Eurasian J. For. Res. 12-1: 47-56 , 2009

Photosynthetic Productivity of Three Coniferous Species in Baikal Siberia, Eastern Russia

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Abstract

This paper explores changes in photosynthetic productivities of common pine (*Pinus sylvestris* L.), Siberian spruce (*Picea obovata* Ledeb.) and Siberian larch (*Larix sibirica* Ledeb.) during several successive years. Considered are both inter-annual and intra-annual changes, with intra-annual periods defined as early spring (April – May 15), spring-summer (May 16 – June 15), summer (June 16 – August 31), and autumn (September 1 – the first week of November). The study has revealed that high annual photosynthetic productivities in the different species concerned correlates with particular weather conditions during the vegetation periods. The total amount of carbon dioxide assimilated by the two evergreen coniferous species in the early spring, spring-summer and autumn exceeded the amount assimilated in the summer and was as large as 50 – 70% of the annual value. Meanwhile larch has been found to assimilate more than half of the total annual CO_2 in the summer. It is concluded that the characteristics of inter- and intra-annual dynamics of photosynthetic productivity identified in this study offer an opportunity to account for some of the ecosystem-specific features of the coniferous species under investigation, for instance, their ability to co-exist with deciduous plants in mixed communities, as well as the possibility of long-term preservation of boreal ecosystems on the same territories.

Key words: conifers, inter-annual and intra-annual changes of photosynthetic productivity, ecosystem-specific features of annual CO_2 gain, Baikal Siberia

Introduction

Coniferous species are dominant in forest ecosystems in North Asia. In the Baikal region conifers not only dominate, but also form highly productive mixed communities. The climate in the western part of the Baikal territory is characterized by high solar irradiation, deep winter freezing of the ground, and moisture deficit in summer. Under such conditions conifers possess plasticity of physiological functions, which allows them to remain in the plant communities and to support their high productivity.

Different sides of photosynthesis, which is a major physiological process in plants, have been studied as to coexistence of species in a community. As shown, there is evidence suggesting a correlation between photosynthesis rate and competitiveness of trees under a forest canopy (Kuppers 1984). Also there are data showing predictable changes in photosynthesis (i.e. under light saturation and at light-compensatory point) in trees at different stages of a serial succession (early-, intermediate- and late-successions) (Bazzaz 1979, Koike 1988). Furthermore, it is believed that photosynthesis is one of the regulatory mechanisms of quantity of spruce sprouts under the forest canopy while competing with herbaceous plants (Starostina 1988). It is also shown that there is a linkage between the value of potential photosynthesis and the status of species in herbaceous plant communities (Slemnev 1990, 1996). In terms of annual CO_2 balance, however, the role of photosynthesis as a mechanism regulating coexistence of species in a community has not been well studied yet.

The aim of this study was to investigate inter- and intra-annual changes in photosynthetic productivity of three coniferous species: common pine (*Pinus sylvestris* L.), Siberian spruce (*Picea obovata* Ledeb.), and Siberian larch (*Larix sibirica* Ledeb.) as a mechanism ensuring their noncompetitive existence in multi-component communities.

Materials and methods

Net photosynthesis of common pine, Siberian spruce, and Siberian larch was measured during the period of 1995 – 1999 in a plantation on the outskirts of Irkutsk (52°14’21”N 104°16’7”E). The plantation was established in 1985 with two-year-old seedlings, grown from local coniferous seeds supplied by a state-owned arboretum located in the settlement of Meget, Irkutsk District, 150 km away from the study plot.

Irkutsk is situated at about 80 km from the southwestern shore of Lake Baikal surrounded by mountain ranges. Geographically, this territory is a part of the Middle-Siberian plateau, an elevated plain predominated by gently sloping hills. The territory is mainly characterized by widespread common pine forests, with inclusions of Siberian larch, spruce, fir, Siberian pine, birch, and aspen. Spruce together with pine and larch form mixed tree stands in the downward

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parts of the relief, i.e. in folds, river heads and terraces. The area under study is 80% forested, with coniferous species accounting for more than half of the forested area (Vashchuk *et al.* 1997).

The climate of the region is largely formed by the Siberian anticyclone. Through most of the year, the weather in this region is dominated by continental air masses. The influence of the Atlantic and Pacific Oceans is rather weak because the area of Pre-Baikalia (west of and south-west of Lake Baikal) is remote from the ocean coasts and surrounded by mountain ranges as well. Normally, it is in the summer season that as the air becomes warmer, conditions favoring rainfall are formed and humid precipitation-bearing winds from the Atlantic penetrate the area (Kartushin 1969; Ladeishchikov 1982). In general, the quantity of summer rainfall is dominate in the annual precipitation.

The study plot is located on a gentle eastern slope (2–3°). The type of soil is gray forest non-podzolized loamy soil, on Jurassic coaly loams underlain by sands. Ground waters lie at a considerable depth (11 – 50 m), so they do not have any pronounced effect on moisture content in the soil.

