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Effect of sulphur dioxide on photosynthesis, photorespiration and dark respiration of Scots pines differing in resistance to this gas

INTRODUCTION

The toxic effect of sulphur dioxide plants has been investigated frequently. Numerous papers published on the subject deal primarily with changes in the metabolism of plants caused by SO_2 (Thomas, et al., 1956; Daines, 1968; Godzik and Piskornik, 1969, 1970; Havas, 1971; Ziegler, 1973, 1975; Malhotra et al., 1976; Knabe, 1976 and others). One of the responses of plants to SO_2 action is a reduction in photosynthesis (Wislicenus, 1898; Wieler, 1903; Keller, 1958; Börtitz, 1964; Vogl, 1964; Vogl et al., 1964) long before necroses of the assimilation organs are observable (Wieler, 1905; Hallgren, 1975; Thomson, 1975). An increase in the sensitivity of photosynthesis in trees to SO_2 occurs parallel with an increase in their biological activity, thus it is greatest in late spring and early summer (Thomas et al., 1956). Sulphur dioxide penetrating through stomata into the plants is accumulated in the form of HSO_3^- or SO_3^{--} ions. Studying the inhibitive effect of SO_3^{--} on the photosynthetic incorporation of CO_2 Ziegler (1972) has shown that this influence is associated with the competition between CO_2 and SO_3^{--} in the active loci of the enzyme RudP-carboxylase, which plays a basic role in the fixation of CO_2. An increase in the concentration of CO_2 hinders the replacement of CO_2 by SO_3^{--} which causes a decline in the sensitivity of photosynthesis to SO_2 (Ziegler, 1973).

Sulphur dioxide influences also the dark respiration. It has been reported that SO_2 inhibits (Gilbert, 1968 b) or stimulates (Keller, 1957) the evolution of CO_2 in darkness. Studying the exchange of CO_2 in pine shoots originating from polluted and non polluted regions Żelawski et al. (1974) report that pines from both these regions do not differ in the intensity of dark respiration. Ballantyne (1973) comparing the effect of SO_2 on respiration in a resistant maize and a susceptible bean plant suggests that the resistance of maize is expressed as a lesser reduction in dark respiration and a lesser inhibition of ATP synthesis in mitochondria following treatment with SO_2 than was the case with the bean plant.

The effect of SO_2 on photorespiration is as yet unknown (Libera et al., 1974). Ziegler (1975) claims that under the influence of SO_2 photorespiration may be drastically reducted or it can be completely inhibited, however this data requires confirmation.

It was a purpose of this work to study the effect of SO_2 on CO_2 exchange in detached shoots from two Scots pine individuals differing in degree of resistance to this gas. In view of differences in reaction of both individuals to SO_2 during the vegetative season an attempt was made to study the effect of this gas on the CO_2 exchange in light, i.e. photosynthesis and photorespiration, and in darkness, that is dark respiration, during four seasons of the year. As it was already shown before (Keller, 1957; Börtitz 1969) the extent of the toxic action of SO_2 depends not only on the degree of resistance of plants to this gas, but also on the concentration and duration of action of this gas. Thus it was decided that regardless of the season the pine shoots will be fumigated for the same period of time and with the same concentration of the pollutant.

MATERIALS AND METHODS

For the study use was made of one year old shoots from two individuals (grafts) of Scots pine (*Pinus silvestris* L.) growing in a seed orchard aged 15 years, and differing in the resistance to SO_2. These individuals have been marked in the Institute of Dendrology as K-08-02 III (the more resistant one) and K-01-16 I (the less resistant one). They have been selected on the basis of five experiments aimed at selecting individuals having a distinct resistance to the action of SO_2. For each of these studies 8 pine clones were used each represented by three grafts. Shoots after being placed in bottles with water have been subjected to the action of SO_2 for a specified period of time and concentration. In order to compare changes caused by the action of this gas with changes assiociated with the ageing of the detached shoots, from the same individuals further 4 shoots were taken and these acted as non-fumigated controls.

