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Proposal of the Environmental Resource Utilization Coefficient (ERUC) - A Tool for Characterizing the Conditions for High Photosynthetic Activity in Conifers in Siberia, Russia -

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Abstract

Normalized values for the optimal ranges of environmental factors, such as air and soil temperatures, air humidity, available soil water supply, and illumination during the growth period are suggested as an environmental resource utilization coefficient (ERUC) for analyzing the photosynthetic activity in many species. Based on graphical and ecophysiological studies, we tested the idea of ERUC for the common pine (*Pinus sylvestris* L.), Siberian spruce (*Picea obovata* Ledeb.) and Siberian larch (*Larix sibirica* Ledeb.) which are native to Siberia, Russia. The numerical value of a ring-shaped area obtained on a petal diagram was taken by us to equal the value of the maximum environmental resource utilization coefficient (ERUC). Changes in the ERUC values for each measurement year were compared to the corresponding annual characteristics of photosynthetic activities (e.g. the absolute seasonal maximum photosynthesis rate, the maximum daily photosynthetic productivity, and the seasonal photosynthetic productivity). It is proposed that the ERUC be used to characterize the environmental niche for coniferous species.

Key words: photosynthetic productivity, conifers, environmental resources, optimal ranges of environmental factors, continental climate, East Siberia

Introduction

Woody plants can live for a long time and can survive even under severe environmental conditions, such as those found especially in the Siberia region where a thick permafrost layer exists. Therefore, each species has high growth performance in the optimal range of the growth environment as well as a threshold of upper and lower limits (e.g. Larcher, 2003).

Photosynthetic activity is a good indicator for any effects of environmental conditions on plants. Photosynthetic characteristics such as leaf structure, primary metabolism and net photosynthesis can be used in investigations concerned with the geographical distribution of plants, their phytocenotic status and the involvement of species in successions (Bazzaz, 1979; Kuppers, 1984; Koike, 1988; Pyankov *et al*., 1992, 1994; Slemnev, 1996, 2000). The ecological niche can also be characterized from the response of photosynthesis to environmental conditions (Barker *et al*., 1997; Benowicz *et al*., 2000).

The ecological niche is defined as a set of environmental conditions that are necessary for the existence of a population (Whittaker, 1980). The concept of niche builds upon the differential response of naturally existing species to stress conditions or to the availability of resources (Leibold, 1995). Earlier it was pointed out that the procedural approaches available were not sufficiently advanced to allow one to make a description of niches for different species and the quantification of niche size (Rabotnov, 1987). Nowadays new techniques have been developed which allow the indicators of plant niches to be graphically determined on the basis of photosynthesis. For instance, a method was developed which on the basis of the light curve for photosynthesis permitted determination of the radiation intensity at which the photosynthetic activities of agricultural crops could reach their highest values (Tooming, 1977). In addition, temperature curves of photosynthesis were used to calculate coefficients of heat and cold tolerance of plants, which characterize the distribution properties of plants in the arid ecosystems of Mongolia (Slemnev, 2000). For cultivated plants the optima of photosynthesis were determined graphically, which were similar in their area or shape to the optima of biomass accumulation (Drozdov and Kurets, 2003).

Over a period of years we have been investigating the photosynthetic activities of conifers under the severe-continental conditions of the Siberian Baikal region. By a severe-continental climate we mean abrupt changes, up to about 20ºC, in day and night temperatures in spring and early summer as well as in autumn, beginning in late August; in addition, there are sharp differences from lows of -40ºC in winter to highs of +34ºC in summer, with summer often being quite dry.

Recent results derived from our experimental research have provided a basis for the development of an environmental resource utilization coefficient (ERUC) describing the integrated effect of five environmental factors on the photosynthetic activity of

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three conifer species. These factors are air and soil temperatures, air humidity, available soil water supply, and illumination. The aim of the present study was to estimate the maximum environmental resource utilization coefficient (ERUC) during the growing season in common pine (*Pinus sylvestris* L.), Siberian spruce (*Picea sibirica* Ledeb.), and Siberian larch (*Larix sibirica* Ledeb.) and to analyze the correlations between the main characteristics of photosynthetic activities, such as maximum daytime photosynthetic rate, maximum photosynthetic daily and seasonal productivity, and the ERUC obtained. The present results are compared with those obtained by us in our earlier investigations. We discuss the possibility of using ERUC to characterize the niche attributes of the three coniferous species in our region.