In September 1999, we characterized the plantation as follows: the species composition was 40% pine, 30% spruce and 30% larch; the crown density was 0.5 – 0.6, the average height of pine, spruce and larch trees was 4.45 m, 3.95 m, and 5.13 m, respectively; and the average stem diameter at the height of 1.5 m, was 68.8 mm for pine, 43.2 mm for spruce, and 50.4 mm for larch. The plantation was arranged in rows: in the first and fourth rows there were pine trees, in the second and third ones - alternating spruce and larch trees.

The carbon dioxide exchange in intact 1-year shoots was studied during 1995-1999 using an IR gas analyzer Infralyt-4 (Germany) slightly modified by A.S. Shcherbatyuk (Shcherbatyuk 1990). The measurements were taken from the beginning of the net photosynthesis till the end of it, that is, from April till November. Net photosynthesis was recorded three times a week (on Tuesday, Wednesday and Thursday) during the whole period. Three trees of each species were chosen each year for simultaneous measurements. Cylinder-shaped assimilation chambers with polyethylene coating and a light-weight rigid framework were fixed in the middle part of the crowns in those trees. Solar radiation incident upon the tree canopy was measured with a pyranometer M-80 (Russia); automatic records were taken by a potentiometer KSP-4 (Russia). The ambient air temperature, the temperature in one of the assimilation chambers, and also the soil temperature at depths down to 120 cm were taken continuously on the measurement days with copper thermocouples, and the parameters were simultaneously recorded by a multi-point register KSM-4 (Russia). Relative air humidity in the middle part of the crown was measured with a hygrograph M-21 AN (Russia), and the parameters were verified using Assman's aspiration psychrometer. Soil moisture content at every 10-cm level down to a depth of 100 cm was determined every ten days using the thermostat-weight method (Nikolayev 1948, Fedorovsky 1975). During the vegetation period the net photosynthesis and environmental factors such as solar radiation, air temperature, soil temperatures, and relative air humidity were recorded every day at 1-hour intervals. Thus, more than 70 patterns of day time variations of net photosynthesis and environmental factors were obtained for each year.

We analyzed the dynamics of net photosynthesis, and the corresponding radiation intensity, air temperature, and air humidity. For the analysis soil temperatures were also taken daily at 1 p.m., as well as the total content of available soil water supply in the upper 0 to 50-cm layer, the latter being determined every ten days. Daily net photosynthesis and daily total radiation were determined as the sum of all the hourly values of day. Annual photosynthetic productivity was determined as the total sum of photosynthesis during the growing months. The monthly value of photosynthesis was estimated as the product of the daily mean photosynthetic productivity (determined on the basis of experimental days) by the number of days in the corresponding month.

[We obtained the daily sum of carbon uptake by adding its hourly values over the entire day. Night time respiration was not taken into account, since it is not large. We did not use light response curves received in lab experiments].

Results

Inter-annual changes in photosynthesis productivity

Inter-annual changes in photosynthesis productivity were analyzed with due regard for i) the climatic conditions of the vegetation periods (Table 1) and ii) annual photosynthesis productivities (Table 2).

The summer of 1995 was characterized by high air temperatures, often reaching 30°C, and by a decrease in available soil water supply in the upper 50-cm layer from 100 mm in the spring to 30 – 35 mm in July and August. On some days, relative air humidity approached the threshold value of 32 – 34%; lower air humidity limits the net photosynthesis in conifers in our area. It was thus possible to characterize all the vegetation period as hot and dry. On the whole, vegetation period that year was favorable only for photosynthesis in pine trees (Table 2).

Frequent atmospheric precipitations in mid-June of 1996 delayed soil warming. Furthermore, frequent summer rains were accompanied by drops in air temperature, which caused the soil temperature to drop below mean annual values. The vegetation period was classified as cool and humid. The uniform optimal soil moisture and relatively low air temperatures favored increase in the photosynthesis in spruce much more than in pine and larch.

The vegetation period of 1997 was characterized by very warm, mild weather conditions. The absence of night frost, together with the rise in air temperature and soil warming in April and in early May, were good contributory factors for the early beginning of photosynthesis which started in evergreen coniferous trees on April 1 compared with, normally, April 10. The middle of the vegetation period was characterized by

Table 1. Hydrothermal conditions of the vegetation periods, 1995-1999.

