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Experimental Studies of the Short-Term Fluctuations of Net Photosynthesis Rate of Norway Spruce Needles under Field Conditions*

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野外條件下에서 독일가문비(*Picea abies* Karst) 針葉의 純 光合成率의 短期 變化에 대한 實驗的 硏究*

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ABSTRACT

Canopy structure conductances of a Norway spruce forest in the Solling Hills(Central Germany) and Central Forest Biosphere Reserve(320㎞ to the north-west from Moscow) were derived from LE(latent heat flux) and H(sensible heat flux) fluxes measured(by Eddy correlation technique and energy balance method) and modelled(by one dimensional non-steady-state) SVAT(soil-vegetation-atmosphere-transfer) model(SLODSVAT) using a rearranged Penman-Monteith equation("Big-leaf" approximation) during June 1996. They were compared with canopy stomatal conductances estimated by consecutive intergrating the stomatal conductance of individual needles over the whole canopy("bottom-up" approach) using SLODSVAT model.

The result indicate a significant difference between the canopy surface conductances derived from measured and modelled fluxes("top-down" approach) and the stomatal conductances modelled by the SLODSVAT("bottom-up" approach). This difference was influenced by some nonphysiological factors within the forest canopy(e.g. aerodynamic and boundary layer resistances, radiation budget, evapotranspiration from the forest understorey). In general, canopy surface conductances derived from measured and modelled fluxes exceeded canopy stomatal conductance during the whole modelled period. The contribution of the understorey's evapotranspiration to the total forest evapotranspiration was small (up to 5 - 9% of the total LE flux) and was not depended on total radiation balance of forest canopy. Ignoring contribution of the understorey's evapotranspiration resulted in an overestimation of the canopy surface conductance for a spruce forest up to 2㎜/s(about 10 - 15%).

要　約

독일 중부(Solling Hills)의 가문비림 임관의 구조적인 수분증산 통도특성은 LE와 H의 유동량으로 측정되고, 1996년 6월중 재배열된 Penman-Monteith 식을 이용하여 SVAT 모형을 설계하여 도출하였다. 또한 SLODSVAT 모형을 통한 전체 임관 내 각 침엽의 연속적인 수분통도성을 평가하여 임관 기공의 통도성을 비교하였다.

이와 같은 결과에서 나온 임관 표면 통도성과 유동량을 설계하고, SLODSVAT 모형에 의해 설계된 기공 통도성 사이에서 중요한 차이점을 알 수 있었다. 이 차이점은 산림 임관의 범위내에 빗물리

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적인 요소에 의해 영향을 받았음을 알 수 있으며, 일반적으로 임관 표면의 통도성은 전체 측정 기간 동안 임관 기공 전도력보다 크게 나타났다. 또한 산림의 전체 증발산량에 대한 하층부의 공헌도는 작았고, 임관의 복사에너지 균형에 의존하지는 않는 것으로 나타났다. 하층부 증발산량의 기각은 독일 가문비림에 대한 임관 표면 전도력의 과대 평가로서 나타난 결과이다.

INTRODUCTION

Many detailed studies of photosynthesis and respiration of coniferous forests are well summarised by Linder(1979) and reviewed, for example, by Ludlow and Jarvis(1989), Katrushenko and Karpov(1983), Kull and Koppel(1987), K. Idso and S. Idso(1994). The main purposes of all these studies were :

- to describe and to quantify the variability of photosynthesis and respiration of forests on different spatial(from the needle and shoot to tree and canopy scale) and temporal scales ;
- to study the photosynthetic response of forests on changes of environmental conditions(incoming solar radiation, air temperature and relative humidity, ambient CO_2 concentration, air pollution, soil water content etc.) and the evaluation of these responses during tree growth.