The climate of the study area

The study area has a severe-continental climate, with a high level of insolation. In winter, a powerful anti-cyclone forms over the southern territory of East Siberia, resulting in predominantly clear, calm weather that favors considerable heat loss from the terrestrial surface. The period from late March to early May in our locality is referred to as “black spring” by phenologists, since there is a large difference between day and night temperatures (about 20ºC) due to which the soil remains hard-frozen, thawing out at the very top layer under the sun rays and freezing again by night. Because of this, deciduous and grassy plants stand leafless making the surroundings look dark and colorless throughout this period. The actual spring (late March to early June) is characterized by low relative air humidity, sometimes as low as 10%, by a high level of insolation and by a gradual rise in air temperature. During this period, the soil is gradually heated and thaws downward. The frost-free summer period lasts for about 100 days. But slight frosts (from -1ºC to -4ºC) may well happen during the growing period in late spring (sometimes up to June 15), and in early autumn (beginning from August 25). The yearly temperature amplitude may reach 80°C, and the daily amplitude can exceed 20°C. The monthly average temperatures in January and July are as low as -23.4ºC and as high as +17.2ºC, respectively. The yearly average temperature is -2.4ºC (Handbooks on the USSR Climate, 1966 a, b). The yearly average precipitation is 359 mm, with most summer precipitation falling during the second half of the summer. Snow cover in the study area is about 40-50 cm deep. The territory is characterized by a predominance of evaporation over precipitation during the warm season.

Materials and Methods

The investigation on the basis of which the ERUC has been developed was carried out during 1995-1999 in a plantation established in 1985 with one-year old conifer seedlings on the research field of the Siberian Institute of Plant Physiology and Biochemistry SB RAS on the outskirts of the City of Irkutsk, Russia (52º 14' N, 104° 16' E). The study area was located on a gentle slope (1-2^{o}) of eastern exposure. The size of sample trees was as in Table 1.

Table 1. Average sizes of trees under study.

Species	Larch	Spruce	Pine
Height (m)	5.2 ± 0.8	4.0 ± 0.5	4.5 ± 0.7
Diameter at the height of 1.5 m (mm)	68.7 ± 0.8	50.4 ± 0.7	43.2 ± 0.8

The soil type, i.e. gray forest, non-podzolic, loamy, and the water table (at a depth of 11-22 m) were typical of the sub-taiga zone of the southern part of Eastern Siberia. In September 1999 the age of the trees was 15 years old, the species composition of the plantation was 40% pine, 30% spruce, and 30% larch, and the ratio of the tree crown area to that of the plantation was 0.5-0.6.