	April	May	June	July	August	September	October
			Atmospheric precipitation, mm				
1995	–	15	48	30	136	38	18
1996	–	18	108	127	85	31	10
1997	7	29	51	120	101	45	18
1998	10	42	128	171	67	53	16
1999	15	29	59	146	49	12	14
long-term mean1	16	32	70	92	85	44	21
			Monthly air temperature mean, °C				
1995	–	9.7*	15.3	18.8	16.8	7.8	3.3
1996	–	15.5*	14.0	20.1	15.6	7.7	2.1***
1997	9.8**	12.2	17.3	19.2	18.0	8.8	5.3***
1998	3.9	9.7	13.4	17.5	17.3	9.7	2.9
1999	2.7	12.4	15.2	19.6	16.2	10.0	1.3
long-term mean1	1.0	8.4	14.8	17.6	15.0	8.1	0.5
			Monthly soil temperature mean at depth of 20 cm, °C				
1995	–	5.0*	9.6	14.2	15.1	10.0	5.1
1996	–	6.5*	8.8	13.2	14.0	8.8	5.6
1997	2.3	6.1	10.7	13.7	15.3	10.3	5.1
1998	0.2	4.6	8.8	13.4	14.9	10.4	4.2
1999	0.0	4.3	9.8	15.2	14.1	9.4	4.2
long-term mean1	0.0	7.0	12,8	16.8	15.9	10.3	3.1
			Monthly total solar radiation mean, mol m^{-2}				
1995	–	2,539	3,314	3,202	2,691	1,329	1,240
1996	–	2,254	2,494	3,214	2,635	1,770	1,135
1997	2,433	3,069	3,429	3,019	2,207	1,200	1,141
1998	2,578	2,513	2,780	2,496	2,427	1,355	982
1999	2,111	3,152	3,366	2,554	2,902	1,518	1,127
long-term mean1	2,150	2,720	2,808	2,637	2,219	1,647	1,076

* mean value for the period 20-31 May ** mean value for the period 10-31 April *** mean value for the period 1-17 October
1 long-term mean for 100 years (In: The Climate of Irkutsk, 1981)

Table 2. Photosynthetic productivity of conifers in different vegetation periods.

Year	Characteristics of a growing season	Photosynthetic productivity mol CO_2 m^{-2} $year^{-1}$		
		Pinus	*Picea*	*Larix*
1995	Hot, dry	9.2	3.1	3.1
1996	Cool-warm, wet	8.7	6.8	4.9
1997	Warm, moderately wet	13.9	6.8	6.2
1998	Warm, wet	7.6	6.3	5.5
1999	Hot, dry	5.3	2.8	2.5

unprecedented warming of the entire soil horizon. The relative air humidity throughout the vegetation period was optimal (above 32 – 34%) so depression of net photosynthesis rate down to zero level was not observed in the conifers under investigation. The vegetation period was classified as warm, and moderately humid. These conditions were more favorable for photosynthesis in common pine and Siberian larch.

The frequent intense rains in 1998 without cooling of the air masses, and a fairly long period with unusually warm (not lower than 20 °C) humid nights in summer characterized the vegetation period as warm and humid. The conditions during that period were the most favorable for photosynthesis in larch and spruce (Fig. 1 and 3).

In 1999, the long period of high temperatures along with drought and soil moisture deficit lasting into middle autumn (Fig. 2) caused both summer and early-autumn depression in photosynthesis in evergreen conifers. It allowed us to characterize 1999 as hot and extremely dry. Except in the spring-summer period, this year was extremely unfavorable for photosynthesis in spruce and larch (Fig. 4).

Our analysis revealed a considerable change in the amount of photosynthesis productivities for the three coniferous species during the vegetation period under different weather conditions, with there being a specific correlation between certain types of weather conditions and highest productivities for each species. The maximum photosynthesis productivity in pine was observed in the hot and dry vegetation period, for spruce it was the cool and humid year, and for larch - warm, moderately humid year. Thus alternation of contrasting weather conditions in successive years allowed the various species to be supplied, in turn, with favorable conditions for their higher photosynthesis and, consequently, for more extensive growth and abundant seed production.

[Larch shows lower values of photosynthesis in all the years because in our study it is calculated as mkmol CO_2 per 1 m^2 of the surface of needles. If we had calculated photosynthesis of conifers as mg CO_2 per 1 g dry weight of needles then the photosynthesis of larch would have been shown to be 4 to 5 times higher than that of pine].

The fact that the highest annual photosynthesis productivities of *Pinus sylvestris, Picea obovata* and *Larix sibirica* depended on the type of weather conditions of a vegetation period is in agreement with the ecological characteristics of these species as xerophyte, mesophyte and xeromesophyte, respectively (Koropachinsky 1983).