The degree of damage to needles caused exclusively by the action of SO_2 has been determined on the basis of a difference between the mean degree of injury on the needles subjected to SO_2 and the untreated controls. Necroses and discolourations have been determined on 50 needles of each shoot using a six point scale where:

0 = lack of injuries,

1 = area of necroses and discolorations represents 1 - 10% leaf surface,

2 = area of necroses and discolorations represents 11 - 30% leaf surface.

3 = area of necroses and discolorations represents 31 - 50% leaf surface,

4 = area of necroses and discolorations represents 51 - 70% leaf surface,

5 = area of necroses and discolorations represents 71 - 100% leaf surface.

On the basis of results from this selection it was found that the shoots of individual K-08-02 III were less injured than those of individual K-01--16 I. Difference in the degree of injury of shoots of these two individuals are shown in Table 1.

Table 1

Mean degree (estimate from 0 - 5) of SO_2 injury to Scots pine shoots

Date	25 - 29 V 1976	27 - 29 VII 1976	24-26 VIII 1976	6 - 8 X 1976	3 - 6 XI 1976
SO_2 conc. Duration of fumigation	8.0 ppm 5×6 hrs	2.0 ppm 3×6 hrs	2.0 ppm 3×6 hrs	2.0 ppm 3×6 hrs	2.0 ppm 4×6 hrs
Individuals					
K-08-02 III	0.0	0.8	0.4	0.1	0.1
K-01-16 I	3.4	2.6	4.1	2.1	4.0

MEASUREMENT OF CO_2 EXCHANGE

For the experiment in each season 20 shoots were collected from each of the two pine individuals. The one-year-old shoots collected from the upper unshaded tree whorls have been exposed to sulphur dioxide at a concentration of 2.0 ppm for three days, 6 hours daily. The control shoots were held in bottles with water in a non-polluted atmosphere. The CO_2 exchange in light and in darkness has been measured after 3 days from cutting the shoots (controls) or immediately after the fumigation treatment on the third day. The measurements of changes in CO_2 have been made with the help of an infra red gas analyser Infralyt III which operated in a closed system. The intensity of apparent photosynthesis (APS) and dark respiration (DR) were measured between the ranges of CO_2 concentration from 350 and 250 ppm recording the time taken for the change and the compensation point for CO_2 (concentration at which no further changes occur).

The intensity of photorespiration was defined as:

$$PR = \frac{APS \times CO_2 \text{ comp.}}{CO_2 \text{ conc.} - CO_2 \text{ comp.}}$$

Where PR is the photorespiration, APS the apparent or net photosynthesis between the given ranges of CO_2 concentration, CO_2 conc. the mean range of CO_2 concentrations, here 300 ppm, and CO_2 comp. the concentration of CO_2 at the compensation point (when PR=APS). TPS is the true photosynthesis defined as APS+PR. (P o s k u t a et al., 1972).

The measurements of CO_2 exchange were made in the following periods: 15 IX - 25 X 1976 — autumn period, 15 I - 25 II 1977 — winter period, 10 IV - 15 V 1977 — spring period, 30 VI - 20 VIII 1977 — summer period.

The results obtained have been verified statistically with the help of variance analysis and the multiple range test of Scheffé (O k t a b a, 1972). A null hypothesis about the lack of differences between individual elements of the experiment was verified at the 0.05 level of significance.

