Relationship between dry matter production and carbon dioxide absorption in seedlings of Scots pine (*Pinus silvestris* L.) in their second vegetation season*

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Abstract

Accumulation of dry matter in needles, lignified stems and roots during the second vegetation season was compared with seasonal changes in photosynthesis and respiration activities of these organs. Whereas growth analysis concerned plants growing at nearly natural course of external conditions, gas exchange determinations were made at constant laboratory conditions. For comparison of dry matter production and photosynthetic ability of a plant new terms „assimilation capacity” and „efficiency of assimilation” were introduced as possible expressions of photosynthetic productivity. Two ecotypes of Scots pine originating from lowland and highland regions of the country exhibited slightly different pattern of the investigated characteristics.

INTRODUCTION

From the results of studies in the field of plant productivity it is already known that the dry matter accumulation of a plant is not directly correlated to its photosynthetic capacity. None or even sometimes negative correlation between the two above-mentioned processes has been found by various investigators; this can be interpreted in terms of variation in efficiency of the particular plants in transforming the carbon dioxide into organic matter but this requires more detailed investigations.

In the present study seedlings of Scots pine were investigated during the second vegetation season by measuring the gas exchange of the particular organs in constant laboratory conditions and by simultaneous determination of the actual dry matter accumulation in a semi-controlled

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greenhouse environment. Seeds from two different sources, were taken for comparative study as representatives of the two main ecotypes of pine occurring on the territory of Poland.

MATERIAL AND METHODS

The seeds originated from natural stands in the highland region (Nowy Targ — φ 49°27', 620 m.a.s.l.) and lowland region (Dłużek — φ 53°32', 135 m.a.s.l.). The seed was sown and germinated in standard pots containing 12 kg of loamy-sandy forest soil. Water content was maintained at the level of 60% of capillary capacity by watering to constant weight. The plants were kept out of doors (under a wire net only), being wheeled under the glass for nights and rainy periods; they also spent the following winter in the unheated greenhouse.

Experiments were begun in the spring of the second vegetation season, when the new shoots had started to grow. They were repeated five times during the vegetation season. Measurements of gas exchange took place in constant laboratory conditions at 25°C, and CO₂ concentration between 350 and 300 ppm. The light source consisted of three 250 W incandescent reflector lamps from above through an 8 cm thick water screen, and of eight 20 W fluorescent lamps at two opposite sides of the photosynthetic chamber; it gave quite uniform partially dispersed illumination diminishing the effect of „mutual shading” of needles, and securing highest photosynthesis rates.

The closed system of the infrared CO₂ analyser was used for determination of CO₂ consumption in light and its evolution in darkness. Plants previously adapted for some time to the measurement conditions were cut into three or four segments, each of which was examined separately in a plexiglass chamber with controlled temperature. After the measurements of photosynthesis and respiration in all parts of the plant had been completed, the root was carefully extracted from the soil, washed, and its respiration was determined. According to Negisi (1966) such a procedure is admissible for estimating respiratory rates comparable with those of attached roots although some traumatogenic effects may also be expected (Żelawski 1962).

The harvested plant material was dried at 105° C. Two groups of plant material were used for growth analysis: 1) consisting of the samples used for gas exchange determinations (means of 10 plants measured separately) and 2) sampled on parallel plants growing in the same conditions (in this case each sample consisted of 21—36 plants). Net assimilation rates were calculated by the simplified formula with assumption of the linearity of the growth course between the two harvests (see review by Nečas et al. 1966).

RESULTS

Growth and dry matter accumulation

The ratio of assimilating to nonassimilating parts considerably increased during the first period of intensive growth of new needles and began to decrease again towards the end of the vegetation season (Fig. 1).

Fig. 1. Dry matter accumulation in particular organs of pine seedlings during their second year of growth (in brackets is given the ratio: assimilatory organs to nonassimilating organs)

Old needles of the previous vegetation season (juvenile needles) made up only a small portion of the total assimilatory organs. At the beginning of June they amounted to 33—47% but at the end of September to as little as 7—11% of the total green tissue. The change in this proportion was due to both, the increase of dry weight of new needles and to the decline in dry weight of old needles almost completely disappearing at the end of the vegetation season.

The two investigated pine strains were not quite equal as regards the course of dry matter accumulation, though the essential trends were almost the same. The lowland pine seems to have a somewhat higher ratio of assimilating to nonassimilating organs, although the difference between both ecotypes is small.

The mean data of dry matter of a single needle (Fig. 2) showed the same trends for the two investigated ecotypes: during the shooting period (June/July) the average dry weight of a single needle was the highest

at the basis of the shoot and decreased towards its top parts; however, when growth had been accomplished (end of August), the top needles became heaviest and the middle part needles the lightest. Juvenile needles of the previous vegetation season did not show any significant change in their dry weight during the period June-October.