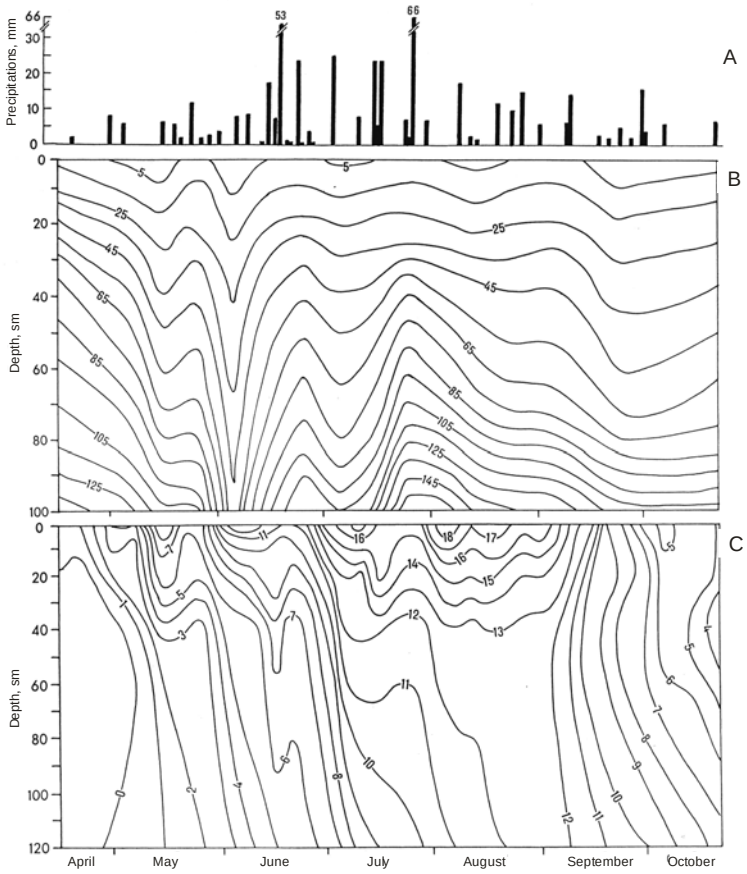

Fig. 1. Changes of environmental factors in 1998: Precipitations, mm (A), available soil water supply, mm (B) and soil temperatures (C) at different depths.

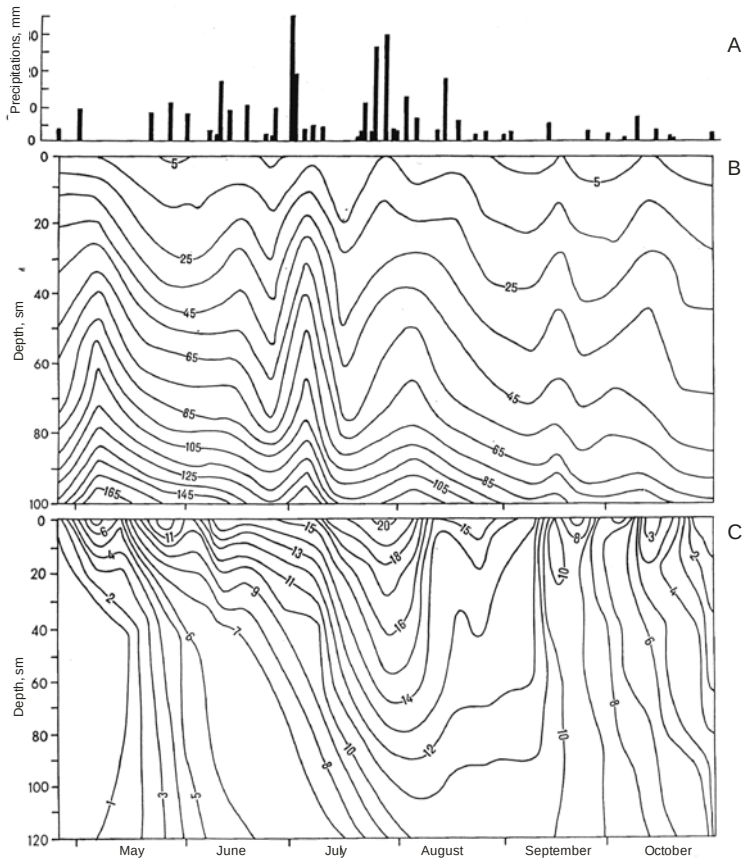

Fig. 2. Changes of environmental factors in 1999. Notations are the same, as in Fig. 1.

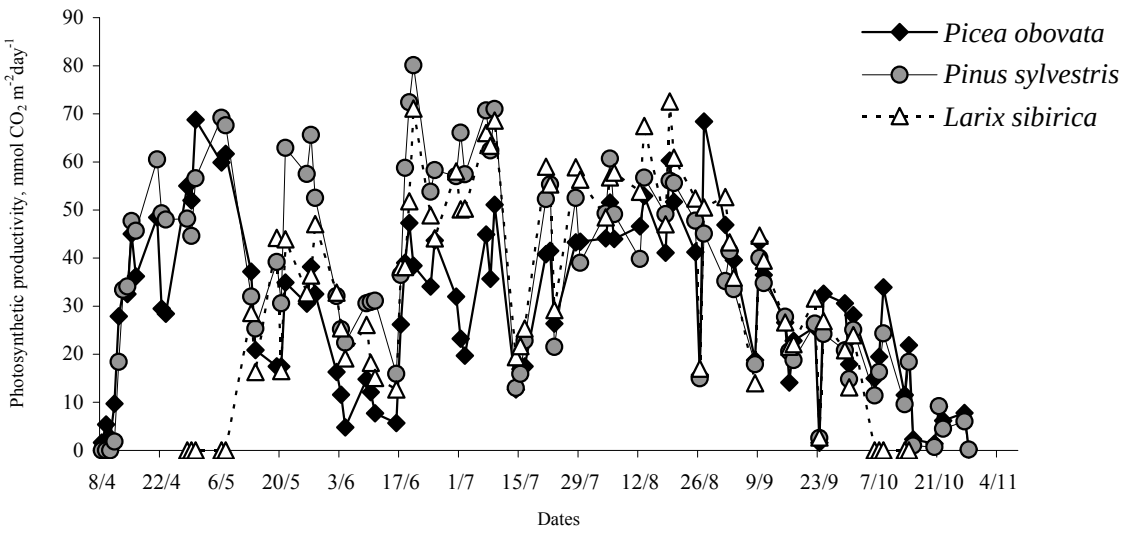

Fig. 3. Dynamics of daily photosynthetic productivities in conifers in 1998.

