Plant Physiol. (1976) 58, 91-94

Physiological Characteristics of Photosynthesis and Respiration in Stems of *Populus tremuloides* Michx.[1]

Received for publication January 19, 1976 and in revised form March 25, 1976

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ABSTRACT

The physiological responses of 6- to 8-year-old aspen (*Populus tremuloides* Michx.) stems to temperature, light, and CO_2 concentration were investigated in the field throughout the year using infrared CO_2 analysis. Light response studies showed that the rate of gross photosynthesis was linear from 0 to 400 ft-c (0 to 1.6 mw/cm^2 of 400-700 nm) with light saturation being reached between 800 to 1400 ft-c (3.2 to 5.6 mw/cm^2 of 400-700 nm). At this light intensity, the respiratory CO_2 loss was reduced to 10 to 15% of dark rates. Net photosynthetic CO_2 uptake was not observed even at intensities as high as 3400 ft-c (13.6 mw/cm^2 of 400-700 nm). The light response curve was similar for both winter and summer stems.

During summer months, the respiratory and photosynthetic rates of the aspen stem increased with temperature at a near constant rate between 5 and 35 C. For winter stems, the gross photosynthetic rate increased in a pattern similar to the dark respiratory rate as the temperature rose from 3 to 17 C. Below 0 C and above 17 C, however, the gross photosynthetic rate fell off in relation to the respiratory rate so that the per cent of CO_2 reassimilated decreased from 75% to less than 50%. Measurable bark photosynthetic activity was not observed below −3 C.

The gross photosynthetic rate of stems was not affected when the gas passing through the cuvette contained concentrations of CO_2 ranging from 0 to 580 μl CO_2/l air.

Twigs and stems of living shrubs and trees have a greenish corticular layer just beneath the bark surface. The green pigment is Chl which is concentrated in photosynthetically active chloroplasts (17). Photosynthesis by the stem is termed corticular photosynthesis (20) or bark photosynthesis.

Most species in which bark photosynthesis has been investigated were not capable of net photosynthesis, but stem photosynthesis did reduce substantially the respiratory loss of CO_2 from the stem (1, 8-10, 13, 16, 19). Little is known, however, about the response of bark photosynthesis to changes in environmental parameters. The purpose of this research was to investigate the effects of light intensity, temperature, and CO_2 concentration on *Populus tremuloides* Michx. (aspen) bark CO_2 exchange. Chl analysis of the green bark layer has revealed that on a surface area basis, the Chl concentration is similar to the Chl content of aspen leaves (3, 14, 17), making it a promising organism for this study of both physiological and ecological aspects of bark photosynthesis (4).

MATERIALS AND METHODS

One dozen 3- to 5-year-old trees from a single clone were transferred to the Syracuse campus in May 1971. Each tree was transplanted into a wooden box (46 cm wide × 46 cm long × 52 cm high) containing a sandy loam soil mixture (pH 6.4-6.8). The boxes were placed in an east-west row with the stem-to-stem distance between the boxes 60 to 75 cm. A superstructure of angle iron was built over the boxes to support experimental equipment.

Each box received a 113-g application of 15-15-15 (NPK) fertilizer supplemented with 1 tablespoon of Sequestrene 330 Fe every 5 to 6 weeks throughout the summers of 1971 and 1972. No fertilizer was added in 1973. The trees were watered every 1 to 3 days so that the soil moisture tension in each box was maintained between 0 and 100 centibars. Extensive use of the trees was started 1 year after the transplanting to allow for site adjustment. The boxed trees were healthy and vigorous as evident from the rates of shoot growth, the color and size of the leaves, and the width of the growth rings. Bud break occurred April 18 to 25, 1973; leaf fall, October 12 to 26, 1973. Bark slippage commenced in mid-April and ceased in October. Stem diameters were observed to increase from mid-May through mid-August.

Photosynthetic and respiratory CO_2 exchange rates were measured using a 30-cm, water-cooled, acrylic plastic cuvette consisting of two halves that could be placed around the stem and sealed with no apparent injury to the stem (5). To reduce water, CO_2, and heat gradients within the cuvette, an air recirculation system was used with the cooling coils submerged in water or a water-ethanol mixture depending on the operating temperature (5).