Experiments on the photosynthetic activities of conifers were carried out from the beginning of photosynthesis in pine and spruce needles in early April to the end of photosynthesis in early November. As for the photosynthesis of the larch trees, it started simultaneously with the beginning of growth of brachyblast needles, about May 15. Measurements were made every week throughout the period of photosynthesis in the following manner. Each Monday the equipment used was set up and recording continued until Friday morning. For analysis we used the data obtained from Tuesday to Thursday. The carbon dioxide gas exchange of one-year-old shoots was recorded with an IR gas analyzer – an “Infralyt 4”-based multi-channel device slightly modified by A.S. Shcherbatyuk (Shcherbatyuk, 1990). Three trees of each species were chosen for the measurements. Nine assimilation chambers, each reinforced with a wire frame and covered with polyethylene, were installed on the southern side of the middle part of the crowns of the trees under study. Along with CO_2 assimilation, also recorded were the dynamics of the environmental parameters. Soil temperatures were taken at the following levels: at a depth of 5 cm and then at 20 cm intervals up to a depth of 100 cm. The soil temperatures, the temperature in one of the assimilation chambers, and the ambient air temperatures all were measured using copper temperature-sensitive sensors with simultaneous registration by a multi-point register KSM-4 (Russia), with the two instruments being interconnected. The radiation intensity under the tree canopy was measured with a M-80 pyranometer (Russia), and readings were also taken using a KSP-4 potentiometer (Russia), with both instruments being connected. Air humidity was determined on a weekly basis by a hygrograph and its readings were verified on a daily basis using an aspiration psychrometer. Soil moisture contents were determined for each 10 cm soil layer to a 100 cm depth every ten days during the growth period using the thermostat-gravimetric method. The available soil water supply was calculated by a commonly used technique (Fedorovsky, 1975) as the difference between the soil moisture content and the moisture inaccessible for plants. The inaccessible moisture was taken to be equal to the maximum amount of hygroscopic water held by soil particles multiplied by a factor of 1.5 (Nikolayev, 1948). The units of measurement of photosynthesis and radiation intensity were µmol CO_2 $m^{-2}s^{-1}$, and µmol $m^{-2}s^{-1}$, respectively. (Long and Hallgren, 1989). To calculate the photosynthesis rate per unit of surface area of the needles, Tselniker's tables were used (Tselniker, 1982, Tselniker and Yelchina, 1996). The tables show the correlation between the mass and surface area of the needles in pine and spruce. We calculated the surface area of larch needles. The absolute value of maximum of the net photosynthesis rate during growing season was assessed from the daytime maxima of the process for all days of the study. The values for the photosynthesis rate for each hour of the day were used to infer the daytime (daily) productivity of photosynthesis. The total monthly productivity was calculated as the product of the daily average photosynthesis productivity and the number of days in a month. The annual (seasonal) photosynthesis productivity of shoots was calculated as the sum of the photosynthesis productivity values for all months of the growth period mentioned above. Optimal conditions for photosynthesis were considered to be those ranges of environmental factors where the values of the CO_2 assimilation rate achieved 80% to 100% of the absolute seasonal maximum net photosynthesis (Larcher, 1978, 2003).

To calculate the ERUC, the optimal ranges of the following factors were used (Suvorova *et al.*, 2004): air temperature and relative humidity, radiation intensity, soil temperature taken at a depth of 5 cm (daily at 1 p.m.), and the available soil water supply in the top 0 to 50 cm deep soil layer. The lower and upper boundaries of the optimal ranges were expressed in terms of the percentage of the maximum value for each factor. A radiation intensity of 4500 µmol $m^{-2}s^{-1}$ (the solar radiation in our region is as high as that in the area of Samara City, in the southern part of European Russia), an air temperature of 35°C, a soil temperature of 23°C, an available soil water supply of 170 mm in the upper 50 cm layer, and 100% relative air humidity were assumed as being the100% values.

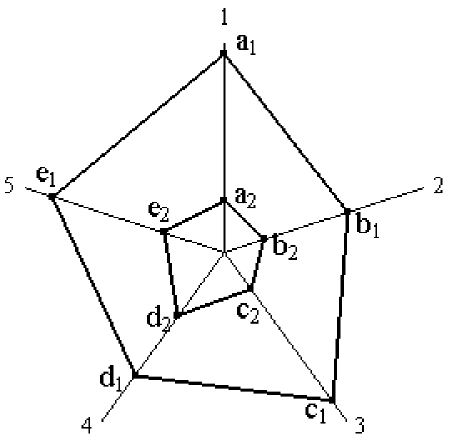

Fig. 1. Graphical representation of the form, components and size of the environmental resource utilization coefficient (ERUC) using a petal-diagram.

If, for example, the optimal range of radiation intensity for pine was 1108 - 3776 µmol $m^{-2}s^{-1}$, then it corresponded to 25% - 84% of the maximum, respectively (see above). The values thus transformed were plotted on a petal diagram. On the diagram the boundaries of the upper ranges were interconnected; the boundaries of the lower ranges of all factors were also interconnected. As a result we obtained a kind of ring-shaped area between the upper and lower boundaries. Then the square of the ring-shaped area was calculated as the difference between the squares of the pentagon produced by the upper ends and that produced by the lower ends of the normalized fragments (Fig. 1).