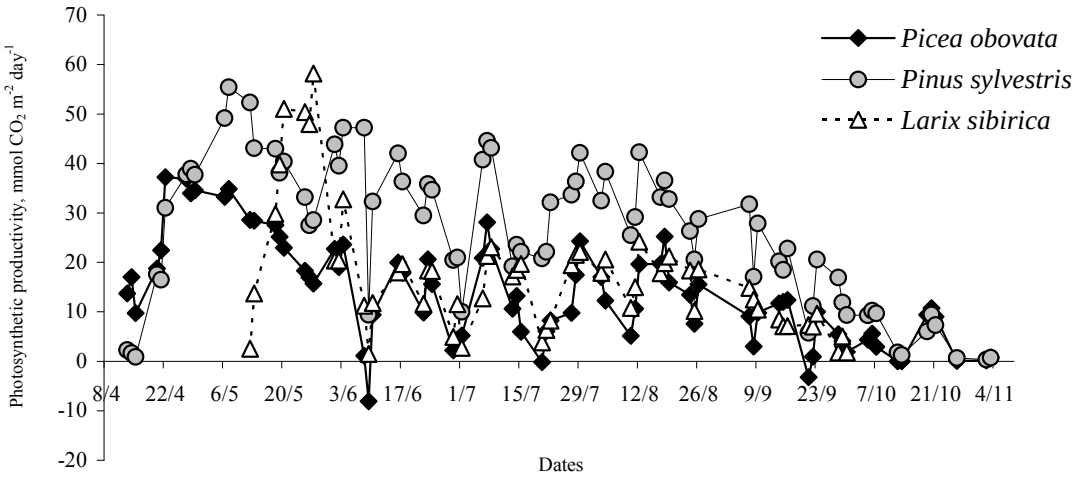

Fig. 4. Dynamics of daily photosynthetic productivities in conifers in 1999.

Table 3. Photosynthetic productivity of conifers in the chosen periods (% of the annual photosynthetic productivity).

Species	Periods			
	Apr. – 15 May	16 May –15 Jun.	16 Jun. – 31 Aug.	1 Sep. – the end of vegetation period
		1997		
Pinus	38.5	25.2	26.2	10.1
Picea	27.2	18.5	35.2	19.1
Larix	*	31.4	54.1	14.5
		1998		
Pinus	19.9	19.1	46.6	14.4
Picea	19.8	14.4	45.2	20.6
Larix	*	19.1	66.4	14.5
		1999		
Pinus	19.8	21.7	45.2	13.3
Picea	28.6	21.4	39.2	10.8
Larix	*	38.0	54.0	8.0

Intra-annual changes in photosynthesis productivity

Annual photosynthesis activity was divided into four periods: early spring, spring-summer, summer, and autumn, which differed in phenological state of conifers (Elagin, 1976) and in the extent of dependence of their photosynthesis on prevailing limiting factors. Actual duration of each period is given below when describing photosynthesis peculiarities characteristic of these periods.

It was found that the early spring period started in early April (within the first ten days) and lasted till about May 15. The first signs of net photosynthesis were observed at the beginning of this period, and low air and soil temperatures acted as prevailing limiting factors (Figs. 1 and 2). In spite of these limiting factors, during this period the evergreen coniferous species assimilated fairly large amounts of CO_2, namely, 20-30% of the total annual photosynthetic productivity (Table 3). For Siberian spruce such photosynthetic productivity was favored by low night air temperatures with abundant moisture in the ground litter, and for common pine by high radiation intensity and rapid warming of the upper soil layers.

During the anomalously warm early spring in 1997 the CO_2-exchange and daily photosynthesis productivity of pine exceeded the observed values in the following years by a factor of more than four. This year warming of the air and soil due to lack of night frosts was so fast that temperatures in April were close to actual temperatures in a spring-summer period. In addition, the total available soil water supply in the litter and the upper 0 to 50 cm soil layer was very high; about 140 mm, with the annual average being not higher than 80 – 100 mm. For pine the increases in daily photosynthesis were attributed, with a high level of confidence, to soil temperature rise at the depth of 5 cm (R^2=0.82 in pine and R^2=0.13 in spruce), whereas in spruce the increases were due to the available water supply in soil (Suvorova *et al.* 1999 a). For the early spring period the amount of assimilated CO_2 for spruce and pine was about 30% of their annual values (Table 3). In the spring-summer and summer periods, with air temperatures still growing and soil moisture lowering, neither pine nor spruce showed such high values of photosynthesis activity.

