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Assessment of Scots Pine (*Pinus sylvestris* L.) Respiration at Culmination Stage of Its Current Growth in Forest-Steppe Zone of Pre-Baikal Area

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Abstract—Respiration and growth of vegetative organs of the Scotch pine model trees have been studied at the culmination stage of its current growth in forest-steppe zone of Pre-Baikal area during vegetation periods in 1976–2005. The presence of a close relationship between vegetative organ respiration and the temperature and processes of their growth is the basis of the assessment of respiration, a calculation of the intensity of which is performed per the surface and absolute dry mass (a.d.m.) of these organs. Regardless of the basis for calculating the respiration rate in the studied organs, its value decreases from apical meristems towards the base of organs. The ratio between the total respiration of over- and underground pine organs during its calculation per the surface and a.d.m. was 3 : 2 and almost 2 : 1, respectively. The pine respiration increased approximately two times from the beginning to the end of the observation period (regardless of the base of calculation its intensity), while its average value calculated per the surface and a.d.m. during this period was 32.8 and 36.9 kg CO_2, respectively.

Keywords: Scots pine (*Pinus sylvestris* L.), stem, roots, branches, needle, respiration of a tree
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INTRODUCTION

It is known that it is possible to calculate the productivity of woody plants through reducing the balance between carbonic acid absorbed in photosynthesis and isolated in respiration (Tsel'niker et al., 1993). However, the result of reducing the balance did not always correspond to the value of productivity determined by direct weighting (Kaibiyanen et al., 1999). Therefore, the problem of the "junction" of productivity indices, obtained based on different approaches, also exists currently (Pretzsch, 2009).

In its time, the insufficient degree of study of woody plants was considered a reason for the discrepancy between their productivity discovered by different methods. Indeed, plant respiration was considered for a long time to be a waste of assimilates. However, the understanding of plant respiration began to change in the course of time; it began to be thought of as a competent element of the production process (along with photosynthesis), which emerges in typical conditions of the plant habitat (Semikhatova et al., 2007). However, emphasizing the significance of respiration in the production process, A.T. Mokronosov (1983, p. 57) considers it "nothing other than photosynthesis prolonged into the night or heterotrophic plant tissues and organs."

A number of methodological and technical difficulties arise during the study of woody plant respiration. This is due to the fact that their size and mass considerably increase as a result of the continuous ontogenesis of this life form. Therefore, the assessment of woody plant respiration is conducted at the level of a separately taken plant organism by a chamber method with respiration measurement in separate organs (Tsel'niker et al., 1993; Molchanov, 2007) or at the level of a whole tree (Mori et al., 2010). Total ecosystem respiration (a part of which includes plant respiration) is determined at the level of ecosystem by the "eddy covariance" method (Wang et al., 2006). These approaches can sometimes complement each other (Zha et al., 2007); nevertheless, the selection of criteria for the assessment of respiration for both vegetative organs and for the woody plant in total remains very topical.

The assessment of respiration at the level of woody plants is associated with the determination of the dependence of respiration of separate metamers or organs on the temperature (Tsel'niker et al., 1993; Wang et al., 2006) or other parameters (Vose and Ryan, 2002; Bosc et al., 2003; Zhang et al., 2006). The respiration intensity of the organs can be expressed on various bases, resulting in differences in its integral values. Thus, it was demonstrated that respiration decreased with an increase in the *Larix decidua* larch

stem and branch diameter (calculated per a.d.m.) and increased when calculated per the surface unit (Larcher, 1978). Therefore, the extent to which the base of the respiration intensity calculation influences the integral respiration assessment in woody plants is still not clear; finally, it affects the value of their productivity determined by a balance method. The aim of the study was to assess the integral value of the Scots pine respiration at the culmination stage of the pine-plantation current growth on the basis of previously obtained ecological and physiological peculiarities of its respiratory CO_2 exchange and vegetative organ growth (using the respiration intensities calculated per the surface and a.d.m. of these organs).

MATERIALS AND METHODS

The experimental material was obtained at an experimental area of 2 ha located within the Ust'-Orda Buryat Autonomous District of Irkutsk oblast in the forest-steppe zone of Pre-Baikal area (52°52′ N, 104°41′ E). The climate in the region of observation is extreme continental and is characterized by large daily and seasonal variations of meteorological indices. The average annual air temperature is minus 3°C. The average annual amount of precipitations is 271 mm, and precipitations are very uneven within a year. The humidification coefficient (HC) is 0.6–0.8 (*Atlas Irkutskoi*..., 2004), indicating the insufficient humidification of the region of observation.

The main environmental factors (air and soil humidity, air and soil temperature, and precipitations) were measured according to generally accepted methods directly at the experimental area, and data from the weather station of the Ust'-Orda settlement (located less than 20 km from the area) were used in years of observation when no measurements of environmental factors were conducted. The observations were performed in 1976–2005 at the experimental area, which is highly complete dead-covered I class quality of locality pinery, II, with its subsequent passage to III age class. In this age class, the pine trees enter the culmination stage of the current growth, for which maximal stem increases in radius, height, and volume are typical. At the beginning of studies, the composition, average height, and diameter were 9S1L, 12.1 m, and 18 cm, respectively; at the end, these indices changed and were 10SL, 22.6 m, and 24 cm, respectively.

The respiration of the pine aboveground organs were measured for 1–2 days (more frequently with a periodicity of 7–10) from May to October in 1976–1986. CO_2 gas exchange of the studied pine organs were registered using multi-channel gasometric plant mounted based on Infralit-III gas analyzer (Junkalor, Germany) with a measurement area from 0 up to 0.05% CO_2 in volume. Specially made chambers were used for determining the stem respiration. The respiration of leaves, shoots, and needle were measured in the leaf chambers out of polyethylene film with a wire framework. The volume of stem and leaf chambers was approximately 180 cm^3. CO_2 isolation from chlorophyll-bearing (at the middle of the crown) and non-chlorophyll-bearing (1.3 m) stem surface were registered separately (Zabuga and Zabuga, 1981). The respiration of the studied organs was studied on three preliminary selected trees that grow near a three-tiered tower, the intensity of CO_2 gas exchange in which minimally deviated from the average value.

