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Influence of shade on productivity of photosynthesis in seedlings of Scots pine (*Pinus silvestris* L.) during the second vegetation period*

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This paper is a continuation of the previous study on the adaptability of pine seedlings to shade (Żelawski and Żelawska 1967; Żelawski and Kinelska 1967 b.) It contains data concerning dry matter production, photosynthesis and respiration rates, as well as the morphological and anatomical structure of needles in pot plants cultivated for two vegetation periods under different conditions of shading. The possible causes of the low tolerance of this species to shade are discussed and the adaptability in pines of various origin is compared.

MATERIAL AND METHODS

The pine of highland provenance (Nowy Targ) which was previously found to be somewhat more shade-tolerant than pines of lowland origin was the object of this more detailed study. Plants cultivated in pots under natural light and those under paper tape screens receiving 60 or 20 per cent of full illumination were examined at the end of the vegetation season 1966. It is understandable that due to the experimental procedure applied not only light intensity was modified during the pretreatment but the whole complex of external conditions (like e.g. air temperature and humidity, evaporation, light quality, and diurnal course of all these influences) was changed and did affect the differentiation of plants growing under the screens. However, from ecological point of view the investigation of the total "shade" influences seems to be more justified than the investigation of the effect of light reduction itself.

Photosynthesis and respiration of the whole shoot was measured after the transfer of plants into laboratory conditions by the use of a closed circuit system of an infra-red-CO_2-analyser, like in our previous works (Żelawski and Kinelska 1967 a, b; Żelawski and Kucharska 1967); air temperature was 25°C, illumination about 10,000 lux, CO_2-concentration within 350—300 ppm. Chlorophyll

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content was determined spectrophotometrically (Mackinney 1942; Bruinsma 1963). Respiration of the whole needle fascicles was determined by the Warburg direct method at water-bath temperature 25°C. Cross and longitudinal sections of needles as well as slices of epidermis were examined under the microscope and planimeter technique on drafts was applied for measurement of the surface area of the main tissue complexes. Dry weight of needles, lignified stems, and roots was determined after drying samples at 105°C.

RESULTS

1. Photosynthesis and respiration rate

Fig. 1 indicates that, within the applied range of illumination, the photosynthetic light curves are linear both for the sun and half shade plants. The curve for "light-starving" plants, receiving only 20% of full light exhibits a slight deviation from linearity but there is no saturation level attained in either of the investigated plant groups. In accordance with our state of knowledge the light compensation point is the lowest in plants cultivated in heavy shade conditions. When fresh or dry matter of needles is used as a reference unit photosynthesis and respiration rates are higher

