Eurasian J. For. Res. 14-1: 29-37 , 2011

Correlation of Photosynthesis and Water Regime of *Pinus sylvestris* L. Under Extreme Environmental Conditions of Pre-Baikal Area

KOPYTOVA Lidia D.*, OSKOLKOV Vladimir A.

Siberian Institute of Plant Physiology and Biochemistry,
Siberian Branch of Russian Academy of Sciences
132, Lermontov st., Irkutsk, 664033, Russia

Abstract

The paper discusses variations in the photosynthesis and water regime for *Pinus sylvestris* L. under extreme conditions of the forest-steppe zone of the Irkutsk Region.

The daily cycle of *Pinus sylvestris* L. is characterized by variations in net-photosynthesis, which reaches a maximum in the early hours, with a simultaneous decrease of gas-exchange intensity and transpiration. This is evidence of the substantial role the stomata plays in the regulation of these processes. The air temperature ($r = -0.65 \pm 0.05$, $n = 12$) is the principal negative factor for carbon dioxide gas exchange. The intensity of transpiration is determined by the level of solar radiation coming into the biocenosis. Insufficient soil moisture, and absolute air humidity ($r = 0.70 \pm 0.04$, $n = 12$) play a very important role in the processes of gas exchange and transpiration, together with such factors as cool cloudy weather.

Therefore, with the solar radiation absorbed by the needles and the elevated air temperature, we observed not only an increase in air humidity in the sub-stomata cavities, but also an increase in the concentration of carbon dioxide in the mezophyll of the needles. Variations in the temperature of the needles provoke an increase of transpiration and the decrease in the intensity of gas exchange. In this case, gas exchange is negatively impacted by the re-assimilation of carbon dioxide discharged in the process of respiration. This dependence is seen from the graphics characterizing the dependences of gas exchange and transpiration upon variations of solar radiation and temperatures. Hence, under extreme conditions, the stomatal mechanism acquires a dominant importance and performs an adaptive function.

Key words: photosynthesis, transpiration, moisture of needles, stoma, water deficiency

Introduction

Sufficient moisture is known to be one of the parameters controlling photosynthesis. Water consumption in vegetative communities takes place at the expense of transpiration. Investigations of both CO_2-gas exchange and transpiration have been conducted over several decades, but the Relationship between these two processes is still being investigated. Experiments have shown that plants of different ecological groups are characterized by substantial differences in all the parameters of water regime, each possessing different, complex adaptive potentialities (Drozdov and Kurec 2003; Berry, Bjorkman 1980). This affects the intensity of their CO_2-gas exchange (Brim 1991; Dang *et al*. 1997). Xerophytes are characterized, as a rule, by a reduced transpiration and gas exchange intensity as compared to mezophytes (Lir *et al*. 1974; Sleicher 1970). At the same time, they possess more efficient adaptation mechanisms, and hence:

– maintain the activity of their photosynthetic apparatus under the conditions of insufficient soil moisture (Pelah *et al*.1995; Vu *et al*. 2001; Zwiefel *et al*. 2007);

– preclude the development of structural changes in the assimilation apparatus (Eastman and Camm 1995);

– do not reduce their physiological processes (Drozdov and Kurec 2003) and do not slow tree growth (Dang *et al*. 1997).

It has been demonstrated that a set of principal factors, which determine the intensity of gas exchange characteristic of pine under forest-steppe conditions, includes not only the level of solar radiation but also soil moisture (Singh and Sasahara 1981; Suvorova *et al*. 2005a; Khalil and Grace 1993; Balaur *et al*. 2009). Under these conditions, water deficiency is the parameter that reflects the adaptive shifts in the balance of water available from the soil and the active fraction that is transpired by the needles (Foyer *et al*. 1990; Sudachkova *et al*. 2002; Zwiefel *et al*. 2005).

This study investigated the dependence that exists between the net-photosynthesis of *Pinus sylvestris* L. and conditions of the water regime, as well as the influence of extreme external environmental factors of the Pre-Baikal area forest-steppe zone.

Materials and Methods

The experimental site is located in the

(Received; Feb. 4, 2011: Accepted; June 1, 2011)
∗ Corresponding author: vosk@sifibr.irk.ru

Olkhon–Priangarsky pine-forest-steppe district (Pre-Baikal area), in the eastern part of the Irkutsk sub-mountain depression (Fig. 1). It is mainly pine forests with some Siberian larch (*Larix sibirica* L.), birch (*Betula pendula* Roth) and aspen (*Populus tremula* L.). The site is about 80% forest (Vashuk *et al*., 1997). The soil is grey forest soils belonging to the long-season permafrost type (The USSR Map of Soils…, 1988). The experimental site is characterized by high-density dead soil cover of the pine forest, yield class I.

