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Influence of SO_2 on CO_2 assimilation and carbon metabolism in photosynthetic processes in Scots pine*

INTRODUCTION

The photosynthetic capacity of plants is inhibited by SO_2 concentrations higher than 0.11 ppm (Börtitz 1964, Vogl 1964, Lorenc-Plucińska 1978b). Such inhibition occurs long before leaf necrosis becomes evident (Hällgren and Huss 1975). In woody plants the sensitivity of photosynthetic processes to SO_2 increases as general metabolic activity increases in late spring and early summer (Lorenc-Plucińska 1978b).

The mechanism of inhibition of photosynthesis by SO_2 is partly explained by Mukerji and Yang (1974) and Ziegler (1972, 1973). The mechanism appeared to be related to „competition" between CO_2 and SO_2^{--} for active places in ribulose-1,5-biphosphate carboxylase or phosphoenolpyruvate carboxylase.

The influence of SO_2 on carbon metabolism in the photosynthetic process has not been satisfactorily explained. Literature data for this topic are fragmentary. Arndt (1970) and Godzik and Linskens (1974) reported an increase in free amino acids in barley, increased radioactivity in glycolic acid and in sugar phosphates with a simultaneous decrease of ^{14}C incorporation into sucrose and photosynthetic pigments (Spedding and Thomas 1973). SO_2 induced higher ^{14}C incorporation by soluble sugars and lower incorporation by starch in bean plants (Mudd 1979).

The details of effects of SO_2 on photosynthetic processes in woody plants have not been adequately studied. The present study was undertaken on the changes occurring under the influence of SO_2 on the CO_2 assimilation rate and on carbon metabolism of Scots pine. Another

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objective was to study the sensitivity to SO_2 of metabolic processes in trees known to vary in SO_2 tolerance.

Abbreviations: RuBP — ribulose-1,5-bisphosphate, PEP — phosphoenolpyruvate, PGA — 3-phosphoglycerate, GDH — glutamate dehydrogenase, ppm — parts per million, dpm — decompositions per minute.

MATERIAL AND METHODS

PLANT MATERIAL

One-year-old shoots of Scots pine were used. They were collected from three specimens c. 15 years old. Two of them registered in the Institute of Dendrology as K-08-02 III and K-01-16 I, were ortets of plus trees, growing in a seed orchard in the Zwierzyniec Experimental Forest near Kórnik. The third specimen, registered as PSI-6 was located in a Scots pine plantation in the vicinity of Kórnik.

Detached shoots were transported to the laboratory with their bases in water. Before the experiment started they were shortened once again under a stream of water.

The three specimen trees were selected on the basis of a series of experiments established in order to determine their sensitivity to SO_2 (Białobok and Karolewski 1978). The excised shoots were placed in vessels with water and exposed to SO_2 according to the scheme presented in Table 1. SO_2 injury was estimated as earlier (Lorenc-Plucińska 1978b). Average data, given in Table 1 for the degree of injuries are calculated from the difference of injuries between the gas treated shoots and the controls. They can be thus considered as the gas-caused injuries. Least injury was observed on specimen K-08-02 III (tolerant), its greater intensity on PSI-6 (relatively tolerant), and most injury on K-01-16 I (susceptible). Measurements of CO_2 assimilation and investigation of the carbon metabolism were carried out on those specimens. Excised shoots are often used in such experiments. Polster and Weise (1962) and Poskuta et al. (1967) reported that data obtained on

Table I

Injuries (averages) on the SO_2 treated shoots

Date	14 - 20 V 1976	25 - 29 VI 1976	27 - 29 VII 1976	24 - 26 VIII 1976	3 - 6 IX 1976
SO_2 concentration	5.0 ppm	8.0 ppm	2.0 ppm	2.0 ppm	2.0 ppm
Duration of SO_2 treatm.	36 h	30 h	18 h	18 h	18 h
	6×6 h	5×6 h	3×6 h	3×6 h	3×6 h
Tree symbol	degree of injuries (average)				
K-08-02 III	0.00	0.05	0.83	0.42	0.12
PSI-6	0.88	0.60	2.57	3.14	0.41
K-01-16 I	1.91	3.42	2.56	4.72	4.05

detached and intact shoots were comparable provided the shoots were well supplied with water.

In order to study the influence of SO_2 on carbon metabolism of leaves of different age experiments were conducted at three different times: spring 10 Apr. — 15 May, summer 15 June — 20 Aug., autumn 15 Sept. — 25 Oct.

Twenty SO_2 — treated shoots and twenty unfumigated controls were used in each experiment.

SO_2 DOSAGE

SO_2 dosage was controlled automatically with a Mikolyt-2 analyzer, produced by Junkalor, Dessau (DDR). The instrument functions as an analyzer as well as an SO_2 metering device. A detailed description of the fumigation chambers as well as metering and analyzing system was given by Białobok et al. (1978).

Experimental shoots were treated with SO_2 at 2.0 ppm, a concentration similar to that used in order studies (Enderlein and Vogl 1966, Constantinidou and Kozlowski 1979). The shoots were exposed to SO_2 for three days, six hours a day, with each fumigation beginning between 7 and 9 A.M. Control shoots, detached simultaneously were put into a similar chamber but with an inside atmosphere free of SO_2. Measurements of CO_2 assimilation and of carbon metabolism during the photosynthesis were made immediately after the third fumigation. Separate shoots were placed in the fumigation chamber at 15 to 30 minute intervals to allow for the difference in time at which shoots were collected following SO_2 fumigation.

Shoots were put into the fumigation and control chamber in vessels with a narrow necks. A hard paper circle was put between the shoot and the opening of the neck and the bottle tightly wrapped with polyethylene foil. The SO_3^{--} — ions content in the water in bottles located in the fumigation chamber was colorimetrically tested in a spectrophotometer by a p-rozalinine method (West and Goeke 1956). There was no increase in SO_3^{--} — ions in water after the end of the fumigation period.

DETERMINATION OF PHOTOSYNTHESIS PRODUCTS LABELLED WITH ^{14}C

Shoots were placed in a chamber for photosynthesis made from metaplex with a water jacket outside. The end of the shoot extending outside the chamber was immersed in water. The shoots were initially illuminated for twenty minutes to adapt them to the conditions of the experiment. Two halogen lamps of 1000 W each served as a light source, the intensity of radiation being 240 Wm^{-2}. Temperature in the chamber was 293 ± 2°K. The chamber itself (marked *KR* on the scheme — Fig. 1) was included in a closed circuit system together with a membrane pump

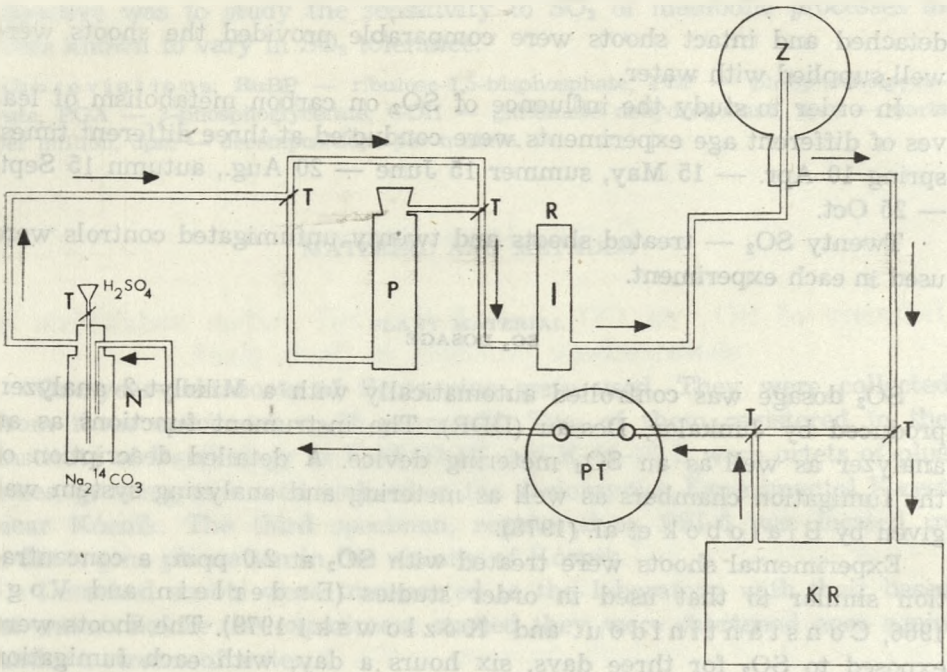

Fig. 1. Scheme of the $^{14}CO_2$ fixation system

(*PT*), a rotameter for gas flow measurement with the system (*R*), a vessel for $^{14}CO_2$ liberation (*N*), three-way valves (*T*), a gas surge (compensation) tank (*Z*) and a $^{14}CO_2$ absorber ($Ca(OH)_2$+NaOH) (*P*). The rate of air flow was 4 l/min and total volume of the measuring device was 2.67 l. Photosynthesis was measured in an atmosphere containing 380 ppm of CO_2 marked with ^{14}C in a ratio of 100 uCi. The radioactive CO_2 has been liberated from $Na_2{}^{14}CO_3$ following addition of 5N H_2SO_4. The shoots were exposed to $^{14}CO_2$ in light for 5 minutes. Needles were than detached from the shoot, weighted, and immersed in a 80% boiling alcohol. Incorporation of radioactive carbon into sugar phosphates, soluble sugars, starch, amino acids and organic acids were determined as well as into particular compounds within those fractions. Ion-exchange chromatography, paper chromatography and autoradiography were used (W j a r k et al. 1968 and G r i s h i n a et al. 1974).