Measurements of photosynthesis on a shoot level have already been made under field and laboratory conditions using both stationary gas-analysers(Katrushenko and Karpov, 1983 ; Kull and Koppel, 1987 ; Ludlow and Jarvis, 1983 ; Bolondinsky and Vilikaynen, 1987) and portable systems(Marek et al., 1989). Since, specific parameters characterising the activity of the photosynthetic apparatus of tall tree branches are often difficult to determine, the method of photosynthesis measurements for detached shoots has also been suggested(Lange et al., 1986). Most of these studies describe either a long-term variability of photosynthesis rate or the response of net photosynthesis on environmental conditions. They did, however, not take into account the analysis of short-term fluctuations and rhythms of photosynthesis and respiration(Gumowski, 1981 ; Bravdo, 1977 ; Edwards and Woker, 1986) due to low frequencies(about 2 - 6 measurements per minute) of direct photosynthesis rate measurements under field conditions. Obviously, these low frequencies don't allow to study the high frequency rhythms of photosynthesis. Short-term fluctuations of photosynthesis rates observed during the experiment are usually characterised either as systematic inaccuracies of the experiment, or as "noise" or as the influence of some unknown factors.

A new generation of the portable photosynthesis measuring systems allows to make rapid (about 1 - 2 seconds) measurements of the photosynthesis rate simultaneously with measurements of other ecophysiological and environmental parameters(e.g. transpiration rate, stomatal conductance, incoming photosynthetically active radiation(PAR), air and leaf temperatures, air relative humidity, CO_2 concentration, etc.).

A study of short-term rhythms of photosynthesis is very important, first of all, because it can be used for diagnostics of the forest state and for prediction of the forest development. The point is that short-term rhythms are most sensitive indicators and regulators of the state functioning and the health of each vegetative system (Kaybiaynen, 1979, Aschoff, 1981). The beginning of disturbance and damage of trees is immediately manifested by the disturbance or change(amplitude, frequency) of their biological rhythms(Tchernyshov, 1974).

The main focus of this paper is to study experimentally short-term fluctuations and rhythms of net photosynthesis of the needles of a Norway spruce trees. The measurements took place at a forest experimental site in the Central Biosphere Forest Reserve in Russia during the second part of June of 1991.

METHODS

1. Experimental site

The experimental site is located in a Norway spruce forest(*Picea Abies* (L.) Karst.) in the

Central Forest Biosphere Reserve(Nelidovo region, Tverskaya district, 320km to the northwest from Moscow). The size of its protected area is about 210km^2. Surrounding buffer zone is 2km wide. Spruce(25 - 35m high and 70 - 120 year old) is dominated species(about 46% of forest trees).

The climate of the Central Forest Biosphere Reserve is temperately continental. The annual precipitation is approximately 700㎜. The average annual temperature is about 3.5C.

During the period of measurements the daily air temperature varied from 20 to 30C, the relative humidity - from 30 to 75%. Incoming PAR varied from 100 to 2000 mol m^{-2}s^{-1} depending on the time of measurements and cloud conditions.

The soil was well-watered and transpiration was not limited during all period of measurements.

2. Instruments

For the measurements of net photosynthesis of the needles the portable photosynthetic system LI-6200(LI-COR, USA) was used. LI-6200 allow to make fast, simultaneous measurements of leaf stomatal conductance and photosynthesis and transpiration rates. The system includes the infrared CO_2 gas-analyzer difference between the sample and the reference concentration is used to calculate the photosynthesis rate of the needle.

In a transient mode with a closed flow path, the CO_2 analyzer is used in an absolute mode. Air from the sealed needle chamber is continuously re-circulated through the analyzer sample cell and the net photosynthesis rate is calculated from the rate of change of CO_2 and other parameters.

3. Measurements

Measurements were performed for one year old needles in well sunlit upper part of the tree crown. For all measuring series the differential measuring mode of the gas-analyzer with open flow path was used. Two different methods were used to study the short-term fluctuations of the net photosynthesis rate depending on fluctuations of incoming PAR :

- the measurements under the natural changes of light conditions and,
- the measurements under the artificial shading of the measuring chamber from direct sun beams by a special screen with different optical density.

CO_2 concentration was measured by LI-6250 one time per two seconds. A duration of each measuring series was about 10 minutes determined by the capacity of LI-6200 RAM memory.

RESULTS AND DISCUSSION

A great variability of the photosynthesis rate was observed under natural changes of incoming solar radiation(Fig. 1, 2).