RESULTS

CO_2 EXCHANGE IN THE NON-FUMIGATED (CONTROL) SHOOTS OF THE MORE SO_2 RESISTANT (K—08—02 III) AND THE LESS RESISTANT (K—01—06 I) INDIVIDUALS DURING FOUR SEASONS OF THE YEAR

Activity of the processes of carbon dioxide exchange in non-fumigated shoots of the two individuals differing in resistance to SO_2 is different during the year but significantly so only in some seasons (Fig. 1). Apparent photosynthesis differs between the more resistant and more susceptible individual only in the autumn (Table 2, Ho_2). At that time the individual more resistant to SO_2 assimilates more CO_2 (68 µg CO_2 × g dry wt. of need-

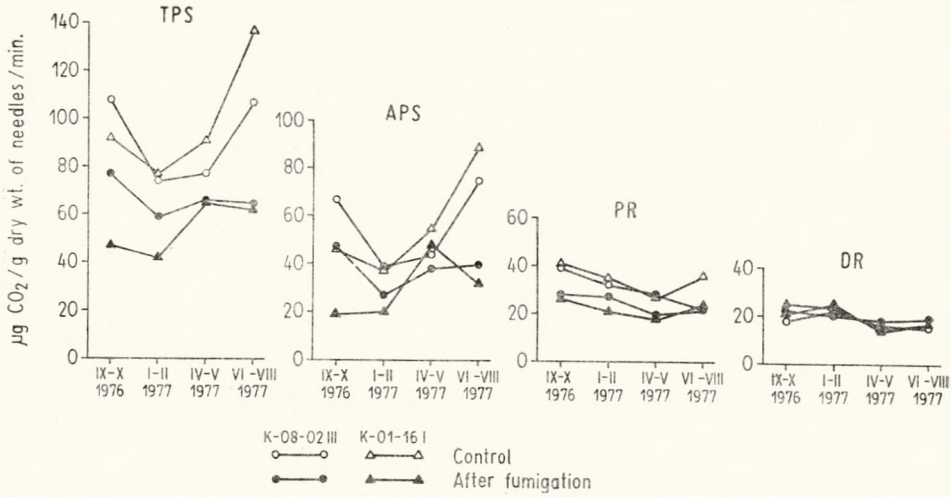

Fig. 1. Exchange of CO_2 in light and in darkness. Apparent photosynthesis (APS), photorespiration (PR), true photosynthesis (TPS), dark respiration (DR) in detached shoots of Scots pine subjected to the action of SO_2 at a concentration of 2.0 ppm for 3 days 6 hrs daily (K-08-02 III — more resistant individual, K-01-16 I less resistant individual)

les × min.—1) than the less resistant individual (46 µg CO_2×g dry wt. of needles × min.—1). In other parts of the season differences in the intensity of apparent photosynthesis for the two individuals where not significant (Table 2, HO_2).

Differences in photorespiration between the two individuals are significant only in the summer (Table 2, Ho_2). At that time the resistant individual emits less CO_2 in light (22 μg CO_2/g dry wt. of needles/min.) than the less resistant one (36 μg CO_2/g dry wt. of needles/min.) (Fig. 1).

The intensity of true photosynthesis differentiates the two individuals in the summer and in the autumn (Table 2, Ho_2). In the summer the less resistant individual has significantly higher TPS (137 μg CO_2) g dry wt. of needles (min.) than the more resistant one (107 $_2$g CO_2/g dry wt. of needles/min.). On the other hand in the autumn the opposite is true the corresponding values being (92 and 114 μg CO_2/g dry wt. of needles/min.) (Fig. 1).

The intensity of dark respiration is significantly different between the individuals differing in SO_2 susceptibility only in the winter period (Table 2, Ho_2). At that time the more resistant individual emits less CO_2 in the dark than the less resistant one (22 and 25 μg CO_2/g dry wt. needles/min. respectively) (Fig. 1). In the other parts of the year the differences in DR were not significant.

THE EFFECT OF SO_2 ON CO_2 EXCHANGE IN SHOOTS OF THE MORE SO_2 RESISTANT INDIVIDUAL (K—08—02 III)

The action of sulphur dioxide at a concentration of 2.0 ppm for 3 days (6 hours daily) on detached pine shoots of the more resistant individual to SO_2 significantly lowers the intensity of apparent photosynthesis throughout the year except for the spring period (Table 2, Ho_1, Fig. 2).