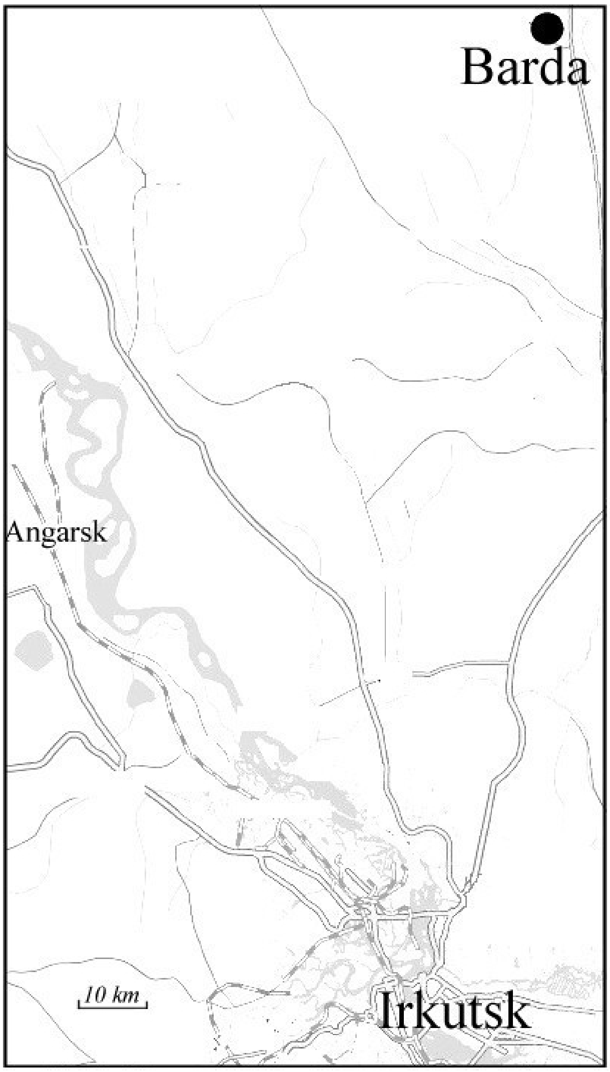

Fig. 1. Map-schema of experimental site.
(show black circle; Pre-Baikal area;
N52°53'38.4" E104°25'0.5" ; scale 1:10,000)

The climate of the site is mainly Siberian anticyclone. On the whole, the climate is sharply continental and is characterized by high level of insolation. The average annual temperatures vary from –1.1°C to –3.0°C; the average temperatures are –30°C in January, and +17°C in July. The area is characterized by low relative air humidity, insuficient precipitation (the average total annual precipitation is 270mm) that is extremely unequal in distribution and has some intervals during the vegetation period that the reserves of available soil moisture approach wilting moisture conditions.

Pinus sylvestris L. (a local species of Scotch pine) was the object of our investigation. This species is known for its high tolerance with respect to water availability, which allows it to grow both in marshes and dry soils (Lir *et al*. 1974; Sen'kina 2002; Sperry and Tyrel 1990). Despite the fact that moving water from the soil to the needles is impeded by substantial resistance in the trunk (Robonen *et al*., 2002), pine needles are capable of withstanding very high (sub-lethal) levels of water deficiency (Sleicher 1970; Pelah 1995). These peculiar water regime properties distinguish the local pine as a representative of euxerophytes (Genkel 1982).

During the vegetation period, the following water regime parameters were investigated: transpiration intensity, water deficiency, moisture content, water-absorption capacity of the needles. Air moisture inside and outside the assimilation chambers was measured with a "Volna-2" hygrometer. Water deficiency in the needles (percentage of damp weight) was determined by saturation in wet chambers for 4 hours at 20°C (Sleicher 1970).

The water potential was measured by the method of refractometry (Maximov 1952; Caff and Carr 1964). The method is based on simultaneous comparisons of the cell sap with sucrose solutions of various concentrations. Correlations of densities of the sap and of sucrose solution determines the water potential.

The degree of stomata openness was evaluated by replicating pieces of needles by microscopic method (Davydov 1991). It was determined that there were two states of stomata: open and closed. Solar Radiation is the main factor that provokes the opening of the stomata. Light influences the stomata both directly and via the CO_2 gradient, which arises between sub-stoma cavities and the external air during photosynthesis. The environmental temperature determines the degree of openness of the stomata indirectly – via variation in the conditions of evaporation and metabolism of CO_2 (Baranova, 1985; Spence, 1987).

The gas-exchange intensity for CO_2 and for transpiration was measured simultaneously on intact needles of different age collected in course one year. They were taken from the twigs of middle part of the southeastern side of the tree crown were taken triple repetitions. The twigs were placed into cylindrical polythene chambers having a wire frame (diameter – 10cm, length – 20cm). The air passing through the assimilation chamber (rate 80 l/h) was split into two flows, one of which was used to determine the intensity of photosynthesis, the other to determine the intensity of transpiration. The concentration of CO_2 in the air and the content of water vapors were determined with a infra-red gas-analyzer (Infralit 4, GDR) (Suvorova *et al*. 2009). The intensity of photosynthesis (mg CO_2 /g*h) and the intensity of transpiration (g H_2O/g*h) were computed per unit of the needles dw.

Results

The results of our experiments showed that during the day Pinus sylvestris L. has two or more increases and decreases of net-photosynthesis with the maximum increase in early hours of the day. During periods of optimum humidity, it is possible to observe – but rather seldom – one-maximum curve of the process.