Our observations over the last thirty years indicate that such climatic conditions occur rather infrequently in East Siberia - once or twice in a decade. But they are very important for understanding the eco-physiological peculiarities of the evergreen coniferous species. Firstly, such anomalous periods revealed a high photosynthetic potential of pine as a factor that accounts for its fast growth. Secondly, high early spring photosynthesis is likely to meet the requirements for assimilates not only for growth, but also for adaptation to subsequent extreme drought conditions owing to the fact that assimilates are consumed to supply maintenance respiration.

Needles of larch start growing after May 15 and so does its photosynthesis, which is why larch is not discussed in the early spring period.

According to the phenological calendar, the spring-summer period was defined as starting after May 15 and lasting till June 13 – 20. There is a specific climatic peculiarity of the region: at the end of the early spring and beginning of the spring-summer period there would sometimes be another cold spell with sharp cold winds and atmospheric precipitation. This is just the time for larch to break its buds. The photosynthesis in pine and spruce under these conditions fluctuated, terminating for several hours. Growth of needles of the larch brachiblasts also slowed down.

The rest of that period was largely characterized by an increasing adverse effect of higher air temperatures on photosynthesis in spruce caused by a considerable concurrent decrease in moisture content in the litter and in the upper 50 cm soil layers. The photosynthesis in pine showed stable increase. Needles of the larch brachiblasts began to grow as photosynthesis in it was proceeding at a higher rate (Fig. 2, 4). Slight night frosts which might happen even in early June had no marked effect on daily photosynthesis productivity, but in the morning hours on such days the beginning of photosynthesis was delayed. Pine and spruce photosynthesis productivities equaled or were slightly lower than their productivities in the early spring period. Larch photosynthesis productivity reached 20 – 40% of the annual value (Table 3).

The summer period started on June 15 and lasted till August 30, with one exclusion. In our region sometimes there may be a delay of warming in the early spring with a following delay of the spring-summer period and a late beginning of summer like it was in 1999 (5 to 7 days). In our study, the summer period was characterized by the most active photosynthesis in larch which assimilated 50 – 70% of the annual amount of carbon dioxide whereas evergreen pine and spruce assimilated less than 40 – 45 % of it (Table 3).

Drought was a key factor in the decrease in photosynthetic productivity during the summer period in all the species. The decrease in available soil water supply down to 30 mm or less in the upper 50-cm layer, accompanied with high air temperatures and low air humidity, could result in a 20% and 40% drop of monthly photosynthesis productivities in pine and larch, respectively, with a 65% loss in spruce photosynthesis productivity during the drought in July 1995 compared with optimal conditions during the same month of 1996.

In the humid cool vegetation period in 1996 the relative rate of CO_2 assimilation of light-requiring pine was exceeded by that of spruce because of the predominance of moderate to low radiation intensity. For May and June it is shown in Table 1. In the remaining part of the vegetation period there was not enough atmospheric heat to compensate for lack of spring soil warming that year, either. Short frequent rains with prevailing cloudiness together with lower soil temperatures limited photosynthesis of pine.

As for spruce, the radiation intensity on cloudy days was optimal, because spruce reaches light saturation of photosynthetic activity within the range of moderate illumination values as has been shown earlier (Shcherbatyuk *et al.* 1991). In addition, we had

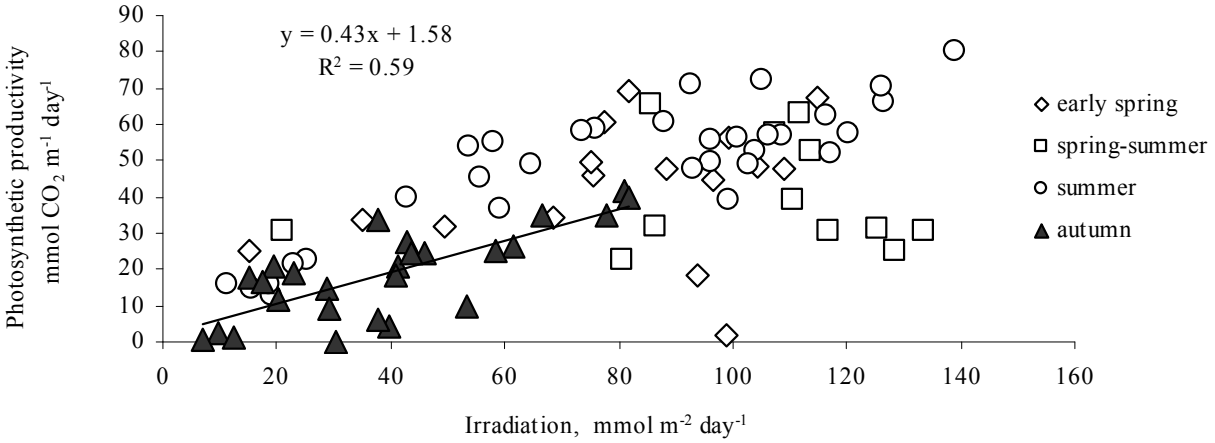

Fig. 5. Correlation of daily photosynthesis productivity of pine with total daily illumination in the autumn period of 1998.

