

## Photosynthetic response of poplar leaves under varying quantum flux density

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### Introduction

Leaf photosynthetic capacities are usually measured under constant quantum flux density (*QFD*). But it could be asked how photosynthesis is established in rapidly changing illumination, as in the natural environment. Three responses are possible: 1) photosynthesis is independent of the previous *QFD*; the rate of the CO<sub>2</sub> metabolism is rapidly set to the photochemical activity; 2) low *QFD* generates an increasing request for photosynthetic products; as a consequence under high *QFD*, photosynthesis can be stimulated (Stitt, 1986); 3) energy is stored during the high *QFD* period and photosynthesis is transiently stimulated during the low *QFD* period. This effect has been reported in shade plants (Sharkey *et al.*, 1986). The response to varying *QFD* depends upon the time constant of various processes involved in CO<sub>2</sub> reduction and metabolism. Some of them are very fast, such as photochemical production of reducing power (1 s). Others are slower, such as the energization of the thylakoid membrane (10 s) and operation of the Calvin cycle (several min). The response depends also upon the frequency of the *QFD* variation (Rabinowitch, 1956; Gau-

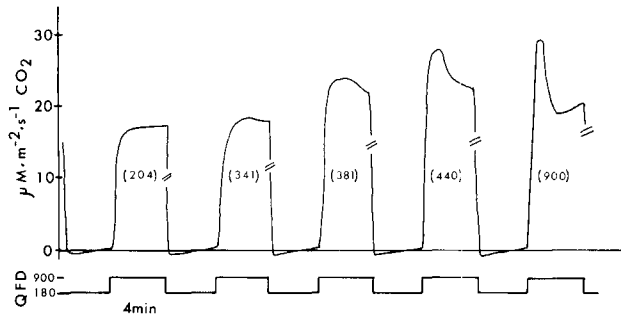
dillère, 1974). This paper reports effects on the photosynthetic rate of poplar leaves illuminated by a low frequency varying quantum flux density. It is concluded that, in poplar leaf, photosynthesis under high *QFD* oscillates after the low *QFD* treatment. This phenomenon depends upon the rate of CO<sub>2</sub> assimilation and the genotype.

### Materials and Methods

Poplar cuttings were grown in a growth chamber under constant high *QFD* (700  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). Net CO<sub>2</sub> and water exchange were measured on attached leaves, studied in a small cuvette (25 ml) to reduce to a minimum the response time of the device (Gaudillère *et al.*, 1987). High *QFD* was 1000  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and low *QFD* was 180  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . High and low *QFD* were applied successively at 4 min intervals (period = 8 min).

### Results

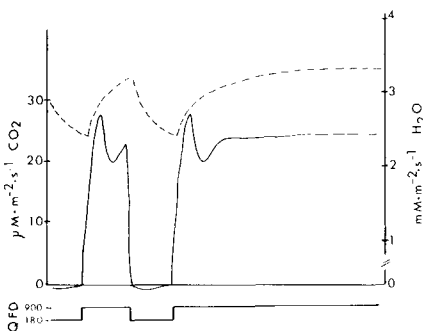
Fig. 1 presents the variations of photosynthesis of *Populus trichocarpa* (cv *Fritzi Pauley*) under varying *QFD* at different CO<sub>2</sub> contents in the gas phase. The net



**Fig. 1.** Kinetics of net  $\text{CO}_2$  exchange of poplar leaves (clone *Fritzi Pauley*) at different internal  $\text{CO}_2$  concentrations (between parentheses), after the increase of the quantum flux density ( $QFD$ ). Duration of the illumination sequences: 4 min.