QUANTITATIVE DETERMINATION OF RADIOACTIVITY

Amounts of ^{14}C absorbed by each fraction and by separate compounds within each fraction were determined by scintillation counting Packard, model 3375 (Packard Instruments Company, Inc. USA). Data from two growing seasons were evaluated to weighed averages according to the least squares method (B r a n d t 1974). Results were tested by analysis of variance and the multiple confidence interval of Tukey. The total

amount of ^{14}C absorbed was considered a measure of the rate of photosynthesis. The rate was expressed as the amount of ^{14}C absorbed (minute) g of fresh weight of needles (dpm $\times$ g^{-1} fr. wt. of needles).

RESULTS

TOTAL ^{14}C INCORPORATION

The rate of $^{14}CO_2$ incorporated differed greatly among trees and during the season (Table 2). Uptake of $^{14}CO_2$ was lowest in autumn, increased in spring and reached a maximum during the summer.

Fumigation with SO_2 caused considerable reduction of ^{14}C uptake in all specimens (Table 2). The greater the sensitivity of a tree to SO_2, the greater was the inhibition (Fig. 2). There was also a significant interaction observed between the SO_2 action (compared with controls) and the degree of sensitivity (of investigated trees) (Table 2). Inhibition by SO_2 of uptake of radioactive carbon in light was greatest during the summer (Fig. 2).

FIXATION OF ^{14}C INTO STARCH, SUGAR PHOSPHATES, SOLUBLE SUGARS, AMINO ACIDS AND ORGANIC ACIDS

In needles of unfumigated trees most of the radioactive carbon was incorporated into starch, followed by soluble sugars, organic acids, amino acids, and sugar phosphates (Fig. 3). In the summer an even higher proportion was incorporated into starch. Uptake of ^{14}C by other fractions was similar to that during the spring. In autumn the proportion of ^{14}C incorporated into sugars increased at the expense of that in starch and other assimilates (Fig. 3).

Sulphur dioxide significantly inhibited uptake of ^{14}C during each

Table 2

snfluence of SO_2 action on the $^{14}CO_2$ assimilation after 5 min of photosynthesis in Scots Pine Ihoots. *T* – specimen tolerant to SO_2, *I* – relatively tolerant specimen, *S* – susceptible specimen, *C* – control, SO_2 – sulphur dioxide treated, $\bar{x}$ – weighed mean, α_1 – significance of differences between C and SO_2, α_2 – significance of interaction between SO_2 treatment and specimens under investigation, * – differences significant at 0.05 level, ** – differences significant at 0.01 level

Radioactive carbon uptake (total)		Spring			Summer			Autumn		
		T	*I*	*S*	*T*	*I*	*S*	*T*	*I*	*S*
		^{14}C[dpm $\times$ g^{-1} fr. wt. of needles] $\times 10^5$								
C	$\bar{x}$	60.41	85.50	63.10	109.60	120.80	129.50	32.00	40.28	47.10
SO_2	$\bar{x}$	31.80	30.60	17.70	34.60	21.30	18.00	20.00	22.91	9.33
	α_1	**	**	**	**	**	**	**	**	**
	α_2		**			**			*	

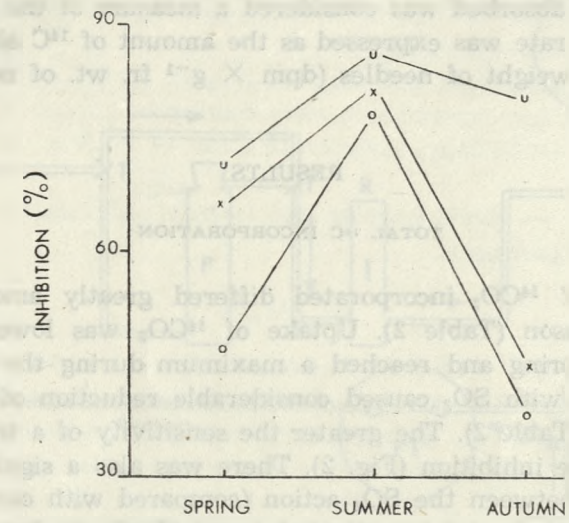

Fig. 2. Inhibition of ^{14}C assimilation rate by SO_2. o —— o — speciment tolerant to SO_2; x —— x — relatively tolerant; u —— u — susceptible specimen

season. The reduced uptake was evident in all products of photosynthesis except the amino acids in the tolerant tree during the autumn (Table 3). During the spring, summer, and autumn SO_2 stimulated the ^{14}C uptake in

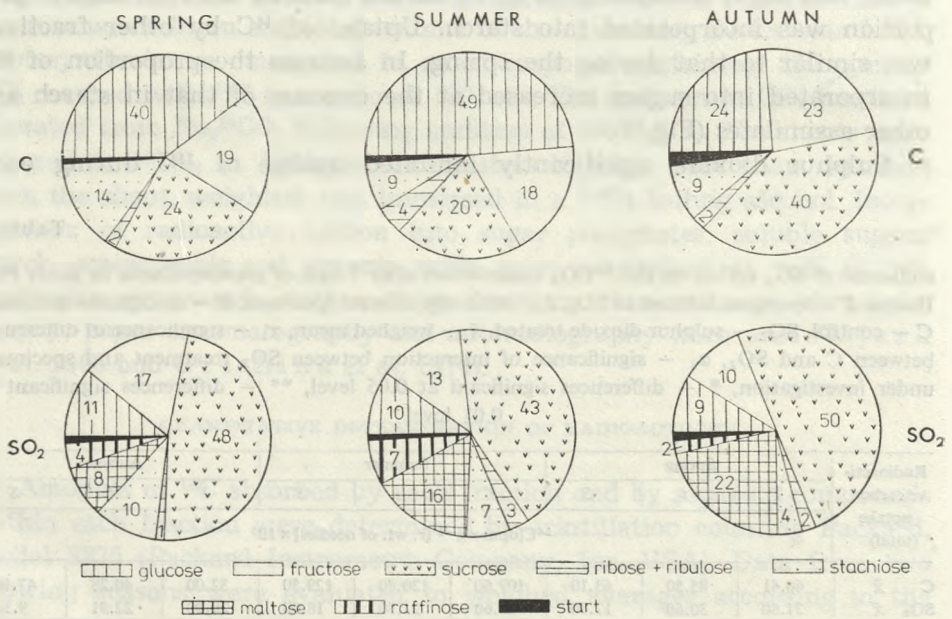

Fig. 4. Incorporation of ^{14}C in sugars after 5 min of exposure of pine shoots to $^{14}CO_2$. Tolerant specimen. C — control, SO_2 — sulphur dioxide treated

Table 3

^{14}C uptake by starch, sugar phosphates, soluble sugars, amino acids and organic acids after 5 min of pine shoots exposition in $^{14}CO_2$ atmosphere. *T* – specimen tolerant to SO_2, *I* – relatively tolerant specimen, *S* – susceptible specimen. *C* – control, SO_2 – sulphur dioxide treated. $\bar{x}$ – weighed mean, α – significance of differences between C and SO_2, * – differences significant at 0.05 level, ** – differences significant at 0.01 level