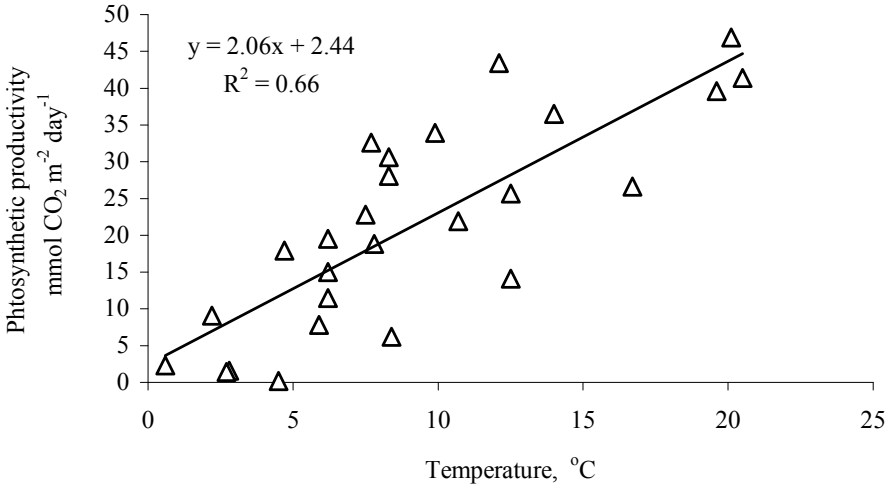

Fig. 6. Correlation of daily photosynthetic productivities of spruce with mean daily air temperatures in the autumn period of 1998.

previously found for the forest-steppe Pre-Baikalia (Suvorova 1992) and have confirmed by the present study that Siberian spruce in the sub-taiga zone is characterized by having the lowest temperature optimum, and the highest optimum for air humidity of the species under study. These photosynthetic properties contributed to the highest values of spruce photosynthetic productivity during a cool humid summer. On the contrary, low radiation intensity suppressed photosynthesis activity in Siberian larch, as did low air and soil temperatures. Larch showed the highest photosynthesis rates in the summer period with optimal soil moisture (over 30 mm in the 0 – 50 cm layer) optimal atmospheric humidity (over 35%) and high air temperatures (20 to 30 °C) (Suvorova *et al.* 1999 a).

According to our classification the autumn period began on September 1 and lasted till the end of the photosynthesis (late October-first ten days of November). In larch the period of photosynthesis attenuation began in late August and ended within the last ten days in September, corresponding with the senescence of its needles. However, with delays in the onset of autumn frosts, low photosynthetic activity of the yellowing needles could last fairly long - until the 28 of September and could contribute more than 10% to its annual photosynthesis (Table 3).

The weather in September during the study period, except for 1999, was characterized by a combination of low night temperatures and moderate humidity which appeared quite favorable for photosynthesis in evergreen coniferous species. Low radiation intensity in this month became the key limiting factor for the light-requiring pine: both the maximum light level and the total daily solar radiation dropped down to 35 – 40% of the highest June averages (Fig. 5). Nevertheless, conditions of clear cool days of so called “golden autumn” were rather favorable for photosynthesis in pine as optimal moisture and temperature for this species prevail at this time. Thus, the long autumn

period of 1995, which started on September 1 and lasted until November 1, ensured a significant contribution (23%) to the annual photosynthetic productivity for pine.

On the other hand, insolation in September was optimal for spruce, because, as mentioned above (Shcherbatyuk *et al.* 1991), its photosynthesis reaches light saturation at a moderate radiation intensity - in the ranges of 1350 – 2250 mkmol $m^{-2}s^{-1}$. The lower and upper points of the range depend on the air temperature: the lower the temperature the higher the light saturation point. For pine it is 3150 – 3600 mkmol $m^{-2}s^{-1}$. In some years, spruce autumn CO_2-gain was equal to about half of that in the summer period (Table 3) and exceeded photosynthetic productivity in pine.

During the autumn drought of 1999 (rather infrequent in this region), even at moderate air temperatures, photosynthesis decreased in both pine and spruce, in the latter to a greater extent than in the former (Fig. 4).

A further decrease in daily photosynthetic productivity was caused by dropping air temperatures as well as by cooling of the soil layer (Fig. 6). The total value of the attenuating photosynthesis in spruce and pine in October amounted to 6% and 4% of their annual quantities, respectively.

Discussion

The characteristics of dynamics of photosynthetic productivity of pine, spruce and larch during their vegetation periods suggest that conditions during the summer period are the least favorable for carbon assimilation due to higher air temperatures, and lower soil and atmospheric moisture. But each species has its own adaptive peculiarities which ensure its survival under unfavorable conditions.

