Relationship between transpiration and respiration in plants during the dark period

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Abstract

Energetic aspects of the relation between transpiration and respiration during the dark period were evaluated. One-year old seedlings of three trees, one bush and one annual plant were grown in controlled conditions. Experiments were performed under uniform environment during the day and two regimes of air relative humidity (RH) during the night, low (50 - 65 %) and high (95 %). For all investigated plant species the dark transpiration rate (E), the free energy of respiratory substrate, the entropy production and the free energy balance (FEB) of the dark respiration were higher at low than at high RH. E was linearly related to the FEB (r^2 ranged between 0.63 and 0.90).

Additional key words: air humidity, free energy balance of dark respiration.

Introduction

Scare studied, but of a special interest is the relation between the main physiological processes during the dark: transpiration and respiration. For a number of species, the existence of such a relation is experimentally established by studies in laboratory (Prokofev and Katz 1963, 1964, Jeanrenaud 1978, Press *et al.* 1988) and nature (Polster 1950, Künstle and Mitscherlich 1976) environment. In all these reports such a relationship has only been noted, but without considering of its physiological significance and role. Some authors consider that the respiration is the source of energy for the transpiration (Jeanrenaud 1978). Others (Stoyanov and Florov 1969, Florov and Stoyanov 1970, Florov 1978) approved that the dark transpiration provides with energy the dark respiration.

The aim of presented work was to evaluate the relationship between

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Abbreviations: RH - air relative humidity; Φ - entropy production; $(\Delta G/\Delta t)$ - free energy of respiratory substratum; $(\Delta G/\Delta t)_a$ - free energy balance (FEB) of dark respiration.

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transpiration and respiration in different plant species during the dark period from energetic point of view.

Materials and methods

Plant material: One-year old trees (*Quercus sessiliflora* Salisb., *Fagus silvatica* L., *Fraxinus oxycarpa* Wild.), a shrub (*Rubus idaeus* L.) and an annual plant (*Phaseolus vulgaris* L.) were used. The plants were grown from seeds or cuttings. After germination, they were grown under controlled environment in air-conditioned chamber: photoperiod 8 h, irradiance 140 W m^{-2} from a mixture of cold and warm white fluorescent lamps, day/night air temperature 24/24 ± 1 °C and air relative humidity (RH) 70 - 75 ± 3 % during the light period. During the night two regimes of RH were maintained: low (50 ± 3 %) and high (90 ± 3 %). Parallel experiments were performed in greenhouse. The only difference was that the parameters were not kept in so narrow limits (for instance the low RH during the night was about 50 - 65 %). The duration of air humidity treatments was different for each plant species (see Table 2). Three or two independent experiments were carried out with each plant species.

Energetic characteristics of dark respiration: Energetic aspects of the dark respiration were characterised on the base of irreversible thermodynamics applied to the plant organism according to the boundary-layer method (Florov 1978, 1988). For thermodynamic description, the free energy of Gibbs (G) (isobaric-isothermal potential) was used. The boundary-layer method is a principally new application of the irreversible thermodynamic laws at whole organism level, namely to the boundary layer between the plant leaves and the ambient air. In brief, the main reasons for that consideration are consequences from: the universal surface law of Rubner (1883), and the anisotropic character of living membranes (Katchalskii and Kedem 1964, Kotyk and Janáček 1980). After thermodynamic analysis of the energetic processes going on the boundary layer between leaves and ambient air, it is obtained that the rate of the energy release from the respiratory substrate is quantified by the equation (Florov 1978, 1988):

$$\frac{\Delta G}{\Delta t} = -LE\eta_0 - P\frac{\Delta T}{T} \qquad [J\ m^{-2}\ s^{-1}] \qquad (1)$$

where: E - transpiration rate [g m^{-2} s^{-1}]; P - leaf-air heat exchange rate [J m^{-2} s^{-1}]; ΔT - leaf-air temperature difference [K]; T - the mean leaf-air absolute temperature [K]; L - latent heat of evaporation (L = 2511 J g^{-1}); η_0 - specific humidity of saturated water vapour at the leaf surface at the corresponding leaf temperature (the leaf surface is considered as saturated) [g g^{-1}]. The release of energy from the respiratory substratum is accompanied by any losses, *i.e.* by any entropy production, quantified by the function of dissipation Φ in equation (Florov 1978, 1988):

$$-\Phi = P\frac{\Delta T}{T} + LE\Delta\eta \qquad [J\ m^{-2}\ s^{-1}] \qquad (2)$$

The sign minus indicates that the released energy is aimed to decline. The parameters P, T, ΔT, E, L are the same as in the equation (1); $\Delta\eta = \eta_o - \eta_a$ [g g^{-1}], where η_o and η_a are the values of specific air humidity at the transpiring leaf level and the surrounding air, respectively. The equation (2) is verified and used by a few other investigators (Batyuk 1973, Galoux 1974, Stoyanov 1975). The difference between the total energy released from the respiratory substrate $\Delta G/\Delta t$ (1) and the dissipated energy as a result from the entropy production ($-\Phi$) (2), represents the free energy accumulated in chemical bounds $(\Delta G/\Delta t)_a$, quantified by the equation (3), (Florov 1978, 1988). This part of the free energy is characterised by an integral criterion for free energy accumulation at plant organism level - the free energy balance (FEB) of a leaf system during the dark respiration:

$$FEB = (\Delta G/\Delta t)_a = -LE\eta_o + LE\Delta\eta \qquad [J\ m^{-2}\ s^{-1}] \qquad (3)$$

Our experimental studies have included the determination of corresponding amounts of free energy released from respiratory substrate according to equations (1), (2) and (3). For that purpose, some measurements were performed.