Radial growth of the stem, branches, and skeletal roots were measured using a microscopic analysis of the wood samples. The wood carvings were cut from a peripheral part of the stem at a height of 1.3 m, the skeletal root (approximately 50 mm in diameter) was cut at a distance 0.5–0.7 m from the root butt, and branches were cut from middle parts of shoots located in the base and at the apex of skeletal branches. In addition, the wood samples of skeletal branch shoots of different ages were additionally taken in the branches of upper, middle, and lower parts of the crown.

Transverse sections, on which morphometric indices of annual growth were determined using an MBI-3 microscope, were made in 1976–1986 and 2003–2005 from the wood samples of the stem, root, and branches on the sledge microtome with a thermo-cooling table (TCT) adapted to it. During the years of observations (1987–2002), indices of the growth-layer structure were measured using a binocular loupe on the wood samples of the studied organs after their appropriate preparation. Annual and average annual ring width (ARW) were used in an analysis of the radial growth of branches (calculated per sample). Each of these values was obtained based on the measurements of the growth ring in four diametrically opposing directions.

The biomass of the studied pine organs was measured according to the method (Molchanov and Smirnov, 1967) using separate methodological recommendations (Semechkina, 1978). The mass of the studied organs was recorded on three (less frequently, five) model pine trees in the middle of autumn, when the dead needle litter is mostly complete. The accuracy of the organ's biomass was kept within ±3–10%.

The mass of needle of different ages was determined in the upper, middle, and lower parts of the crown. In separate years, three average trees, in which three branches from lower and middle parts of the crown were cut and the whole needle was plucked (taking into account its age), were used for obtaining more reliable results on the ratio of the mass of needle of different ages. At the same time, the needle of the upper part of the crown were plucked completely. The needle surface area (as well as the mass) was determined in three parts of the crown according to (Tsel'niker et al., 1993).

The stem mass was calculated based on its volume and wood density. The stem volume was mainly calculated using quadratic parabolic formula (Zakharov, 1961), as well as determined experimentally. The stem

was divided on sections during the determination of the surface area, and the surface area was calculated for each of them according to truncated cone formula. The wood density, which was determined at different height of the stem, was on average $0/40 \pm 0.01$ g/cm^3.

The branch mass was determined directly, separately measuring the mass of young shoots of branches of upper, middle, and lower parts of the crown. The branch and shoot mass was recorded by thick ($d > 1$ cm) and thin ($d \leq 1$ cm) fractions (Semechkina, 1978). The surface area of branches and shoots were calculated using the ratio of surface and mass in middle samples of each fraction in three parts of the pine crown.

The literature data were used for determining the total biomass of the pine roots (Prokushkin, 1982). According to them, the root biomass from the stem biomass was approximately 1/3. At the same time, we demonstrated that the average growth of skeletal roots by the radius and in length was also approximately one-third of the stem growth by the radius and in height during the period of observations. In addition, in 1988, 1993, and 2002–2004, the "root base and skeletal roots with a diameter over 30 mm" fraction (thick skeletal roots) was experimentally recorded on seven model trees; in 2002–2004, "skeletal roots from 30 to 2 mm" (thin skeletal roots) fractions were recorded on three trees. This made it possible to determine the average portions of the biomass of thick and thin skeletal root fractions (46 and 40%, respectively) and consider that the remaining 14% accounted for the portion of physiologically active growth and absorbing roots with a diameter less than 2 mm (thin roots and lobes). The results also indicated the rightfulness of the ratio of pine stem and roots that we accepted. The surface area of the root fraction was calculated through the values of their specific surface mass (expressed in $g_{a.d.m.}/dm^2$) obtained by direct measurements.

The pine respiration was measured taking into account the phenological phases of its development (Elagin, 1976). A statistical treatment of the results was conducted using Excel and Statistica v. 5.5 programs.

RESULTS AND DISCUSSION

The respiration of the Scots pine model tree was represented as a sum of respiration of aboveground and underground organs using L.A. Ivanov's approach (Tsel'niker et al., 1993). The intensity of CO_2 isolation was calculated for different bases (surface and absolutely dry mass (a.d.m.)) using the required ratios of the mass and pine organ surfaces or specific surface density (SSD). It was established that the mass of the stem surface unit increased approximately 20 times from upper parts of the stem towards its lower parts. The thick skeletal branch SSD was significantly higher in the lower part of the pine crown than in the upper part; its value in skeletal roots changed depending on the diameter of their fraction (SSD increased with an increase in the root diameter).

When determining the surface area of the pine crown needle, it was established that the surface density of needle of different ages decreased from the top to the crown base and was 1.02 ± 0.04 $g_{a.d.m.}/dm^2$ in the upper part of the crown, 0.87 ± 0.03 in the middle, and 0.76 ± 0.02 in the lower. The averaged SSD (for the needle of all pine crown) was close to the value of this index for its middle part (0.86 ± 0.05 $g_{a.d.m.}/dm^2$). The average SSD value for thin roots (less than 2 mm in diameter (fine root)) was 0.33 ± 0.02 $g_{a.d.m.}/dm^2$ for the model pine tree.

The change in SSD over the pine skeletal organs caused differences in the intensity of respiration CO_2 isolation calculated per different bases (Fig. 1). Regardless of the base for the respiration intensity calculation, its value decreased from the central shoot to lower parts of the stem (height 1.3 m) and increased from thick to thin skeletal roots. The amplitude of fluctuations among the respiration intensities calculated per a.d.m. of these organs was significantly more than calculated per the surface.

It should be noted that, in the light chlorophyll-bearing cortex layer of upper two-thirds of the stem length, part of respiration CO_2 reassimilated (Zabuga and Zabuga, 1981).Therefore, respiration CO_2 isolation by the stem parts in the crown was measured in light and in a dark chamber in order to take into account the ability of the cortex chlorophyll-bearing layer to reduce CO_2 losses during the assessment of the stem respiration.