Figure 2 shows the data obtained under the soil moisture values close to optimum ones. Under these conditions, there is a high level of correlation (r = 0.75±0.06, n = 12) between the daily dynamics of photosynthetic activity and transpiration of the needles. Morning maxima of these processes do not coincide, since the intensity of transpiration reaches the largest values 1–1.5 hours after the corresponding maximum of photosynthesis. No dependence of transpiration on stomata activity in the morning hours was seen.

In the afternoon hours, a decrease of moisture content was accompanied by a decrease in the CO_2-gas exchange rate (Fig. 2). A further parallel decrease in photosynthesis and transpiration intensity was not related to changes in the degree of stomata openness.

The most probable cause of the simultaneous reduction in intensity of these processes is the shortage of transpired water. This results in a decrease in transpiration and an increase in the temperature of the needles, which provokes an increase in part of respiration in the value of visible photosynthesis (Foyer

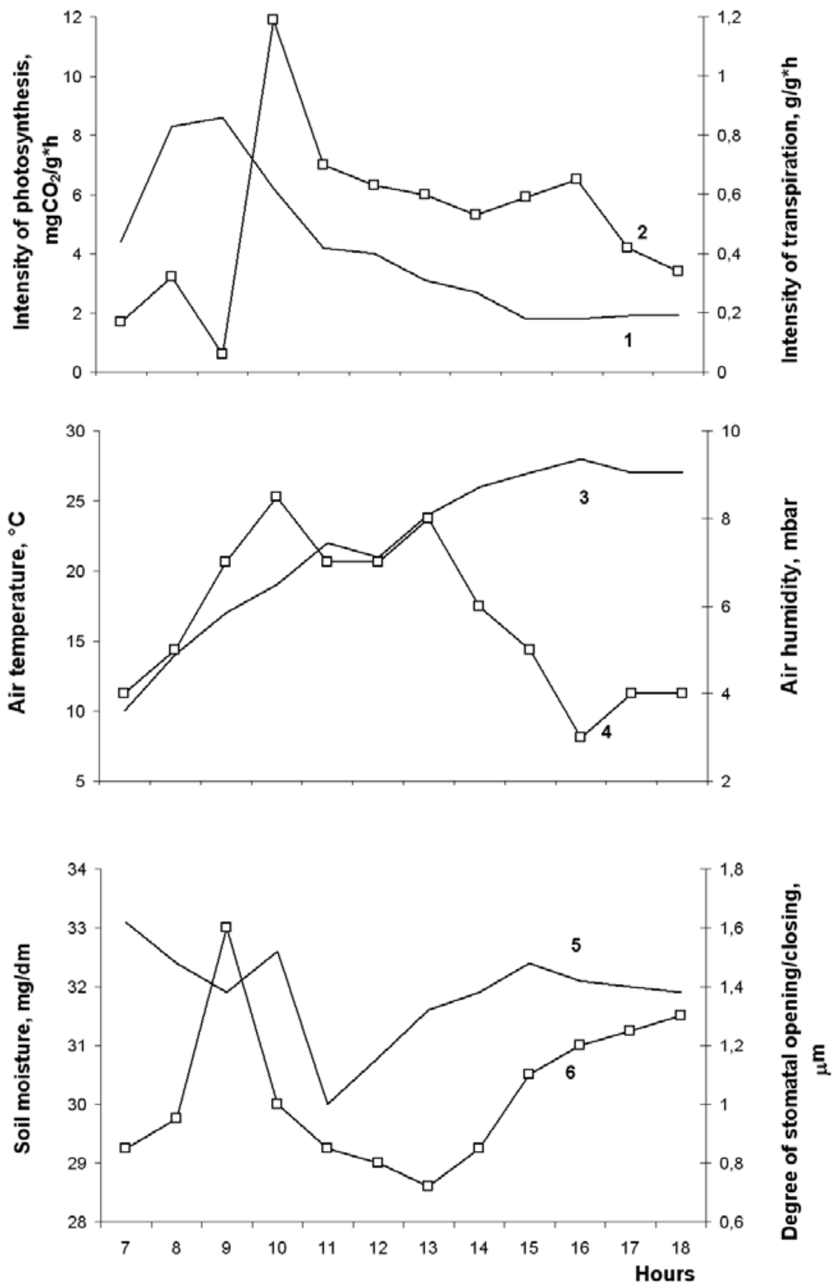

Fig. 2. Changes of the factors under optimum conditions for a day: Photosynthesis (1) Transpiration (2) Air Temperature (3) Air Humidity (4) Moisture (5) and Degree of Stomatal Opening/Closing (6).

et al. 1990; Zou and Kahnt 2008).

The daily dynamics of water deficiency in the needles is characterized by several curves depending on external factors (Fig. 3). When there is insufficient water, the maximum water saturation of the needles is observed between 5 to 6 a.m. (the stock of productive soil moisture in a soil layer of 0 to 50cm amounts to 46cm). Furthermore, the value of residual water deficiency is 13 to 15%, 2–3 times as large as in case of some optimum soil moisture (4 to 6%). The maximum of water deficiency is normally registered between 11 to 12 a.m. (Fig. 2), whereas in the case of sufficient soil moisture – between 3 to 4 p.m.