		Spring						Summer						Autumn					
		T		*I*		*S*		*T*		*I*		*S*		*T*		*I*		*S*	
		C	SO_2	C	SO_2	C	SO_2	C	SO_2	C	SO_2	C	SO_2	C	SO_2	C	SO_2	C	SO_2
		^{14}C incorporated (dpm × g^{-1} fr. wt. of needles) × 10^5																	
Starch	$\bar{x}$	22.77	7.55	35.72	7.63	23.67	4.90	57.25	3.41	64.00	4.70	66.69	4.10	10.15	5.46	10.23	4.81	12.50	1.92
	α	**		**		**		**		**		**		**		**		**	
Sugar phosphates	$\bar{x}$	1.31	0.44	2.15	0.32	2.81	0.41	2.50	0.75	4.83	0.45	4.82	0.40	0.45	0.25	0.90	0.32	1.00	0.15
	α	*		**		**		**		**		**		*		*		*	
Soluble sugars	$\bar{x}$	22.53	16.25	27.83	14.23	22.84	8.00	24.22	16.64	26.60	10.50	33.67	8.62	17.45	11.44	20.36	13.75	25.49	5.61
	α	**		**		**		**		**		**		**		**		**	
Amino acids	$\bar{x}$	6.16	4.20	9.22	4.07	6.69	2.40	11.62	4.32	12.10	3.00	11.01	2.79	1.47	1.44	2.54	1.99	2.73	0.95
	α	*		**		**		**		**		**				*		**	
Organic acids	$\bar{x}$	7.67	3.40	14.59	4.38	7.07	2.16	14.03	4.53	13.30	2.80	13.34	2.12	2.51	1.46	4.27	2.04	4.85	0.70
	α	**		**		**		**		**		**		**		**		**	

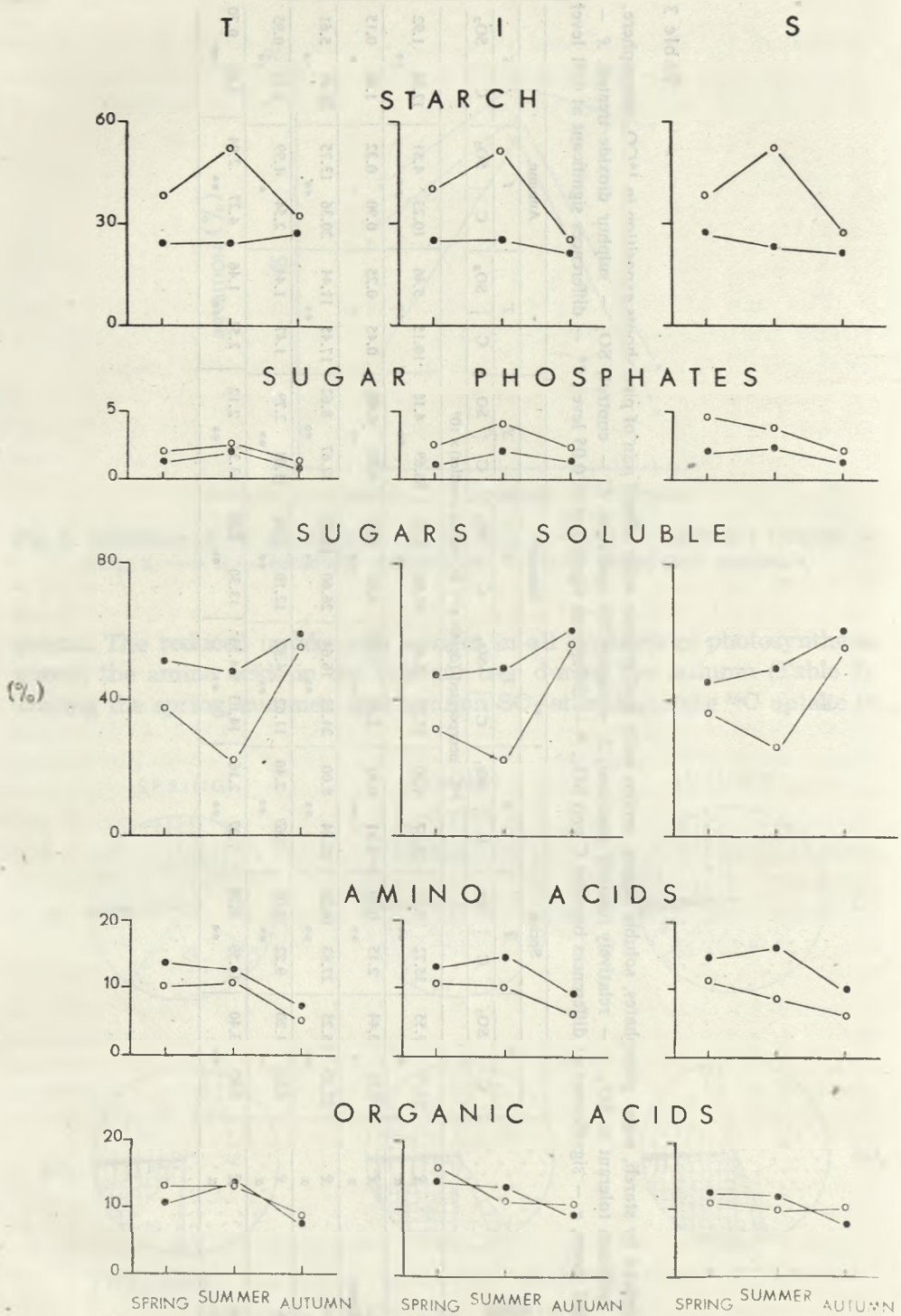

Fig. 3. Incorporation of ^{14}C in starch, sugar phosphates, sugar soluble, amino acids, and organic acids after 5 min exposure of pine shoots to $^{14}CO_2$ ○ — ○ — control, ● — ● — SO_2 treated, T — specimen tolerant to SO_2, I — relatively tolerant specimen, S — susceptible specimen

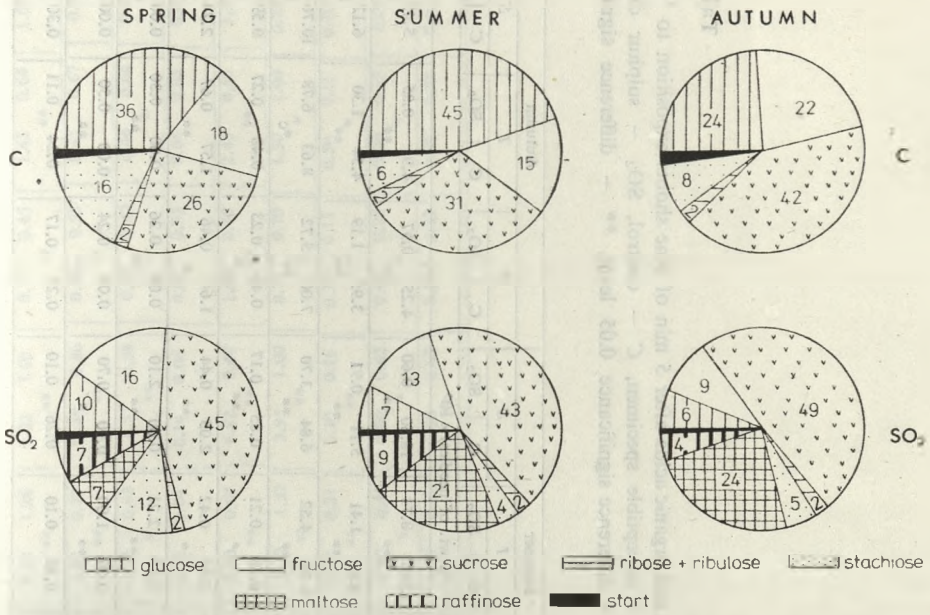

Fig. 5. Incorporation of ^{14}C in sugars after 5 min of exposure of pine shoots to $^{14}CO_2$. Relatively tolerant specimen. C — control, SO_2 — sulphur dioxide treated

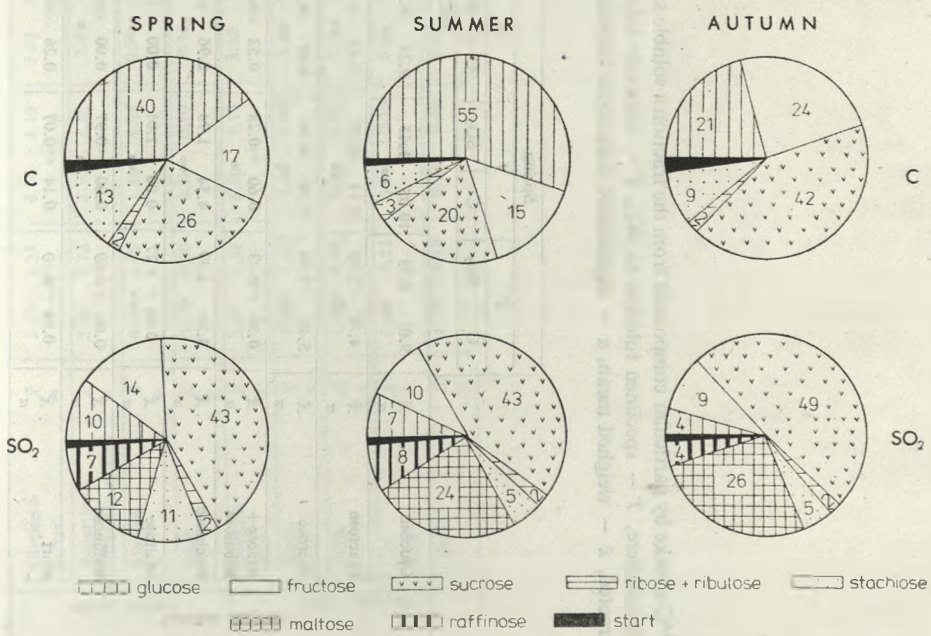

Fig. 6. Incorporation of ^{14}C in sugars after 5 min of exposure of pine shoots to $^{14}CO_2$. Susceptible specimen. C — control, SO_2 — sulphur dioxide treated