For our region the threshold reserve of available soil water supply in the upper 50-cm layer is 30 mm, as inferred empirically from experimental data spanning over seven years (Shcherbatyuk *et al.* 1991). It was shown by Suvorova *et al.* (1999 b) that when air humidity does not drop below 35%, larch has an advantage in maintaining normal photosynthesis: its daily productivity, as a result of soil water deficit, decreased only down to 21%, whereas pine and spruce decreased their photosynthetic productivities down to 14% and 8%, respectively. The data obtained for the forest-steppe Pre-Baikalia for a 10-year period showed that with a decrease in available soil water supply below 30 mm in the upper 50-cm layer and a decrease in relative air humidity to 15 – 20%, pine had the advantage in maintaining a stable level of photosynthesis productivity (Suvorova 1992).

In contrast, moderate temperature, and optimal soil moisture in spring and autumn are used to their advantage by evergreen coniferous species to attain higher photosynthetic productivity.

In our view, the specific characteristics of spring and autumn photosynthesis in the conifers allow us to account for the following phenomena.

1. **Co-existence of coniferous and deciduous species at different stages of development in mixed communities.** With the weather conditions changing every year, different species may in turn, experience favourable conditions facilitating higher productivity of photosynthesis, thus ensuring long term co-existence of various species. Peculiarities of “non-summer” photosynthesis and its predominant share in the annual photosynthetic productivity of the evergreen conifers contribute to preserving the heterogeneity of forest ecosystems, which happens as follows. Deciduous trees, such as aspen and birch that grow in boreal ecosystems, actively assimilate CO_2, just like larch, in the summer period. Growth and reproduction processes in them take place at the expense of their summer assimilates. Thus due to the fact that active CO_2 assimilation in evergreen and deciduous trees occur in different time periods, conditions for their coexistence in mixed forest communities are formed, which makes them more stable self-reproducing structures.

2. **Long-lasting existence of spruce undergrowth under the canopy of deciduous plants.** Spruce is capable of accumulating a large amount of assimilates during periods of open canopy in early spring, the spring-summer period (prior to the complete unfolding of leaves in the upper canopy layer), and in autumn after canopy leaf fall. Young spruce trees are known to keep a positive carbon balance in the summer season under a closed forest canopy owing to the adaptation of photosynthetic capacity to a low irradiation level. При этом Under these conditions the light compensation point and the plateau of photosynthesis saturation go down, the dark respiration and transpiration rates decrease, and the efficiency of photochemical reactions increase (Alexander *et al.* 1995, Man and Lieffers 1997).

3. **Fast rehabilitation of pine in East Siberia after forest fire, in uncultivated areas, and along railways.** Pine requires the high irradiance of open areas and their quickly warming soil in early spring to achieve the highest value of photosynthetic activity. These characteristics seem to provide a physiological basis for pine being one of the pioneer species in East Siberia (Shimanyuk 1962).

4. **Long-lasting existence of relic plant communities, formed during periods of local warming in the Pleistocene and Holocene, on limited territories of Siberia under atypical conditions.** These communities are represented by tundra sparse forests of *Larix sibirica* on the peaty soils of the Southwestern Yamal (Aleksandrova 1971, 1978, Telyatnikov and Pristyazhnyuk 1999), spruce forests in areas of calcareous soils along the Lena River valley and its tributaries (Utkin 1965, Shcherbakov 1975, Timofeyev 1980), pine communities on lake quagmires in the Kurgan region, and pine-covered crests among swamps in the Barabinsk forest-steppe (Kats 1971, Starikov *et al.* 1989, Liss *et al.* 1981, Valutsky 1991). [Relic communities are those which used to be widely spread before or within past geological ages**,** which nowadays have only locally remained]. We believe that these communities have survived until the present because of the peculiar characteristics of coniferous photosynthesis. Despite changes in the relief and climate, these areas

still preserved the conditions favoring periods of high photosynthesis of coniferous forests, most likely in early spring and in autumn, and in the case of communities in the polar regions, spring-summer and summer. Owing to ability to augment photosynthesis in favorable periods, conifers form reserves of assimilates which are necessary for adaptation of plants and reproduction of their new generations. These patterns also suggest that photosynthetic productivity ensures the long-term persistence of the boreal ecosystems.

Based on the results of the analysis and their discussion, we can conclude that ability of evergreen conifers to effectively assimilate CO_2 during cold and humid periods in spring and autumn, ability to stand droughts and changes in irradiation during the vegetation period, ability to significantly increase photosynthesis in years which are favorable for only some of the species are the traits of photosynthesis that supply opportunity for sustainable coexistence of coniferous species in multicomponent boreal communities and possibility of long-term preservation of boreal ecosystems on the same territories.

Acknowledgements

We would like to thank V. Voronin (Dr. Sci.), V. Oskolkov, and A. Deloverov for their help with the experimental part of this study. Our thanks go to A.D. McGuire, B. Amiro, M. Apps and L.A. Platonova, who reviewed an earlier draft of the manuscript.

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