In the case of a growing deficiency of soil moisture,

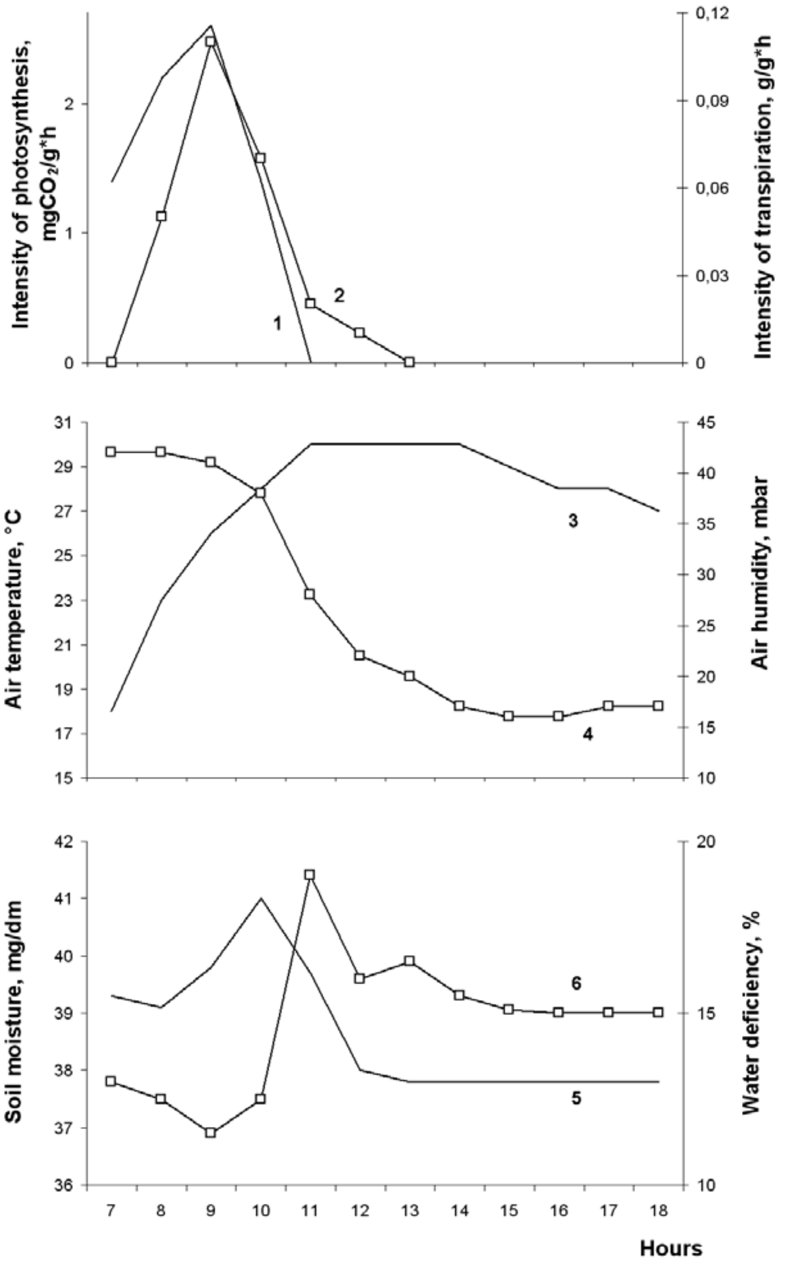

Fig.3. Changes of the factors under drought conditions for a day: Photosynthesis (1) Transpiration (2) Air Temperature (3) Air Humidity (4) Moisture (5) and Water deficiency (6).

daily maxima of CO_2-gas exchange shifted towards earlier hours of the day. In the case of intense soil drought (when the stock of productive soil moisture in the soil layer of 0 to 50cm is 36cm), the photosynthesis curve assumes becomes asymmetric, with the maximum at 7 to 9 a.m. Therefore, a decrease in the supply of water from the soil, plays a key role in the gas exchange dynamics of the early occurrence of water deficiency maximum. Furthermore, a simultaneous reduction in the gas exchange and transpiration intensities shows the substantial role of stomata in the regulation of these processes (Fig. 2).

In the case of an extreme reduction of available soil moisture reserves (productive soil moisture being 28cm in a 50cm soil layer) the maximum of water deficiency was registered between 7–9 a.m. Variations in transpiration and photosynthesis in related to maximal values of water deficiency were owing to stomata (Tuzet *et al*. 2003).

A comparison of the values of water deficiency in the needles of different age groups under drought showed that the current year's needles in the beginning of their growth are characterized by low values of this parameter, i.e. 5 to 6%. Together with the development of the needles, the water deficiency increases, and at the termination of needle growth it reaches a level equal to the moisture deficiency in the second year and third year needles (Fig. 4). This means that the water consumption of growing needles is determined to a large extent by the hormonal status of the plant, not external factors (Tuzet *et al*. 2003).

The dynamics of water deficiency in simultaneous daily variations of transpiration and photosynthesis reflects the process of adaptation of the plant to a limited supply of water to the needles.In order to identify the external factors, which regulate the dynamics of gas exchange and transpiration, we conducted multiple regression analysis of these processes to determine their dependence on air temperature, solar radiation and air humidity.