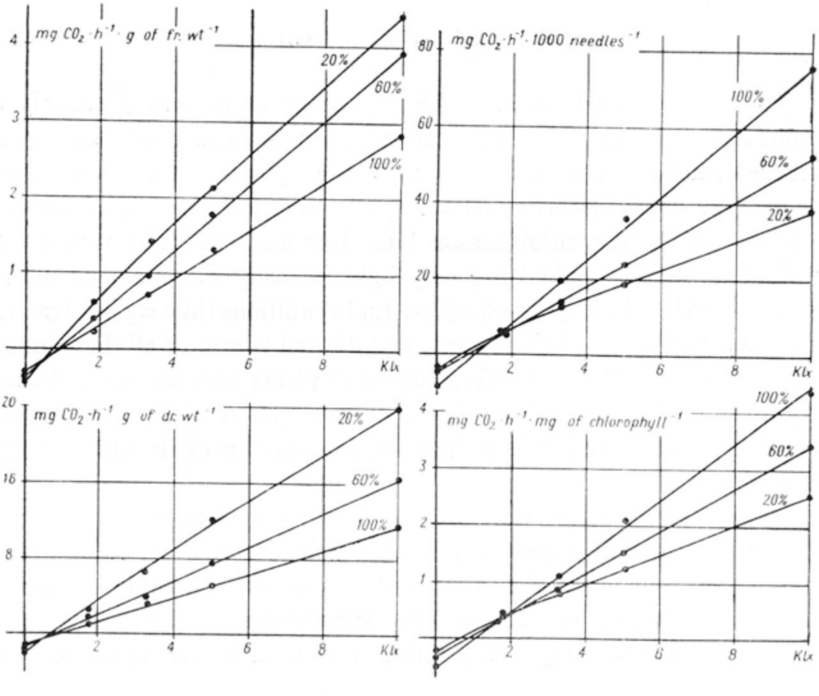

Fig. 1. Photosynthetic light curves of the sun and shade (60% and 20% of full light) plants in calculation per various reference units.

in shade-cultivated plants or vice versa when calculation is made per number of assimilatory organs or per amount of chlorophyll.

Extrapolation of the CO_2 photosynthetic curves to zero concentration of carbon dioxide (Żelawski 1967b) gave the estimated value of the CO_2-evolution in light (for the whole shoot); in these experimental conditions the rate of the "photorespiration" was always higher than that of dark respiration, but the same relation was observed when comparing shade cultivated plants and those grown in full light (Tab. 1).

Table 1

Comparison of the rates of dark respiration and light CO_2-evolution from the whole shoot (extrapolated from the net photosynthesis rate and CO_2-compensation point)

Rate of the process (mg CO_2 h^{-1} × × g of fr. wt^{-1})	Light conditions of the culture		
	100%	60%	20%
Respiration in darkness (air temp. 25°)	0.31	0.34	0.41
CO_2-evolution in light (at about 10 Klux, air temp. 25°)	0.57	0.71	0.74

Table 2

Respiration rate (in μl O_2 per hour) in plants grown in various conditions of illumination; Average data from 32 replication (8 plants, 4 samples from each plant)

Reference unit	Light conditions		
	100%	60%	20%
1 g of dry weight	544	580 (107%)	623 (115%)
1 g of fresh weight	198	180 (91%)	174 (88%)
100 needles	657	391 (60%)	176 (27%)
1 m of needles' length	816	414 (51%)	237 (29%)

The rate of O_2-consumption in darkness measured on needles alone is lower in shade than in sun plants when calculated per 1 g of fresh weight, per 100 needles or per 1 m of needles length (Tab. 2). However this is not the case when respiration is expressed per 1 g of needles dry weight perhaps not only because of different water content but also owing to different development of mechanical tissues.

2. Morphology and anatomy of needles

Needle length was not much different between the experimental variants: needles from half-shade conditions were, on the average, somewhat longer than those from control plants and in heavy shade they were somewhat shorter (Tab. 3). Width, thickness, and consequently surface area of the cross-section were more affected than length and were strongly reduced in worse illumination conditions. Fresh and dry weight of a single needle were consequently lower in shade conditions; moreover the dry weight of a needle decreased almost proportionally with the reduction of light whereas fresh weight diminished less. The water content of needles was in shade needles distinctly higher than in sun needles.

Table 3

Average data on morphological features of a single needle in plants grown under various conditions of illumination

Morphological feature	Light conditions			Number of replications
	100%	60%	20%	
Length (mm)	80	94 (117%)	72 (90%)	8 plants, 16—36 needles from every plant
Width (mm)	1.13	0.98 (87%)	0.67 (59%)	2 plants, 16 needles cross-sections from every plant
Thickness (mm)	0.53	0.47 (89%)	0.34 (64%)	
Thickness/width ratio	0.47	0.48	0.50	
Surface area of the maximum cross-section (mm^2)	0.473	0.377 (80%)	0.192 (41%)	8 plants 16-36 needles from every plant
Fresh weight (mg)	33	23 (70%)	10 (30%)	
Dry weight (mg)	12	7 (58%)	3 (25%)	
Water content (%)	64	70 (109%)	71 (110%)	

The density of stomata decreases when the light conditions of culture become worse and the decrease is more evident on the flat than on the convex side of the needles. This is evident not only when giving the number of stomata per 1 mm^2 of needle surface but also when the number of epidermis cells per unit of surface area was taken as reference unit. These numbers are higher in sun than in shade plants (Tab. 4).