The pine stem respiration was determined according to the formula

$$R_s = 10^{-3} R_{1.3}(A_{ncl} + kA_{cl}), \quad (1)$$

where R_s is stem respiration during vegetation, CO_2 kg; $R_{1.3}$ is the intensity of respiration CO_2 isolation by the stem region at height 1.3 m in g/($g_{a.d.m.}$ vegetation) or in g/(dm^2 vegetation); A_{ncl} is the surface or mass of the stem, the cortex of which does not contain a chlorophyll-bearing layer, dm^2 or $g_{a.d.m.}$; A_{cl} is the surface or mass of the stem, the cortex of which contains a chlorophyll-bearing layer, dm^2 or $g_{a.d.m.}$; and k is the CO_2 reassimilation coefficient.

The intensity of the respiration CO_2 isolation of the stem region at a height 1.3 m per vegetation was found on the curve (Fig. 2a), calculating the average air temperature per vegetation. When determining the stem respiration, its intensities (expressed per surface unit) was recalculated per a.d.m. unit using the ratio of mass and surface of appropriate stem regions. The results of a calculation of the stem respiration are given in Table 1. From the beginning to the end of the period of observations, the stem mass and surface changed 2.8 and 3.0 times, respectively, while its respiration changed 2.3 times calculated per surface and 2.5 times calcu-

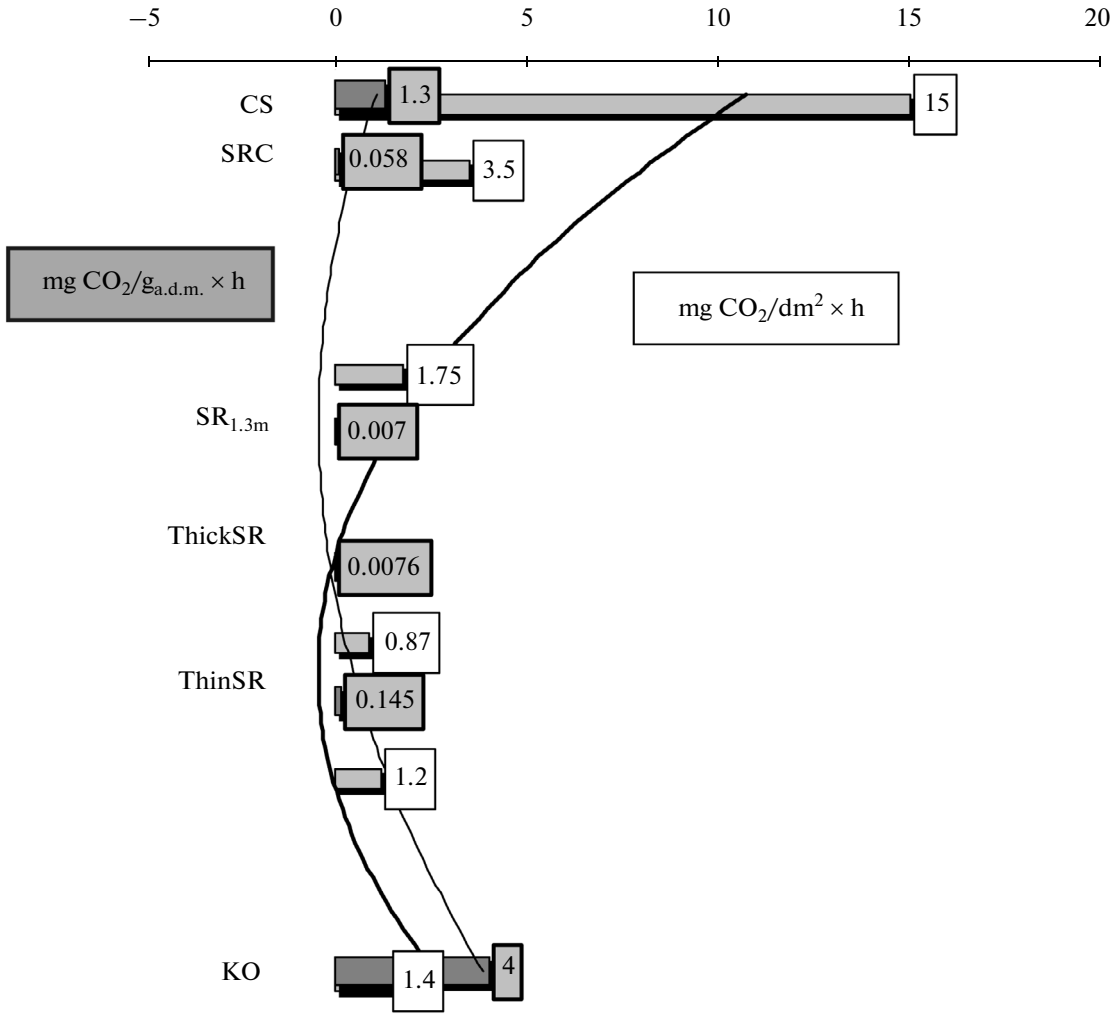

Fig. 1. Respiration intensity of over- and underground organs of the Scots pine. The maximal value of the pine vegetative organ respiration at air temperature 10°C is presented in the figure. The specific surface density of the pine skeletal organs (used in a recalculation of the respiration intensity) is given in the table.

Designations: CS is central shoot, SRC is stem region in the middle of the crown, $SR_{1.3m}$ is stem region at height 1.3 m, ThickSR is thick skeletal roots, ThinSR is thin skeletal roots, and TR is thin roots (fibrils). Respiration intensity calculated per surface and mass is demonstrated on the abscissa axis. Respiration intensity of vegetative organs calculated per dm^2 is shown as a thick line; per $g_{a.d.m.}$ is shown as a thin line.

lated per mass (Table 1). During the period of observations, the stem respiration calculated per surface was 35–48% smaller than that calculated per a.d.m.

