Photosynthesis and respiration of Scots pine (*Pinus silvestris* L.) seedlings grown in water culture from seed of various provenance*

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In spite of numerous publications on the physiology of Scots pine (literature review: Żelawski 1967), the effect of light intensity and CO₂ concentration on the photosynthetic rate in this species has not been sufficiently studied. It seemed therefore interesting to investigate the photosynthetic light and CO₂-concentration curves. The study comprised the linear parts of the curves, i.e. the light conditions up to about 10,000 lux at CO₂-concentration 0—500 ppm. The shifting of the carbon dioxide compensation point at varying light intensity was precisely determined. The experiments were carried out on seedlings grown in water culture. Seed from three different sources was used for comparison of the photosynthetic efficiency of various provenances of pine.

MATERIAL AND METHOD

Scots pine seedlings of three provenances (Dłużek, Spała and Nowy Targ) representing various regions of the country were used in this research, as in our previous study on photosynthesis (Żelawski, Góral 1966). Seedlings were cultivated in the water solution recommended for pine by Ingestad (1960, 1962/63). The whole plant material grew under natural light conditions in one common container standing at a southern window of a room. The seed germinated in March and plants 10—13 weeks-old were used for gas exchange determination.

Measurements of the net photosynthesis and dark respiration were carried out by means of an infra-red gas analyser in a closed circuit system. The time of CO₂-uptake was determined at 50 ppm intervals, as the concentration slowly decreased from 0.05 v% to the carbon dioxide compensation point. The photosynthetic light curve determinations are based on measurements of the rate of CO₂-uptake between 350 and 300 ppm. During the measurements the plants were placed in a double-walled plexiglass chamber connected with an ultrathermostat. In this way the temperature of the air surrounding the seedling was kept at a constant level of 25°C, both during the light and dark periods of the experiment.

The illumination was adjusted so that the plants received light from three direc-

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tions simultaneously. Fluorescent tubes were set on the two opposite sides of the chamber; they gave up to 2×2500 lux inside the chamber. Additional 5000 lux came from the incandescent lamps placed above the upper, 8 cm thick water screen. The total amount of light obtainable from the combined light sources was estimated to be at least 10,000 lux but it should be borne in mind that it is not easy to define the true light intensity when the radiation comes from several directions. Yet, the illumination chamber applied in this experiment provided for the whole plant more uniform conditions than the one-sided light sources. The reduction of the light intensity, achieved by use of neutral screens, was expressed as a percent of the maximum illumination applied.

The photosynthetic CO_2 -concentration curves were determined at two light intensities (maximum and about half of that).

All data were calculated for fresh and dry weight units and also expressed per 1000 needles and per 1 mg of chlorophyll. The chlorophyll content determinations were carried out spectrophotometrically and the calculations of chlorophyll *a* and *b* were based on the MacKinney (1941) formula in the modification of Bruinsma (1960).

Ten plants of each provenance (altogether 30) were examined. The average data for the investigated pine strains are presented in fig. 1—3 and in table 1.

RESULTS

Figure 1 presents average data of photosynthesis rate at varying light intensity. It can be seen, that the applied illumination does not provide condition for the maximum photosynthesis rate of this species, the saturation level not being reached. The relation of photosynthesis rate to light intensity is linear in character within the investigated illumination range. The light compensation point i.e. the intensity of light at which the equilibrium between uptake and evolution of CO_2 occurs, takes place in the given experimental conditions between 9 and 10% of light. Within the investigated range of illumination provenance does not seem to affect the reaction of photosynthesis to varying light intensity.

Within the CO_2 -concentration range 200—400 ppm, the rate of photosynthesis is almost directly proportional to the concentration of carbon dioxide (fig. 2). However, higher concentrations of CO_2 do not seem to cause any further increase of the photosynthetic rate. In the given experimental conditions the photosynthetic saturation level begins already between 450 and 500 ppm. The character of the photosynthetic CO_2 -concentration curves are similar at two different light intensities and CO_2 -compensation point occurs at exactly the same concentration of carbon dioxide (about 65 ppm).

There is only a very slight difference in absolute values of photosynthesis rates of the investigated pine strains but the character of the influence of carbon dioxide on the photosynthesis rates is very much the same in all of them.

Fig. 1. Effect of light intensity on photosynthesis rate of Scots pine seedlings (each value is an average from 10 plants).

Fig. 2. Effect of CO_2 -concentration on photosynthesis rate of Scots pine seedlings (each value is an average from 10 plants).

The relationship between the position of the carbon dioxide and the light-compensation points is shown in fig. 3. It is seen that the equilibrium between the photosynthesis and respiration rates takes place at various CO_2 levels, depending on light intensity. At lower light intensities near to the light-compensation point, a very slight change of illumination results in a remarkable shift of the CO_2 -compensation point, whereas at relatively higher intensities there is no effect of light on the position

Fig. 3. Position of CO_2 -compensation point as related to light intensity.

of the CO_2 -compensation point. In the investigated plant material and in the given experimental conditions the constant level of the CO_2 -compensation point was attained at light intensity near to 50% of illumination applied. No significant differences in the position of the compensation point were found between the seedlings of different provenance.