Fig. 1(a) shows typical examples of short-term variation of PAR, needle temperature (T_{leaf}), relative humidity (F) and net photosynthesis rate (P) on 25 June 1991. One can see no dependence of P on incoming PAR(period of PAR fluctuations was about 20 - 30 s, their amplitude was about 300 - 500(mol/m^{2}s, incoming PAR flux was higher than the quantum efficiency). The variation of P was closely correlated with a variation of F. It indicates that the fluctuations of P rate are essentially dictated by the same mechanisms which are responsible for the changes of F in the measuring chamber. Since, the trend of F depends mainly on the transpiration rate, it can be proposed that a common biological rhythm of the tree regulate the rates of photosynthesis and transpiration through the stomatal functioning. The analysis of the time series confirms partly this hypothesis. Fig. 1(b) demonstrates the power spectral density functions ($G(f)$) for PAR, T_{leaf}, F and P. The local maximums of $G(f)$ were registered on frequencies (f) about 0.008 - 0.011 s^{-1} for F and P. They correspond to the frequencies of natural rhythm of P which can be visually observed in Fig. 1(a). A response of P to PAR fluctuations(the main frequency about 0.025 - 0.04 s^{-1}) could not be found. There is only a small local maximum in PAR spectrum (f0.012 s^{-1}), which overlaps with the maximum of the photosynthesis spectrum.

