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Thermodynamic balance of photosynthesis and transpiration at increasing CO_2 concentrations and rapid light fluctuations☆

Dolores Marín[a], Mercedes Martín[b], Patricia H. Serrot[b], Bartolomé Sabater[b,*]

[a] Department of Physical Chemistry, University of Alcalá, Alcalá de Henares, 28871 Madrid, Spain
[b] Department of Plant Biology, University of Alcalá, Alcalá de Henares, 28871 Madrid, Spain

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ABSTRACT

Experimental and theoretical flux models have been developed to reveal the influence of sun flecks and increasing CO_2 concentrations on the energy and entropy balances of the leaf. The rapid and wide range of fluctuations in light intensity under field conditions were simulated in a climatic gas exchange chamber and we determined the energy and entropy balance of the leaf based on radiation and gas exchange measurements. It was estimated that the energy of photosynthetic active radiation (PAR) accounts for half of transpiration, which is the main factor responsible for the exportation of the entropy generated in photosynthesis (S_g) out of the leaf in order to maintain functional the photosynthetic machinery. Although the response of net photosynthetic production to increasing concentrations of CO_2 under fluctuating light is similar to that under continuous light, rates of transpiration respond slowly to changes of light intensity and are barely affected by the concentration of CO_2 in the range of 260–495 ppm, in which net photosynthesis increases by more than 100%. The analysis of the results confirms that future increases of CO_2 will improve the efficiency of the conversion of radiant energy into biomass, but will not reduce the contribution of plant transpiration to the leaf thermal balance.

1. Introduction

Radiant energy is mainly consumed in the leaf to fuel photosynthesis and transpiration the estimations of which are essential for climate modelling and the understanding of vegetation (Berner, 1997; Chen et al., 2011) and water dynamics (Jasechko et al., 2013). The thermodynamics of the two processes have been frequently investigated both theoretically and experimentally (Ksenzhek and Volkov, 1998). From the agronomic perspective, attention has mainly focussed on the yield of chemical energy, from radiant energy, as an indicator of photosynthetic efficiency and on the concomitant water consumed and, mainly, lost in transpiration. In fact, the entropy production per unit of biomass synthesized is higher the lower the efficiency of energy use and the production of entropy in photosynthetic systems, as in microbial growth (von Stockart and Liu, 1999), reflects the Gibbs energy dissipation accompanying the production of biomass. However, formal estimations of the production of entropy are interesting in other aspects as well. As a measure of organization (Ksenzhek and Volkov, 1998; Marín et al., 2009; Davies et al., 2013), low entropy content is associated with the maintenance of leaf structure and function. Therefore, at least for a comparison with the magnitude of the low entropy associated with life, the production of entropy in the leaf is relevant. Photosynthesis and transpiration produce entropy that must be exported to maintain leaf structure and function, therefore increasing the global entropy as required for all irreversible processes (Schrödinger, 1944). However, due to the scant knowledge of entropy balances in photosynthesis and transpiration to date, a comparison with the estimations of negative entropy associated to cell organization is not possible.

On the other hand, most investigations so far have focussed on steady-state systems in which the leaf receives a constant light intensity at actual and free-air enriched CO_2 concentrations (Leakey et al., 2009). However, in the field, the leaf is very frequently exposed to rapid changes in light intensity (typically from 50 to about 1500 μmol photon m^{-2} s^{-1} PAR) due to transitory shadow produced by clouds, by other leaves fluttering in the wind and by animals (Külheim et al., 2002; Smith and Berry, 2013) that could differently affect photosynthesis and stomata aperture and transpiration. In addition, the responses to fluctuating light should be affected by the concentration of CO_2, which is the main substrate of photosynthesis and a negative modulator of stomata aperture. Taking also into account the concern regarding increasing

Abbreviation: PAR, photosynthetic active radiation.

* Corresponding author. Tel.: +34 918854934; fax: +34 918855066.
E-mail address: bartolome.sabater@uah.es (B. Sabater).

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concentrations of atmospheric CO_2, we have investigated how this affects the efficiency of energy use and the entropy production of the leaf under fluctuating light.

To investigate the thermodynamic parameters associated to photosynthesis and transpiration of leaves under rapid light intensity changes, we implemented a reference light fluctuation treatment previously assayed (Martín et al., 2009) consisting of 15 min of leaf acclimation at 130 μmol photon m^{-2} s^{-1} PAR, followed by four 6-min light phases of 870, 61, 870 and 130 μmol photon m^{-2} s^{-1} PAR at leaf surface. Tobacco leaves were used as the experimental model. The laboratory results were analysed with a thermodynamics model of fluxes that can be applied for field-based measurements.

2. Materials and methods

2.1. Plants culture

Assays were performed with tobacco (*Nicotiana tabacum*, cv. Petit Havana) plants cultivated as previously described (Martín et al., 2009). Seeds were sown in pots with compost soil substrate, germinated and grown in a glasshouse and regularly irrigated with Murashige/Skoog nutrient solution.