Table 4

^{14}C uptake by particular compounds from the fractions: soluble sugars, amino acids and organic acids after 5 min of pine shoots exposition to $^{14}CO_2$ atmosphere, *T* – specimen tolerant to SO_2, *I* – relatively tolerant specimen, *S* – susceptible specimen, *C* – control, SO_2 – sulphur dioxide treated, $\bar{x}$ – weighed mean, α – significance differences between, C and SO_2, * – difference significance 0.05 level, ** – difference significant at 0.01 level

			Spring						Summer						Autumn					
			T		*I*		*S*		*T*		*I*		*S*		*T*		*I*		*S*	
			C	SO_2	C	SO_2	C	SO_2	C	SO_2	C	SO_2	C	SO_2	C	SO_2	C	SO_2	C	SO_2
			^{14}C incorporated (dpm × g^{-1} fr. wt. of needles) × 10^5																	
Soluble Sugars	Glucose	$\bar{x}$	9.01	1.78	10.05	1.45	9.23	0.80	12.00	1.60	12.02	0.74	18.60	0.60	4.25	0.97	4.91	0.85	5.45	0.25
		α	**		**		**		**		**		**		**		**		**	
	Fructose	$\bar{x}$	4.37	2.70	5.14	2.32	3.85	1.14	4.27	2.23	4.00	1.41	5.11	0.91	3.95	1.19	4.54	1.30	6.12	0.50
		α	**		**		**		*c		**		**		**		**		**	
	Sucrose	$\bar{x}$	5.48	7.90	7.36	6.41	6.01	3.41	4.84	7.25	8.25	4.52	6.84	3.70	7.00	5.72	8.63	6.78	10.76	2.72
		α	**		*c		**		**		**		**		**		*c		**	
	Ribose + Ribulose	$\bar{x}$	0.36	0.23	0.60	0.28	0.52	0.20	0.90	0.20	0.53	0.21	0.85	0.17	0.40	0.23	0.48	0.27	0.59	0.12
		α			*				*		*		**		*				*	
	Stachiose	$\bar{x}$	3.29	1.59	4.54	1.73	2.96	0.90	2.14	1.20	1.60	0.42	2.05	0.44	1.64	0.46	1.57	0.67	2.24	0.30
		α	*		**		**		*		*		**		*		**		**	
	Maltose	$\bar{x}$	0.00	1.27	0.00	1.01	0.00	1.00	0.00	2.70	0.00	2.21	0.00	2.10	0.00	0.26	0.00	0.30	0.00	1.45
		α	**		**		**		**		**		**		**		**		**	
	Raffinose	$\bar{x}$	0.00	0.69	0.00	0.97	0.00	0.60	0,00	1.13	0.00	1.00	0,00	0.70	0.00	0.24	0.00	0.50	0.00	0.23
		α			**		*		**		**		*		λ		**		*	
	Start	$\bar{x}$	0.10	0.10	0.14	0.07	0.26	0.10	0.11	0.13	0.30	0.10	0.26	0.10	0.27	0.17	0.24	0.11	0.30	0.06
		α																		

Amino Acids	Glycine+ Serine	$\bar{x}$	3.13	1.33	4.70	1.16	3.57	0.65	8.62	1.91	9.08	1.26	8.02	1.08	0.77	0.45	1.43	0.64	1.63	0.25
		α	**		**		**		**		**		**		**		**		**	
	Aspartic+ Glutamic acids	$\bar{x}$	2.05	1.72	2.95	1.58	2.07	0.94	1.64	1.22	1.57	0.79	*1.49	0.80	0.42	0.55	0.61	0.67	0.57	0.29
		α	*		**		**		*		**		**		*				**	
	Alanine	$\bar{x}$	0.89	1.05	1.38	1.23	0.94	0.76	1.19	1.11	1.34	0.93	1.37	0.88	0.27	0.42	0.46	0.64	0.47	0.38
		α	*		*		*		*		*		* **		*		*		*	
	Start	$\bar{x}$	0.15	0.10	0.18	0.10	0.11	0.10	0.12	0.10	0.12	0.04	0.14	0.06	0.02	0.03	0.06	0.05	0.03	0.04
		α																		
Organic Acids	Glycolic acid	$\bar{x}$	3.67	1.21	6.60	1.13	3.02	0.62	6.34	1.37	5.90	0.67	6.82	0.48	1.50	0.40	2.43	0.53	3.31	0.14
		α	**		**		**		**		**		**		**		**		**	
	Malic acid	$\bar{x}$	1.89	1.21	4.40	1.90	2.22	0.91	4.50	1.92	5.10	1.32	3.95	1.00	0.73	0.70	1.30	1.00	0.73	0.35
		α	*		**		**		**		**		**		*		*		*	
	PGA	$\bar{x}$	1.95	0.70	3.31	0.76	1.70	0.34	2.96	0.61	2.13	0.31	2.30	0.16	0.33	0.15	0.50	0.15	0.70	0.06
		α	*		**		**		**		**		**		*		*		**	
	"y" acid	$\bar{x}$	0.00	0.23	0.00	0.50	0.00	0.30	0.00	0.60	0.00	0.45	0.00	0.42	0.00	0.22	0.00	0.35	0.00	0.14
		α	*		**		*		**		*		*		*		*		**	
	Start	$\bar{x}$	0.20	0.10	0.23	0.10	0.13	0.05	0.31	0.10	0.27	0.10	0.30	0.05	0.10	0.03	0.09	0.04	0.10	0.02
		α																		

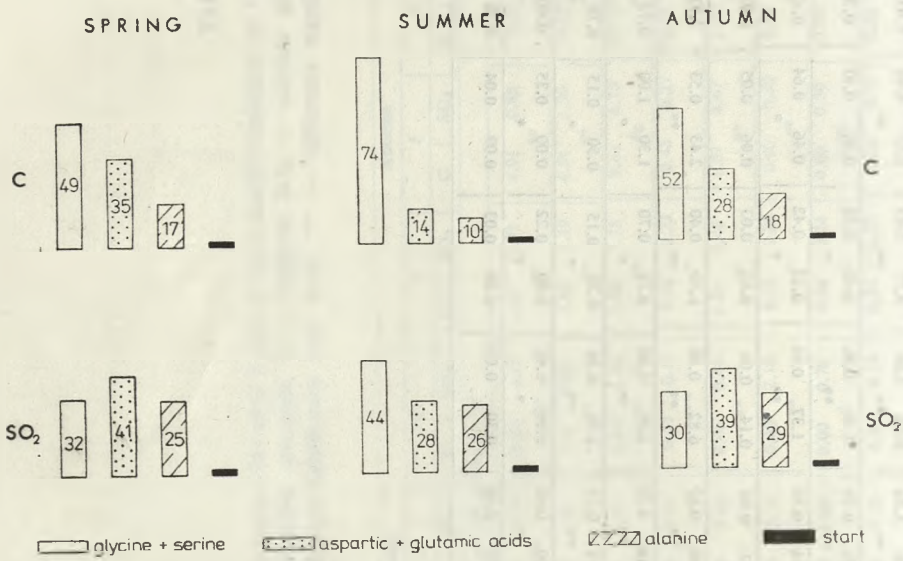

Fig. 7. Incorporation of ^{14}C in amino acids after 5 min of exposure of pine shoots to $^{14}CO_2$. Specimen tolerant to SO_2. C — control, SO_2 — sulphur dioxide treated

soluble sugars, with a corresponding decrease in radioativity of starch (Fig. 3). Changes in sugar synthesis were followed by a lowering of radioactive sugar phosphates with simultaneous increase of ^{14}C in amino acids and its lowering or slight increase in organic acids (Fig. 3).

^{14}C UPTAKE BY INDIVIDUAL SOLUBLE SUGARS

During the spring, in the needles of control shoots the radioactive carbon was incorporated mostly in glucose, followed by sucrose, fructose, and ribose + ribulose (Fig. 4 to 6). During the summer glucose labled in the soluble fraction increased followed by a continued lowering of sucrose as well as stachiose and fructose. In the tolerant and SO_2 — susceptible specimens there was a simultaneous increase in ^{14}C in ribose + +ribulose. In autumn, however, ^{14}C was mostly incorporated in sucrose and to a lower degree, by other sugars (Fig. 4 to 6).