Fig. 2. Mean dry weight of a single needle (mg) in top, middle, and basal parts of a new shoot and mean dry weight of a single juvenile needle (mg) of the previous year of growth

Net assimilation rates calculated for the period June 1—30 amounted to 34.4 (lowland pine) and 42.3 (highland pine) mg of dry weight per g of needles dry weight and day, and they gradually decreased reaching zero for the period September-October (Table 2, Fig. 7).

Photosynthesis and respiration

The rates of photosynthesis and respiration exhibited a typical seasonal decline (Fig. 3 and 4).

Systematic but slight differences appear when pines of different provenience are compared. Juvenile needles of the previous year are always more active in highland than in lowland pine both as regards photosynthesis and respiration rates. The seasonal course of photosynthesis was not the same and the typical for highland pine earlier advance of the photosynthetic winter depression was noticeable in secondary needles.

Fig. 3. Seasonal changes of photosynthesis and respiration of new needles (paired needles in fascicles)

Fig. 4. Seasonal changes of photosynthesis and respiration rates of the previous year's juvenile needles

Fig. 5. Photosynthesis and respiration rates in top, middle, and basal needles of the new developing shoot

Photosynthesis as well as respiration expressed per 1000 needles showed in paired needles a constant difference between the investigated pine strains, which mainly resulted from difference in the average dry weight of needles.

Differentiation of physiological activities along the shoot is even more pronounced than the differentiation of dry weight of needles. Distinctly higher photosynthesis rates were usually observed in the middle and base than in the top parts of the shoot, but a seasonal change in this regularity was seen in both investigated ecotypes (Fig. 5).

In respiration rates another regularity was observed: at the beginning of the vegetation season, the respiration rate decreased from the top needles to the base needles and towards the end of the growing period an opposite trend was noted. The ratio photosynthesis:respiration (A/R) reached its maximum in the September measurements, and in most cases it was the highest in the middle part of the shoot (Tab. 1).

Table 1

Various indices concerning the ratio of shoot to root activity

Ratio	Ecotype	Date of the experiment				
		June 1	July 1	August 5	Sept. 25	Oct. 28
Photosynthesis (shoot): respiration (root)	lowland	34	47	21	28	19
	highland	31	32	16	19	14
Photosynthesis (shoot): respiration (shoot)	lowland	7.2	10.0	9.0	12.3	9.6
	highland	7.3	8.7	8.3	12.8	8.2
Photosynthesis (shoot): respiration (shoot+root)	lowland	5.8	8.3	6.3	8.5	6.4
	highland	5.9	6.8	5.5	7.6	5.2
Respiration (shoot): respiration (root)	lowland	4.9	4.7	2.3	2.2	1.9
	highland	4.3	3.7	2.0	1.5	1.7
Dry weight (shoot): dry weight (root)	lowland	1.9	3.8	3.0	2.0	2.5
	highland	1.7	3.4	3.0	2.2	1.9

The respiration rates of the root system are least reliable owing to the known difficulties in precise extraction from the soil. In calculations per 1 g of dry weight the respiration rates of root amounted, on the average to about 0.4–1.0 mg per hour, a value of the same order of magnitude as shoot respiration in late summer and autumn. The maximum respiration rate was found to occur in full summer time this being related in part with the change in the proportions of active and dead tissues in the total dry matter of the root (Fig. 6). Higher rates of root respiration were observed in the highland ecotype at every sampling date.

Fig. 6. Root respiration in seedlings of different provenience

The ratios: 1) photosynthesis of the shoot to respiration of the shoot, 2) photosynthesis of the shoot to respiration of the root, 3) respiration of the shoot to respiration of the root, 4) photosynthesis of the shoot to respiration of the shoot and root, as well as 5) dry matter of the shoot to dry matter of the root were in most cases higher in the lowland than in the highland ecotype (Table 1).

Capacity of assimilation and assimilation efficiency

Larcher (1969 a, b) suggested the term „capacity of net photosynthesis” (F_{cap}) to express the maximum rates of CO_2 uptake occurring at natural partial pressure of carbon dioxide, other conditions being favourable. An analogous term „capacity of net assimilation” (NAR_{cap}) could be introduced for indicating the maximum ability to accumulate dry matter by plants growing in such optimum conditions. This „assimilation capacity” and laboratory data on photosynthesis and respiration are related according to the equation given in the above mentioned paper (Larcher 1969a). However, estimation is also possible by the use of a simplified formula where, instead of the integrated daily course of photosynthesis and respiration, the average rates of the processes (assumed as capacity of net photosynthesis and capacity of dark respiration) are multiplied by their average time of duration:

$$NAR_{cap} = \frac{[F_{cap} d - R_s (24 - d) - R_r \cdot 24] c}{[d (F_{cap} + R_s) - 24 (R_s + R_r)] c}$$

where:

- F_{cap} — capacity of net photosynthesis,
- R_s — respiration rate of the shoot,
- R_r — respiration rate of the root, (all these values calculated in $mg\ CO_2$ per hour per 1 g of dry weight of assimilatory organs),
- d — length of the day in hours, average for the period concerned,
- c — coefficient of conversion between carbon dioxide and dry matter (mg) (assumed to be roughly 0.7)

By comparing the true rates of net assimilation determined directly by growth analysis and the calculated values of assimilation capacity obtained indirectly from gas exchange measurements at nearly optimum conditions, it is possible to estimate the efficiency of assimilation

$$\frac{NAR_{true}}{NAR_{cap}} \times 100$$

The assimilation efficiency was first calculated for the period of highest photosynthetic activity, i.e. for the time of active growth, of the longest days and of highest photosynthesis rates. In two groups of plant material (1. harvested at the beginning and at the end of June, and 2. harvested June 10 and July 15) pine of lowland provenience showed higher assimilation capacity (NAR_{cap}) and lower net assimilation rate (NAR_{true}) than pine of highland provenience. As a result the assimilation efficiency (AE %) was in both cases much higher in highland than in lowland provenience (Table 2).

Table 2

Comparison of true rates of net assimilation and calculated values of assimilation capacity in pine seedlings of different provenience

Period of investigation (Dates of sampling for growth analysis)	Provenience	Assimilation capacity (NAR _{cap})	Net assimilation rate (NAR _{true})	Assimilation efficiency (AE %)
		mg dr. wt. day ⁻¹ ·g needles dr wt ⁻¹		
June 1—30	lowland	141.3	34.4	24
	highland	136.7	42.3	31
June 10 — July 15	lowland	127.5	23.3	18
	highland	101.1	32.1	32

During the vegetation season the assimilation efficiency decreased considerably. In mid July this efficiency was as low as 8—12% and it gradually diminished to zero in mid October when the net assimilation rate

Fig. 7. Net assimilation rates calculated from gas exchange measurements as the assimilation capacity and determined directly from growth analysis data

of plants growing out-of-doors was zero, but assimilation capacity estimated from laboratory data in optimum conditions was still almost one third of its maximum value (Fig. 7).

DISCUSSION

Some aspects of shoot formation in pine seedlings has been described in the reviews by Jankiewicz (1967), and Hejnowicz (1967), and also in the work by Gowin and Góral (1968). The present paper supplies some further information concerning the different pattern of needle growth in the top, middle, and basal parts of the shoot. This may be of some importance for sampling of representative needle material as well as in interpreting the data on physiological processes occurring within the shoot.

It is seen that the previous year's juvenile needles do not increase in weight during the summer time of the second vegetation season; this is in agreement with the earlier observation by Gowin and Góral (1968). Owing to the gradual dying and dropping off the role of these assimilatory organs is almost negligible towards the end of the second vegetation season.

Accumulation of dry weight in root and stem continues to occur longer in the autumn months than the increase of needle weight. The ratio of assimilating to nonassimilating organs increases in June and July but exhibits almost the same values at the beginning and at the end of the vegetation season. The ratio shoot/root is also the highest in the period June/July. This indicates that in spring time the photosynthates are used at first to produce active assimilatory organs, and only later dry matter accumulates in other parts of the plant. This is in agreement with the facts established previously by Larson (1964), Gordon and Larson (1968), and Larson and Gordon (1969), in their experiments with translocation of ^{14}C -photosynthetic products.

The differentiation of needles along the shoot brings about some differences in the rates of physiological processes. However, different rates of photosynthesis and respiration do not directly reflect the morphological variation. Irrespective of the change in the proportions of needles size during the growth period the middle part of the shoot is always most active in photosynthesis. The basal needles showed exactly the same photosynthesis rate as the middle part needles, except at the earliest date of measurement in the beginning of June what might be related with earlier growth of basal needles as seen from the dry weight data. Further evidence that needles along the shoot are not uniform in physiological respects, and that this physiological differentiation does not directly correlate with the needle size variation is seen from the data concerning

respiration, where neither direct nor inverse proportionality of both values could be detected.

The data of this work confirm the previous information on the seasonal course of photosynthesis (Żelawski and Góral 1966) completing it in some details. The rates of photosynthesis in juvenile needles of the previous year are distinctly lower during the second vegetation season as compared with photosynthesis rates of the new developing secondary needles. This means that in the second vegetation season the juvenile needles do not attain the high photosynthetic capacity typical for the first year (Żelawski and Kinelska 1967), even though they exhibit some recovery of photosynthesis after the winter depression (Żelawski and Kucharska 1967). Thus the contribution of these assimilatory organs to the total production of dry matter is certainly limited to the spring period only before the new shoot begins to elongate. Young needles of the new growth become photosynthetically active already in early stages of their growth, and soon after they begin to prevail in weight, their production starts to play a decisive role. Comparing the data of this paper with previous results Żelawski and Góral (1966), Żelawski, Kucharska and Łotocki (1969) we come to the conclusion that the period around June 1 is the time of maximum photosynthesis activity for Scots pine growing under the climatic conditions of this country.