The respiration of the pine model tree aboveground part includes not only the stem respiration, but also the crown (branches and needle) respiration. The formula for calculating the branch respiration was as follows:

$$R_b = 10^{-6} K_i^{\mathrm{I(II)}} T \sum_{i=1}^{n=3} (J_i^{\mathrm{I(II)}} A_i^{\mathrm{I(II)}}), \qquad (2)$$

where R_b *is* respiration, CO_2 kg; T is the duration of the vegetation period, days; $K_i^{\mathrm{I(II)}}$ is the physiological activity coefficient; $J_i^{\mathrm{I(II)}}$ is the respiration intensity of the crown branches (either in mg $CO_2/(g_{a.d.m.}$ day) or in mg $CO_2/(dm^2$ day); $A_i^{\mathrm{I(II)}}$ is the mass in $g_{a.d.m.}$ or branch surface in dm^2; i is the lower index for designating the crown part (1 upper, 2 middle, and 3 lower); I(II) is the upper index for designating thin and thick branch fractions, respectively.

The respiration intensity of skeletal branches (consisting of shoots of different ages) was determined according to the dependence of respiration on the width of the annual ring of their growth (Fig. 2b), and the branch respiration intensity, initially calculated per the surface unit, was recalculated per mass unit using the ratios (as in case of the stem). The results of a calculation of the pine crown branch respiration (without growing shoot respiration) are given in Table 2. The respiratory costs of the shoots of the current year of

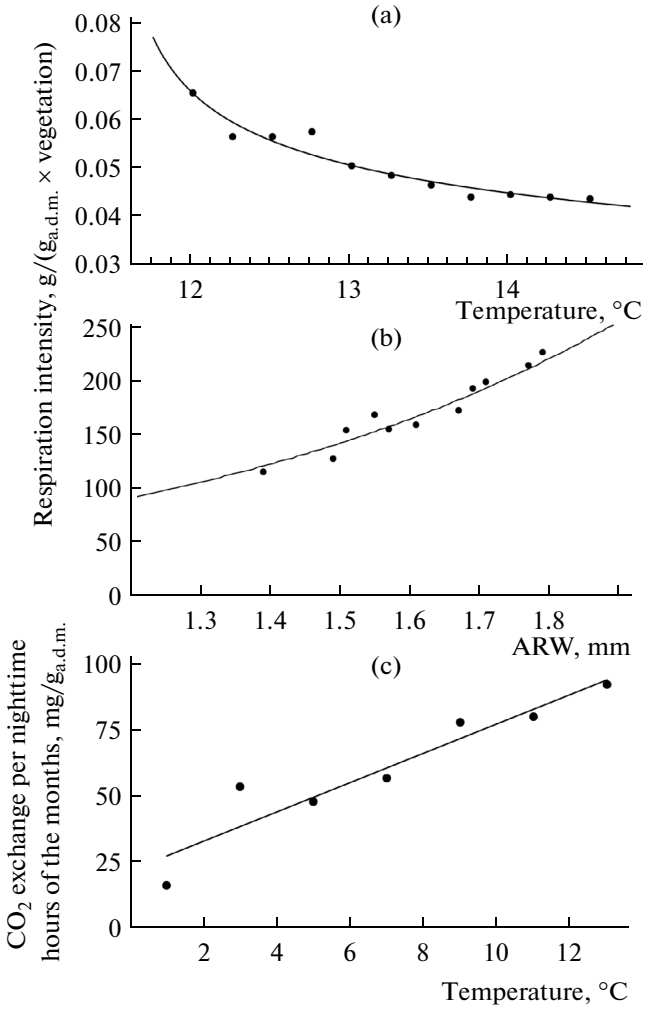

Fig. 2. Dependence of the respiration intensity of the stem region at a height 1.3 m (a) and two-year needle (c) on the air temperature; crown branches on the annual ring width (b).

Designations: Average per vegetation (a) and average per nighttime hours of the month (c) air temperatures are given on the abscissa axis of the figure. ARW is annual ring width (b).

life, the respiration of which constituted from 20 to 30% out of the total respiration of the pine crown branches, were taken into account during the assessment of the total value of the pine crown skeletal base respiration altogether (Zabuga and Zabuga, 2006a).

Within the considered approach, it was obtained that the respiration of the skeletal base of the pine model tree crown (taking into account the respiration of growing shoots) changed from the beginning to the end of the period of observation less than 2 times (both calculated per the surface and per the mass). At the same time, the respiration of the pine crown skeletal base calculated per the surface was 9–14% smaller than that calculated per a.d.m.

The respiration of the pine crown needle was assessed by the results of measurements of the intensity of its nighttime respiration:

$$R_n = 10^{-3}(J_{nb}A_b + J_{na}A_a), \quad (3)$$

where R_n is needle nighttime respiration per vegetation, kg CO_2; J_{nb} is the respiration intensity of needle until July 20 in g $CO_2/g_{a.d.m.}$ or g CO_2/dm^2; A_b is the mass (surface) of needle until July 20, $g_{a.d.m.}$ (dm^2); J_{na} is the respiration intensity after July 20, g $CO_2/g_{a.d.m.}$ or g CO_2/dm^2; and A_a is the mass (surface) of needle after July 20, $g_{a.d.m.}$ (dm^2).

A calculation of total carbonic acid isolation in respiration of the pine assimilating organs was reduced to a determination of the sum of night CO_2 emissions in 2-year needle, for which the temperature dependence of its nighttime respiration (Fig. 2c), the duration of nighttime period, and the average temperature of this period for each month of vegetation were used. A selection of the needle of this age group was caused by the fact that, first, it was distinguished by a considerable portion (18–31%) in total mass of the crown needle and by a positive balance of gas exchange during all vegetation. Second, the values of nighttime respiration intensity in needle of different ages (2 years and older) that have different locations in the crown had almost no significant differences (Zabuga and Zabuga, 2009). The mass (surface) of the needle, which was registered at the end of the last vegetation period, was used in calculations of nighttime CO_2 isolation by the crown needle until July 20; after July 20, the mass (surface) of the needle, which was determined at the end of current vegetation was used, since in this period of vegetation the growth of young needle mostly ended and the mass yellowing of all needle started in the pine under conditions of forest–steppe zone of Pre-Baikal area. Since the mass and surface ratio of needle of different ages for all pine crown was at the average close to one, no differences were obtained in the assessment of its respiration during the use of its intensities represented to different bases (Table 2).