Comparison of the investigated pine strains can also be carried out on the basis of the average data listed in table 1. As seen, there is no marked difference as regards provenance either in the respiration rate or in the photosynthetic efficiency calculated per number of assimilatory organs and per 1 mg of chlorophyll content. Yet, the rates of photosynthesis expressed per fresh and dry weight units as well as growth characteristics, like average weight of needles, and proportions between the organs of the plant are somewhat different in seedlings of different provenance. This indicates that in spite of the uniform conditions of water culture, certain developmental differences between them may occur and manifest themselves even at a very early stage.

Table 1

Growth characteristics, chlorophyll content, photosynthesis and respiration rates in pine of different provenance (each number is calculated as an average from 10 seedlings; chlorophyll determinations are based on 3 replications)

Characteristics	Provenance		
	Dłużek	Spała	Nowy Targ
Growth characteristics			
Dry weight of needles (mg)	29,9	34,5	38.5
Number of needles on shoot	61	65	70
Dry weight of a single needle (mg)	0.49	0.53	0.55
Dry matter content in needles (%)	19,0	18,4	18,9
Dry weight of lignified stem (mg)	10,1	10.6	13.9
Dry weight of root system (mg)	4,4	5,1	8.2
Dry weight of whole plant (mg)	44,4	50,2	60,6
Shoot/root ratio (based on d. wt. determinations)	9.4	8.6	6.4
Stem/needles ratio (based on d. wt. determinations)	0.34	0.31	0.36
Chlorophyll content ($a+b$)			
per g of fresh weight of needles (mg)	2.4	2,2	2.0
per 1000 needles (mg)	5.4	5.6	5.4
chlorophyll a / chlorophyll b	2.1	2.0	2.0
Apparent photosynthesis*			
mg CO ₂ /g of fresh weight/ hour	5.45	5.16	4.80
mg CO ₂ /g of dry weight/ hour	28.9	28.6	25.1
mg CO ₂ /1000 needles/ hour	13.8	14.3	13.7
mg CO ₂ /mg of chlorophyll/ hour	2.56	2.55	2.54
Dark respiration			
mg CO ₂ /g of fresh weight/ hour	0.51	0.52	0.52
mg CO ₂ /g of dry weight/ hour	2.9	2.9	3.0
mg (CO ₂ /1000 needles/ hour	1.3	1.4	1.4

* At maximum light intensity applied in experiment and at natural (350—300 ppm) CO₂-concentration.

DISCUSSION

In the data published on photosynthesis of Scots pine the relation of this process to light intensity has not been sufficiently described. Most of the investigators did not find the light saturation level even under full illumination in natural summer conditions (Stålfelt 1921, 1924; Ivanow and Kossovitch 1930; Polster 1950; Decker 1954), others however, were able to show that photosynthesis in Scots pine reaches a constant value at 30, 20 or even 8—10 thousand lux, depending on the influence of growth conditions (Sokołova 1964) or nitrogen deficiency (Keller and Wehrmann 1963).

Our investigation carried out at relatively low light intensity could not give any further elucidation of the problem of light saturation, but it has shown clearly that in good conditions of growth the photosynthetic light curve is still linear in character up to the highest light intensity applied (at least 10,000 lux). Keller and Wehrmann (1963) who also experimented with pine seedlings grown in water culture did not find the maximum rate of photosynthesis even at 50,000 lux when the plants contained greater amounts of chlorophyll, but they were able to show that, in plants with low chlorophyll content, the photosynthetic saturation level had been reached already at 15,000 lux. However, it should be mentioned here, that these authors did not analyze in detail the course of the photosynthetic light curves.

Our study concerning the position of the CO_2 compensation point at varying light intensity threw some new light on the question which also has not been sufficiently described in the earlier literature. From the papers of Egle and Schenk (1952, 1953), Bruckner and Urbach (1958) and Egle (1960), general information could be gathered on the mutual influence of light intensity, CO_2 -concentration and temperature on the state of equilibrium between the uptake and evolution of CO_2 . However, there were only very few plant species, the compensation points of which had been defined in this way. The determination of the relation between the CO_2 - and the light-compensation points has given some more precise information about this state in Scots pine seedlings at 25°C. It should, however, be borne in mind that in these experiments the gas exchange determinations were not made on single leaves but included the entire above-ground parts of the plant. Therefore, the data does not represent the actual photosynthesis and respiration rates in leaves, but show an equilibrium which is also affected by the ratio of assimilatory organs and non assimilating, but respiring parts of the plant.

The data on the influence of CO_2 on the photosynthetic rate within the natural range of CO_2 -concentration show that in pine, the photosynthetic CO_2 -saturation level can be reached at relatively low CO_2 -concentration when low light intensity is applied. However, already a long time ago, Stålfelt (1924) demonstrated that Scots pine was able to use carbon dioxide even in concentrations 10 times higher than its natural content in the air, when the light intensity amounted to 30% of the natural full illumination. The results of our experiment seem to indicate that other limiting factors, (like for instance the degree of stomata closure) may have been involved here.