The rates of the respiration in the above ground parts are the highest in spring time. However, this is not the case in the root system which shows its maximum respiration later in the vegetation season. Also Shiroya et al. (1966) and Lister et al. (1967) have established that the maximum rates of root respiration and photosynthates' translocation in white pine seedlings grown in Canada occur in August-September.

As far as the physiological differentiation of ecotypes is concerned, the following characteristics were typical: 1) not quite the same seasonal course of photosynthesis and earlier advance of winter depression in pine of highland provenience (like in the previous research — Żelawski and Góral 1966), 2) a different course of growth and various proportions between the organs, 3) higher values of the ratio photosynthesis to respiration in the lowland than in the highland ecotype, 4) higher values of respiration of the root in the highland ecotype, 5) net assimilation rates higher and assimilation capacities lower in pine of highland origin, and consequently much higher assimilation efficiency in highland than in lowland pine, 6) previous year's juvenile needles continue to be photosynthetically active longer in pine of highland origin, although abscission proceeds in the same way in both ecotypes.

It has already been shown (Żelawski and Gowin (1966), Żelawski and Niwiński (1966) that smaller needles are typical for pine of highland ecotype. However, in this study like in some previous

works carried out with two-year-old plants, this regularity did not always occur. It appears that secondary needles formed in fascicles during the second vegetation season are not yet quite typical in size and usually excessively elongated. Assimilatory organs typical for the ecotype begin to develop only since the third year of growth.

An attempt to estimate the correlation between dry matter production (net assimilation rate) and the direct data received from gas exchange measurements (photosynthetic capacity) indicate that both values do not quite parallel each other either in the seasonal course or when comparing different ecotypes. Thus, the assimilation efficiency (%) indicating the percentage of dry matter accumulation, as compared with the maximum productivity attainable at most favourable conditions, exhibits a fast decrease towards the end of the vegetation season; it is also quite different for both investigated ecotypes. However, the significance of the index (AE %) should not be overestimated when evaluating plant objects; its high value rather indicates a better reaction of the plant to the actual growth conditions than its ability of being generally more efficient. The diversity of ecotypes is better recognisable when using the discussed index than if only photosynthetic capacity or dry matter production are taken into consideration. At the most favourable time of the year, during the longest days when light intensity and temperature were most favourable and photosynthetic capacity was the highest, assimilation efficiency amounted only to about 32%. This means that the average daily course of production attains only up to about 1/3 of the level assumed as a possible maximum.

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Związek pomiędzy produkcją substancji organicznej a pobieraniem CO₂ u siewek sosny zwyczajnej (Pinus silvestris L.) w ciągu drugiego okresu wegetacji

Streszczenie

Praca stanowi próbę porównania w przebiegu sezonowym nagromadzenia suchej masy i procesów wymiany gazowej siewek sosny zwyczajnej w ciągu ich drugiego okresu wegetacyjnego. Badano wzrost roślin i nagromadzenie suchej masy w doświadczeniu wazonowym w hali wegetacyjnej stosując metodę analizy wzrostowej. Jednocześnie na tym samym materiale badano w standardowych warunkach laboratoryjnych procesy fotosyntezy i oddychania poszczególnych części pędu i korzenia stosując metodę analizatora CO₂ w podcierwieniu. Podjęto próbę oceny produktywności procesu fotosyntezy wprowadzając pojęcie „zdolności asymilacyjnej”

i „wydajności asymilacji”. Pierwszy z wymienionych terminów oznacza maksymalną produkcję suchej substancji netto obliczoną na podstawie wyników pomiarów wymiany gazowej w optymalnych warunkach, a drugi wyraża procent realizacji tej produkcji w rzeczywistej asymilacji netto.

Badania dostarczyły informacji w sprawie zróżnicowania morfologicznego i funkcjonalnego igliwia sosny wzdłuż pędu wierzchołkowego, jak również rozszerzyły wiadomości o sezonowej zmienności procesów wzrostu, gromadzenia suchej masy oraz fotosyntezy i oddychania w poszczególnych częściach rośliny. Badania potwierdziły i rozszerzyły dotychczasowe wiadomości o fizjologicznym zróżnicowaniu sosny pochodzenia niżowego i podgórskiego. Obok różnic sezonowych w przebiegu procesu fotosyntezy stwierdzono także, że badane ekotypy różnią się pod względem wydajności asymilacji.

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