The square of the ring-shaped area was determined by the formulas:

$$S_1 = 1/2*\sin \pi/180*72*(a_1b_1+b_1c_1+c_1d_1+d_1e_1+a_1e_1) ;$$
$$S_2 = 1/2*\sin \pi/180*72*(a_2b_2+b_2c_2+c_2d_2+d_2e_2+a_2e_2) ;$$
$$S_{ERUC} = S_1 - S_2$$

where axis 1 is for radiation intensity, axis 2 – air temperature, axis 3 – soil temperature, axis 4 – available soil water supply, axis 5 – air humidity; a_1, b_1, c_1, d_1, e_1 are the upper boundaries of normalized optimal ranges of environmental factors; a_2, b_2, c_2 d_2, e_2 are the lower boundaries of normalized optimal ranges of environmental factors.

S_1 is the square of the large pentagon, S_2 – that of the small pentagon, S_{ERUC} – the square of the ring-shaped area.

We assumed that the ring-shaped area corresponded to a set of environmental conditions that a conifer needs to reach its highest values of photosynthesis rate during a growing season. The numerical value of the ring-shaped area was taken by us to be equal to the value of the maximum ERUC, the environmental resource utilization coefficient. Changes in the ERUC values for each measurement year were compared to the corresponding annual characteristics of photosynthetic activities, that is, to the absolute seasonal maximum photosynthesis rate (A_{max}), the maximum daily photosynthetic productivity (P_{daily}), and the seasonal photosynthetic productivity (P_{season}). The values of the upper and lower boundaries of the ranges, as the components of the ERUC, were compared with the absolute seasonal maximum of photosynthesis. The results are given in Tables 2 and 3.

Results and Discussion

The values for the ERUC were determined for growing seasons which differed in the level of heat and moisture supply, that is, for 1995 – hot, dry, 1996 – cool, humid, 1998 – warm, humid, and 1999 – hot, dry (Suvorova *et al.*, 2002).

The results of the analyses revealed changes of the ERUC from 9413 to 12775 units in pine, from 11091 to 13359 units in spruce, and in larch from 1697 to 12565 units (Table 2). For pine, the highest ERUC values were observed in the hot, dry year of 1995 that was characterized, however, by high soil moisture content in the early spring; the lowest values were determined for the hot, extremely dry year of 1999. For spruce, the highest ERUC value was observed during the cool,

Table 2. Correlation of the basic indicators of photosynthesis for the conifers with the environmental resource utilization Coefficient (ERUC).

	Year	Seasonal P (mol CO_2 m^{-2} g^{-1})	Daytime P (mmol CO_2 m^{-2} g^{-1})	A max (μmol CO_2 m^{-2} s^{-1})	ERUC
PINE	1995	9.2	121.7	3.73	12,775
	1996	8.7	92.8	3.37	11,639
	1998	7.6	80.1	2.9	9,801
	1999	5.3	55.4	2.01	9,413
	r^2 with ERUF	**0.88**	**0.95**	**0.91**	
SPRUCE	1995	3.1	59.8	3.21	11,500
	1996	6.8	77.2	2.56	13,359
	1998	6.3	68.8	2.49	12,458
	1999	2.8	37.2	1.47	11,091
	r^2 with ERUF	**0.96**	**0.91**	0.31	
LARCH	1995	3.1	56.5	1.77	9,445
	1996	4.9	71	2.34	12,461
	1998	5.5	72.6	2.25	12,565
	1999	2.5	58.2	2.01	1,697
	r^2 with ERUF	**0.87**	**0.96**	0.48	

Note : seasonal P – seasonal photosynthetic productivity, daytime P – maximum daytime productivity of photosynthesis, A max – absolute value of the maximum of photosynthesis rate during the growth period.
From here on, the correlation coefficients in excess of 0.80 are significant when P = 0.90.

Table 3. Correlation of the absolute seasonal maximum of photosynthesis rate for the conifers (A max) with environmental factors on the boundaries of the optimal ranges of the ERUC.