The experimental conditions of this work could not provide the optimum light intensity and increased CO_2 -concentration in order to measure the maximum rates of photosynthesis. In spite of this, the average data obtained in this work exceed the values published for Scots pine by other authors. Especially the data expressed per 1 g of dry matter of needles are very high. Keller and Wehrmann's (1963) data, the best comparable with ours showed considerably lower photosynthetic rates, despite the fact that the authors had the possibility of using an illumination up to 50,000 lux. The difference between the photosynthetic efficiency in both papers discussed is probably due to the different age of the plant material or to the various

temperature conditions used in these experiments. However, it is worth stressing that the photosynthesis rate calculated per 1 mg of chlorophyll was in our experiments similar as that reported by Keller and Wehrmann for seedlings with the highest chlorophyll content, i.e. in conditions of sufficient N supply.

Relatively little can be said as regards the comparison between seedlings of different provenance. There is a slight difference in the average photosynthesis rates calculated per weight units of needles, but this difference is probably due to the different growth rates of the investigated pines. The conditions of water culture provided a very uniform milieu for development of all seedlings but, in spite of this, the differences of origin manifested themselves in needles' size and in the total amount of dry matter produced in needles, lignified stems, and roots. From the data presented in table 1 it can be seen that the plants from Nowy Targ, deriving from the highland area exhibit somewhat outstanding dimensions.

The picture of differences between plants of different provenance obtained in this study with young seedlings seems to be different as compared with the results of our previous work carried out on two-year-old pot seedlings (Żelawski and Góral 1966). However, the divergence is only apparent since in both experimental series various developmental stages of plants were compared. As has already been shown (Żelawski and Góral 1966), the photosynthesis rate in plants of highland provenance may exceed the rate of lowland pines at the beginning of the vegetation season, but during the summer and autumn months the situation may be reversed. The relatively faster development of Nowy Targ seedlings in the water culture experiment might have caused the decrease of photosynthesis rate, since even-age plants may have been not equally "aged". None the less, the photosynthetic rate expressed per number of assimilatory organs or per chlorophyll content of needles was very much the same in the investigated pine strains, and the question of physiological differences between the ecotypes remains still unsolved and requires further research.

CONCLUSIONS

1. In the investigated seedlings the dependence of photosynthesis rate on light intensity was linear in character in the illumination range up to about 10,000 lux.
2. The beginning of the photosynthetic CO_2 -saturation level was reached at about 450–500 ppm, in both variants of light intensity, this indicating that for pine seedlings other factors, besides illumination, may have limited the rate of photosynthesis.
3. At lower values of illumination, the position of the CO_2 -compensation point depends markedly on the light intensity but it is constant within the range of illumination from about 45 to 100% of the light intensity applied in the experiment.
4. In spite of the fact that the experiments were carried out below the light-saturation level and at concentrations of carbon dioxide near to natural, the values of photosynthesis rate found in these experiments exceed those published for Scots pine in earlier literature.

5. In this experiment the pine seedlings of different provenance were very much the same in their photosynthetic efficiency though in calculations per weight units there was slight difference between the lowland and highland plants perhaps connected with their different course of growth.

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Fotosynteza i oddychanie siewek sosny zwyczajnej (Pinus silvestris L.) wyhodowanych w kulturach wodnych z nasion różnego pochodzenia

Streszczenie

Badano zależność intensywności fotosyntezy od natężenia światła i stężenia CO_2 oraz położenie punktu kompensacyjnego u 10—13 tygodniowych siewek sosny zwyczajnej trzech proveniencji (Dłużek, Spała, Nowy Targ). Pomiarów przeprowadzono w warunkach laboratoryjnych, przy temperaturze 25° , stosując analizator gazowy (IR) w układzie zamkniętym. Wyniki pomiarów przeliczono na 1 g świeżej i suchej masy igliwia, na 1000 igieł i na 1 mg chlorofilu ($a+b$) oznaczonego spektrofotometrycznie.

W zakresie intensywności światła stosowanych w tych badaniach krzywa świetlna fotosyntezy miała charakter liniowy, natomiast krzywa CO_2 wykazywała początek poziomu wysycenia przy stężeniu 450—500 ppm.

Położenie punktu kompensacyjnego (CO_2) jest stałe przy wyższych intensywnościach światła natomiast zmienia się coraz wyraźniej w pobliżu świetlnego punktu kompensacji, w miarę jak maleje oświetlenie.

Mimo, że doświadczenia przeprowadzono w warunkach poniżej poziomu wysycenia świetlnego i przy stężeniu dwutlenku węgla zbliżonym do naturalnego, stwierdzone intensywności fotosyntezy netto, szczególnie w przeliczeniu na 1 g suchej masy igliwia, przewyższają dane ustalone dla sosny przez innych autorów.

W pracy nie stwierdzono zasadniczych różnic w wydajności fotosyntetycznej igliwia sosen różnego pochodzenia; pewne drobne różnice intensywności fotosyntezy w przeliczeniu na masę igliwia pomiędzy sosną pochodzenia górskiego (Nowy Targ), a sosną z niżu (Dłużek i Spała) mogą być związane z niejednakowym przebiegiem wzrostu badanych proveniencji.