When assessing the respiration of thin and thick skeletal roots, it was assumed, first, that the stem and skeletal roots are covered by a lateral meristeme, which annually develops annual growth rings similar in their organization, and, second, the presence of a close relationship between the width of the annual ring growth and total carbonic acid isolation from the stem surface. Therefore, it was assumed that such a relationship is also typical for skeletal roots (Zabuga and Zabuga, 2006b). The respiration of the pine skeletal roots was determined according to the formula

$$R_{cr} = 0.0023(J_{crh}A_{crh} + J_{crt}A_{crt}), \quad (4)$$

where R_{cr} is the respiration of skeletal roots, kg CO_2; J_{crh}, J_{crt} is the intensity of CO_2 isolation by thick and thin skeletal roots, respectively, in mg/($g_{a.d.m.}$ h) or in mg/(dm^2 h); A_{crh}, A_{crt} is the surface or mass of thick and thin skeletal roots, dm^2 or $g_{a.d.m.}$; and 0.0023 is the coefficient that takes into account the physiological activity of skeletal roots, kg CO_2/(mg CO_2 h).

Table 1. Stem and skeletal root respiration CO_2 isolation in Scots pine

Model tree-stem diameter at a height of 1.3 m, cm	Respiration intensity of the stem regionat a height 1.3 m, mg CO_2/dm^2 h	Stem surface, dm^2		Stem mass, $g_{a.d.m.}$		Stem respiration CO_2 isolation in kg calculated per	
		chlorophyll-bearing	non-chloro-phyll-bearing	chlorophyll-bearing	non-chloro-phyll-bearing	surface	mass
18	3.6	283	121	39714	29786	5.7	7.7
19	3.3	334	145	50000	37500	6.1	8.8
20	3.9	410	176	62057	46543	8.9	13.0
21	3.6	472	203	71886	53914	9.5	13.9
22	3.2	575	247	87371	65529	10.2	15.0
23	3.2	680	294	104057	78043	12.1	17.9
24	3.0	780	335	120686	90514	13.0	19.4
Model tree-stem diameter at a height of 1.3 m, cm	Intensity of thin and thick skeletal root respiration, mg CO_2/dm^2 h	Skeletal root surface, dm^2		Skeletal root mass, $g_{a.d.m.}$		Skeletal root respiration CO_2 isolation in kg calculated per	
		thick (base and roots witha diame-ter of ≥30 mm)	thin with a diameter from 2 up to 30 mm	thick (base and roots with a diameter of ≥30 mm)	thin with a diameter from 2 up to 30 mm	surface	mass
18	1.1/0.9	60	900	7500	6500	2.4	2.1
19	1.0/0.9	110	1410	11600	10000	3.5	3.0
20	0.9/0.7	140	1780	14800	12900	3.9	3.4
21	1.3/1.1	150	2080	17200	15200	6.6	5.9
22	0.9/0.8	200	2560	21400	18500	5.7	4.9
23	0.9/0.8	230	2980	25500	21800	6.6	5.8
24	1.8/1.5	250	3440	29200	25000	12.7	11.3

The results of a calculation of the skeletal root respiration are given in Table 1. During the period of observations, the value of the skeletal root respiration calculated per the surface increased more than 5 times; calculated per the mass, it increased 4.5 times. As opposed to stem respiration, the skeletal root respiration (when calculating its intensity per the surface) was 12–17% larger than per a.d.m.

When assessing the thin root respiration, we relied on literature data on its intensity measured in the Scots pine in the subzone of southern taiga (Tsel'niker et al., 1993). At the same time, the influence of the so called "concentration" factor on the respiration intensity of thin roots were taken into consideration (Vose and Ryan, 2002; Tsel'niker, 2005). The respiration of thin roots was discovered according to the formula

$$R_{fr} = K_{fr}A_{fr}, \quad (5)$$

where R_{fr} is the respiration of thin roots, kg CO_2; A_{fr} is the mass and surface of thin roots, kg a.d.m. or dm^2; and K_{fr} is the coefficient. When calculated per the mass, the K_{fr} value was 1.36 kg $CO_2/g_{a.d.m.}$; per surface, 0.45 kg CO_2/dm^2.

The assessment of thin root respiration was conducted based on the averaged value of its intensity and average (for the whole mass of the pine thin roots) its ratio with the surface of thin roots. No differences in integral values of the thin root respiration either calculated per the surface or calculated per the mass were obtained with such an approach. According to the calculations, the values of the pine thin root respiration for the model pine trees with the stem diameter 18, 19, 20, 21, 22, 23, and 24 cm at a height of 1.3 m per vegetation were 4.2, 5.4, 6.4, 7.2, 8.6, 9.9, and 11.3 kg CO_2, respectively.

As a result, it was obtained that the respiration of the model pine tree at the culmination stage of its current growth was on average 36.9 kg CO_2 calculated per the mass and 32.8 kg CO_2 calculated per the surface. The pine model tree respiration increased from the beginning to the end of the period of observations approximately two times, regardless of the base for the

Table 2. Crown respiration CO_2 isolation in Scots pine model tree

Stem diameter at a height of 1.3 m, cm	Branch surface in three parts of the crown, dm^2			Branch mass in three parts of the crown, kg			Crown needle mass and surface, kg/m^2*
	upper	middle	lower	upper	middle	lower	
18	92	485	477	0.9	5.1	5.8	12.7/146.5
19	95	610	500	0.9	6.5	6.5	10.4/119.9
20	163	769	583	1.6	7.7	7.7	13.8/159.1
21	210	869	779	2.0	8.9	10.4	14.8/170.4
22	313	858	916	2.5	9.5	11.7	14.2/162.9
23	269	838	1027	2.7	9.6	12.7	14.2/162.9
24	301	1006	944	2.9	11.1	12.0	14.0/161.4