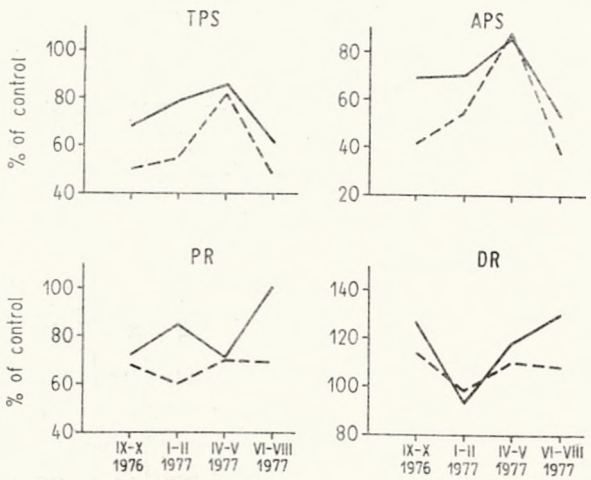

Fig. 2. Effect of SO_2 on apparent photosynthesis (APS), photorespiration (PR), true photosynthesis (TPS) and dark respiration (DR) of detached pine shoots from the more resistant individual (continuous line) and the less resistant one (broken line) to the action of this gas

Table 2

Exchange of CO_2 in light and in darkness. Apparent photosynthesis (APS), photorespiration (PR), true photosynthesis (TPS), dark respiration (DR) in detached shoots of Scots pine subjected to the action of SO_2 at a concentration of 2.0 ppm over 3 days, 6 hrs daily (K-09-02 III – more resistant indivual, K-01-16 – less resistant individual)

		Autumn 15 IX – 25 X 1976				Winter 15 I – 25 II 1977				Spring 10 IV – 15 V 1977				Summer 20 VI – 20 VIII 1977			
		μg CO_2/g dry wt. needls/min.				μg CO_2/g dry wt. needls/min.				μg CO_2/g dry wt. needls/min.				μg CO_2/g dry wt. needls/min.			
		TPS		APS		PR		DR		TPS		APS		PR		DR	
Plant		K	SO_2	K	SO_2	K	SO_2	K	SO_2	K	SO_2	K	SO_2	K	SO_2	K	SO_2	K	SO_2	K	SO_2	K	SO_2	K	SO_2	K	SO_2	K	SO_2	K	SO_2
K-08-02 III																													
	$\bar{x}$	114	77	68	47	39	28	18	22	74	59	39	27	32	27	22	21	77	66	44	38	28	20	16	18	107	65	75	40	22	22	15	19
	σ	22	20	18	15	7	6	4	4	13	14	9	8	9	10	2	2	16	22	16	19	9	7	4	6	25	9	24	9	10	7	3	5
	Ho_1	+		+		+		+		+		+		–		–		–		–		+		–		+		+		–		+	
	α_1	0,01		0,01		0,01		0,05		0,05		0,01		0,1		0,1		0,1		0,1		0,05		0,1		0,01		0.01		0,1		0,05	
K-01-16 I																													
	$\bar{x}$	92	47	46	19	40	27	22	25	77	42	37	20	36	21	25	24	92	76	55	48	27	19	14	15	137	62	88	32	36	25	16	17
	σ	19	13	18	7	6	7	5	6	13	8	9	5	8	4	2	4	30	27	26	24	10	8	7	4	23	23	30	16	10	11	2	5
	Ho_1	+		+		+		–		+		+		+		–		–		–		+		–		+		+		+		–	
	α_1	0.01		0,01		0.01		0,1		0,01		0,01		0,01		0,1		0,1		0,1		0,05		0,1		0,01		0,01		0,05		0,1	
	Ho_2	+		+		–		–		–		–		–		+		–		–		–		–		+		–		+		–	
	α_2	0,05		0,01		0,1		0,1		0,1		0,1		0,1		0,05		0,1		0,1		0,1		0,1		0,01		0,1		0,01		0,1	
	Ho_3	–		–		–		–		+		–		+		–		–		–		–		+		–		+		–		+	
	α_3	0,1		0,1		0,1		0,1		0,01		0,1		0,05		0,1		0,1		0,1		0,1		0,1		0,05		0,1		0,05		0,1	