Also the width of the endodermis cells is reduced in shade though their number around the conducting elements is not so much affected. The number of assimilation mesophyll cells per surface unit of the cross-section preparation was considerably lower in full light plants than in shade plants indicating that the size of these cells must be greatly reduced by shading. The total surface of the assimilatory tissue is reduced by shade nearly in the same degree as the whole cross-section surface and consequently the percentage of assimilatory tissue is only very little influenced. On the contrary the reduction of the total surface of conducting elements is not so strongly marked; this results in a relative increase of these tissue complexes in conditions of lower light intensity during the culture. On the other hand the percentage of epidermis varies only little and that of the surface area of resin ducts is slightly higher only in heavy shade conditions.

Table 4

Anatomical features of needles from plants grown under various conditions of illumination

Anatomical feature	Light conditions			Number of replications for calculation of averages
	100%	60%	20%	
Number of stomata per 1 mm² of surface area (flat/convex side respectively)	88/69	65/61 (74%/88%)	58/52 (66%/75%)	7 needles, 10 measurements on each needle
Number of epidermis cells per 1 mm² of surface area (flat/convex side respectively)	115/88	98/84	93/74	
Density of stomata per 1 epidermis cell (flat/convex side respectively)	0.77/0.78	0.66/0.73	0.62/0.70	
Width of the epidermis cells (μ)	15	14 (93%)	14 (93%)	3 needles, 1 preparation from each needle
Width of the endodermis cells (μ)	46	41 (89%)	37 (80%)	
Number of assimilation mesophyll cells per 1 mm² of the cross-section	200	370 (185%)	600 (300%)	
Surface area of the assimilation mesophyll (mm²)	0.267	0.211 (79%)	0.104 (39%)	2 plants, 16 needle cross sections from each plant
Per cent of the assimilation mesophyll	56.4	56.0 (99%)	54.2 (96%)	
Surface area of the conducting elements (mm²)	0.109	0.091 (83%)	0.049 (45%)	
Per cent of the conducting elements	23.1	24.1 (104%)	25.5 (110%)	
Surface area of the epidermis (mm²)	0.070	0.056 (80%)	0.027 (39%)	
Per cent of the epidermis	14.7	14.9 (101%)	14.1 (96%)	
Surface area of the resin ducts (mm²)	0.026	0.019 (73%)	0.012 (46%)	
Per cent of the resin ducts	5.5	5.0 (91%)	6.3 (115%)	
Per cent of intercellular spaces within assimilation tissues (%)	28	36	36	

Very difficult is the estimation of the volume of intercellular spaces. From the investigation made on a few longitudinal sections it cannot be excluded that the percentage of these spaces within assimilation mesophyll is somewhat higher, and the data certainly indicate that it is never lower in shade than in sun needles.

3. Habitus of plants and dry matter distribution

Seedlings grown in half-shade conditions (60% of full light) exhibited a typical shade habitus with slightly elongated stem and delicate but dark green needles. Seedlings cultivated in heavy shade conditions (20% of full light) were of the shade type too, showing however signs of starvation and growth reduction.

Table 5

Dry matter production in seedlings cultivated in various illumination conditions; average data from 70, 70, and 9 replications, respectively

Feature	Light conditions				
	100%	60%		20%	
Dry weight of the whole plant (mg)	1130	716	(63%)	118	(10%)
Dry weight of needles (mg)	523	399	(76%)	58	(11%)
Dry weight of the stem (mg)	147	159	(108%)	26	(18%)
Dry weight of the root (mg)	460	159	(35%)	34	(7%)
Shoot/root ratio	1.5	3.5		2.5	
Stem/needles ratio	0.28	0.40		0.45	
Root/stem ratio	3.1	1.0		1.3	

The total dry matter production (Tab. 5) was closely related to the light condition of the culture but the change of weight under the influence of shade was not the same in the particular organs, the root system being more affected than the needles; the stem of half-shade plants was markedly elongated and its dry weight was even somewhat higher than in control plants. The strong reduction in dry weight of all organs including the stem was observed in plants receiving only 20% of full light.