Year	A max, (μmol CO_2 m^{-2} s^{-1})	Upper boundary of ranges: T air, (°C)	Rad. int., (μmol m^{-2} s^{-1})	T soil, (°C)	Moisture reserve, (mm)	Air humidity, (%)	Lower boundary of ranges: T air, (°C)	Rad. int., (μmol m^{-2} s^{-1})	T soil, (°C)	Moisture reserve, (mm)	Air humidity, (%)
PINE											
1995	3.73	23.7	4,279	20.1	123.0	83	12.1	1,373	5.0	62.9	46
1996	3.37	26.2	4,430	18.4	97.6	86	13.1	2,658	8.4	39.0	30
1998	2.90	21.5	3,776	17.5	74.0	99	8.5	1,108	7.0	32.0	74
1999	2.01	22.0	3,145	17.8	84.3	97	7.0	1,285	5.8	39.6	62
r^2 with A max		0.60	**0.95**	0.74	0.72	**-0.82**	**0.90**	0.37	0.08	0.58	-0.57
SPRUCE											
1995	3.21	17.3	3,948	20.2	124.5	99	11.6	665	12.0	55.0	62
1996	2.56	25.8	4,209	17.2	99.0	98	9.0	522	7.9	46.5	36
1998	2.49	26.0	3,455	17.5	84.0	99	4.0	576	0.0	32.0	40
1999	1.47	16.6	4,430	15.0	84.3	92	6.0	620	0.0	39.6	28
r^2 with A max		0.20	-0.51	**0.97**	**0.81**	**0.91**	0.64	0.15	**0.80**	0.59	**0.90**
LARCH											
1995	1.77	22.0	3,101	21.0	109.4	90	12.7	1,196	15.3	38.9	64
1996	2.34	27.5	3,854	20.8	97.6	98	11.8	665	12.8	55.9	55
1998	2.25	30.0	4,253	17.5	74.0	93	10.0	1,772	6.0	47.0	26
1999	2.01	20.5	2,968	15.0	48.0	53	20.0	2,791	12.5	45.6	32
r^2 with A max.		**0.80**	**0.80**	-0.05	-0.16	0.35	-0.37	-0.25	-0.61	**0.92**	-0.40

humid year of 1996, and the lowest value was typical of the extremely dry year of 1999, when this species showed a long-lasting photosynthesis depression, with CO_2 release (maintenance respiration) starting sometimes around midday and continuing on till the end of the daytime. For larch, the largest ERUC value was observed during the warm, humid growing season of 1998. The lowest ERUC value for this species could not be determined sufficiently clearly because in 1999 the larch trees were severely infested by plant pests.

Positive correlation of ERUC with the corresponding annual characteristics of photosynthetic activities listed above appeared to be specific for each coniferous species (Table 2).

In pine, ERUC varied with changes in all the characteristics of photosynthetic activity: the seasonal and daily photosynthesis productivities, and the absolute value of maximum photosynthesis rate in the season (R^2=0.88-0.95). In larch and spruce, ERUC varied with changes in the seasonal and maximal daily photosynthetic productivity (R^2=0.87-0.96). The absolute seasonal maximum photosynthesis rate was found to show a significantly lower correlation (R^2=0.31-0.48), which seems to be caused by a higher lability of photosynthetic activity in these species. Hence the set of conditions (ERUC) under which a maximum level of photosynthetic potential is realized determines the highest level of production potential in coniferous species. This is most conspicuous in pine.

The lowest variability of the ERUC for pine, in 1995-1996 and 1998-1999, was due to the relative stability of the optimal ranges of air temperature and soil moisture (Fig. 2 A). In spruce, the ERUC values remained relatively stable owing to the shift of the lower boundaries of the optimal ranges of solar radiation and air and soil temperatures toward their lower values (Fig. 2 B). The graphical form of the ERUC was found to be the most dynamical in larch - its optimal ranges of factors in some years were either very narrow or very broad. In the physiologically weakened larch trees damaged in 1999, the optimal ranges of environmental factors narrowed to a minimum size (Fig. 2 C). Hence the graphical form and size of ERUC for different species are not the same. This led us to conclude that the complex of environmental resources, which is needed by each species for realization of its highest photosynthetic activities, is not quite the same for all the species. The graphical forms demonstrate that these sets partially overlap, still there are particular differences between them. Therefore, the diagrams reflect the varying needs of species in natural resources as well.