Fig. 2(a, b) shows other variations for P,

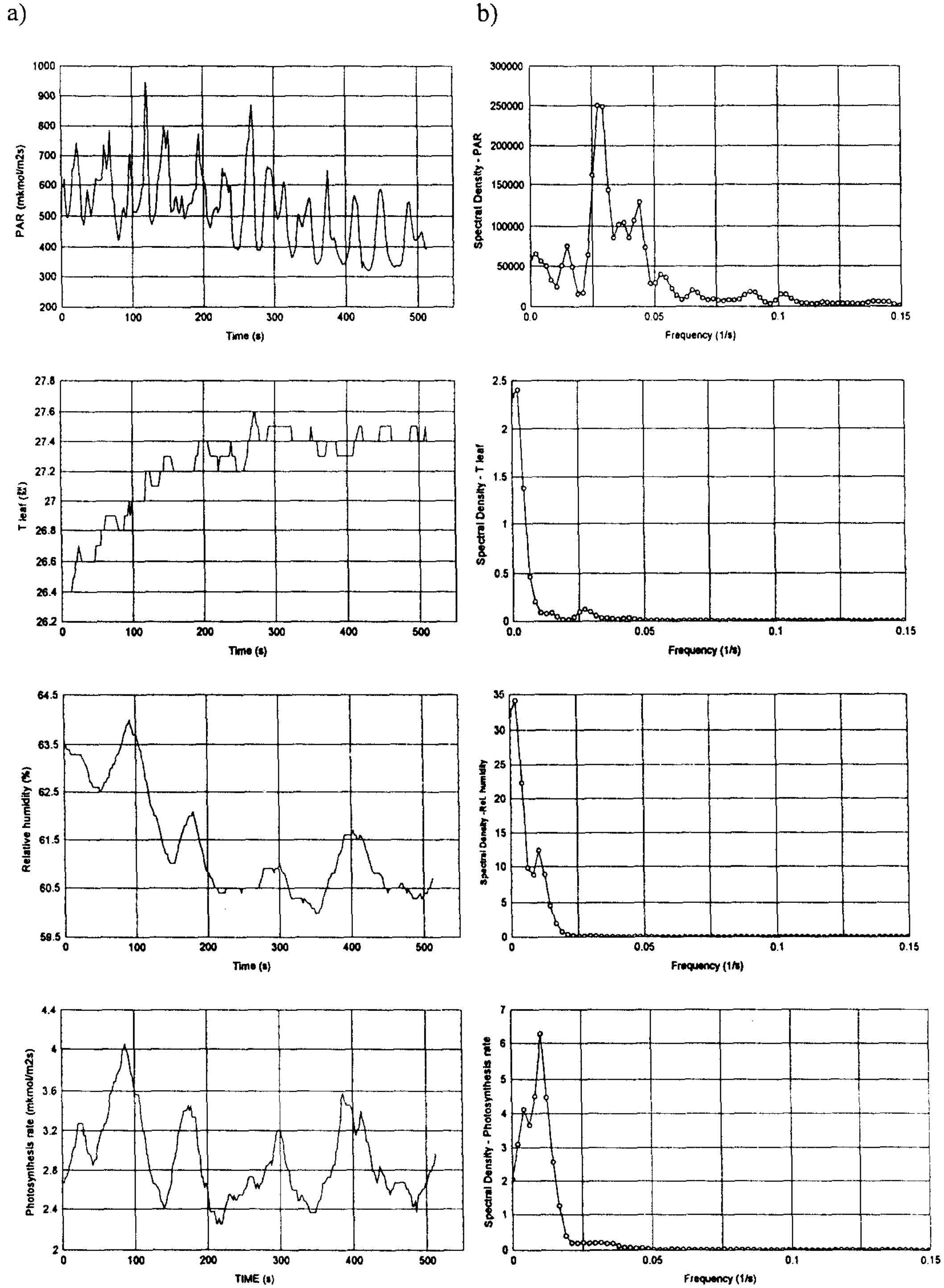

Fig. 1. Time variability of incoming PAR, needles temperature, relative humidity and photosynthesis rate (a) and theirs spectral density distributions (b) during the first 10 minutes period on 25 June 1991.

