Seasonal changes in the photosynthesis rate of Scots pine (*Pinus silvestris* L.) seedlings grown from seed of various provenances *

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Changes in the photosynthesis rate of evergreen woody plants, during their vegetation and rest period have been investigated by many authors (Zacharova 1929; Ivanov and Orłowa 1931; Freeland 1944; Mc Gregor 1958; Pisek and Rehner 1958; Neuwirth 1959; Bourdeau 1959; Parker 1961; Polster and Fuchs 1963; Tranquillini 1963). The rate of photosynthesis of Scots pine under laboratory as well as field conditions has also been measured by several authors (Ivanov and Kossowitsh 1929; Stålfelt 1921, 1924; Polster 1959; Keller and Wehrmann 1963). However, the seasonal changes of the photosynthetic ability of this widely spread species are not yet sufficiently known. Especially various ecotypes of pine were not been investigated in this respect. Some observations on growth of plantations, cultivated from seeds of various origin indicate that they may differ in the rate of photosynthesis.

In this study the progeny of pine deriving from various climatic regions and cultivated in uniform conditions was compared as regards the photosynthetic ability at various times of the vegetation period.

MATERIAL AND METHOD

As in the previous morphological study of Scots pine assimilatory organs (Żelawski, Gowin 1966; Żelawski, Niwiński 1966; Żelawski 1966) pines of the same three Polish provenances, i.e. Dłużek, Spała and Nowy Targ, representing two lowland and one highland ecotypes were used in these experiments. The plants were grown in pots, under greenhouse conditions at the Experimental Forest Station Rogów (100 km south-west of Warsaw).

During the whole vegetation season (1964) carts with the pots stood under a wire net and were wheeled for the nights and in rainy periods into an open greenhouse under glass. Winter time plants were kept in an unheated greenhouse where temperature was similar as out of doors.

At the end of the rest period, i.e. in March, measurements of photosynthesis and respiration rates were started and successively carried out at four week inter-

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vals, during the whole vegetation season 1965. For photosynthesis and respiration determinations the plants were always brought from greenhouse into the laboratory where possibly constant conditions were secured. An Infra-red-gas-analyser (IRGA) in a closed circuit system was used (see literature Żelawski, Góral 1966). The air in the system circulated between the plant chamber and IRGA, with a flow speed of 40 l/h, and the time was measured in seconds while the CO_2 concentration decreased from 350 to 200 ppm.

The experiments were carried out in plexi-glass chambers, fastened on intact plants. The final determination of the photosynthesis rate took place after the "steady state" had been established. Adaptation of plants to the conditions of experiment occurred in the open system at a concentration of carbon dioxide near to that of atmospheric air.

Light conditions which could be provided without overheating, from two incandescent lamps 500 W each, gave illumination which was approaching of the photosynthetic saturation level. The plants were illuminated from one side and from above, the light being filtered through a 6-cm running water screen. Mirrors were arranged on the other sides of the plant in order to obtain possibly uniform dispersion of light. Such arrangement provided better light conditions but caused difficulty in determination of light intensity. The use of photo-cells, set perpendicularly to the light sources, showed about 22 000 lux from the side lamp and 30 000 lux from the upper one. In this case neither total nor physiologically active radiation could be determined accurately, but possibly constant light conditions were kept during the series of experiments.

The air temperature was usually $27 \pm 1^\circ\text{C}$ during the illumination period. Respiration in darkness was always measured at a temperature lower by 3° to 4°C . The fastening of chambers on growing seedlings made the application of temperature conditioned chambers difficult. Therefore it was not possible to keep exactly the same temperature level after switching on the light source.

Except for first and second spring series, when only three plants of each provenance could be simultaneously examined, other series were usually represented by 7 to 9 seedlings as replicates.

RESULTS

Comparison of the meteorological data for the year 1965 with average values calculated for a period of 22 years leads to the conclusion that the vegetation season 1965 was somewhat cooler and more humid than usual. Low minimum temperatures and retarded spring time may have influenced the development of plants and this influence may not have been the same for plants originating from various regions (tab. 1). Thus, the results of investigation presented in this paper are valid for the given experimental conditions of the year 1965 but for a full comparative study on ecotypes further research, during the next years is necessary.