In both shade variants of the experiment, the amount of dry matter in root equalled nearly that found in the stem, while in the unscreened, control plants this proportion was more than 3:1. The shoot/root ratio was the highest at 60% of light and the stem/needles ratio increased with deteriorating light conditions.

DISCUSSION

The great number of publications dealing with photosynthesis and respiration of shade-affected plants has been recently revieved in several papers (Simonis

1960; Gabrielsen 1960; Bourdeau and Laverick 1963; Kozlowski and Keller 1966; Żelawski 1967 a). Various species of pines were also investigated in this respect and the main conclusions concerning their photosynthetic activity are as follows:

1. Pines usually do not reach the photosynthesis light saturation level up to the highest natural illumination; this is probably due to the mutual shading of their leaves (Stålfelt 1924; Kramer and Clark 1947).

2. Shade needles exhibit higher photosynthesis rates than sun needles if the comparison is made at lower light intensity (up to the natural diffuse light under overcast sky), and fresh or dry weight is applied as a reference unit (Stålfelt 1921, 1924; Ivanoff and Kossowitsch 1929; Oskretkov 1959; Żelawski and Kinelska 1967 b — *P. silvestris*; Tranquillini 1955, Pisek and Winkler 1959 — *P. cembra*; Bourdeau and Laverick 1958 — *P. resinosa*, *P. strobus*).

3. Neither is there sufficient information on the attainment of the photosynthetic light saturation level in the shade-adapted pine needles; the possible influence of the simultaneous temperature increase or of inhibition due to the duration of irradiation (Kozłowski 1957; Jarvis 1964) make the problem of photosynthesis measurements at higher light intensities not easy to approach.

4. The dark respiration rate (per needles weight and surface area unit) is lower in shade than in sun plants (Chlebnikowa 1962; Oskretkov 1959).

The results presented here did not give any further information as to the photosynthesis rates at higher light intensities, but they demonstrated that, within the applied range of illumination, the photosynthetic light curves do not show any distinct bend even in heavily shaded plants.

The data also indicate the relative value of comparison between the photosynthetic activities of shade- and sun-grown plants, since the conclusions may be different depending on the basis of calculation itself; in terms of the chlorophyll unit, for instance, the shade plants were less active than sun plants. This is also true for respiration data notwithstanding that the measurements are often made on the whole shoot (including respiration of the stem with active zones of cambium and parenchyma cells) and calculated per needles only. It is seen from IRGA-determinations that the dark respiration rate as well as the extrapolated evolution of CO_2 in light was in our research greater in shade than in sun plants (when calculated per weight units). It was also the case in Warburg measurements but only when dry weight of needles was used as the reference unit. The data from CO_2 and O_2 measurements are not directly comparable but it is seen that the relative increase of the respiration rate was 107, 115% (Warburg) and 112, 143% (IRGA) in half-shade and in heavy-shade plants, respectively. This divergence is probably due to the increased proportion of stem to needles (Tab. 5) in the shaded plants. Only the data obtained for detached needles and calculated per fresh weight, needles' number, or length are in accordance with the general assumption that sun leaves respire more intensively than the shade ones.