Stem diameter at a height of 1.3 m, cm	CO_2 isolation in three parts of the crown calculated per branch surface, mg/days			Branch respiration calculated per surface, kg CO_2	CO_2 isolation in three parts of the crown calculated per branch mass, mg/days			Branch respiration calculated per mass, kg CO_2	Crown needle respiration, kg CO_2
	upper	middle	lower		upper	middle	lower		
18	2517.6	10903.4	8356.3	2.2	3184.1	12222.5	9454.3	2.5	5.3
19	2551.5	13660.8	8574.7	2.5	3116.3	14763.58	9678.7	2.8	3.8
20	4364.3	17476.5	9920.4	3.2	5133.4	19262.1	11300.4	3.6	5.2
21	6257.7	19600.8	13184.4	3.9	6415.1	21360.0	14925.6	4.3	5.1
22	8628.3	18949.0	15765.8	4.4	9159.6	20852.1	17520.4	4.8	6.1
23	7184.6	18315.7	17861.6	4.4	8635.2	20057.6	19597.7	4.9	6.2
24	8189.9	22214.3	16238.8	4.7	8695.7	24047.5	18927.2	5.2	5.7

* Needle mass on the left, surface area of the crown needle on the right.

calculation of its intensity. The pine model tree growth in height and diameter was 10.5 m and 6 cm, respectively, which caused the change in the surface and mass of vegetative organs several times (Tables 1 and 2). The ratio between the respiration of above- and underground pine parts when calculated per the surface was 3 : 2; per the mass it was almost 2 : 1 (Fig. 3). The respiration ratio for "crown : stem" and "skeletal roots : thin roots" calculated per the surface was 1 : 1 and 2 : 3, respectively; when calculated per the mass, the same ratios were the same and were 2 : 3.

The respiration intensity of assimilating organs of coniferous woody plants is usually calculated per a.d.m. unit; while for their skeletal parts it is per the surface unit (Tsel'niker et al., 1993; Molchanov, 2007). This is caused by the fact that it is easier to measure the mass for the needle and the surface for skeletal organs. Regardless of the fact on which base the respiration intensity was calculated, the assessment of its integral value was conducted on similar algorithms, which require, on the one hand, information about the mass or surface of the studied organs and, on the other hand, information about the rate of their respiration.

At the beginning of the observation period, aboveground and underground skeletal organs of the pine model trees were already characterized by a considerable length and had a larger surface and mass, which increased several times more at the end of the observation period. The ratio of the mass and surface of the Scots pine studied organs, which was expressed by a specific surface density index, considerably changed primarily throughout its skeletal organs (Fig. 1). Due to the annual generation of annual rings and the increase in the growth of biomass (deposited in the wood of aboveground and underground skeletal pine organs), their SSD increased in the direction from apical meristems towards the root collar. The ratio of the mass and surface has relatively small value in the youngest and functionally active parts of these organs, such as thin branches and thin skeletal roots. Therefore, the intensity of respiration CO_2 isolation when calculated per different bases was maximal in young parts of the pine skeletal organs (Fig. 1), characterized by a high growing activity of the complex of living external tissues (Zabuga and Zabuga, 1985). The SSD value of the Scots pine needle obtained in conditions of forest-steppe zone of Pre-Baikal area is in agree-