Experimental measurements: Transpiration rate during the dark (E) [g(H_2O) m^{-2} s^{-1}] was determined by the mass of single pot plants (five replicates), measured twice a day (down and dusk) and expressed on a leaf area basis; in order to prevent evaporation from the soil the entire pot surface was covered with plastic bags, tied around the plant stems. Leaf area was determined planimetrically. Leaf and air temperatures were measured with a system of five copper-constantan thermocouples, (with diameters 0.013 mm and 0.50 mm respectively). $\eta_o \cong 0.622\ e_o/p_s$, where p_s = 0.1 MPa is the standard atmospheric pressure, e_o - partial pressure of saturated water vapour was determined psychrometrically on the base of leaf temperature data. The specific humidity of the air $\eta_a \cong 0.622\ e_a/p_s$ was determined as η_o, but considering the partial water vapour pressure of the air e_a (on the base of the air temperature and relative humidity data). P [J m^{-2} s^{-1}] was calculated on the base of the radiation budget (R) equation during the dark period, R = 0 = P + LE. Measurements were performed daily in five replicates. All data were tested for significance by the analysis of variance (completely randomised design) and the *t*-test was used to evaluate the significance of RH treatments. Regression analysis was used to fit the studied relationships.

Results

The obtained data have indicated that air humidity during the dark has a significant influence on E, $\Delta G/\Delta t$, Φ, and FEB (Table 1) in all species examined. As it could be expected, E is significantly higher at the lower RH (~ 50 %) in the night-time. At the lower RH, an increase of $\Delta G/\Delta t$ values was observed, too. In spite of the higher values of Φ at these conditions, $(\Delta G/\Delta t)_a$ was also higher.

FEB of dark respiration was calculated daily for each plant species, and the sums for the whole period of RH treatment are presented in Table 2. The higher air humidity (RH ~ 95%) caused a statistically significant ($P < 0.001$) decrease in the FEB.

The close relationship between E and FEB of leaves during the dark $(\Delta G/\Delta t)_a$ was analytically described (Fig. 1). It is striking that, linear regression models fit the dependencies under high r^2 values (0.63 - 0.90) and 95 % coefficient of probability. Similar patterns were obtained for all examined species.

Table 1. Influence of air relative humidity, RH, on dark transpiration rate, E [$\times 10^{-2}$ g(H_2O) m^{-2} s^{-1}], free energy released during dark respiration, $\Delta G/\Delta t$ [$\times 10^{-1}$ J m^{-2} s^{-1}], entropy production, Φ [$\times 10^{-1}$ J m^{-2} s^{-1}], and FEB of leaf system during the dark, $(\Delta G/\Delta t)_a$ [$\times 10^{-1}$ J m^{-2} s^{-1}] in different plant species. Means (n = 5) ± S.E.

Species	RH ≈ 50 %				RH ≈ 95 %			
	E	$\Delta G/\Delta t$	Φ	$(\Delta G/\Delta t)_a$	E	$\Delta G/\Delta t$	Φ	$(\Delta G/\Delta t)_a$
*Quercus sessiliflora***	0.30 ±0.08	0.92 ±0.02	0.46 ±0.02	0.46 ±0.00	0.11 ±0.03	0.39 ±0.01	0.02 ±0.01	0.36 ±0.00
*Fagus silvatica***	0.28 ±0.03	0.98 ±0.02	0.29 ±0.02	0.69 ±0.00	0.11 ±0.01	0.60 ±0.02	0.16 ±0.01	0.45 ±0.01
*Fraxinus oxicarpa**	0.44 ±0.08	1.00 ±0.04	0.22 ±0.02	0.78 ±0.02	0.17 ±0.06	0.53 ±0.02	0.17 ±0.02	0.36 ±0.00
*Rubus idaeus**	0.47 ±0.11	1.30 ±0.10	0.22 ±0.03	0.80 ±0.08	0.22 ±0.06	0.56 ±0.09	0.14 ±0.03	0.41 ±0.06
*Phaseolus vulgaris***	2.47 ±0.33	11.24 ±1.45	5.50 ±1.42	5.74 ±0.02	0.92 ±0.06	4.22 ±0.33	0.38 ±0.05	3.84 ±0.28

Differences between two RH: * - $P < 0.05$, ** - $P < 0.001$.