Our analysis showed that during the periods of hot sunny weather air temperature acts as the principal negative factor for CO_2 gas exchange ($r = -0.65 \pm 0.05$, $n = 12$). Otherwise, the intensity of transpiration is determined by the level of radiation absorbed by the biocoenosis. Under cool cloudy weather conditions combined with insufficient soil moisture, absolute air humidity ($r = 0.70 \pm 0.04$, $n = 12$) plays a substantial role in the process of gas exchange and transpiration. Consequently, the processes of gas exchange and transpiration take place at the expense of the absorbed solar energy (Foyer *et al.* 1990), but these are regulated by air temperature and humidity (Suvorova *et al.* 2005b).

This regularity is reflected in the average daily dynamics of these processes (Fig. 5). Their averages were determined using accidental functions to reveal typical (recurrent) regularities and the level of accidental variations (Ventzel 1969). When comparing curves the CO_2-gas-exchange and the transpiration can find that both follow the dynamics of total radiation. This research revealed the explicit dependencies

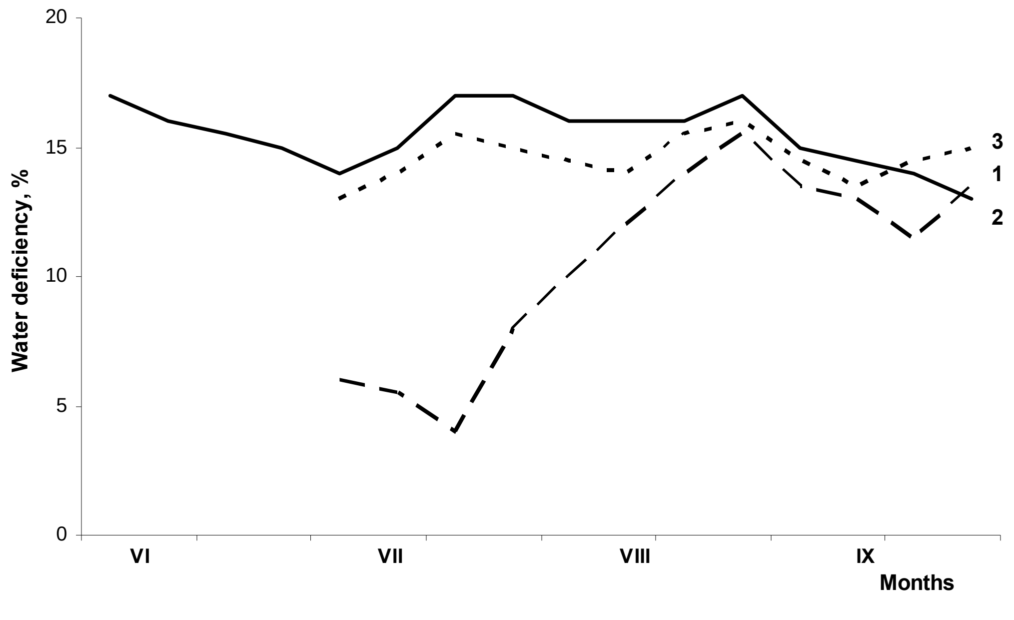

Fig. 4. Seasonal change of the water deficiency in the this year (1), two year (2) and three year (3) needles.

between transpiration and solar radiation (r = 0.74 ± 0.04, n = 12), and between gas-exchange and solar radiation (r = 0.71 ± 0.05, n = 6). During the day, the energy distribution between gas exchange and transpiration constantly varies. In order to explain these phenomena, diagrams of dependences of gas exchange and transpiration with respect to solar radiation have been constructed. Figure 6 shows that under low radiation levels the rate of transpiration growth is smaller than the rate of gas exchange. In case of an increase in the radiation level, there is an inverse relationship. The radiation level, under which the saturation takes place, is higher for transpiration than CO_2-gas exchange.

Our investigation of the dependence of photosynthesis and transpiration intensity on air humidity showed that with an increase in the latter the intensity of gas exchange increases. Transpiration under high humidity conditions has an explicit oscillatory (fluctuating) character. With a temperature increase under a constant radiation level, transpiration intensity decreases (Fig. 7). This probably is the result of the rapid increase in the needle temperature. At a definite radiation level, there exists a temperature under which the maximum intensity of visible photosynthesis is reached and the most efficient water consumption occurs.

