calvin's cycle may result.

The results presented have demonstrated that: 1° during the winter under the influence of SO<sub>2</sub> there occur abnormalities in the carbon metabolism during photosynthesis evidenced by an increased labelling primarily of malate and sucrose, which was also observed during the summer (Lorenc-Plucińska 1982); 2° the direction of metabolic changes in carbon assimilation are similar under the influence of an SO<sub>2</sub> stress as during the winter depression; 3° the pine clones previously selected on the basis of differences in visible needle injuries following SO<sub>2</sub> treatment (Lorenc-Plucińska 1982) maintain their differential sensitivity to this gas also during the winter.

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#### SUMMARY

The effect of sulphur dioxide was examined on the uptake of <sup>14</sup>CO<sub>2</sub> and the distribution of <sup>14</sup>C among photoassimilates during the winter depression of activity and emergence from it in SO<sub>2</sub>-tolerant, SO<sub>2</sub>-relatively tolerant and SO<sub>2</sub>-susceptible clones of Scots pine (*Pinus sylvestris* L.). Detached twigs were treated with 1.0 ppm SO<sub>2</sub>, 6 h daily over 3 consecutive days. The fumigated twigs were then exposed to <sup>14</sup>CO<sub>2</sub> for 5 min. The labelled soluble sugars, starch, amino acids and dicarboxylic acids were fractionated and determined using ion-exchange chromatography, paper chromatography and autoradiography. Low winter temperatures and exposure to SO<sub>2</sub> inhibited the subsequent total <sup>14</sup>CO<sub>2</sub> uptake, decreased the percentage of label in starch, glycolate, glycine and serine. The degree of inhibition varied with the susceptibility of trees to SO<sub>2</sub> and was greatest in the most susceptible one. On the



other hand there was a marked increase in the percentage of label in sucrose, aspartate, glutamate, alanine and malate. Changes in  $^{14}\text{C}$  labelling of sucrose and especially of malate increased to a much greater degree in susceptible individuals than in tolerant ones. It is concluded that cold winter temperatures and  $\text{SO}_2$  fumigation alters  $^{14}\text{CO}_2$  uptake and the carbon reduction in photosynthesis in a similar manner. Fumigation with  $\text{SO}_2$  during wintertime (in controlled conditions) distinctly hampered the labelling of the  $\text{C}_3$  pathway and the products of  $\beta$ -carboxylation increased. These disturbances are dependent on the degree of susceptibility of trees to  $\text{SO}_2$ .

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### *Wpływ $\text{SO}_2$ na metabolizm sosny zwyczajnej podczas zimy. II. Wpływ na metabolizm węgla w fotosyntezie*

#### Streszczenie

Badano wpływ dwutlenku siarki na asymilację  $^{14}\text{CO}_2$  i metabolizm węgla w fotosyntezie podczas zimowej depresji i po jej przełamaniu wraz z ociepleniem u  $\text{SO}_2$ -tolerancyjnego,  $\text{SO}_2$ -względnie tolerancyjnego i  $\text{SO}_2$ -wrażliwego klonu sosny. Obcięte pędy traktowano  $\text{SO}_2$  w stężeniu 1,0 ppm przez 3 dni po 6 godz. dziennie. Ekspozycja pędów w atmosferze znacznego dwutlenku węgla trwała 5 min i następowała bezpośrednio po ukończeniu fumigacji. Zawartość radioaktywnych cukrów rozpuszczalnych, skrobi, aminokwasów i kwasów dwukarboksylowych oznaczano za pomocą chromatografii jonowymiennej, bibulowej i autoradiografii.

Niska temperatura podczas zimy oraz dwutlenek siarki hamują asymilację  $\text{CO}_2$  i obniżają procentową zawartość radioaktywnej skrobi, glikolanu, glicyny i seryny. Obniżenie zależało od stopnia wrażliwości badanych klonów na  $\text{SO}_2$  i było największe w klonie wrażliwym. Z drugiej



strony notowano znaczny wzrost zawartości radioaktywnej sacharozy, asparagianu, glutamianu, alaniny i jabłczanu. Zmiany w znakowaniu sacharozy, a szczególnie jabłczanu były znacznie większe w klonie wrażliwym w porównaniu z tolerancyjnym.

### ГАБРИЭЛЯ ЛОРЕНЦ-ПЛЮЦИНЬСКА

*Влияние SO<sub>2</sub> на метаболизм углерода сосны обыкновенной в зимний период.*  
2. *Влияние на метаболизм углерода в фотосинтезе*

#### Резюме

Исследовали влияние сернистого ангидрида на ассимиляцию <sup>14</sup>CO<sub>2</sub> и метаболизм углерода в фотосинтезе в период зимней депрессии и после ее прохождения во время оттаивания у SO<sub>2</sub> — устойчивого, SO<sub>2</sub> — относительно устойчивого и SO<sub>2</sub> — чувствительного клона сосны. Срезанные ветки обрабатывали SO<sub>2</sub> в концентрации 1.0 частей/млн в течение 3 дней по 6 часов в день. Побеги экспонировали в присутствии меченой двуокиси углерода в течение 5 минут непосредственно после газации. Содержание меченых растворимых сахаров, крахмала, аминокислот и дикарбоксиловых кислот определяли путем ионообменной и бумажной хроматографии и автордиографии.

Низкая температура в зимний период, а также сернистый ангидрид тормозили ассимиляцию CO<sub>2</sub> и понижали процентное содержание меченого крахмала, гликолевой кислоты, глицина и серина. Понижение зависело от степени чувствительности исследуемых клонов к SO<sub>2</sub> и было самым значительным в чувствительном клоне. С другой стороны, отмечено значительный рост радиоактивного сахара, аспарагиновой, глутаминовой и яблочной кислот, а также аланина. Изменения в мечении сахара, а в особенности яблочной кислоты были значительно большими у чувствительного клона по сравнению с толерантным.