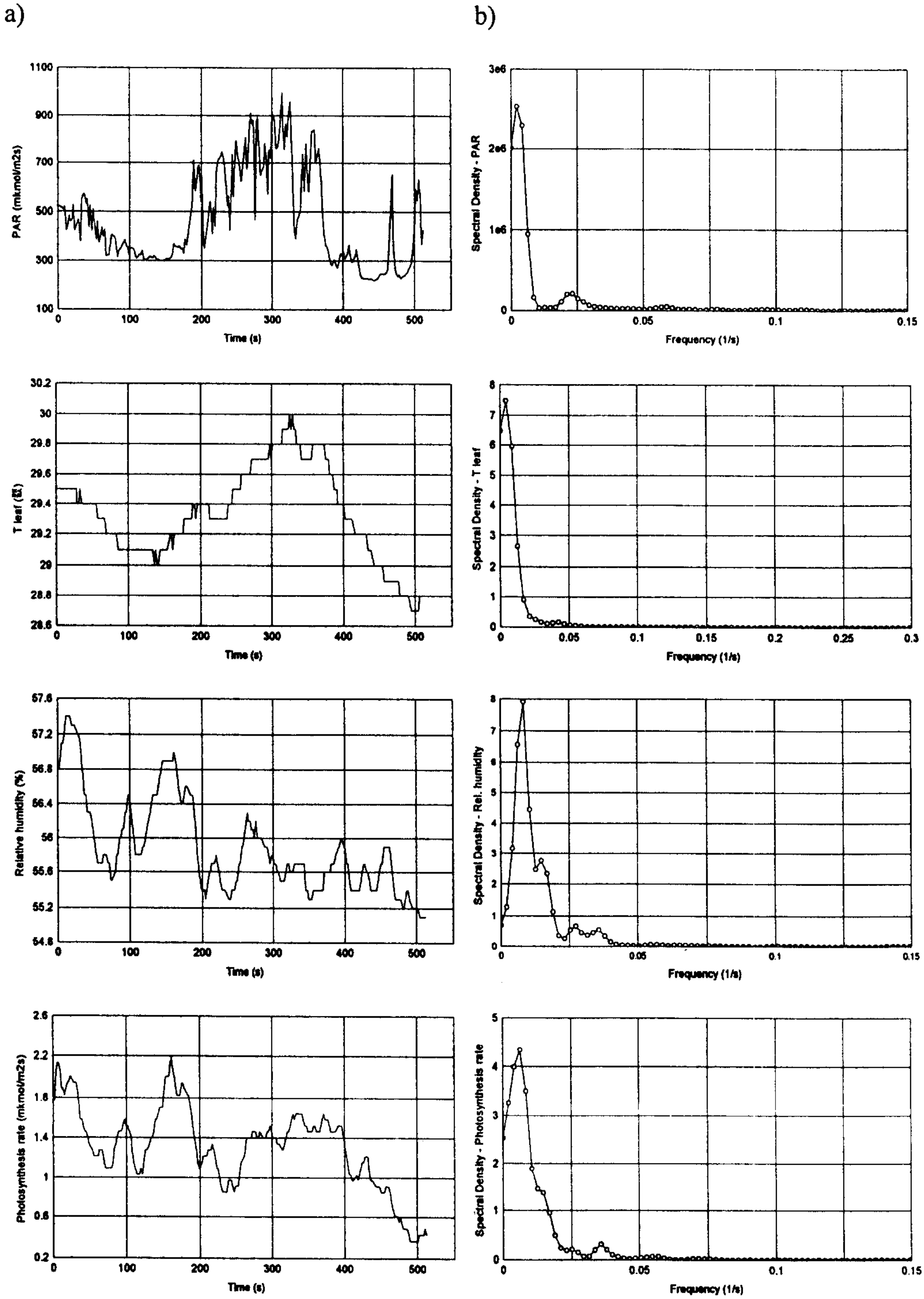

Fig. 2. Time variability of incoming PAR, needles temperature, relative humidity and photosynthesis rate (a) and theirs spectral density distributions (b) during the second 10 minutes period on 25 June 1991.