$\text{CO}_2$  uptake increased with the  $\text{CO}_2$  content. Photosynthesis increased transiently when high  $QFD$  was applied. A low light treatment was followed by a transitory stimulation of photosynthesis under high light. If high  $QFD$  was maintained for a long time, a 2nd induction of photosynthesis occurred. The stomatal conductance increased but the change in the internal  $\text{CO}_2$  content was not sufficient to explain the change in the photosynthetic rate (Fig. 2). A periodic variation of  $QFD$  showed that this oscillatory phenomenon was reversible. It was induced by the low

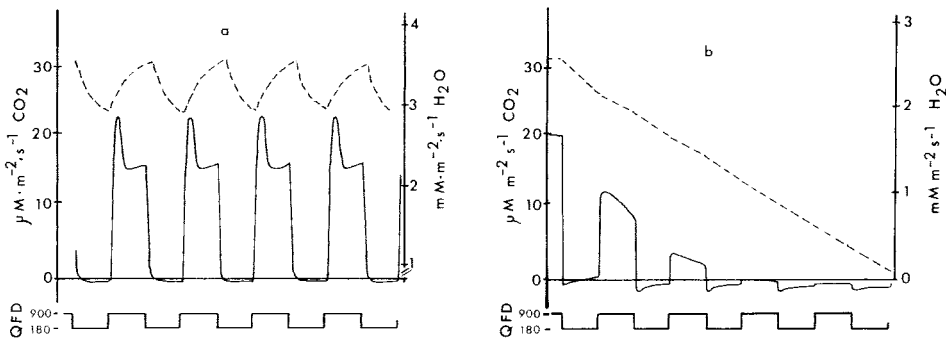
light period (Fig. 3a). Different cultivars of poplars have been examined in this respect (*Populus trichocarpa* clone *Fritzi Pauley*; *P. trichocarpa* x *P. deltoides*, clones *Unal*, *Beaupré*; *P. x euramericana*, clone *1214*, *P. deltoides*). One clone (*Beaupré*) responded differently. When varying  $QFD$  was applied, photosynthesis was rapidly inhibited (Fig. 3b). The low  $QFD$  period induced a general inhibition of the photosynthetic apparatus. Re-activation of leaf photosynthesis could be obtained only when high constant  $QFD$  was maintained for a long time.



**Fig. 2.** Kinetics of net  $\text{CO}_2$  and  $\text{H}_2\text{O}$  exchanges of poplar leaves (clone *Fritzi Pauley*) under varying  $QFD$  then under permanent high  $QFD$ .

## Discussion and Conclusion

The photosynthetic response during the low  $QFD$  phase was not significantly different from the constant low  $QFD$  control. Conversely, during the high  $QFD$  phase, the net  $\text{CO}_2$  assimilation rate oscillated. An internal regulatory process in the  $\text{CO}_2$  metabolism occurred. This phenomenon was amplified when environmental conditions favored a high net  $\text{CO}_2$  uptake (high  $\text{CO}_2$  content in the gas phase). The photosynthetic threshold was approximately  $20 \mu\text{mol}$  of  $\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . This



**Fig. 3.** Kinetics of net CO<sub>2</sub> and H<sub>2</sub>O exchanges of poplar leaves under varying QFD, each sequence 4 min. **a.** Clone *Fritz Pauley*. **b.** Clone *Beaupré*.

regulatory process has already been observed during the induction of photosynthesis or after an increase of the CO<sub>2</sub> concentration in the gas phase (Walker *et al.*, 1983). The phosphate metabolism could be involved, since it has been demonstrated to be critical at saturating light and CO<sub>2</sub> (Dietz and Foyer, 1986).

In the *Beaupré* clone, we observed a new response to varying illumination. The low QFD time initiated an inhibition of the net CO<sub>2</sub> uptake. The phenomenon continued during the following high QFD period and photosynthesis was rapidly totally inhibited. These leaves were able to photosynthesize under constant illumination. We suggest that they are unable to establish efficiently the different fluxes involved in carbon metabolism under fluctuating environmental conditions. Photosynthesis collapsed rapidly. The same clone cultivated in a greenhouse was not inhibited by varying illumination (data not shown). Constant illumination of the leaves in the growth chamber could explain their behavior.

The net CO<sub>2</sub> uptake of leaves under varying illumination at a low frequency involves many physiological and genetic characteristics. The response depends upon the accuracy of the initiation of the

photochemical, biochemical and translocation processes. This procedure is slow. Fluctuating illumination is always less effective for photosynthesis than constant illumination. These experimental conditions can be used to measure the metabolic setting capabilities of a clone to a fluctuating environment.

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