Table 1
Some meteorological data of the year 1965 and arithmetical means for the period of 22 years (Experimental Forest Station Rogów)

Mean temperature (C°)	Arithmetical means for 22 years	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	year
	1965	-3.1	-3.4	0.8	6.7	13.1	16.1	17.9	16.8	13.1	8.0	3.1	-0.8	7.3
Mean maximum temperature (C°)	Difference	-1.5	-5.7	0.2	7.3	9.4	15.6	15.9	14.8	13.3	6.4	-1.4	-0.1	6.2
		+1.7	-1.7	-0.6	+0.6	-3.7	-0.5	-2.0	-2.0	+0.2	-1.6	-4.5	+0.7	-1.1
Mean minimum temperature (C°)	Arithmetical means for 22 years	-0.6	-0.3	5.1	11.7	18.5	21.5	23.4	22.4	18.7	12.4	5.8	1.4	11.6
		1.4	-1.7	6.4	11.2	15.7	22.2	23.4	22.6	22.1	13.2	2.0	2.3	11.8
Mean minimum temperature (C°)	Difference	+2.0	-1.4	+1.3	-0.5	-2.8	-0.7	0.0	+0.2	-3.4	+0.8	-3.8	+0.9	+0.2
		-6.2	-7.0	-3.4	1.7	6.8	9.7	12.1	11.4	8.1	3.7	0.1	-3.6	2.8
Rainfall (mm)	Arithmetical means for 22 years	-5.5	-2.5	-6.0	0.1	2.4	8.5	8.9	8.0	6.4	0.3	-5.8	-3.8	0.1
		+0.7	-5.5	-2.6	-1.6	-4.4	-1.2	-3.2	-3.4	-1.7	-3.4	-5.7	+0.2	-2.7
Rainfall (mm)	Difference	26.9	35.4	31.1	36.5	51.1	65.6	89.3	77.0	52.8	38.0	41.1	35.2	578.0
		23.8	29.7	16.2	69.1	127.7	74.9	99.9	64.7	83.5	5.7	34.7	51.2	681.1
Rainfall (mm)	Difference	-3.1	-5.7	-14.9	+32.6	+76.6	+9.3	+10.6	-12.3	+30.7	-32.3	-6.4	+16.0	+110.1

Table 2

Average fresh and dry matter of needles on pine seedlings during their formation in the second vegetation season (in g)

Date of experiment	Fresh weight			Dry weight			Per cent of dry matter		
	Provenance			Provenance			Provenance		
	Dłużek	Spała	Nowy Targ	Dłużek	Spała	Nowy Targ	Dłużek	Spała	Nowy Targ
March 17—18	1.11	0.84	0.64	0.41	0.29	0.23	36.9	34.5	35.9
April 12—13	1.25	0.68	0.69	0.45	0.24	0.25	36.0	35.3	36.2
May 13—16	0.69	0.87	0.68	0.31	0.40	0.31	44.9	46.0	45.6
June 8—9	1.55	1.77	1.61	0.46	0.53	0.45	29.7	29.9	28.0
July 9—16	2.82	2.49	2.13	0.79	0.70	0.57	28.0	28.1	26.8
August 4—6	5.91	6.05	4.05	1.69	1.66	1.04	28.6	27.4	25.7
August 30-Sept. 3	5.73	5.67	5.55	1.70	1.94	1.69	29.7	34.2	30.5
Sept. 27-Oct. 2	7.60	7.07	4.65	2.66	2.50	1.61	35.0	35.4	34.6
Oct. 26—28	7.08	6.28	7.10	2.67	2.41	2.49	37.7	38.4	35.1
Dec. 1—10	5.31	6.15	8.06	2.11	2.68	3.14	39.7	43.1	39.0

Table 3

Average fresh and dry matter of a lignified stem during the second vegetation season (in g)