σ – standard deviation; Ho_1 – result of verification of the null hypothesis about there being a lack of differences between the control and the material fumigated with SO_2; Ho_2 – result of verification of the null hypothesis about there being a lack od differences between the two individuals; Ho_3 – result of verification of the null hypothesis about there being a lack of interaction between the SO_2 treatment and the pine individuals; – – indicates lack of differences (Ho accepted); + – indicates presence of differences (Ho rejected) both at the 0.05 level of significance; α_{1-3} – maximal level of significance when Ho accepted and minimal when rejected.

The inhibition of true photosynthesis under the influence of SO_2 is observable in the same periods of time (summer, autumn and winter) while it is not significantly lower in the spring (Table 2, Ho_1, Fig. 1, 2).

Sulphur dioxide will also reduce the intensity of photorsespiration, particularily in the spring and autumn (Fig. 2). In the other seasons the inhibition is not significant (Table 2, Ho_1).

The intensity of dark respiration is stimulated by SO_2 action in the summer and autumn while in the winter and spring changes in the intensity of this process are not statistically significant (Table 2, Ho_1, Fig. 1).

EFFECT OF SO_2 ON THE CO_2 EXCHANGE IN SHOOTS OF THE LESS RESISTANT INDIVIDUAL TO THIS GAS (K—01—16 I)

The action of sulphur dioxide at a concentration of 2.0 ppm. for 3 days (6 hours daily) on detached shoots of the pine individual characterised by lesser resistance to this gas significantly lowers the intensity of apparent and true photosynthesis in summer, autumn and winter (Fig. 1, 2). In spring the inhibition of these processes is not significant (Table 2, Ho_1). SO_2 causes also a decline in the intensity of photorespiration throughout the year. On the other hand dark respiration is not affected significantly by SO_2 (Table 2, Ho_1, Fig. 1, 2).

DISCUSSION

The presented results indicate that there is a considerable influence of sulphur dioxide on the intensity of CO_2 exchange in light and in darkness, both in the more and in the less resistant individual. The extent of changes in CO_2 exchange caused by SO_2 differs depending on the vegetative season in which the detached shoots have been treated with SO_2. It appears that the changes depend on the physiological age of the shoots.

Van Haut (1961) claims that in the summer the undeveloped shoots are more susceptible to SO_2 than the last year's shoots, which sometimes remain uninjured. Also Mamajev (1976) reports that two-and three--year old shoots are characterised by greater resistance than one-year old shoots. On the other hand Żelawski and Łotocki (1974) when studying the intensity of photosynthesis in a pine stand from a polluted areas and from a non-polluted one have found that in needles of the current season it is almost identical, and that in older needles it is only slightly lower in the material from the polluted stand.

In the study reported here the intensity of apparent and true photosynthesis is significantly lowered by SO_2 throughout the year except for the spring period, and this is so both in the more resistant and in the more susceptible individual (Table 2). However the extent of inhibition of APS

and TPS is greatest in the summer and towards the end of the season (autumn and winter) it declines in both individuals, which is in agreement with the studies of Katz and McCalum (1952). The high sensivity of photosynthesis to SO_2 in the summer appears to be associated with the physiological activity of the process in that period. The photosynthetic maximum for pine occurs in August and sometimes even in June (Żelawski and Góral, 1966), depending on the weather. Pine shoots assimilate at that time large quantities of CO_2 and absorb SO_2 with it (Van Haut, 1961). Considering the competitive nature of SO_3^{--} relative to CO_2 in the active parts of the RudP-carboxylase enzyme (Ziegler, 1972) which plays an important role in the fixation of carbon, it is hardly surprising that the sensitivity of photosynthesis to SO_2 is greatest during the summer.