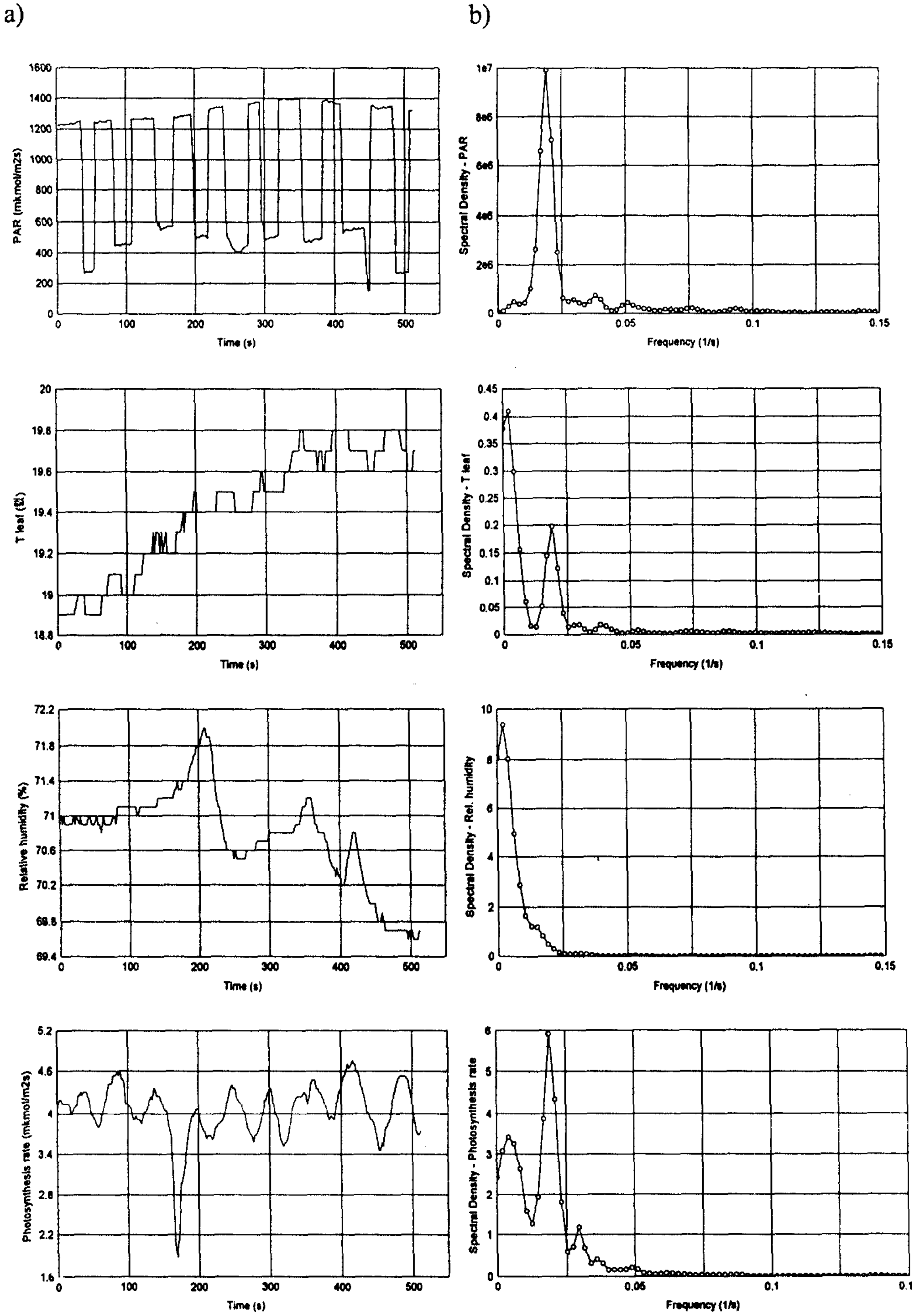

Fig. 3. Time variability of incoming PAR, needles temperature, relative humidity and photosynthesis rate (a) under the artificial shading of measuring chamber and theirs spectral density distributions (b) during the first 10 minutes period on 26 June 1991.