Date of experiment	Fresh weight			Dry weight			Per cent of dry matter		
	Provenance			Provenance			Provenance		
	Dłużek	Spała	Nowy Targ	Dłużek	Spała	Nowy Targ	Dłużek	Spała	Nowy Targ
March 17—18	0.49	0.24	0.30	0.10	0.06	0.08	20.4	25.0	26.7
April 12—13	0.48	0.24	0.33	0.14	0.07	0.08	29.2	29.2	24.2
May 13—16	0.94	0.94	0.65	0.11	0.15	0.11	11.7	16.0	16.9
June 8—9	0.94	1.08	1.00	0.18	0.22	0.21	19.1	20.4	21.0
July 9—16	1.05	0.92	0.90	0.27	0.25	0.29	25.7	27.2	32.2
August 4—6	1.87	1.51	1.31	0.59	0.45	0.48	31.6	29.8	36.6
August 30-Sept. 3	2.30	2.15	1.84	0.68	0.62	0.66	29.6	28.8	35.9
Sept. 27-Oct. 2	2.44	2.32	1.71	0.86	0.72	0.60	35.2	31.0	35.1
Oct. 26—28	2.52	2.90	2.85	0.94	1.05	1.13	37.3	36.2	39.6
Dec. 1—10	2.38	3.07	3.04	0.97	1.18	1.22	40.8	38.4	40.1

Average data concerning fresh and dry matter of plants which were subjected to photosynthesis measurements are given in Tables 2 and 3. Though the number of plants examined was not large enough to study dry matter production throughout the vegetation season, it may be interesting to mention the general character of the formation of assimilatory organs and stem in these seedlings. Development of the new shoot began only in May, and lasted until late autumn. In spite of the fact that the extension growth of the new shoot ends rather quickly in pine, the increase

in the average dry matter was noticeable during the whole vegetation period, not only in stem but also in the assimilatory organs.

There was no marked difference in the course of dry matter accumulation of the plants of various provenance though the formation of needles in the Nowy Targ seedlings seemed to be slightly retarded in comparison with the others.

Seasonal changes in the percentage of dry matter content in needles and stem are shown in Tables 2 and 3. Dry matter content of the old needles significantly increases at the moment of development of the apical bud. At the same time a decrease of that percentage in the lignified stem was observed.

When development of the new shoot has started new needles begin to dominate and the water content in the whole assimilatory organs remarkably increases.

Distinct changes in the dry matter content of needles occur only during autumn, when again an increase of the percentage was noted. In the stem a gradual but considerable increase of the dry matter content connected with formation of the lignified wood tissue, is observed during the whole vegetation season.

A strikingly rapid increase in dry matter content of the stem, and a slight decrease in the needles of the seedlings from Nowy Targ provenance during the summer indicates that, in comparison to lowland pines, differences in water relations can be expected in that highland ecotype.

Table 4

Average photosynthesis (apparent) of Scots pine seedlings during the second vegetation and rest period

Date of experiment	mg CO ₂ /h/ 1 seedling			mg CO ₂ /h/g fr. w. of needles			mg CO ₂ /h/g dry. w. of needles		
	Provenance			Provenance			Provenance		
	Dłużek	Spała	Nowy Targ	Dłużek	Spała	Nowy Targ	Dłużek	Spała	Nowy Targ
March 17—18	1.88	1.36	1.47	1.73	1.60	2.30	4.59	5.35	6.40
April 12—13	3.57	2.42	2.57	2.90	3.43	3.81	7.86	10.17	10.45
May 13—16	2.43	3.24	2.98	3.68	3.80	4.47	8.11	8.27	9.94
June 8—9	3.32	4.00	3.91	2.17	2.29	2.35	7.44	7.65	9.42
July 9—16	6.02	5.32	5.29	2.11	2.14	2.51	7.54	7.86	8.59
August 4—6	13.62	14.61	10.30	2.39	2.49	2.50	8.40	8.83	8.94
August 30—Sept. 3	12.31	12.36	9.72	2.14	2.20	1.78	7.43	6.50	5.86
Sept. 27—Oct. 2	12.83	13.05	6.65	1.70	1.82	1.43	4.95	5.03	3.86
Oct. 26—28	10.20	8.93	8.45	1.41	1.50	1.21	3.75	3.88	3.32
Dec. 1—10	0	0	0	0	0	0	0	0	0

Apparent photosynthesis (average per one seedling) mainly reflects the changes in size of the assimilatory organs (Table 4) However, during spring time, before development of the new shoot had started, some increase in the photosynthetic activity could be observed in old needles. On the other hand the net photosynthesis was found to reach maximum already in August. From that time the process began

to decrease in spite of further continuous growth of needles. The differences in growth of the plants of various provenance were manifested in lower values of photosynthesis in the Nowy Targ ecotype during the summer and autumn.