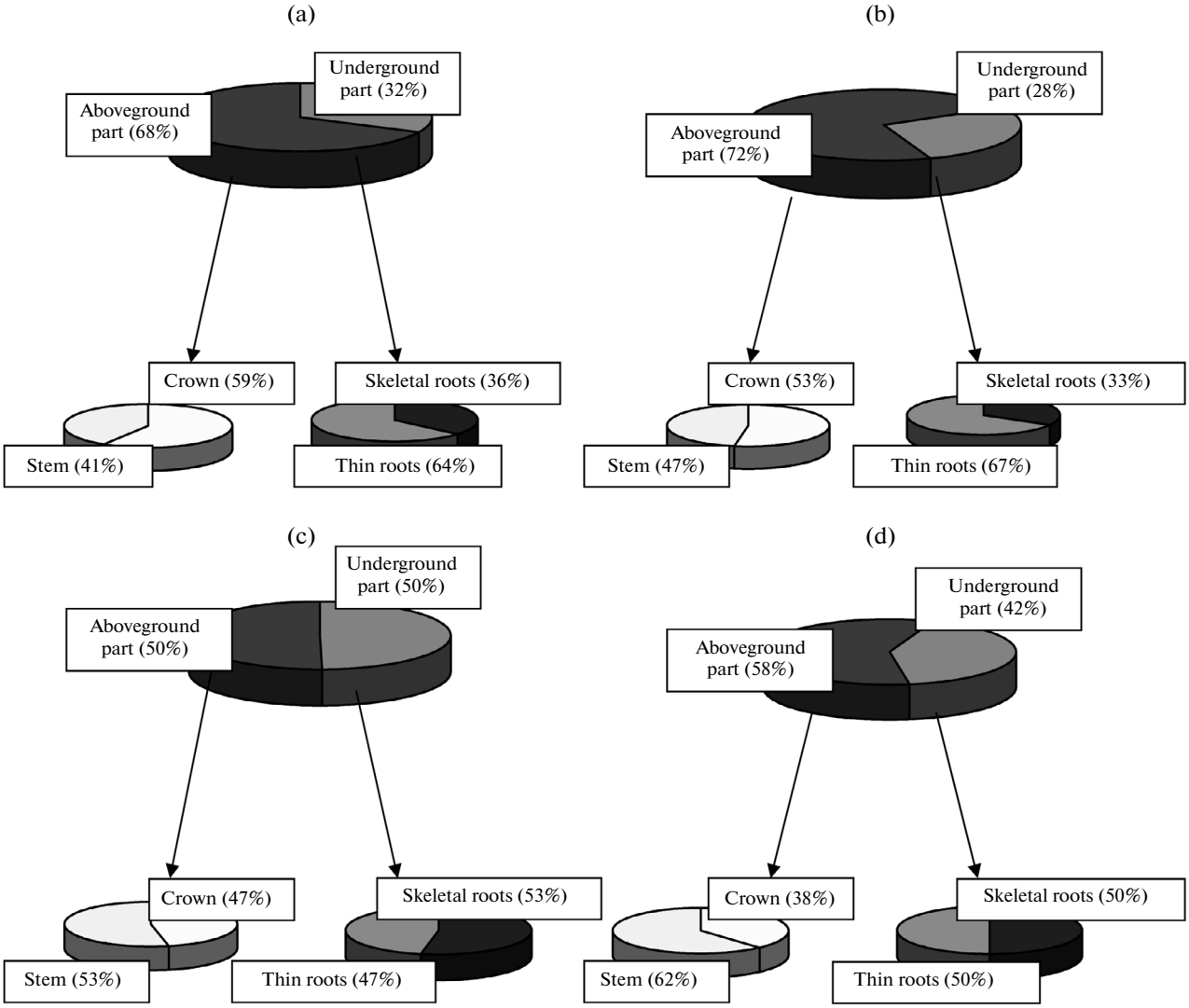

Fig. 3. Ratio of the Scots pine aboveground and underground organ respiration in portions calculated per the surface (a, c) and mass (b, d) with stem diameter at heights of 1.3 m 18 cm (a, b) and 24 cm (c, d).

ment with the literature data both for the studied pine species (but of a different age and habitat) (Bobkova, 2005) and for other species (*Pinus ponderosa*) (Nagel and O'Hara, 2001).

The respiration intensity of the stem and crown needle was determined according to its dependence on the temperature. The temperature dependence of the stem and crown needle respiration, constructed based on data on measuring its intensity and air temperature (calculated for different time periods), differed by the type of its course (Figs. 2a and 2c). According to the literature data (Saveyn et al., 2008), the temperature dependence of respiration is not the only instrument which can be used during its integral assessment. According to these authors, dependences with other factors controlling the rate of respiration processes can be used during its integral assessment. Growth processes should be first attributed to such factors that considerably change the respiration intensity. Thus, it was demonstrated for the stem region at height 1.3 m (Zabuga and Zabuga, 2006b) that the dependence of the respiration intensity on the width of the annual ring provided close values to those determined by the temperature dependence. As was found, a close relationship of respiration with the processes of radial growth was typical not only for the stem, but also for the pine branches (Zabuga and Zabuga, 2005), which made it possible to use it for an integral assessment of respiration of the latter (Fig. 2b). Such a relationship of the radial growth with a woody plant stem and branch respiration was also registered in other conifers (for example, *Pinus taeda* L. (Moore et al., 2008), *Licea abies* (L.) Karst. (Acosta et al., 2010). The relationship of respiration and radial growth was used for the assessment of the Scots pine skeletal root respira-

tion and the determination of its integral value by a calculated method (Zabuga and Zabuga, 2006b).

The fact that a reassimilation phenomenon was taken into account in the algorithm of calculation of the stem respiration value was a specific feature of the method of its assessment. As was demonstrated previously (Zabuga and Zabuga, 1981) and recently (Wittmann and Pfanz, 2008), the cortex of aboveground skeletal organs of woody plants (which contains a chlorophyll-bearing layer) reassimilates part of respiration CO_2 in the light. In the pine stem, the reassimilation capacity of the cortex pigment layer decreased from the top towards the stem regions in lower part of the pine crown (Zabuga and Zabuga, 1981). In natural conditions (that is, without a dark chamber, which was used in studying of CO_2 reassimilation), the intensity of respiration CO_2 isolation by the central shoot or by the stem regions in the crown was closer in value to the intensity of respiration CO_2 isolation for the stem region at a height 1.3 m (in the cortex of which there were no pigments). Nevertheless, the pine stem regions in the crown (regardless of whether they were covered by a dark chamber or not) almost always had a higher respiration intensity when compared with the stem region at a height 1.3 meters. Therefore, the final value of the stem respiration in the adult *Chamaecyparis obtusa* (Sieb. et Zucc.) Endl. tree depended on the amount of the stem regions, the respiration intensity of which was used in the model of its integral value calculation (Araki et al., 2010).

It is known that thin roots of woody plants consist of several fractions, each of which has typical structural and functional peculiarities (Prokushkin and Kaverzina, 1988, pp. 22–24). However, a determination of the thin root respiration is to a lesser extent attached to the fractional composition (Lipp and Andersen, 2003), while it is attached to a larger extent to their diameter (Vose and Ryan, 2002; Jia et al., 2010). As was found, the intensity of the thin root respiration is caused by the method of its determination, associated with the extraction of roots from the soils and measuring respiration at atmospheric CO_2 concentration (lower than in the soil). The measurement gave overestimated intensities of the respiration CO_2 isolation by thin roots in conditions of lower concentration of carbon dioxide in the air; with an increase in CO_2 concentration in the soil, the *Pinus radiata* root respiration considerably decreased in the experiments with sodium hydrocarbonate solution (Sands et al., 2000). Therefore, a number of authors (Vose and Ryan, 2002; Tsel'niker, 2005) corrected the thin root respiration measured at the atmospheric CO_2 concentration (decreasing its value several times). The pine thin root respiration was assessed using the averaged value of its intensity measured in the Scots pine (Tsel'niker et al., 1993).

The considered algorithms, despite their peculiarities, allowed us to calculate the respiration value for both separate organs (Tables 1 and 2) and the model Scots pine tree in general at the culmination stage of its current growth (Fig. 3). It was found that, during the observation period, the portion of the stem respiration in its total average value remained the most considerable (regardless of the calculation base) and was 29 and 37% when calculated per the surface and mass, respectively. When averaging the results obtained, the portion of aboveground organ respiration was higher than of underground organs of the Scots pine, regardless of the base for a calculation of its intensity). On the contrary, when assessing the pine plantation (*Pinus ponderosa*) respiration by the method of vortex covariance, the root respiration exceeded the respiration of aboveground organs (Xu et al., 2005).

According to the obtained assessments (Fig. 3), the stem respiration at the beginning of the observation period was smaller than the crown respiration both calculated per the mass and calculated per the surface; at the end of the observation period, it was on the contrary larger. The carbon flow (caused by stem respiration) was obtained in 50-year pine plantation (Finland) by vortex covariation; it did not exceed 25% from the respiration of the aboveground part (Zha et al., 2007). However, the stem respiration intensity values calculated per the surface (measured by a chamber method in the same pine plantation in 2001–2003 (Zha et al., 2004)) were quite close in value to those that were determined in our studies.