Expression of the photosynthetic activity per 1 cell of assimilation mesophyll would be the most proper basis for comparison of shade- and sun-grown plants since photosynthesis rates calculated per weight units do not have the same physiological meaning on both types of needles due to differences in water content and various development of mechanical tissues. There are great technical difficulties of exact estimation of the number of assimilating cells but if one assume no essential effect of shading on quantity of differentiated mesophyll cells per 1 assimilatory organ and only the diminution of sizes the values of photosynthetic activity expressed per single needle (or 1000 needles) make a good approximation of such physiological index; by such comparison the photosynthetic activity of shade needles is certainly never higher than that of sun needles, even if only the linear section of photosynthetic light curve has been taken into account.

Shade-grown plants and, in particular, light demanding pines usually exhibit strong reduction of the root-system and increased shoot/root ratio (Kozlowski 1949; Bourdeau and Laverick 1963; Lyr and coworkers 1963, 1964; Jarvis 1964; Bellon 1967). This fact was now confirmed for two-year-old Scots pine plants. Probably the changes in the proportion of organs are mostly responsible for the low tolerance of the species to shade, since a small root is not able to maintain the positive water balance of the shoot (Lyr and coworkers 1963; Jarvis 1964; Kozlowski and Keller 1966).

The restricted supply of photosynthetic products could be a limiting factor for the development of a sufficiently extensive root system if the total photosynthetic activity of the whole aerial part is, in shade, distinctly lower than in sun. Light deficiency alone determines low actual photosynthesis rates, but besides this, changes in the photosynthetic activity of the whole plant may have been involved. The ability to increase the photosynthetic efficiency in culture in shade could be considered as a measure of shade tolerance, since only in tolerant plants the poor illumination conditions are partially compensated by an increased efficiency of assimilatory organs. Yet, there is much difficulty in estimating this ability when only artificial light sources, below saturation light intensity, are applied for gas exchange determinations. However, taking into account the average photosynthesis rates for plants grown under 100, 60 and 20% of natural illumination (fig. 1, or data from experiment I and II — Żelawski and Kinelska 1967 b) and the average data for dry weight of needles per 1 plant (Tab. 5), one can estimate the photosynthetic activity of a whole seedling to be 6.1, 6.6, and 1.2 mg CO_2 per hour, respectively, when photosynthesis is measured under the same external conditions. Only the heavily shaded plants, where not only the size but also the number of assimilatory organs were considerably reduced, exhibit low photosynthetic activity despite the fact that their photosynthesis rate (per 1 g of needle dry weight) was almost 100% higher than in control plants; the ful-light and half-shade plants showed similar activities, the advantage of the latter was not great.

The corresponding figures for loss of organic matter per plant, estimated from respiration rates, are 0.68, 0.56 and 0.13 mg CO_2 per hour when only the aerial parts are taken into account. Assuming that the reduced root system respires less in shade than in sun plants one can see that the total loss of organic matter per plant is lesser in shaded plants; the ratio of true photosynthesis to dark respiration of the aerial parts is the highest in seedlings grown under 60% of natural light (10, 13 and 10, respectively).

The conclusion of these considerations is that, in spite of somewhat higher photosynthetic activity at low light intensity and lower respiration losses, the pines growing under half-shade conditions are not able to increase their efficiency to such a degree as would be necessary for better compensation of the light deficiency. As a result they are limited in photosynthetic production and this appears initially in the suppression of root development without much influence on dry matter production in stems (see also Jarvis 1964; Lyr and coworkers 1963, 1964); only in light-starving plants, both the decreased efficiency of the reduced assimilatory organs and the poor conditions of photosynthesis affect the production of dry matter in the stem. Moreover, Shiroya et al. (1966) reported that pines grown at high light conditions translocated to their roots a larger percentage of their photosynthates than those grown at low light intensity.

The explanation for this still too low photosynthetic efficiency of shade grown pines is to be found in the changes of needle structure. The data presented show in this respect, some deviation from the typical picture known for more tolerant plant species (see e.g. Jarvis 1964).