Fig. 1. Seasonal changes in apparent photosynthesis of Scots pine seedlings

The rate of net photosynthesis calculated per unit of needles fresh weight (Fig. 1) showed the highest values in May, just before the development of buds. The change in the type of the needles formed during the second vegetation period may have caused lower values of the photosynthesis rate soon after the extension growth of shoots had started. However, the intensity of the process was quite high, even in young developing needles, and remained at a similar level until August when the second slight peak of the curve occurred. Successive measurements made in September, October, and November showed a gradual decrease in photosynthesis. At the beginning of December, after the first period of frost the photosynthesis of plants was below the compensation point and CO₂ evolution, occurred even in full light.

Between the plants of various origin slight difference occurred in the course of photosynthesis. The difference between the averages within the particular series

of experiments was not statistically proved but for the whole vegetation season it was found to be similar. The highland pine, from Nowy Targ always showed the highest value of photosynthesis rate. The two lowland pines, from Spała and Dłużek, had similar rates of photosynthesis though a systematic difference between them also existed. The curves of seasonal changes were parallel; that for the Dłużek plants being always below the others.

The differences between the ecotypes were manifested not only during the spring and summer time. The reduction of activity during the autumn months was much more pronounced in the Nowy Targ pine than in other ecotypes.

When the photosynthesis rate is expressed per dry matter unit, the spring maximum of photosynthesis occurs earlier (Fig. 1). This is due to the decrease of water content in old needles after the development of the new bud had begun. A distinct rise in the photosynthesis rate takes place in late summer when the new assimilatory organs are already fully developed; this second peak is followed by a rapid drop of the curves. The difference between the highland pine and those of other provenance during the summer time was in this case even more distinct than was the difference in the fresh weight relation, because the investigated plant groups also differed in the water content of needles.

Although the increase in dry matter content towards the end of the vegetation period was rather similar in the needles of pines of all the investigated provenances, the pines from Nowy Targ showed the most rapid reduction of photosynthetic ability when rate of photosynthesis was calculated per gram of dry weight.

Table 5

Average dark respiration of Scots pine seedlings during the second vegetation and rest period

Date of experiment	mg CO ₂ /h/ 1 seedling			mgCO ₂ /h/g fr. w. of the shoot (stem+needles)			mg CO ₂ /h/g dry w. of the shoot (stem+needles)		
	Provenance			Provenance			Provenance		
	Dłużek	Spała	Nowy Targ	Dłużek	Spała	Nowy Targ	Dłużek	Spała	Nowy Targ
March 17—18	0.60	0.44	0.42	0.36	0.42	0.45	1.44	1.60	1.86
April 12—13	0.80	0.54	0.59	0.47	0.57	0.57	1.37	1.70	1.77
May 13—16	0.53	0.66	0.58	0.33	0.37	0.43	1.24	1.24	1.45
June 8—9	0.80	1.06	1.07	0.35	0.35	0.43	1.37	1.39	1.79
July 9—16	1.09	0.86	0.71	0.28	0.26	0.25	1.03	0.93	0.89
August 4—6	2.32	2.26	1.57	0.30	0.31	0.30	1.42	1.08	1.06
August 30—Sept. 3	2.55	2.68	2.40	0.31	0.35	0.33	1.08	1.08	1.03
Sept. 27—Oct. 2	3.16	2.67	2.20	0.32	0.30	0.34	0.91	0.88	0.88
Oct. 26—28	3.73	3.38	3.67	0.39	0.37	0.38	1.05	0.99	0.99
Dec. 1—10	2.28	2.59	2.89	0.30	0.29	0.27	0.77	0.77	0.70

No noticeable difference was found in the course of seasonal changes of dark respiration in the provenances examined (Table 5); the decrease of respiration rate

throughout the vegetation period is probably due to the relative change in the amount of living cells with ageing and lignification of plant tissues.

Relatively small changes in respiration with simultaneous change in photosynthesis result in a conspicuous increase of the ratio photosynthesis: respiration, when the assimilatory organs become fully developed. This ratio expressed by

Fig. 2. Seasonal changes of the ratio true photosynthesis: dark respiration in developing seedlings of Scots pine, during the second year of growth

the relation of the average true photosynthesis (apparent photosynthesis + dark respiration) to dark respiration of one seedling shows the lowest values during the rest period, an increase during the spring time, a temporary diminution after the development of buds, maximum values in full summer, and a gradual decrease towards the end of the vegetation season (Fig. 2). The earlier maximum of summer activity in the Nowy Targ pine can also be recognized from the above given data.