Thus even with the same environment resources, different plant species have different resource usage. This is apparently achieved by every species having its own pattern of environment resource usage through its own inherent form of interaction of regulatory mechanisms. This is consistent with the definition of "niche" by Jiller (1988) according to which "niches" of different species are not fully coincident.

To provide insight into the influence of the individual ERUC elements on the realization of photosynthetic potential we examined the correlation of the upper and lower boundaries of the optimal ranges of environmental factors with the absolute seasonal maximum photosynthesis of the conifers for the same years (Table 3). It was assumed that positive correlation with the upper boundary of the factors indicates that the

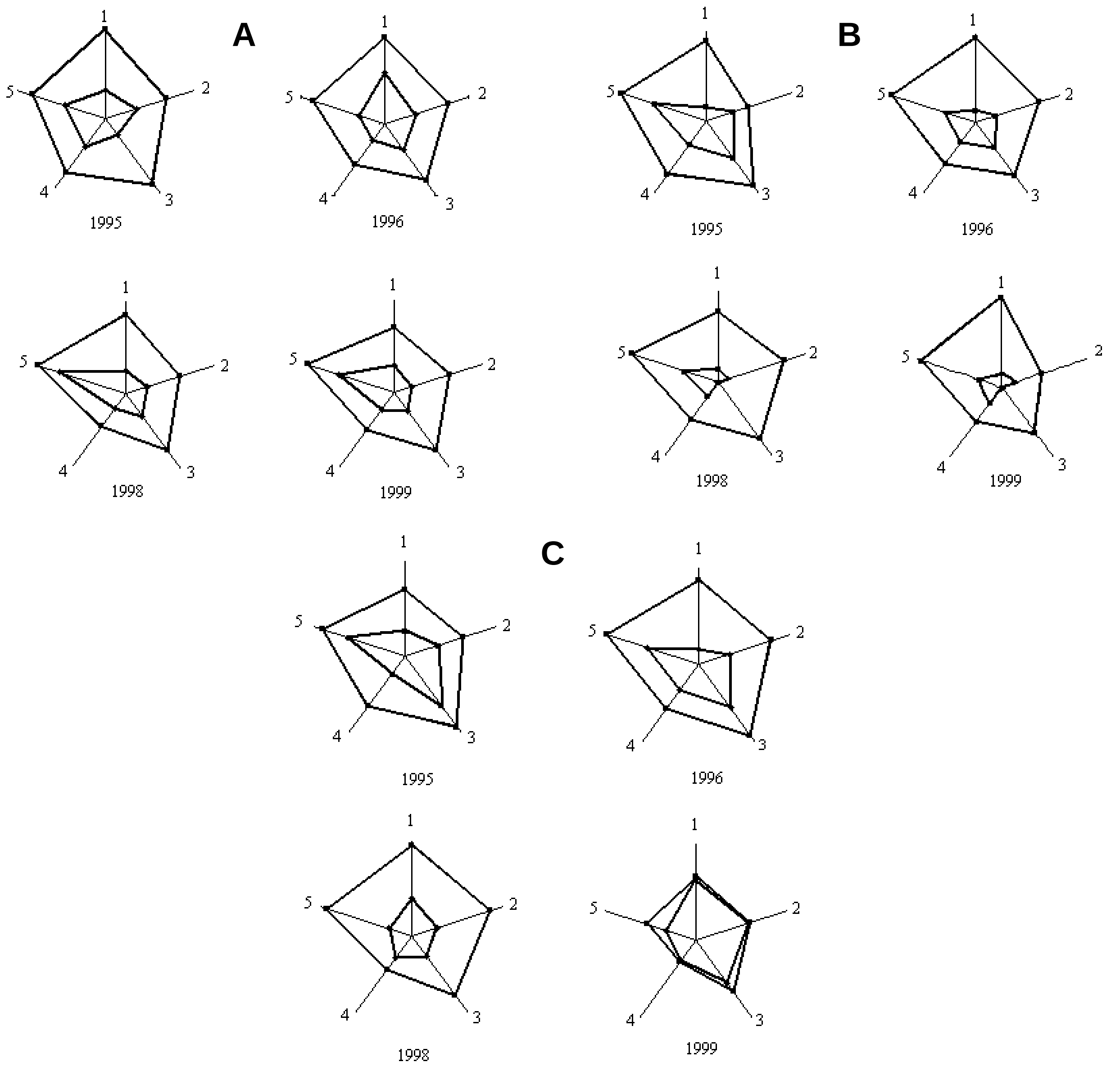

Fig. 2. A – ERUC for common pine, B – for Siberian spruce, C – for Siberian larch.
The axes of the diagrams: 1 – radiation intensity, 2 – air temperature, 3 – soil temperature, 4 – soil moisture reserves, 5 – relative air humidity.

factors are involved largely in enhancing the level of photosynthetic potential. On the other hand, correlation with the lower boundary of the factors was regarded as indicating the factors that impose the greatest limitation on the photosynthetic potential of a given species.

We found that the maximum rate of photosynthesis in pine varies according to the upper boundaries of all the environmental factors with the boundary of the radiation intensity range being especially significant. A reverse dependence is observed when comparing the photosynthesis maximum with the upper boundary of the relative air humidity range. On the lower boundaries of optimum values, the photosynthetic potential of pine is limited by air temperature.

In larch, the absolute seasonal maximum of the photosynthesis rate varies according to the upper boundaries of the optimum for air temperature and the radiation rate. On the lower boundaries of the optima the absolute maximum of photosynthesis in larch is correlated with the boundary of the optimal range of available soil water supply (Table 3).

A high level of absolute maximum photosynthesis in spruce is sustained by the upper boundaries of soil temperature, soil moisture and relative air humidity. On the lower boundaries the changes in photosynthesis are correlated with soil temperature and relative air humidity variations.