The main features of the shade needles in two year-old Scots pine seedlings are: reduction of width and thickness but not of length (in half-shade conditions), reduction in the average dry matter of a single needle (almost proportional to the deterioration of light conditions), increase of water content, diminution of the number of stomata, diminution of the diameter of the epidermis, endodermis and especially mesophyll cells, an only slight tendency to a change in the proportions of the particular tissue complexes within the cross-section surface area (decrease of assimilation mesophyll, increase of conducting elements), higher percentage of the intercellular spaces, increase of the green pigments concentration and a tendency to a decrease in chlorophyll *a*/*b* ratio (2.5, 2.2, and 2.0 respectively). No increase of the leaf surface area can be expected (as is usually the case — see Jarvis 1964) since the needles are not flatter in shade than in sun. Although the direct measurement of the leaf surface area can never be precisely made on pine needles, from the data concerning length and width it can be concluded that the surface area of a single organ is reduced by about 20 or 50% in half-shade and heavy-shade plants, respectively. It means that also the chlorophyll content calculated per surface area unit must be higher in shade plants what is usually not the case in more tolerant, especially broad-leaved species (Egle 1960; Björkman and Holmgren 1963; Gabrielsen 1960) at least not in the same degree as the change of concentration expressed per weight unit (Jarvis 1964).

In pines growing under moderate shading the number of cells which are to be provided with carbon dioxide does not seem to be smaller or is even greater (per needle) than in control plants; cells are only concentrated on a smaller space. That is why photosynthesis rates calculated per dry weight of needles are much higher in shade than in sun plants, while when computed per single organ, they do not differ much, at least not in the same degree as the size of needles itself.

The limited space distribution of all cells within a needle probably brings about some deterioration of the illumination conditions in chloroplasts. It is, to some extent, connected with an increased concentration of chlorophyll since the smaller needles from half shade conditions contain even more chlorophyll per one organ then big needles from the sun plants. Taking into account the average data of chlorophyll concentration and the average sizes of needles, one can see that the amount of chlorophyll contained in a single organ (15.4, 20.2, 11.2 μg respectively) is higher in half shade needles and is not much lower in the light-starved plants, in comparison with the sun ones. However, this increased quantity of assimilatory pigments does not bring about any proportional change of the photosynthetic activity of a single organ which at most remains either at the same level in half shade as in sun plants (**Żelawski** and **Kinelska** 1967) or is even lower in shade (results of this experiment and those in earlier stages of vegetation from the previous work). Consequently, the assimilation numbers were distinctly lower in shade-adapted pines amounting on the average to 4.3, 2.8, and 2.2 for the examined variants of illumination. There is some data in **Björkman** and **Holmgren's** (1963) paper indicating that the reduction of the chlorophyll unit efficiency, after cultivation in shade, is smaller in tolerant plants than in intolerant ones: after some transformation of the results given in the above mentioned paper, the average assimilation numbers for clones of *Solidago virgoaurea* L. cultivated under high or low light intensity were calculated to be 4.3, or 3.7 for the shade-tolerant ecotype and 5.1 or 3.5, respectively for the ecotype originating from exposed habitats. On the other hand **Bourdeau** and **Laverick** (1958) did not find any significant difference in the assimilation numbers of *Pinus resinosa* and *Pinus strobus* young seedlings grown under various degrees of shading. However, the low numbers (not exceeding 1.8 mg CO_2/1 mg of chlorophyll/hour, even at saturation light intensity — 2,500 f.c.) indicate that in

Table 6

Changes in needles length, thickness and width under the influence of reduced illumination in pines of various provenance

Provenance			Length			Tchickness			Width		
			Light conditions (%)								
			100	60	20	100	60	20	100	60	20
Lowland (less tolerant)	Dłużek	mm	80	89	76	0.57	0.48	0.34	1.17	0.88	0.64
		%		111	95		74	50		75	55
	Spała	mm	82	94	67	0.54	0.42	0.33	1.18	0.84	0.63
		%		115	82		78	51		71	53
Higland (more tolerant)	Nowy Targ	mm	80	94	72	0.53	0.47	0.34	1.13	0.98	0.67
		%		117	90		89	64		87	59

their experiment the control plants, cultivated in greenhouse, were of shade type too.