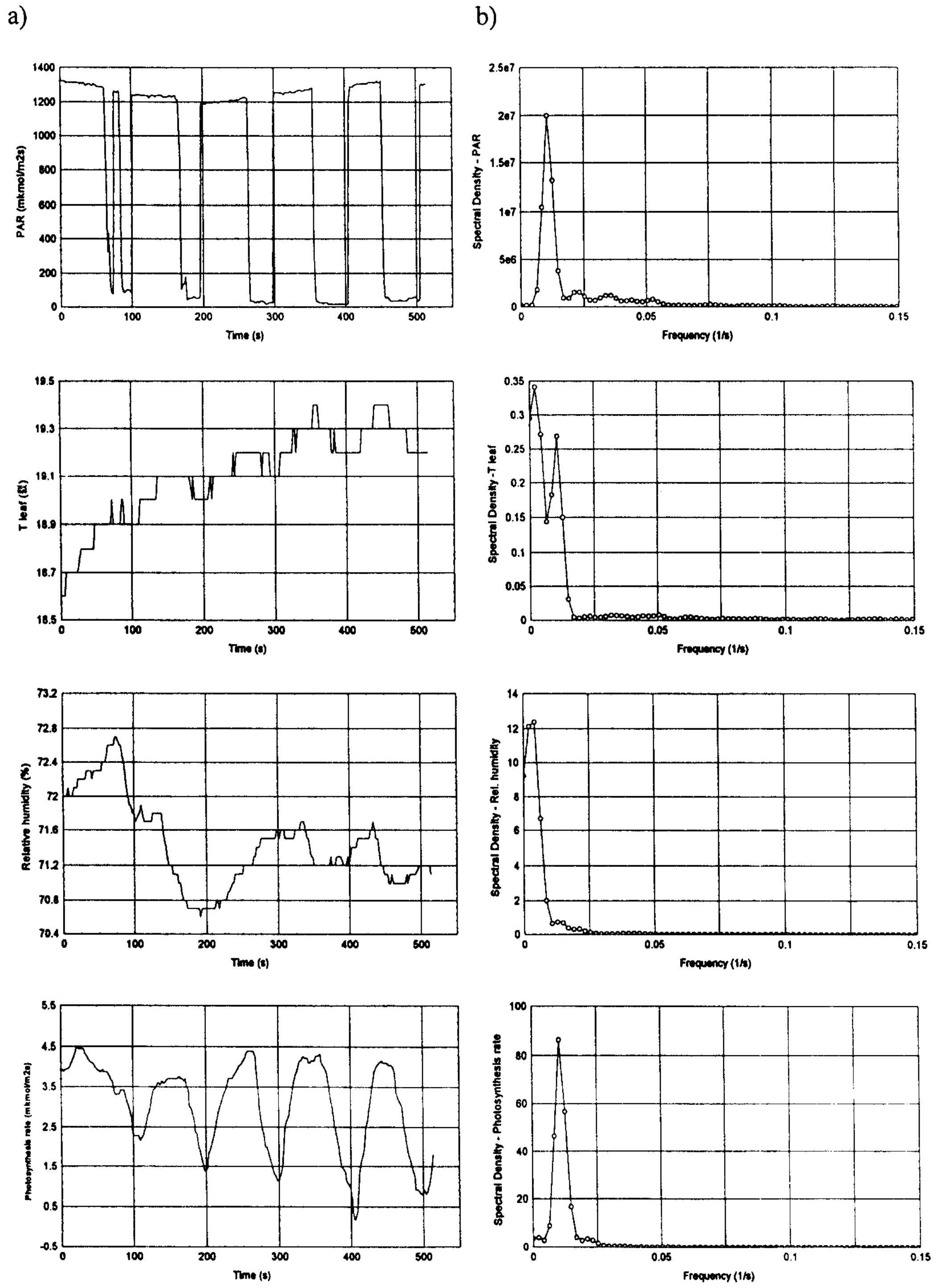

Fig. 4. Time variability of incoming PAR, needles temperature, relative humidity and photosynthesis rate (a) under the artificial shading of measuring chamber and theirs spectral density distributions (b) during the second 10 minutes period on 26 June 1991.

PAR, F and T_{leaf} and their spectral density distributions, respectively, under the natural changes of incoming PAR on 25 June 1991. The close dependence between F and P and very low correlation between P and PAR trends are remained.

During the second part of the experiment the measurements were made under cloudless weather conditions. The measuring chamber has been periodically shaded by special screens with different optical densities. The net photosynthesis response on changes of the light conditions depending on air and leaf temperatures, relative humidity and other factors were studied.

Figs. 3a and 4a demonstrate examples of P variation with time and some environmental parameters under the periodical shadings of the measuring chamber. The amplitude of the fluctuations of PAR was about 1200 - 1400mol/m^{2}s. The duration of shading varied between 10 and 60 seconds.

The measuring results show that under short-time shadings(about 10s) a very small P decreasing was observed only Fig. 3a, 4a. Longer shadings(about 30 - 40 seconds) resulted in detectable changes of P(Fig. 4a). P rate restored to the initial level after taking away the shading screen within about 20 - 50 seconds depending on the shading intensity. For all measuring series P was positive during all shading time. The time of delay of the net photosynthesis response on changes of light conditions varied from 10 to 20 seconds. Decreasing of the shading screen density reduced amplitude and smoothed of P fluctuations(Fig. 3a, 4a).

The natural fluctuations of P adapts to PAR fluctuations have already been observed during the first part of the experiment(Fig. 2a). This effect has more clear noticed under artificial then under natural shading(Fig. 3a and 4a). Generally, adaptation of P fluctuations to PAR changes can be observed via :

- the response time of P rate to a change in light conditions decreases,
- the restoration time of P rate after shading decreases,
- the amplitude of P fluctuations increases.

Figs. 3b and 4b demonstrate the spectral density distributions of fluctuations of incoming PAR, T_{leaf}, F and P on 26 June 1991 under artificial shading. The spectral density shown maximum for frequencies of about 0.020 s^{-1}(for the first period) and of about 0.013 s^{-1}(for the second period) both for PAR and for P fluctuations. These frequencies correspond to the main frequencies of the artificial shading. The initial photosynthesis rhythm(the frequencies are about 0.008 - 0.011 s^{-1}) is strongly suppressed by the rhythm of PAR and slightly noticed as a local maximum, only.

CONCLUSIONS

Measurements of short-term fluctuations of the net photosynthesis rate for a Norway spruce twigs show the existence of a natural rhythm (f0.008 - 0.011 s^{-1}, period about 90 - 120 seconds) regulating the processes of CO_2 and H_2O exchange between the leaf and surrounding air through the stomata functioning. This rhythm was a very stable and it was not significantly changed under the variable environmental conditions.

The periodical fluctuations of the incoming PAR depending on their amplitude provoke a disturbance of this P rhythm and can lead to the change of the frequency and the amplitude of P fluctuations.

The reasons for these fluctuations of net photosynthesis and transpiration and rhythms were not investigated. Short-term 10 minute time series of the measurements, unfortunately, do not allow to get full information about the entire structure of the rhythms of net photosynthesis on a twig level in a spruce forest and to uncover their mechanisms and causes. These question will be the aims of further investigations.

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