According to the results in Tables 1 and 2, the pine stem respiration exceeded the crown branch respiration regardless of the base for its intensity calculation throughout the entire study period. It was consistent with one literature data (both for coniferous (Janouš et al., 2000) and evergreen broad-leaved woody plant breeds (Xiao Fu-ming et al., 2006) and was not consistent with other data (Xu et al., 2005; Miao et al., 2006).

As was previously demonstrated (Zabuga and Zabuga, 1985), the respiration and growth rates decreased in drought conditions; however, the multiplicity of the respiration intensity decrease was considerably smaller than radial growth. During the specific index calculation (used in the algorithm of the skeletal root respiration assessment), it resulted in a considerable amount of the respiration CO_2 calculated to a millimeter of the annual ring growth as compared with other integer values of the stem diameter. As a result, the development of the pine biomass in droughty conditions "was more expensive" from the point of view of respiratory costs when compared with vegetations when such environmental conditions were not registered. Thus, the isolation of the skeletal root respiration CO_2 was characterized by high values (Table 1), which was caused by the influence of draughty conditions of this vegetation.

The thin root respiration exceeded the skeletal root respiration at the beginning of the observation period

(Figs. 3a and 3b). Portions of thin and skeletal root respirations became close in value by the end of the observation period (Figs 3c and 3d). The intensities of the Scotch pine thin root respiration that we used (Tsel'niker et al., 1993), even taking into account their correction (Tsel'niker, 2005), exceeded the maximum of the white pine thin root respiration rate by almost two orders (Fahey and Yavitt, 2005). However, carbon flow caused by the root system respiration (quite comparable with a similar flow in the *Pseudotsuga menziesii* plantation) was obtained when passing from the respiration assessment at the level of model tree to an approximate respiration assessment at the level of the pine plantation (Lalonde and Prescott, 2007).

Despite the fact that, at present, tree respiration is usually measured and assessed through ecosystem carbon flows using a method of eddy covariance, the necessity of measuring the respiration of separate organs and parts of trees in chambers arises within this approach (Wang et al., 2006; Zha et al., 2007). Moreover, the respiration of not only separate organs or parts of a tree, but of a whole woody plant, can be registered by a chamber method (Mori et al., 2010). Final values of respiration of its separate organs and parts are included in the integral value of the tree respiration in the ecosystem approach; it is presented as a carbon mass calculated per the surface unit per year. In this case the problem of the base for respiration intensity calculation per the organ surface or mass (which exists during the study of respiration at the level of biosystem of woody plant organism) becomes not so topical. When studying the whole tree respiration using a large chamber, the value of its intensity is expressed in $\mu mol\ CO_2/tree^{-1}\ s^{-1}$ (Mori et al., 2010), and the calculation base per the mass or surface also loses its significance.

Finally, assessing the whole tree respiration ($kg\ CO_2/tree^{-1}$ $vegetation^{-1}$) using the respiration intensities of vegetative organs calculated per different bases, it was obtained that the calculation base caused the most considerable differences in the skeletal organ respiration and almost did not influence its value in assimilating and thin roots (lobes) in the Scots pine.

CONCLUSIONS

The integral assessment of the Scots pine model tree respiration (expressed by the sum of respiration values of its vegetative organs) was associated with a direct measurement or calculation of the intensity of this process, using the ecological physiological dependence of respiration and growth or temperature dependence of respiration. The respiration assessment was conducted by its intensity in vegetative pine organs calculated per the surface or absolutely dry mass. When calculating the respiration per different bases, we relied on appropriate ratios of the mass and surface of pine organs, or specific surface density. The largest values of specific surface density were in the stem regions in close proximity to its base; the smallest were found in the needle and thin roots (fibrils). A change in the specific surface density along the length of pine skeletal organs determined the differences in respiration intensity and total value calculated per different bases. The most considerable differences of the latter (up to 50%) were obtained in the case of the pine stem, while in its other skeletal organs (branches and skeletal roots) similar respiration differences were smaller (no more than 20%). The average whole tree respiration values for the observation period (which falls on the culmination stage of the pine plantation current growth), obtained using its intensities expressed per different calculation bases, differed even less (up to 15%). Regardless of the calculation base, the respiration of pine aboveground organs remained higher than that of underground organs, while the thin root respiration in underground organs exceeded the skeletal root respiration.

A comparison of the results obtained for the Scots pine with the literature data (in which the assessment of woody plant respiration was given) made it possible to establish both correspondence and divergence in the distribution of respiratory costs between vegetative organs, as well as above- and underground parts of trees. It should be noted that the pine respiration assessment conducted at the level of a model tree biosystem was compared with literature data, including assessments obtained at the ecosystem level. It was found that respiration intensity of the stem at a height 1.3 m calculated per the surface (close in value to the respiration intensity measured in forest-steppe zone of Pre-Baikal area) was previously obtained by a chamber method close by the age of Scotch pine trees growing in Finland. However, a portion of the stem respiration in a total respiration of the aboveground part (considerably smaller when compared with a similar value found in our studies) was later obtained in the same trees by the method of vortex covariance; apparently it is caused by differences in the aboveground part at the considered levels of the living organization. The problem of using the base for calculating the respiration intensity in the ecosystem approach or when using a large chamber in which the woody plant was placed entirely has lost its topicality, since the whole tree respiration became part of the CO_2 flow in the studied system and an assessment of respiration components of the tree itself has required additional measurements.

Thus, different bases for the respiration intensity calculation were the most important for assessing the stem respiration when compared with other vegetative organs or the whole pine tree. The assessment of the Scots pine respiration at the level of woody plant biosystem and its comparison with respiration assessments of the same and other woody plant species, including those obtained at the ecosystem level, demonstrated that there were considerable differences

sometimes. It was concluded that the necessity of further studies and developing algorithms for a quantitative assessment of the autotrophic respiration of woody plants remains topical.

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