Thus, the low productivity of pine seedlings growing under shade conditions can be interpreted in terms of morphological unadaptability of their assimilatory organs to shade. Pine needles, when growing under shade conditions are unable to develop an extended, flat leaf-blade surface which would improve sufficiently the optical capacity of the assimilatory system as it is usually the case in other particularily broad-leaved and more tolerant species of trees, e.g. oak seedlings in Jarvis's (1964) experiments. Unfortunatelly, there is no data abailable for other conifers to compare the shade- induced changes of needle structure. However, from the paper of Taubert (1926) caried out on various species of *Abies* one may conclude, that in shade resistant coniferous plants the changes in width and thickness of needles as well as in sizes of assimilation mesophyll cells are essentially of the same character as in broad-leaved plants.

Also the type of arrangement of the needles fascicles on a shoot — different from other coniferous plants — is probably involved in low tolerance to shade in pines. It causes a relatively high effect of "mutual shading" (Kramer and Clark 1947) and the diminution of assimilatory organs in shade does not change much the conditions of their illumination.

At the beginning of this paper it was explained that seedlings from Nowy Targ had been chosen for this research, since it was already suspected that they would be somewhat more shade-tolerant than other investigated pines. Table 6, which comprises the data for the whole plant material under study shows that in fact, the changes in the morphological features of the needles are in agreement with the above discussed hypothesis: in lowland pines (Dłużek and Spała) the needle length is increased less and the width and thickness is reduced more, in plants grown in shade, than is the case in the highland pine (Nowy Targ).

SUMMARY

Low tolerance of pine seedlings to shade seems to be connected with the type of structural changes of needles in plants grown under conditions of light deficiency. More or less proportional diminution of all structural elements in needles developing under the influence of shade (which is rather not the case in tolerant plants) is probably responsible for insufficient adaptation of assimilatory organs to carry on more efficient photosynthesis at lower light intensities.

Ecotypic differences in shade tolerance are adequate with the type of structural changes of their needles when seedlings of different provenance grown under semi-controlled conditions with differentiated shade influences have been compared.

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Wpływ ocienienia na produktywność fotosyntezy siewek sosny zwyczajnej (Pinus silvestris L.) w drugim roku wegetacji

Streszczenie

Praca stanowi dalsze rozwinięcie naszych poprzednich badań nad zdolnością przystosowawczą siewek sosny do wzrostu w warunkach ocienienia. Badania przeprowadzono na siewkach pochodzenia nowotarskiego, co do których istniało przypuszczenie, uzasadnione wynikami poprzednich prac, że wykazują one nieco większą tolerancję na ocienienie w porównaniu z sosną pochodzenia niżowego. Końcowe wyniki badań zestawiono z danymi uzyskanymi u sosen dwóch innych proweniencji uzyskując dalsze potwierdzenie wysuniętej poprzednio tezy o zróżnicowaniu ekotypów pod względem wytrzymałości na ocienienie (tab. 6).

Badania przeprowadzono na roślinach wyhodowanych w ciągu dwóch okresów wegetacji w doświadczeniu wazonowym, w hali wegetacyjnej przy trzech różnych poziomach naturalnego oświetlenia: 100, 60 i 20% pełnego światła. Przy pomocy analizatora CO_2 w podczerwieni wykonano pomiary oddychania i fotosyntezy całych pędów, a stosując bezpośrednią metodę Warburga pomierzono intensywność oddychania oddzielnych krótkopędów (fig. 1 tab. 1 i 2). Badania wymiany gazowej uzupełniono porównaniem morfologii i anatomii organów asymilacyjnych oraz określeniem ogólnej produkcji suchej masy w nadziemnych i podziemnych częściach rośliny tab. 3, 4 i 5).