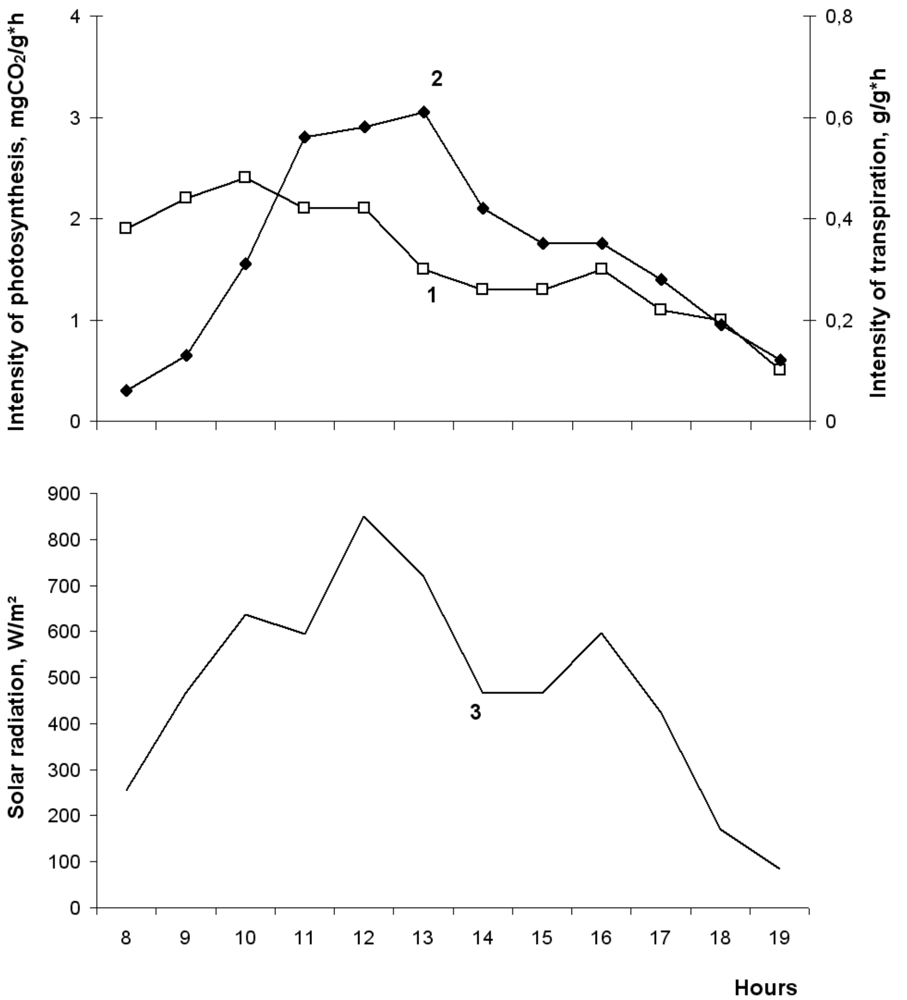

Fig. 5. Factors of the Photosynthesis (1) for a day: Transpiration (2) and Summary Solar Radiation (3).

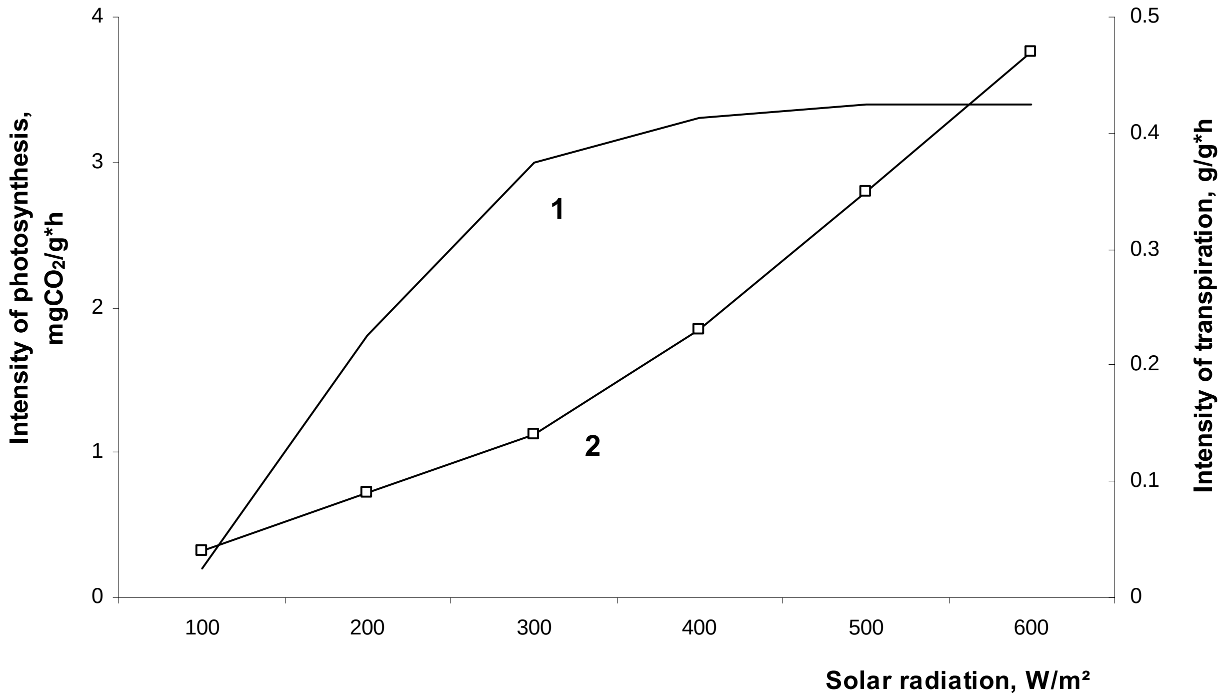

Fig. 6. Correlation CO_2-gas exchange (1) with Transpiration (2) under different solar radiation conditions.