The SO_2 action lowered incorporation of ^{14}C in glucose, fructose, sucrose, ribose +ribulose and stachiose in all specimens (Table 4). However, in the SO_2 — tolerant tree the radioactivity of sucrose was almost doubled during spring and summer (Table 4). In the fumigated tree incorporation of ^{14}C in maltose and raffinose was noted. This was not the case in unfumigated controls (Table 4). The percentage content of incorporated ^{14}C in these sugar fractions after SO_2 treatment was similar in all specimens (Fig. 4 to 6). The gas caused a decrease of the content of all radioactive sugars except of sucrose, which increased after fumigation.

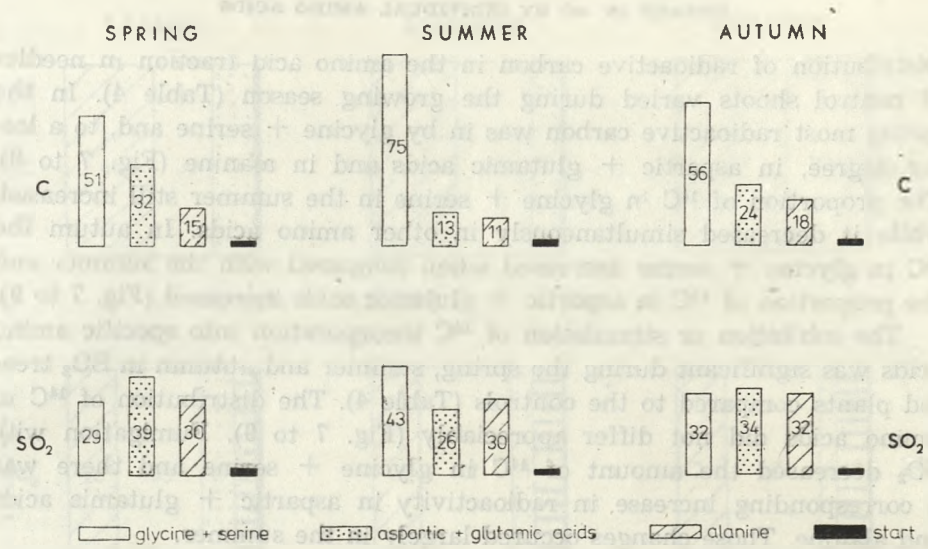

Fig. 8. Incorporation of ^{14}C in amino acids after 5 min of exposure of pine shoots to $^{14}CO_2$. Relatively tolerant specimen. C — control, SO_2 — sulphur dioxide treated

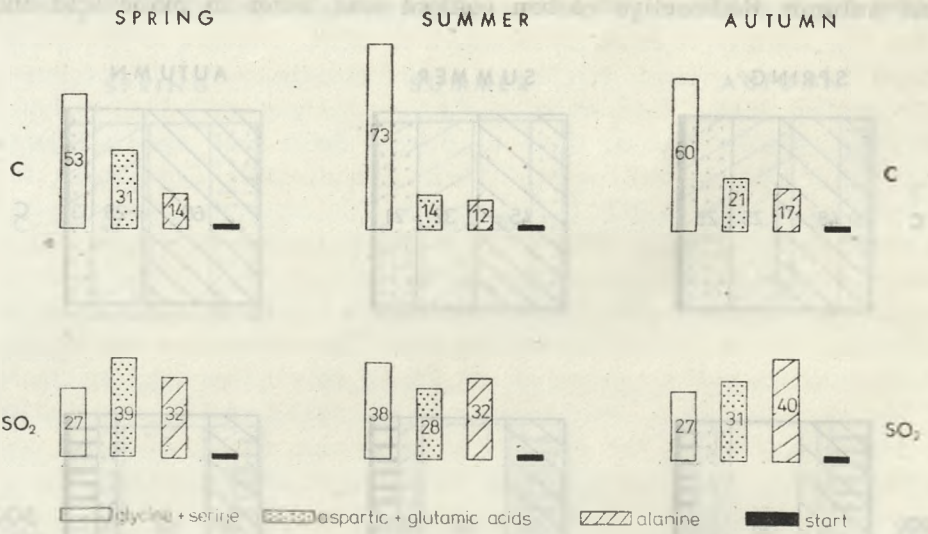

Fig. 9. Incorporation of ^{14}C in amino acids after 5 min of exposure of pine shoots to $^{14}CO_2$. Susceptible specimen. C — control, SO_2 — sulphur dioxide treated

These changes in the ^{14}C content of certain sugars were especially obvious in the summer. The share of maltose and raffinose in the soluble sugar fraction increased after the SO_2 treatment corresponding to the susceptibility of the investigated specimen (Fig. 6).

UPTAKE OF ^{14}C BY INDIVIDUAL AMINO ACIDS

Distribution of radioactive carbon in the amino acid fraction in needles of control shoots varied during the growing season (Table 4). In the spring most radioactive carbon was in by glycine + serine and, to a lesser degree, in aspartic + glutamic acids and in alanine (Fig. 7 to 9). The proportion of ^{14}C in glycine + serine in the summer still increased, while it decreased simultaneously in other amino acids. In autum the ^{14}C in glycine + serine decreased when compared with the summer and the proportion of ^{14}C in aspartic + glutamic acids increased (Fig. 7 to 9).

The inhibition or stimulation of ^{14}C incorporation into specific amino acids was significant during the spring, summer and autumn in SO_2 treated plants compared to the controls (Table 4). The distribution of ^{14}C in amino acids did not differ appreciably (Fig. 7 to 9). Fumigation with SO_2 decreased the amount of ^{14}C in glycine + serine and there was a corresponding increase in radioactivity in aspartic + glutamic acids and alanine. Those changes occured largely in the summer.

^{14}C UPTAKE BY INDIVIDUAL ORGANIC ACIDS

Enhanced incorporation of ^{14}C in glycolic acid occured in needles of control shoots of the three Scots pine specimens during the spring, summer and autumn. Radioactive carbon content was lower in malic acid and

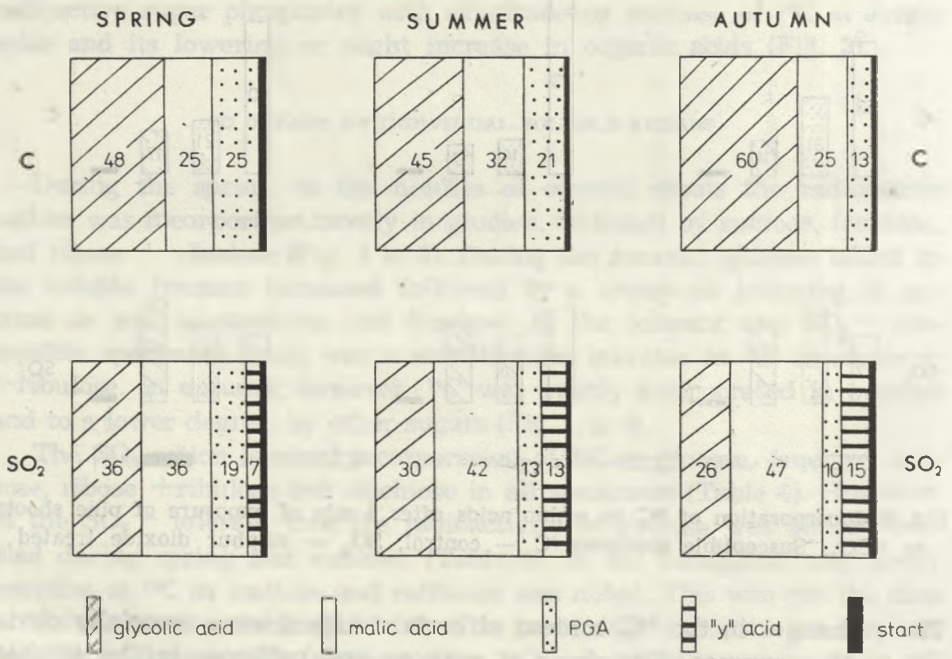

Fig. 10. Incorporation of ^{14}C in organic acids after 5 min exposure shoots to $^{14}CO_2$. Tolerant specimen. C — control, SO_2 — sulphur dioxide treated