W porównaniu z igliwiem roślin kontrolnych, hodowanych w pełnym słońcu, główne cechy drugorocznego igliwia sosny rosnącej w ocienieniu są następujące: mniejsza szerokość i grubość przy jednocześnie zbliżonej długości igły (u roślin w warunkach umiarkowanego ocienienia), mniejsza przeciętna sucha masa jednej igły (zmniejszenie jest niemal wprost proporcjonalne do stopnia redukcji oświetlenia), większa procentowa zawartość wody, mniejsze zagęszczenie aparatów szparkowych na powierzchni epidermy, mniejsze wymiary komórek epidermy, endodermy, a w szczególności miękiszu asymilacyjnego, przy jednocześnie nieznacznej tendencji zmian w proporcjach poszczególnych zespołów tkanek na powierzchni przekroju poprzecznego igły (niewielkie zmniejszenie udziału procentowego miękiszu asymilacyjnego i zwiększenie udziału elementów przewodzących) wyższy udział przestrzeni międzykomórkowych, wzrost koncentracji chlorofilu i spadek stosunku chrolofilu a/b, niższa liczba asymilacyjna przy jednocześnie wyższej intensywności fotosyntezy w przeliczeniu na jednostkę masy igliwia, wyższe intensywności oddychania pędu i niższy punkt kompensacji świetlnej.

Analiza uzyskanych wyników prowadzi do wniosku, że niski stopień tolerancji sosny na ocienienie związany jest z typem przekształceń budowy organów asymilacji, jakie zachodzą pod wpływem

warunków ocienienia. Nie ma bowiem w igłach typu „cienistego" istotniejszych zmian ilościowych w proporcjach poszczególnych zespołów tkanek występujących w igłach wykształconych w pełnym świetle, lecz obserwuje się mniej lub bardziej proporcjonalne zmniejszenie (miniaturyzację) wszystkich elementów liścia. Taka zmiana budowy, nie wykazująca cech spłaszczenia blaszki liściowej typowego dla gatunków dobrze znoszących ocienienie (szczególnie wśród drzew liściastych) nie sprzyja zwiększeniu wydajności fotosyntetycznej zredukowanych organów asymilacji. Liczby asymilacyjne roślin wyrosłych w ocienieniu wykazują znaczne zmniejszenie w porównaniu z kontrolą w pełnym świetle, a ogólna aktywność fotosyntetyczna całej części nadziemnej nie wzrasta u tych roślin w stopniu, który by mógł kompensować ogólne zmniejszenie produkcji fotosyntetycznej spowodowane brakiem światła. Niewysoka zdolność asymilacyjna igliwia roślin wyrosłych w ocienieniu odbija się bardzo silnie na rozwoju systemu korzeniowego, co ma oczywiście poważne konsekwencje dla dalszej egzystencji siewek wyrosłych pod okapem macierzystego drzewostanu; warunki ocienienia zmniejszające wyraźnie wielkość i ogólną masę igliwia i systemu korzeniowego sosny nie wpływają jednak istotnie na ilość suchej masy nagromadzonej w strzałce, o ile warunki ocienienia nie osiągną poziomu „głodowego", przy którym ograniczony dopływ asymilatów ze zredukowanych organów asymilacji odbija się również na ogólnej masie części zdrewniałej pędu.

Wyniki przedstawionych badań w pewnym stopniu wyjaśniają przyczynę nietolerancji sosny w stosunku do warunków ocienienia: jest nią niezdolność przystosowania się organów asymilacyjnych do bardziej wydajnego wykorzystywania złych warunków oświetlenia. Różnice reakcji poszczególnych ekotypów sosny na warunki ocienienia ujawniły się w niniejszych badaniach niejednakowym stopniem redukcji wymiarów liniowych liścia, co oczywiście pociąga za sobą różnice w ogólnej powierzchni organów asymilacyjnych u roślin poszczególnych pochodzeń wyrosłych w ocienieniu.