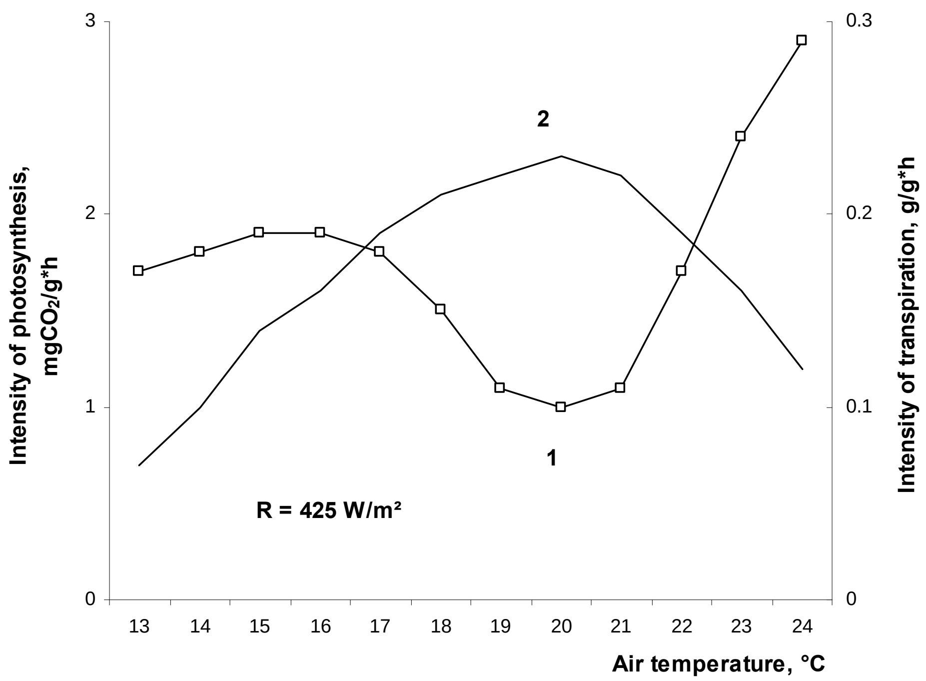

Fig. 7. Correlation CO_2-gas exchange (1) with Transpiration (2) under conditions of constant Solar Radiation (R = 425 W/m2) and different air temperature.

Discussion

Several researchers have stated that the intensity of photosynthesis and the productivity of plants under extreme conditions depend on the functions of the two optimization systems:

– tendency of the plants to rational water consumption under conditions of water stress;

– maintenance of the optimum temperature of the needles in order to maximize the intensity of photosynthesis (Slemnev 2000; Brim 1991; Eastman and Camm 1995).

According to our observations, under conditions of soil moisture deficiency and with substantial variations in water content in the needles, observed is a third variant, but a combination of these two systems, which favorably influence the intensity of photosynthesis. This characteristic may be responsible for *Pinus sylvestris* L.'s ability to accumulate biomass under a combination of various unfavorable water supply conditions.

When the processes of gas exchange and transpiration are considered jointly, it is possible to register a "competitive" type of interaction between these processes. The increase in the intensity of one of these processes is accompanied by the reduction of intensity of the other process. This relationship is explicitly traced to the results of the experiments related to the daily dynamics. This can also be seen from the light (solar radiation) and temperature curves constructed for definite radiation levels.

Pinus sylvestris L. is known to belong to type C_3 plants, one of the gas exchange constituents of which is photo-respiration. The process of photo-respiration has a temperature ratio of 3.6 (Vu *et al*. 2001), while true photosynthesis normally varies within the range of 1.1 to 1.5, and only at a high level of solar radiation does it reach values of 2 to 5 (Rubin and Gavrilenko 1977). In the case of an increase in the radiation level and the temperature, the air humidity in the sub-stomatal cavities increases, and the concentration of CO_2 in the mesophyll of the needles increases too. The change in needle temperature results in an increase in transpiration, which cools the surface of the needles. This change plays a role of the negative feedback to lower the level of gas exchange. The process of gas exchange may take place at the expense of re-assimilation of the CO_2 discharged during the process of respiration. This regularity can be seen in the light and temperature curves of gas-exchange and transpiration. Under extreme conditions, the stomatal mechanism of regulation provides an adaptive function and acquires dominant importance.

References

Balaur N.S., Vorontsov V.A., Kleiman E.I. Ton Yu.D. (2009) Novel technique for component monitoring of CO_2 exchange in plants, Russian Journal of Plant Physiology. 56: 423–427.

Baranova M.A. (1985) Grouping of the morphological types of stomata. Botanic journal. 70, 12: 1585–1595. (in Russian)

Berry, J., Bjorkman, O. (1980) Photosynthetis response and adaptation to temperature in higher plants, Plant Physiol. 31: 491–543.

Brim, W. (1991) Photosynthesis and transpiration of banana leaves as effected by severing vascular system, Plant Physiol. 36: 577–580.

Caff, D.E., Carr, D.J. (1964) Examination of the refractometris method for determining the water potential of plant tissues, Ann. Bot. 28: 351–368.

Dang O.-K., Margolis H.A., Coyea M.R., Collalz G.J. (1997) Regulation of branch level gas exchange of boreal trees: roles of shoot water potential and vapor pressure difference, Tree Physiol. 17: 521–535.