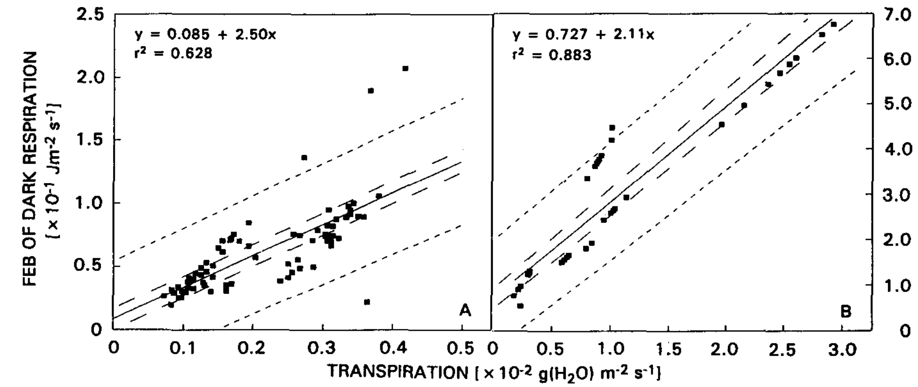

Fig. 1. Linear regression between FEB of dark respiration and dark transpiration rate for *Quercus sessiliflora* (*A*) and *Phaseolus vulgaris* (*B*). Doted lines indicate 95 % predicted limits of the regression model and dashed lines 95% confidence limits.

Table 2. Influence of RH regimes during the night on the FEB of dark respiration [$\times 10^{-1}$ J m^{-2} s^{-1}] for different plant species. Each FEB value is sum of the daily determined values over the whole experimental period.

Species	RH treatment [d]	FEB RH ≈ 50 %	RH ≈ 95 %
Q. sessiliflora	40	29.58	17.92
F. silvatica	30	20.72	13.41
Fr. oxicarpa[g]	65	30.18	21.22
R. idaeus	52	23.13	10.70
P. vulgaris	25	70.80	42.93

[g] - plants grown in greenhouse, other species were grown in air-conditioned chamber

Discussion

This study was provoked by the vision of Florov (1978, 1988) that the source of energy for biochemical reactions during the dark respiration is the free energy of moving water through a plant in the dark. This vision was stated after a thermodynamic description of the relationship between the processes going on the boundary leaf-air and the processes on molecular level. As a result, the quantitative expressions for the released free energy from respiratory substrate (1), its accompanied entropy production (2) and the free energy balance (FEB) of the dark respiration (3) were obtained. Florov (1978, 1988) has also experimentally established a quantitative coincidence between the dark respiration rate of leaves, determined according to the released CO_2 (in energetic units) and the free energy released from the respiratory substratum determined according to equation (1). These facts were considered as theoretical base of the presented study.

Hence in the present study the experimental plants were grown at uniform shoot environment during the light period and under well-watered conditions, the studied relationship was provoked by the differences in the RH during the dark. The principal difference of our experimental design in comparison with all previous (studying the humidity effects) is that we elucidate the effect of varying RH only during the dark. The choice of this experimental scheme was not accidental. We have considered that the FEB of dark respiration has a maximum value under 50 % RH, and it increase with the increase in air temperature till 30 °C (Florov 1983).

The results from this study have demonstrated a significant influence of the air humidity during the dark on all studied parameters E, $\Delta G/\Delta t$, Φ and $(\Delta G/\Delta t)_a$. E for all examined plants in our study was significantly reduced by the higher air RH during the dark (at least $P < 0.001$, Table 1). This is in conformity with the other authors (*e.g.* Rawson and Begg 1977, Hagemeyer and Waisel 1989). There was observed also a close agreement between the dark transpiration rate and the dark respiration (characterised by the free energy released from respiratory substratum and the FEB of dark respiration). Despite some differences in experimental conditions, plant species, duration in RH treatments, precision of environmental control (phytoclimatic chamber or greenhouse), the tendency of this relationship was uniform. Plants grown in the lower RH during the night had higher $\Delta G/\Delta t$ (Table 1). These results are in agreement with the those reported by Florov and Stoyanov (1970) who used different tree species and different RH. They emphazised the determining role of transpiration rate with respect to the dark respiration rate. At the lower RH the accumulation of free energy during the dark respiration, *i.e.* $(\Delta G/\Delta t)_a$ was also higher ($P < 0.05$, Table 2). The established dependencies are valid and statistically evaluated for different plant species - trees, bush and annual plant. The relationship between the FEB of dark respiration and E was fitted with linear regression models (Fig. 1). Press *et al.* (1988) have also found a close linear relationship between night-time rates of transpiration and respiration for hemiparasitic angiosperms. They have explained their results with the difference in the available photosynthate pool assured by the different transpiration rates, and as a consequence the observed increase in respiration. But we do not engage with such an explanation of the obtained results.

In conclusion, proceeding from the irreversible thermodynamics, this study highlights an energetic aspect of the relationship between transpiration and respiration during the dark period. This may be of use in directing future investigations, concerning plants metabolic response to different FEB of dark respiration.

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