Also it needs to be mentioned that in these studies the shoots used in the summer from both the individuals where the current year's shoots that have expanded in the spring, and therefore according to several authors (Van Haut, 1961; Mamajev and Makarov, 1976; Börtitz, 1964) most sensitive to SO_2. Both the individuals have had nonsignificant changes in the intensity of apparent and true photosynthesis in the spring (Table 2, Fig. 2) that is during the time when new shoots were beginning to elongate and the existing one-year-old shoots were becoming two-year-old ones, and therefore more resistant to SO_2.

Vogl, Börtitz and Polster (1970) when studying the effect of SO_2 on photosynthesis of resistant and susceptible pine clones have found that SO_2 causes a depression in the assimilation of CO_2 in both the groups of individuals. However in the resistant individuals it was not as great and it remained reversible loger. These individuals almost did not differ in the intensity of CO_2 assimilation in pure air.

In these experiments the treatment of detached Scots pine shoots with SO_2 at a concentration of 2.0 ppm for three consecutive days, 6 hours daily, has also caused a stronger depression in the intensity of APS and TPS in the less resistant individual than in the more resistant one (Fig. 2). This interaction between individuals and treatments was significant only for TPS in summer and in winter. On the other hand differences in the extend of APS depression between the two individuals were not significant throughout the year (Table 2, Ho_3). These individuals differed also significantly in the TPS in the summer and autumn and in APS in autumn in the non-fumigated control conditions.

The treatment of detached pine shoots with SO_2 has caused a reduction in the CO_2 emission in light (Fig. 2). Inhibition of photorespiration can be the result of the inhibitive action of SO_3^{--} on the activity of glycolic acid oxidase, as suggested by Zelitch (1957), Asada and Kasai (1962), Liebera et al. (1974) and Ziegler (1975). Inhibition of the peroxysomal (Jackson and Volks, 1970) oxidase of glycolic acid (Zelitch,

1957), caused an accumulation of glycolic acid (Spedding and Thomas, 1973) and the lowering of glycine and serine content (Asada and Kasai, 1972; Tanaka et al., 1972).

In the individual more resistant to SO_2 a lowering of photorespiration by this gas was observable in spring and in autumn, while in the summer it did not change. In the less resistant individual fumigated shoots have had a significantly lower photorespiration throughout the year compared with shoots untreated with SO_2 (Fig. 2). In spite of the differences between the two individuals in response of photorespiration to SO_2 treatment the variance analysis has shown that the differences in photorespiration inhibition are significant only in the summer and winter. This differentiation is caused by the greater sensivity of photorespiration to SO_2 in the less resistant individual (Table 2, Ho_3).

Acting with SO_2 at a concentration of 1.6 ppm on pine and spruce Keller (1957) has observed that in the first days of fumigation there is a stimulation of dark respiration. On the other hand a longer exposition of a forthight or so has caused a reduction in the CO_2 emission in darkness.

In this study the exposition of pine shoots to SO_2 has also caused an increase in the intensity of dark respiration both in the more resistant and in the less resistant individual. However significant changes in this respect were observable only in the more resistant individual and only in the summer and autumn. There was no interaction between the SO_2 treatment effect and individual variation at any time in the year (Table 2, Ho_3).

Studying the effect of SO_2 on CO_2 exchange in light and in darkness in individuals differeing in resistance could be helpful in the determination of the causes for differences in sensitivity of pine trees to SO_2. On the basis of the presented results it can be concluded that the individuals differing in resistance to SO_2 have different sensitivities of true photosynthesis to this gas.