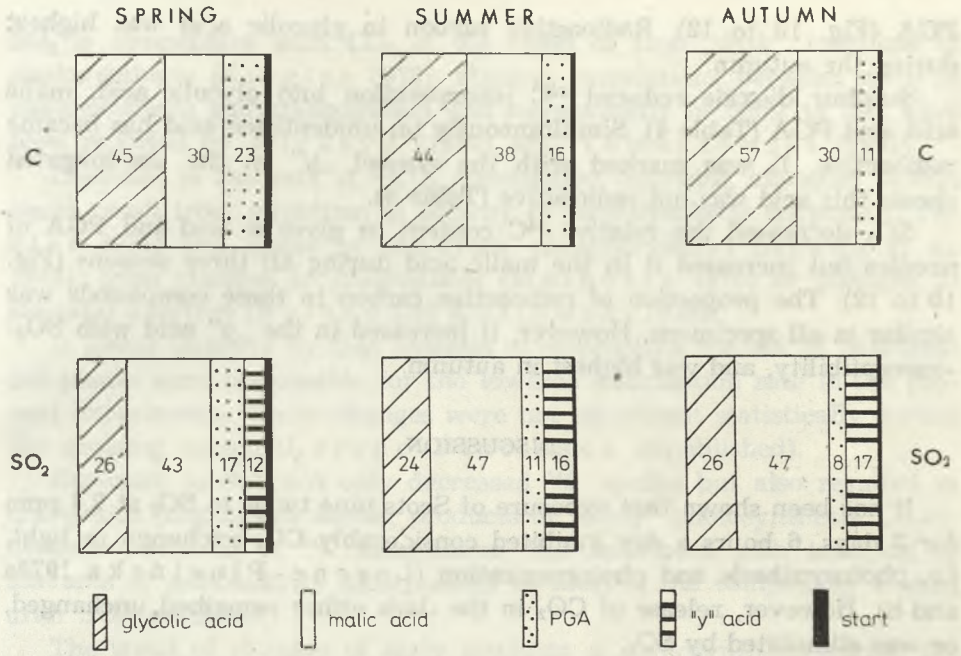

Fig. 11. Incorporation of ^{14}C in organic acids after 5 min of exposure of pine shoots to $^{14}CO_2$. Relatively tolerant specimen. C — control, SO_2 — sulphur dioxide treated

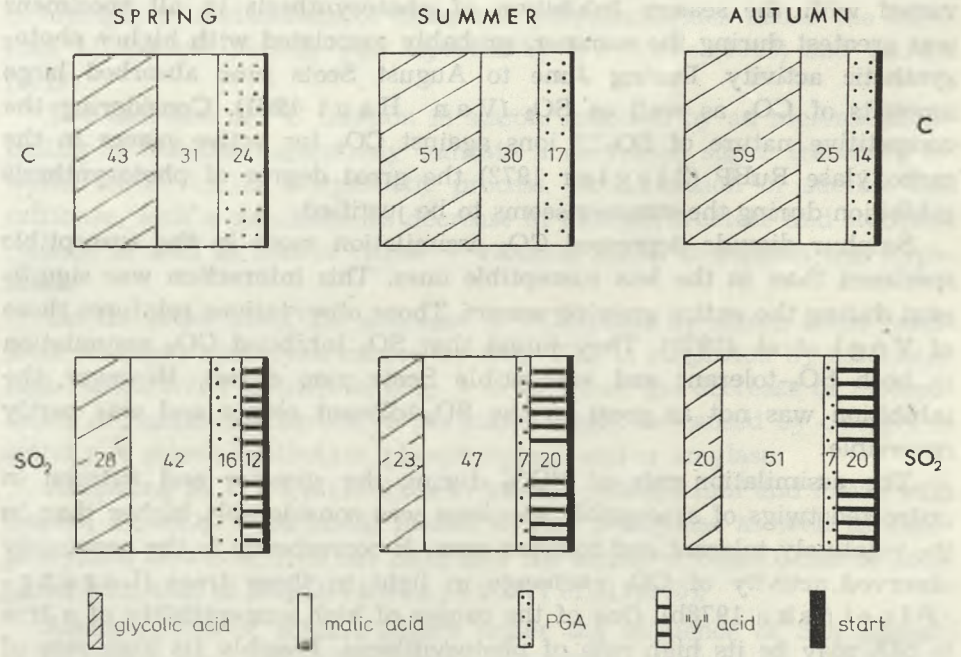

Fig. 12. Incorporation of ^{14}C in organic acids after 5 min of exposure of pine shoots to $^{14}CO_2$. Susceptible specimen. C — control, SO_2 — sulphur dioxide treated

PGA (Fig. 10 to 12). Radioactive carbon in glycolic acid was highest during the autumn.

Sulphur dioxide reduced ^{14}C incorporation into glycolic acid, malic acid, and PGA (Table 4). Simultaneously on unidentified acid has became radioactive. It was marked with the symbol „*y*" In the unfumigated shoots this acid was not radioactive (Table 4).

SO_2 decreased the relative ^{14}C content in glycolic acid and PGA of needles but increased it in the malic acid during all three seasons (Fig. 10 to 12). The proportion of radioactive carbon in those compounds was similar in all specimens. However, it increased in the „*y*" acid with SO_2-susceptibility, and was highest in autumn.

DISCUSSION

It has been shown that exposure of Scots pine twigs to SO_2 at 2.0 ppm for 3 days, 6 hours a day inhibited considerably CO_2 exchange in light, i.e. photosynthesis and photorespiration (Lorenc-Plucińska 1978a and b). However, release of CO_2 in the dark either remained unchanged, or was stimulated by SO_2.

In the present study investigation of carbon metabolism in the photosynthetic process has shown that SO_2 also inhibited CO_2 assimilation after five minutes of exposure of shoots to $^{14}CO_2$. Changes in ^{14}C uptake varied with the season. Inhibition of photosynthesis in all specimens was greatest during the summer, probably associated with higher photosynthetic activity. During June to August Scots pine absorbed large amounts of CO_2 as well as SO_2 (Van Haut 1961). Considering the competitive nature of SO_3^{--} ions against CO_2 for active places in the carboxylase RuBP (Ziegler 1972) the great degree of photosynthesis inhibition during the summer seems to be justified.

Sulphur dioxide depressed CO_2 assimilation more in the susceptible specimen than in the less susceptible ones. This interaction was significant during the entire growing season. Those observations reinforce those of Vogl et al. (1970). They found that SO_2 inhibited CO_2 assimilation in both SO_2-tolerant and susceptible Scots pine clones. However, the inhibition was not as great in the SO_2-tolerant clones and was partly reversible.

The assimilation rate of $^{14}CO_2$ during the summer and autumn in untreated twigs of susceptible specimen was considerably higher than in the relatively tolerant and tolerant ones. It corresponds to the previously observed activity of CO_2 exchange in light in those trees (Lorenc-Plucińska 1978b). One of the causes of high susceptibility of a tree to SO_2 may be its high rate of photosynthesis. Possibly its high rate of CO_2 absorption is associated with absorption of large amounts of SO_2. Consequently severe injury follows. This hypothesis seems reasonable

SO_2 is competitive with CO_2 in the chain of first „dark" reactions of photosynthesis (Ziegler 1972). Positive correlations between rates of photosynthesis and transpiration and susceptibility of trees to SO_2 have been reported by Oleksyn (1982) and Tomaszewski (1981).

Decrease in the rate of $^{14}CO_2$ assimilation following exposure to SO_2 could result from inhibition of activity of photosynthetic enzymes (Ziegler 1975) and cyclic or non-cyclic phosphorylation (Asada et al. 1968), from changes in chloroplasts (Malhotra 1976) or changes in stomatal aperture (Noland and Kozlowski 1979).

It seems unlikely by that changes in chlorophyll content of SO_2-treated plants were responsible for the lowered assimilation rate in the present experiments. Those changes were not significant statistically during the growing season (Lorenc-Plucińska, unpublished).

Exposure to SO_2 not only decreased ^{14}C uptake but also resulted in changes in proportions among products of „early" photosynthesis. Considerable inhibition of ^{14}C assimilation was associated with lowering of amounts of radioactivity incorporated in most of the compounds studied after SO_2 treatment.

The trend of changes of early products of photosynthesis during the growing season under the influence of SO_2 on shoots of SO_2-tolerant and susceptible trees was similar. There was decrease of ^{14}C in starch and a simultaneous increase in soluble sugars (Fig. 3). A similar trend of changes in metabolism of mono-and polysaccharides under the influence of sulphur dioxide was reported by Börtitz (1968) and Mudd (1979).

The decrease of ^{14}C fixation in starch, followed by an increase of labelling of soluble sugars may indicate a decreased sugar transport towards starch in its biosynthetic process. Accumulation of sucrose and raffinose, with a simultaneous decrease of glucose, fructose and stachiose content as well as that of ribose + ribulose seems to support this hypothesis.

On the other hand, the decrease of ^{14}C uptake by starch could result from its rapid hydrolysis caused by SO_2. This is supported by associated high radioactivity in maltose (Fig. 4 to 6). Thus, the decrease of incorporation of radioactive carbon in the starch might be caused by changes in activity of starch synthetase, phosphorylase, and/or amylase.