2.2. Measurement of net photosynthetic and transpiration rates and stomatal conductance

Assays were carried out in the glass house with intact attached fully-expanded healthy leaves (containing around 25 μg chlorophyll cm^{-2}) of the mid-stem of tobacco plants at the beginning of flowering. Photosynthetic activity, transpiration and stomatal conductance were measured during a light sequence treatment (in μmol photon m^{-2} s^{-1} PAR, photosynthetic active radiation, at leaf surface) with abrupt changes in intensity according to the sequence: 15 min acclimation at 130, 6 min at 870, 6 min at 61, 6 min at 870 and 6 min at 130 μmol photon m^{-2} s^{-1} PAR. Data collected each min and at light intensity transitions were directly represented using the Origin software (Princeton, USA). Experiments were repeated two to ten times. Net photosynthetic rates (in μmol consumed of CO_2 m^{-2} s^{-1}), transpiration (in mmol of H_2O m^{-2} s^{-1}) and stomatal conductance (in mol CO_2 m^{-2} s^{-1}) were determined in the glasshouse at 25 °C in 6.25 cm^2 leaf sections fitted on the chamber of the LCpro+ portable photosynthesis system (ADC BioScientific Ltd., Hertfordshire, UK) as previously described (Martín et al., 2009), except for the CO_2 concentration which, having been programmed as fixed during the light sequence treatment, varied as indicated. Registered data indicated that the sub-stomatal CO_2 concentration was stabilized (<5% variation) from the end of 15 min acclimation through the following 24 min incubation. PAR light was provided by mixed red (peak at 660 nm) and blue (peak at 470 nm) LED array unit monitored with a silicon-based sensor, which adjusts the power for constant output at the value set. Changes in light intensity was completed in less than 15 s, which the shortest possible time between two successive graphic lectures in the LPCpro+ photosynthesis system.

3. Results

3.1. Photosynthetic and transpiration rates under fluctuating light intensities. Effect of the concentration of CO_2

Net photosynthesis and transpiration rates varied for the same plant from one day and leaf to another. However, relative rates for different CO_2 concentrations were highly reproducible with differences that never exceeded 5%. Therefore, we determined

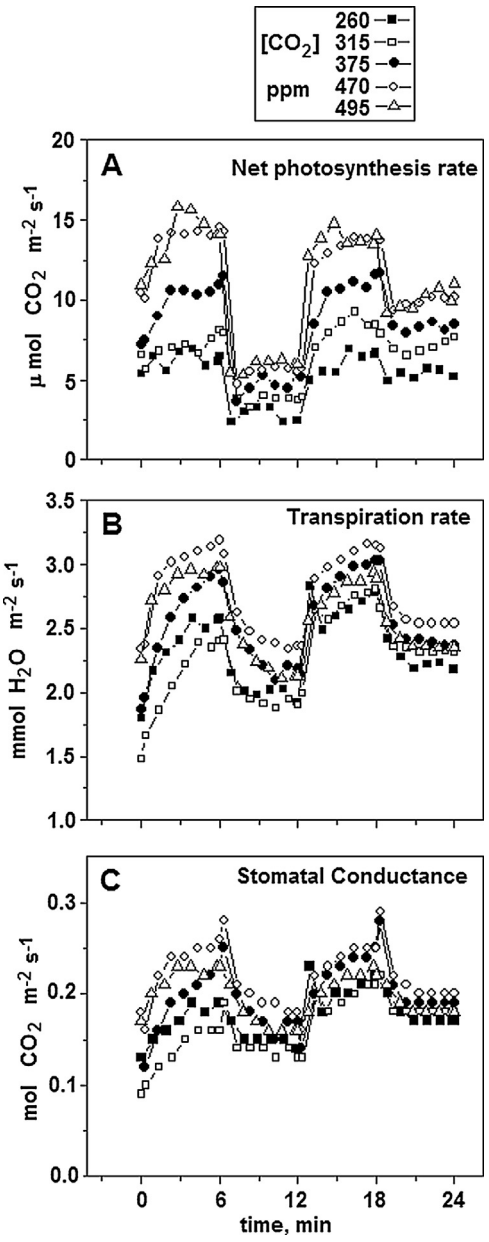

Fig. 1. Effects of the concentration of CO_2 on the photosynthetic (A) and transpiration (B) rates and stomatal conductance (C) under fluctuating light. After 15 min acclimation at 130 μmol photon m^{-2} s^{-1} PAR, the leaf region entrapped in the climatic chamber was subjected to successive 6 min periods (starting at 0 time in the figure) of light intensities, abruptly changing according to the sequence 870, 61, 870 and 130 μmol photon m^{-2} s^{-1} PAR. The concentration of CO_2 varied for each sequence of light treatments as indicated in the box.

rate responses for different CO_2 concentration assays carried out successively with the same leaf section by changing the CO_2 concentration. The 15 min acclimation was repeated for each CO_2 concentration and the order of the assays with different CO_2 concentrations (increasing or decreasing) did not affect the responses of photosynthesis and transpiration rates. Over 100 data of photosynthesis and transpiration rate data were collected in a single experimental session. Experiments were repeated without significant differences two to ten times and all curves in Fig. 1 correspond to one representative complete experiment.

Fig. 1A shows the evolution of photosynthetic rates during the four light phases after the 15 min acclimation of tobacco leaf at CO_2 concentrations ranging from 260 to 495 ppm. As expected, photosynthetic rates were greater at high than at low