Davydov V.A. (1991) Simple method of receipt epidermal imprint with assistance scotch and organic glass, Physiology of plants. 38: 605–609. (in Russian)

Drozdov S.N., Kurec V.K. (2003) There aspects of the ecological physiology of plants. Petrozavodsk: 172. (in Russian)

Eastman P.A.K., Camm E.L. (1995) Regulation of photosynthesis in interior spruce during water stress: changes in gas exchange and chlorophyll fluorescence, Tree Physiol. 15: 229–235.

Foyer C.H., Lelandais M., Yfrbimon J. (1990) Control of quantum effienciis of photosystems I and II, electron flow, and enzyme activation following clark- tolight transition in pea leaves, Plant Physiol. 92: 1053–1061.

Genkel P.A. (1982) Physiology heat- and drought-resistant Plants, Moscow: 280.

Khalil A.A.M., Grace J. (1993) Doe's xylem ABA control the stomatal behavior of water stressed sycamore, Exp. Bot. 44: 1127–1134.

Lir H., Pol'ster G., Fidler G.I. (1974) Physiology of Plants, Moscow: 424. (in Russian)

Maximov N.A. (1952) Elect proceeding unter drought resistance and winter resistance of plants, Moscow: 576. (in Russian)

Pelah D., Shoseyov O., Altman A. (1995) Characterization of BspH, a major boilingstable water-stress-responsive protein in aspen (*Populus tremula*), Tree physiol. 15: 673–678.

Robonen E.V., Chernobrovkina N.P., Kolosova S.V. (2002) Water Flow Rate in Scotch Pine Stem in inundation of Roots and Different CO_2 Concentration in Soil Air, Lesovedenie. 1: 18–23. (In Russian with summary English)

Rubin B.A., Gavrilenko B.F. (1977) Biochemistry and Physiology of Photosynthesis, Moscow: 242. (in Russian)

Sen'kina S.N. (2002) Changes in Water Regime of Scotch pine Needles Related to Enviromental Conditions, Lesovedenie. 1: 24–29. (In Russian with summary English)

Singh M.K., Sasahara T. (1981) Photosynthesis and Transpiration in Rice as Influenced by Soil

Moisture and Air Humidity, Annals of Botany. 48: 513–518.

Sleicher R. (1970) Water regime of plants, Moscow: 362. (in Russian)

Slemnew N.N. (2000) Reaction of photosynthesis of plant of arid ecosystem Gobi (Mongolia) by temperature, Bot. jour. V. 85: 63–77. (In Russian with summary English)

Spence R.D. (1987) Problem of variability in stomatal responses, particulary aperture variance, to environmental and experimental conditions, New Phytol. 107, 2: 303–315.

Sperry J.S., Tyrel M.T. (1990) Water stress xylem embolism in three species of conifers, Plant Cell and Environm. 23: 427–437.

Suvorova G.G., Yankova L.S., Kopytova L.D., Filippova A.K. (2005a) Maximal Photosynthesis Intensity in Scots Pine and Siberian Spruce in Baikal Region, Sib.ecol.journal. 1: 97–108. (In Russian with summary English)

Suvorova G.G., Yankova L.S., Kopytova L.D., Filippova A.K. (2005b) Optimal Environmental Factors and Photosynthesis Intensity of Scots Pine and Siberian Larch in the Baikal Region, Sib.ecol.journal. 1: 85–95. (In Russian with summary English)

Suvorova G.G., Yankova L.S., Kopytova L.D. (2009) Photosynthetic productivity of three coniferous Species in Baikal Siberia, Eurasian J. For. Res., 12, 47–56.

Sudachkova N.E., Milutina I.L., Semenova I.P. (2002) Influence of water deficit on contens of carbohydrates and nitrogenous compaunds in *Pinus sylvestris* L. and *Larix sibirica* Ledeb. Tissues, Eurasian J. For. Res. 4: 1–11.

The USSR Map of Soils in scale 1:1,500,000 (1988), Moscow: 2. (in Russian)

Tuzet A., Perrier A., Leuning R. (2003) A coupled model of stomatal conductance, photosynthesis and transpiration, Plant, Cell and Environment. 26: 1097–1116.

Vashuk L.N., Popov L.V., Krasny N.M. *et al.* (1997) Forest and forestry of the Irkutsk region. Irkutsk: 288. (in Russian)

Ventzel E.C. (1969) Theory of Probability, Moskow: 572. (In Russian)

Vu O., Gourdrian J., Wang T.D. (2001) Modeling diurnal courses of photosynthesis and transpiration of leaves on the basis of stomatal and nostomatal responses, including photoinhibition, Photosynthetica. 39: 43–51.

Zhang R. *et al.* (2003) Determination of regional distribution of crop transpiration and soil water use efficiency using quantitative remote sensing data through inversion, Science in China (Series D). 46, 1: 10–22.

Zou D.S., Kahnt G. (2008) Effect of Air Humidity on Photosynthesis and Transpiration of Soybean Leaves, Journal of Agronomy and Crop Science. 161: 190–194.

Zwiefel R., Zimmerman L., Newbery D.M. (2005) Modeling tree water deficit from microclimate: an approach to quantifying drought stress, Tree physiol. 25: 147–156.

Zwiefel R., Steppe K. Sterck F.J. (2007) Stomatal regulation by microclimate and tree water relations: interpreting ecophysiological field data with a hydraulic plant model, Exp. Bot. 58: 2113–2131.