According to Ilkun (1971), who treated pelargonium and maize with Na_2SO_4 the SO_4^{--} ion could inhibit α- and β-amylase as well as phosphorylase. However, it is not clear how the action of Na_2SO_4 can be compared with that of SO_2 (Nikolajevski et al. 1975).

Accumulation of soluble sugars under the influence of SO_2 appears to be unfavorable for plants. Such accumulation may cause inactivation of RuBP carboxylase, followed by a decrease in the rate of photosynthesis (Rubin and Gavrilenko 1977).

Decrease of radioactivity in ribose + ribulose within the soluble sugar fraction (Fig. 4 to 6) points to changes in reproduction of the CO_2 acceptor. It is consistent with the observed decrease in the $^{14}CO_2$ assimilation rate.

Exposure of shoots to SO_2 was followed by a rise in the radioactive carbon uptake by the amino acid fraction (Table 3), as also reported for Norway spruce (Jäger and Grill 1975), Scots pine (Malhotra and Sarkar 1979) and birch (Nikolajevski et al. 1975).

It has been suggested that the rise of amino acids content under the influence of sulphur dioxide may be caused by hydrolysis of proteins (Fisher 1971) or by an inhibition of their biosynthesis (Mudd 1979).

Analysis of the total amino acids fraction showed that its percentage increase in the total amount of ^{14}C uptake was due to considerable labelling of alanine and aspartic + glutamic acids, with a simultaneous decrease in radioactivity of serine + glycine (Fig. 7 to 9). Increased incorporation of radioactive carbon into the aspartic + glutamic acid fraction could be caused by changes in activity of glutamate or aspartate dehydrogenase, or even one of the synthetases under the influence of SO_2. Investigations by Pahlich et al. (1972) and Jäger et al. (1972) point to the activation of glutamate dehydrogenase (GDH) under the influence of SO_2 toward reductive amination, and its inactivation towards an oxidative deamination. Pahlich (1971) also reported that allosteric control of GDH by α-ketoglutaric acid in the substrate was bound by the sulphite created from SO_2. Hence the sulphite, as an activator, damped the effect of the interaction of α-ketoglutaric acid, possibly resulting in uncontrolled synthesis of glutamic acid.

The increase in aspartic + glutamic acid in the amino acid fraction after exposure to SO_2 could be also caused by a change in the activity of glutamate-oxaloacetate (GOT) and glutamate-pyruvate (GPT) transaminases (Horsman and Wellburn 1975) or malate dehydrogenase (Mudd 1979). The increase could also result from the susceptibility to SO_2 of the RuBP carboxylase being greater than that of the PEP carboxylase (Libera et al. 1975).

The increase in the amount of radioactive aspartic + glutamic acid was correlated with a considerable inhibition of labeling of alanine (Fig. 7 to 9). Kostir et al. (1970) and Tanaka et al. (1972) also observed an increase in alanine of peas and wheat under the influence of SO_2. According to Godzik and Linskens (1974) a stimulation of ^{14}C incorporation into alanine under the influence of sulphur dioxide is due to inbibition of decarboxylation of pyruvate and its utilisation for synthesis of alanine.

Inhibition of uptake of radioactive carbon by glycine + serine appears to be the result of an inhibitory influence of SO_2 on photorespiration

(Lorenc-Plucińska 1978b) and on the content of glycolic acid (Fig. 10 to 12). The lowering of the glycine + serine content in the amino acid fraction could also reflect a transformation of serine to carbohydrates (Goldsworthy 1970), previously to sucrose (Thamas and Bidwell 1970).

Metabolism of organic acids was also altered under the influence of SO_2. Inhibition of incorporation of labeled carbon into PGA and into sugar phosphates might be associated with rapid accumulation of soluble sugars. A decrease in radioactivity of PGA also suggested that its metabolism of malic acid through PEP was accelerated.

Exposure to SO_2 caused an increase in the proportion of malic acid in the organic acid fraction (Fig. 10 to 12). This is a characteristic compound for the C_4 pathway.

Scots pine, like other C_3 plants, is able to absorb carbon through the carboxylation of PEP only to a very small degree (Raghavendra and Das 1977). Synthesis of malic acid is catalyzed by PEP carboxylase, malate dehydrogenase, and glutamate-oxaloacetate transaminase. Changes in activity of those enzymes under the influence of SO_2, as described by Osmond and Avadhani (1971), Ziegler (1974a and b) and Sarkar and Malhotra (1979), could account for the increased rise of radioactivity of malic acid within the organic acid fraction.

Increased labelling of malic and aspartic + glutamic acids following exposure to SO_2, on the other hand, may indicate a change in the metabolic pathway, C_3 to C_4 of the products of photosynthesis, and to a promotion of β-carboxylation. This possibility had been also suggested by Libera et al. (1975). Sulphur dioxide also inhibited the glycolic acid content within the entire radioactivity of the organic acid fraction (Fig. 10 to 12). This occured in all specimens during the growing season. This decrease in labelling of glycolic acid corresponded to a reduction in the rate of photorespiration previously observed (Lorenc-Plucińska 1978b). Inhibition of ^{14}C uptake by glycolic acid as well as by serine + glycine appeared to be caused not only by altered activity of glycolate oxidase under the influence to SO_2 (Soldatini and Ziegler 1979), but also by lowered synthesis of glycolic acid due to inhibition of RuBP carboxylase or a glycolaldehyde transcetolase complex.

Exposure of detached pine shoots to SO_2 greatly accelerated uptake of labelled carbon by an acid under the symbol „*y*" (Table 4). Radioctivity in that acid was not observed in unfumigated shoots. The amount of radioactivity in acid „*y*" was greater in the tree susceptible to SO_2 than in the less susceptible trees (Fig. 12). Chromatographic analysis excluded the following acids citric, izo-citric, succinic, fumaric, tartaric, oxalic, since R_f of them on the model chromatographs did not cover the R_f of the acid „*y*". Identification of this acid needs further investigation.

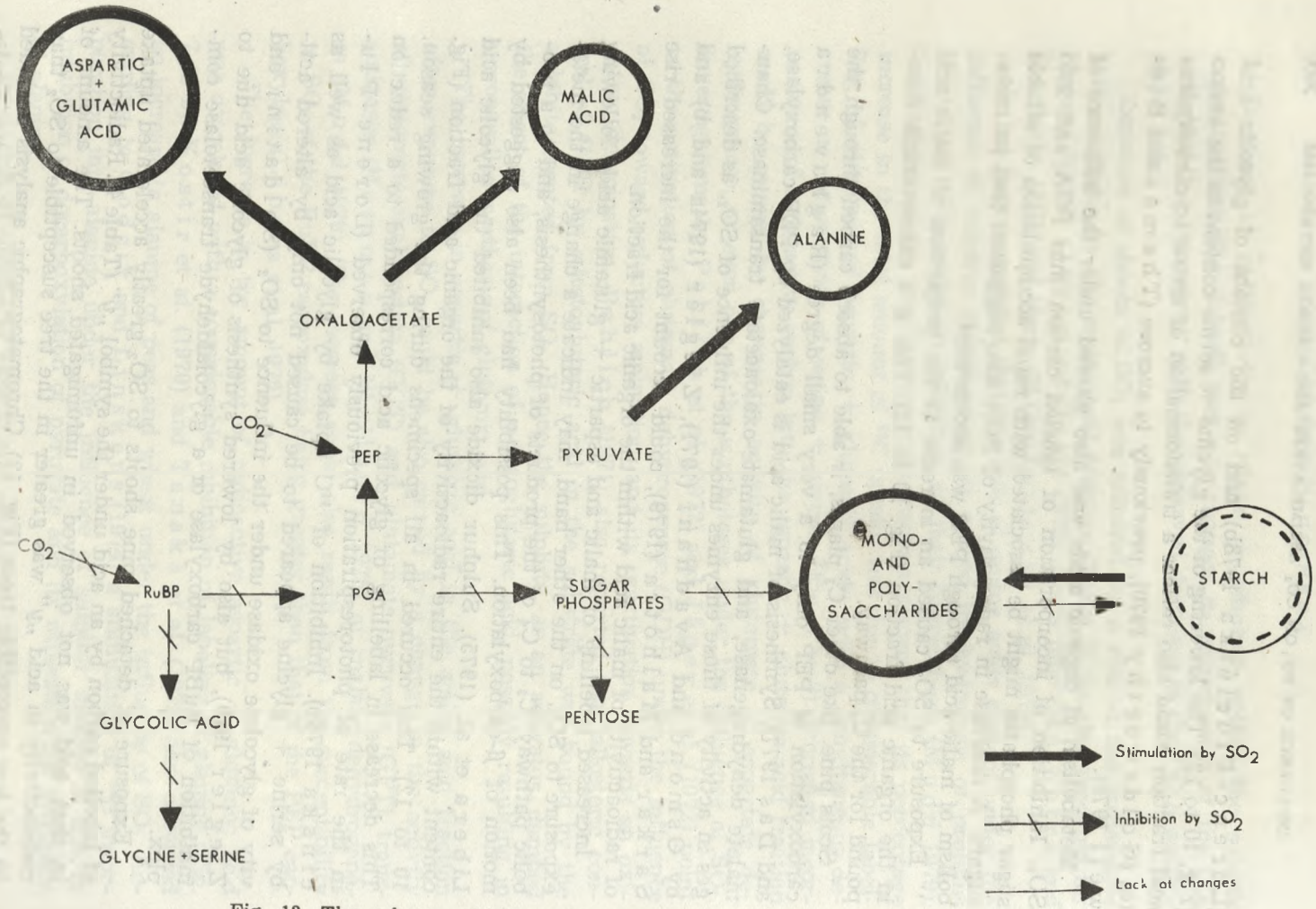

Fig. 13. The scheme of the carbon metabolism in the photosynthesis process in Scots pine shoots exposure to an SO_2 action

From the results of the present study the following model of carbon metabolism in the photosynthesis process, as modified by SO_2 is proposed (Fig. 13).