The results derived from analyzing the correlation of the absolute seasonal maximum of photosynthesis with the upper and lower boundaries are in agreement with an environmental description of the optimal ranges for each coniferous species recently made by the authors (Suvorova *et al*., 2004). Thus the high degree of correlation between the absolute maximum of the photosynthesis rate and the upper boundary of the radiation intensity range is in good agreement with pine being a light-requiring tree. Correlation of the absolute maximum of photosynthesis with the lower boundary of air temperature corresponds to a high degree of correlation between the maximum daytime photosynthesis rate of pine and air temperature in early spring (Suvorova *et al*., 2002).

In larch, correlation of the absolute seasonal maximum of photosynthesis (A_{max}) with the boundaries of the ranges of air temperature, radiation intensity and moisture reserves implies its ability to assimilate CO_2 at a high rate with optimal soil moisture content over a broad range of solar radiation levels and air temperatures (Suvorova *et al*., 1999).

Correlation of the absolute photosynthetic maximum in spruce with the boundaries of the ranges of soil temperature, moisture reserves and relative air humidity corresponds to its environment requirements for attaining a high level of assimilation activity in its needles during the growth period (Shcherbatyuk *et al*., 1999). Thus the intrinsic correlation of the individual ERUC elements with photosynthesis indicators is in good agreement with the environmental properties of each species.

Conclusion

The ERUC expresses the maximum quantity of consumption of environmental resources needed for a high level of photosynthetic activity of the conifers studied. Optimal conditions of high photosynthetic potential are known to be responsible for high biological productivity of species (Drozdov and Kurets, 2003). Hence the set of conditions where a maximum level of photosynthetic potential is realized determines in coniferous species the highest level of production potential. Practical implementation of these conclusions would involve calculation of the correlations between the ERUC and the parameters of both the photosynthetic and biological productivities of conifers.

The differences in the graphical forms and values of ERUC in pine, spruce and larch can be interpreted as one of the characteristics of co-existence of these species in multi-component plant communities. With the same environmental resources, different plant species have varying combinations of usage mechanisms. This is consistent with the definition of “niche” by Jiller (1988) according to which “niches” of different species are not fully coincident. The results of our analysis made in this paper leads us to believe that the ERUC can be used as one of the quantitative characteristics of the ecological niche of each species and its modification in particular habitats.

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