SUMMARY

A study was made of the effect of sulphur dioxide at a concentration of 2.0 ppm on the intensity of apparent and true photosynthesis, photorespiration and dark respiration in detached pine shoots from two individuals differing in resistance to this gas. The CO_2 exchange was measured during four seasons of the year with the help of an infra red analyser in a closed system. It was shown that SO_2 lowers apparent photosynthesis, photorespiration and true photosynthesis and stimulates dark respiration. Inhibition of CO_2 exchange in light is stronger in the less resistant individual. On the other hand the stimulation of dark respiration is stronger in the more re-

sistant individual. There are differences between the seasons in these responses, summer being the most sensitive period.

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GABRIELA LORENC-PLUCIŃSKA

Wpływ dwutlenku siarki na fotosyntezę, fotooddychanie i oddychanie ciemniowe sosny zwyczajnej o różnej odporności na ten gaz

Streszczenie

Badano wpływ trzydniowego działania dwutlenku siarki (po 6 godzin dziennie) w stężeniu 2.0 ppm. na wymianę CO_2 odciętych pędów sosny, osobnika bardziej i mniej odpornego na ten gaz. Oznaczano natężenie fotosyntezy netto, fotoodychania, fotosyntezy rzeczywistej i oddychania ciemniowego za pomocą analizatora CO_2 w podczerwieni. Wykazano, że SO_2 hamuje natężenie fotosyntezy netto i rzeczywistej. Hamowanie asymilacji CO_2 jest najsilniejsze latem, natomiast jesienią i zimą jest wyraźnie słabsze. Wiosną obniżenie asymilacji CO_2 jest nieistotne. Zmiany w natężeniu fotosyntezy netto i rzeczywistej są silniejsze u osobnika mniej odpornego na SO_2. Wykazano, że dwutlenek siarki hamuje natężenie fotooddychania. U osobnika mniej odpornego hamowanie wydzielania CO_2 na świetle jest istotne w ciągu całego roku. Natomiast u osobnika bardziej odpornego na SO_2 obniżenie natężenia fotooddychania jest istotne tylko wiosną i jesienią. Stwierdzono, że dwutlenek siarki stymuluje natężenie oddychania ciemniowego u obu osobników wiosną, latem i jesienią. Zimą — oddychanie ciemniowe jest hamowane. Powyższe zmiany w natężeniu wydzielania CO_2 w ciemności są wyraźniejsze u osobnika bardziej odpornego na SO_2.

ГАБРИЕЛЯ ЛОРЕНЦ-ПЛЮЦИНЬСКА

Влияние сернистого ангидрида на фотосинтез, фотодыхание и темновое дыхание сосны обыкновенной, обладающей различной устойчивостью к этому газу

Резюме

Было исследовано влияние трехдневного действия сернистого ангидрида (по 6 часов в день) в концентрации 5,34 mg/м³ на обмен CO_2 отрезанных побегов сосны у особи более или менее устойчивой на действие этого газа. Была определена интенсивность фотосинтеза нетто, фотодыхания, действительного фотосинтеза и темнового дыхания с помощью инфракрасного газоанализатора CO_2. Выявлено, что SO_2 тормозит интенсивность фотосинтеза нетта и действительного фотосинтеза. Наибольшее торможение ассимиляции CO_2 летом. Осенью и зимой оно значительно меньше. Весной уменьшение ассимиляции незначительно. Изменения интенсивности фотосинтеза нетто и действительного значительнее у особи менее устойчивой к SO_2. Выявлено, что сернистый ангидрид тормозит интенсивность фотодыхания. У особи менее устойчивой выделение CO_2 на свету существенно тормозится в течение всего года, в то время как у более устойчивой особи уменьшение интенсивности фотодыхания является существенным лишь весной и осенью. Зимой темновое дыхание тормозится. Выше указанные изменения интенсивности выделения CO_2 в темноте отчетливей у особи более устойчивой к SO_2.