DISCUSSION

Scots pine has often been the subject of investigations which aimed at elucidation of the problem of winter assimilation in evergreen plants. Though the question of photosynthesis at temperatures below freezing point has not been definitely settled yet (Zacharowa 1930; Ivanow, Orłowa 1931; Freeland 1944; Pisek, Rehner 1958; Bourdeau 1959; Parker 1961; Polster, Fuchs 1963) the authors are in agreement as to the phenomenon of winter depression of photosynthetic activity. Lowering of temperature in late autumn and winter not only affects the actual rate of photosynthesis according to the change of external factors but also affects the ability of plants to carry on photosynthetic process after being transferred to favourable conditions. This photosynthetic ability depends on the intrinsic properties of the plant and is considerably reduced during the rest period. It usually

takes a few days before the photosynthesis of dormant plants shows signs of recovery.

Although "winter assimilation" was not the subject of this investigation the data obtained immediately after the plants had been transferred into the laboratory at various times of the spring period show a gradual increase of the photosynthetic rate with the rise of out-of-doors temperature. The significance of juvenile needles for the balance of organic matter, before the development of a new shoot, was in these experiments clearly demonstrated. Juvenile needles may play an important role in supplying photosynthates to the developing shoot.

There are also indications that last years juvenile needles may lose water when the new shoot begins to develop; it would support the thesis of Čatsky (1962) and other authors as to the preference of young leaves in water supply and possible translocation of water from old to young leaves.

Although our measurements during the development of a new shoot were not continuous but were carried out only in 4 weeks intervals, we did not find any signs of a negative CO_2 balance as reported by Neuwirth (1959) for older trees. The results are not fully comparable since Neuwirth investigated pines in field conditions, and in his experiments changes in gas exchange were determined more frequently during the whole period of development. However, in our determinations in May when buds had already begun to extend, the apparent photosynthesis was high and dark respiration was weak. Four weeks later, when the newly appearing needles were still short and not fully developed, the rate of photosynthesis already reached a level which was only slightly lower than "summer maximum". This means that either the stage of negative CO_2 balance is very short-termed and is not noticeable in four week intervals determinations, or the juvenile needles contrary to the old ones in older trees are photosynthetically more active and the said phenomenon is difficult to detect in two-year old seedlings.

Not many authors have carried out investigations on the seasonal course of photosynthesis in pines in constant comparable conditions. Measurements of McGregor (1958) on *Pinus strobus* and *Pinus taeda* showed a gradual increase and decrease of this activity, maximum value being reached in July and August. Pisek and Winkler (1958) investigated *Pinus cembra* from the upper altitudinal boundary in the Alps. They observed a decrease in the rate of photosynthesis in October and November. Nelson (1964) found the highest photosynthesis for *Pinus strobus* in September, and a quite rapid decrease in the following months. All the above quoted data, however concerning other species of pine show the same regularity as did those for Scots pine in our study. The decrease of photosynthesis rate usually begins relatively early, in full vegetation season, long before any considerable change in weather conditions occurs. The results of the present investigations also show that the autumn decrease in photosynthesis occurs at the same time when the dry matter content in needles begins to increase.

The results of our investigation on pines of three different provenances support the thesis that the seasonal rhythm of photosynthesis seems to be under genetic control. In our experiments, pine seedlings grown in standard conditions

throughout two vegetation seasons were always treated in the same way. In spite of this, the highland plants behaved differently and showed increased rates of photosynthesis during spring and summer, but more rapid transition to the "winter stage" in comparison to the pines of other provenances. It is also interesting to note that water relations in the stem and needles, as well as the growth curves of the needles were here somewhat different too.

The conditions of pot culture were sufficiently uniform to produce a great conformity of the physiological processes in the plants with the new rhythm of the vegetation season. Nevertheless the differences due to origin, though in this case they could not have been very pronounced, were still significant and speak for ecotypic differentiation of the pine strains examined. There is no evidence so far for distinguishing the two lowland groups from each other. However, the results of the investigations provide new data supporting the thesis that the highland pine from Nowy Targ constitutes a distinct ecotype, the characteristics of which reveal themselves in the progeny cultivated in another climatic region.