Sulphur dioxide inhibits the photosynthetic carbon flow toward the PGA, sugar phosphates, and pentose (ribose + ribulose). As a consequence the rate of assimilation CO_2 decreases due to limited reproduction of CO_2 acceptor.

The starch content is lowered by SO_2 through reduced starch synthesis and/or increased activity of amylase. These changes are reflected in accumulation of soluble sugars. Sugar surplus inhibits the activity of RuBP carboxylase/oxygenase, which in turn causes a decrease in the rate of photosynthesis. Inhibition of RuBP carboxylase/oxygenase by SO_2 as well as of the glycolaldehyde transketolase complex decreases synthesis of glycolic acid, leading to lowered metabolism of the glycolic acid cycle which is typical for C_3 plants. This trend is confirmed by the decrease in the rate of photorespiration by SO_2 (Lorenc-Plucińska 1978b). Sulphur dioxide stimulates synthesis of malic, aspartic + glutamic acides and alanine. Increase in amounts of these compounds results from increased flow of carbon from PGA through PEP, a pathway of carbon metabolism which is not limited by SO_2.

I am grateful to Professor Dr. S. Białobok for his advice during preparation of this work.

SUMMARY

Influence of sulphur dioxide on CO_2 assimilation and carbon metabolism during the photosynthesis in Scots pine needles was studied. Experiments were performed during spring, summer and autumn on detached shoots of trees varying in susceptibility to SO_2. After 5 minutes of exposure to $^{14}CO_2$ the radioactivity of the sugar phosphate, soluble sugar, starch, amino acids, and organic acid fractions as well specific compounds within those fractions was studied by ion-exchange chromatography, paper chromatography, and autoradiography. Sulphur dioxide inhibited the $^{14}CO_2$ assimilation rate. The degree of inhibition varied with susceptibility to SO_2 and was greatest in the most susceptible tree. Sulphur dioxide inhibited ^{14}C assimilation mostly during the summer. Assimilation varied with physiological age of shoots. After fumigation with SO_2 ^{14}C incorporation was lowered in glucose, fructose, stachiose, ribose + ribulose, whereas in sucrose it increased especially during the summer. Under the influence of SO_2 radioactive carbon was also incorporated by maltose and raffinose, but was not found in those compounds in unfumigated controls. The amount of those two sugars increased with the susceptibility of trees to SO_2. Uptake of ^{14}C by starch was inhibited ir-

respective of tree susceptibility to SO_2 and during the entire growing season. Exposure of shoots to SO_2 caused a decrease of the glycine + serine content, with a simultaneous increase of ^{14}C in aspartic + glutamic acid and in alanine. This increase under the influence of SO_2, occurred also in malic acid but in PGA and glycolic acid there was a decrease in ^{14}C. Changes in ^{14}C labelling in amino acids and organic acids were independent from the degree of susceptibility to SO_2 and such changes occurred during all seasons. A model of carbon metabolism during photosynthesis under the influence of SO_2 is proposed.

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GABRIELA LORENC-PLUCIŃSKA

Wpływ SO_2 na asymilację CO_2 i metabolizm węgla w fotosyntezie u sosny zwyczajnej

Streszczenie

Badano wpływ dwutlenku siarki na asymilację CO_2 i metabolizm węgla w fotosyntezie igieł sosny zwyczajnej u osobników różniących się stopniem wrażliwości na ten gaz. Doświadczenia wykonano na odciętych gałązkach w okresie wiosennym, letnim i jesiennym. Za pomocą metod chromatografii jonowymiennej, bibułowej i autoradiografii, po 5 minutowej ekspozycji w $^{14}CO_2$ oznaczano radioaktywność frakcji fosforanów cukrów, cukrów rozpuszczalnych, skrobi, aminokwasów i kwasów organicznych oraz poszczególnych związków tych frakcji. Stwierdzono, że dwutlenek siarki hamował natężenie asymilacji $^{14}CO_2$. Obniżenie asymilacji zależało od stopnia wrażliwości badanych osobników na SO_2 i było największe u osobnika wrażliwego na ten czynnik. Wpływ dwutlenku siarki na przyswajanie ^{14}C był największy latem. U wszystkich osobników, po ekspozycji w SO_2, stwierdzono obniżenie zawartości ^{14}C w glukozie, fruktozie, stachiozie, rybozie+rybulozie i zwiększenie w sacharozie. Pod wpływem SO_2 obserwowano także włączanie ^{14}C do maltozy i rafinozy, tj. do związków, które nie znakowały się w kontroli. Radioaktywność tych dwóch fotoasymilantów wzrastała wraz ze wzrostem wrażliwości badanych osobników na SO_2. Dwutlenek siarki hamował włączanie ^{14}C do skrobi u wszystkich osobników sosny. SO_2 powodował obniżenie radioaktywności glicyny+seryny, z równoczesnym wzrostem udziału ^{14}C w kwasach asparaginowym+glutaminowym oraz w alaninie. SO_2 przyczyniał się do wzrostu ^{14}C w kwasie jabłkowym oraz obniżenia udziału radioaktywnego węgla w PGA i w kwasie glikolowym. Zaburzenia w znakowaniu aminokwasów i kwasów organicznych nie zależały od stopnia wrażliwości badanych osobników sosny na SO_2 i były podobne w ciągu sezonu wegetacyjnego. W pracy przedstawiono zmodyfikowany mechanizm przemian węgla w procesie fotosyntezy pod wpływem SO_2.

ГАБРИЕЛЯ ЛОРЕНЦ-ПЛЮЦИНЬСКА

Влияние SO_2 на ассимиляцию CO_2 и метаболизм углерода в фотосинтезе сосны обыкновенной

Резюме

Исследовали влияние сернистого ангидрида на ассимиляцию CO_2 и метаболизм углерода в фотосинтезе сосны обыкновенной у различных особей отличающихся степенью устойчивости к этому газу. Опыты проводили весной, летом и осенью на срезанных ветках. С помощью методов ионообменной и бумажной хроматографии, а также авторадиографии, после 5-минутной экспозиции в $^{14}CO_2$ определяли радиоактивность фосфатов сахаров, растворимых сахаров, кахмала, аминокислот и органических кислот, а также соединений входящих в состав упомянутых фракций. Отмечено, что сернистый ангидрит тормозис ассимиляцию $^{14}CO_2$. Уменьшение ассимиляции зависило от степени чувствительности исследуемой особи и было большим у дерева чувствительного

к действию этого фактора. Влияние сернистого ангидрида на усвоение ^{14}C было самым большим летом. У всех особей после газации SO_2 отмечено уменьшение содержания ^{14}C в глюкозе, фруктозе, стахиозе, рибозе+рибулозе и увеличение в сахарозе. Под влиянием SO_2 отмечено также включение ^{14}C в мальтозу и рафинозу, то есть в соединения, которые не метились в контроле. Активность этих двух фотоассимилятов росла по мере роста чувствительности исследуемых особей к SO_2. Сернистый ангидрид тормозил включение ^{14}C в крахмал у всех особей сосны. Он вызывал также уменьшение радиоактивности глицина+серина, при одновременном росте содержания ^{14}C в аспарагиновой+глутаминовой кислот и аланина. CO_2 содействовал росту ^{14}C в яблочной кислоте и уменьшению участия радиоактивного углерода в ФГА и гликолевой кислоте. Нарушение в мечении аминокислот и органических кислот не зависило от степени чувствительности исследуемых особей к SO_2 и было схожим в вегетационном периоде. В работе представлена модифицированная схема механизма превращения углерода в процессе фотосинтеза под влиянием SO_2.