It is worth noting that the Nowy Targ plants, in comparison with other ecotypes, showed some morphological differences in the earlier comparative investigations on the provenance plantation (Żelawski, Gowin 1966), in native sites (Żelawski, Niwiński 1966) and in pot culture during the first year of growth (Żelawski 1966).

CONCLUSIONS

1. Measurements of photosynthesis carried out on Scots pine seedlings during the second vegetation season showed the highest values of photosynthesis rate (expressed per weight unit) in last year's juvenile needles.

2. The increase of the photosynthesis rate before the development of a new shoot indicates that the old assimilatory organs may play an important role in supplying photosynthates to the developing bud.

3. In summer, after the new needles had fully developed, a second though slight maximum of photosynthesis occurs.

4. The autumn decrease of photosynthesis rate begins relatively early and seems to be correlated with the time of considerable increase in the dry matter content of needles.

5. Higher rates of photosynthesis during the whole vegetation season, more rapid decrease of the activity at the end of the vegetation period, significantly faster decrease of water content in the lignifying stem, and some slight difference in dry matter content of needles during the summer time distinguished the plants of highland provenance from the two lowland strains.

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*Sezonowe zmiany intensywności fotosyntezy u siewek sosny zwyczajnej
(Pinus silvestris L.) wyhodowanych z nasion różnego pochodzenia*

Streszczenie

Przeprowadzone badania dotyczyły zmian aktywności fotosyntetycznej w ciągu sezonu wegetacyjnego u dwuletnich siewek sosny zwyczajnej pochodzących z trzech różnych rejonów Polski.

Pomiary fotosyntezy i oddychania wykonano przy pomocy analizatora gazowego (IR) w układzie zamkniętym. W stałych warunkach laboratoryjnych porównywano intensywność fotosyntezy netto i oddychania w ciemności u siewek hodowanych w hali wegetacyjnej w ciągu dwóch sezonów wegetacji. Przedstawione dane zawierają również charakterystykę przebiegu wzrostu siewek w ciągu drugiego sezonu wegetacyjnego oraz zmian suchej i świeżej masy w igliwiu i w części zdrewniałej pędu.

W porównywalnych warunkach doświadczenia najwyższą intensywność fotosyntezy stwierdza się u siewek w okresie wiosennym przed rozwojem nowego pędu. Wskazuje to na dużą rolę igieł młodocianych w zaopatrzeniu w asymilaty nowopowstających pędów. Zmiana typu powstającego igliwia w początkach drugiego sezonu wegetacyjnego zaznacza się wyraźnym spadkiem intensywności fotosyntezy wyrażonej w stosunku do świeżej i suchej masy organów asymilacji. W ciągu lata, gdy nowopowstałe igły na krótkopędach całkowicie się uformują, zaznacza się drugie, aczkolwiek znacznie mniejsze maksimum intensywności fotosyntezy. Po tym okresie — na długo przed końcem okresu wegetacyjnego rozpoczyna się stopniowy spadek aktywności fotosyntetycznej siewek; w doświadczeniach przeprowadzonych na początku grudnia nie stwierdzono w ogóle pochłaniania CO₂ w pierwszych godzinach po przeniesieniu roślin z hali wegetacyjnej do warunków laboratoryjnych. Jesienny spadek zdolności asymilacyjnej wydaje się być skorelowany ze zmianą stosunku suchej masy i wody, jaka zaznacza się wyraźnie w igliwiu w ciągu sierpnia.

Badane dwa typy sosny pochodzenia niżowego (z rejonu Pojezierza Mazurskiego i z centralnej Polski) nie różniły się między sobą istotnie w przebiegu zmian intensywności fotosyntezy, ale sosna z Podhala wykazywała wyraźnie wyższą zdolność asymilacyjną w ciągu okresu wegetacyjnego i szybszy spadek aktywności w końcu lata i jesienią. Również odmienny przebieg zmian zawartości wody i suchej masy w części zdrewniałej pędu i w igliwiu wyróżnia ten ekotyp sosny od pozostałych typów innego pochodzenia.