An open system was used from June to August when gas exchange rates were high. During the remainder of the year, measurements were carried out with a closed system (5). The closed system was connected with 92 m of tygon tubing (0.6 cm i.d., 0.9 cm o.d.), and the open system with one-half of this amount. Even though tygon tubing has the lowest CO_2 permeability of a number of different types of tubing (11), the leakage rate of the tubing was determined with the cuvette placed on a 2.5-cm diameter copper pipe. With 440 μl CO_2/l air, the leakage rate was 0.1 mg CO_2/dm^2·hr at 20 C for the closed system and one-half of this rate for the open system. This rate decreased at lower temperatures. To minimize this error, the CO_2 concentration was not allowed to increase by more than 50 μl CO_2/l over ambient levels (320 ± 20 μl/l) in the open system and 30 μl CO_2/l in the closed system.

The air intake for the open and closed systems was located 10 m above the ground to reduce CO_2 concentration fluctuations in the entering air. The air from the cuvette was pumped with diaphragm pumps to an adjacent laboratory for measurement of CO_2 content. After adjustment of the gas temperature to a constant value (20 C) followed by dehydration, the CO_2 content

[1] This research is part of the dissertation submitted by K. C. F. in partial fulfillment of the Ph.D. requirements.

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of the air in both systems was measured with a Beckman 215A IR gas analyzer.

Temperatures were measured on two sides of the stem within the cuvette and compared with the temperatures of similarly placed thermocouples on an adjacent stem (5). The temperature was determined using 0.125-mm diameter copper-constantan thermocouples. The measuring junctions were gently pushed into the periderm-corticular region. The two lead wires, each 25 cm long, were extended above and below the measuring junction and secured to the stem with nylon monofilament fishing line to expose them to similar isotherms.

In the following studies, to avoid complications arising from fluctuating sunlight, the stems were exposed to artificial illumination provided by six new Sylvania 300-w flood lamps which provided up to 3600 ft-c (14.4 mw/cm^2 of 400–700 nm). Three ring stands were positioned around the cuvette at a distance of 25 cm, and two bulbs were mounted on each stand. In front of the bulbs on each stand was a 6-mm-thick sheet of acrylic plastic.

Light intensity and quality of the artificial light source were measured using a Weston light meter calibrated with an ISCO SRR spectroradiometer to permit determination of the energy output by the flood lamps between 400 and 700 nm.

RESULTS

Stem Response Times to Light and Temperature Changes. Two different measurements were performed using IR gas analysis: the CO_2 release rate in the dark to estimate the rate of dark respiration, and the CO_2 release rate in the light to determine the effect of light on the rate of CO_2 release. Exposure to saturation light intensity resulted, not in net CO_2 uptake by the chlorophyllous stem, but only in a reduction in the rate of CO_2 release from the stem (see under "Light Response Studies"). Therefore, the difference between the dark and light release rates represents the gross (total) rate of photosynthesis of the stem.

To assure that all measurements were steady state, it was essential to know the time required for the stem CO_2 release rate to reach a dynamic equilibrium during the light-dark transitions. This transition time would also give insight into the response of a stem to sudden natural changes in light intensity such as sunflecks penetrating the canopy.

Figures 1 and 2 show the time necessary for the CO_2 release rate to reach a steady state during dark to light and light to dark transitions. Achievement of a steady state required 20 to 30 min. As expected, such changes in illumination were accompanied by changes in temperature. A comparison of Figure 1 (constant temperature) with Figure 2 (changing temperature) suggests that the change in flux rate was apparently independent of temperature within the limits of the sensitivity of the over-all system. This result suggests that the changes in measured CO_2 fluxes during dark to light transitions are not under simple kinetic control.

Light Response Studies. The effect of light on the CO_2 release rate from the stem was determined on January 26, February 22, July 3, 10, 11, and 16, 1973. To insure complete control over light conditions, the winter curves were determined at night, and the summer light curves during the daytime necessitating that a large enclosure of black polyethylene be built around the lights and the cuvette. Light intensity was varied by placing up to 10 layers of 1.5-mm mesh aluminum screening on the sheet of acrylic plastic in front of the bulbs. Temperature control was maintained by the water-cooling system in the cuvette water jacket, the air recirculation system of the cuvette, the 6-mm-thick acrylic plastic sheets which acted as IR heat filters, and a 35-cm-diameter fan used to dissipate heat from the flood lamps. The light intensity was measured by placing the target of a Weston illumination meter No. 756 at 18 different positions around the outside wall of the cuvette and averaging the values. The mean value was adjusted for the 2.5-cm distance between the outer cuvette wall where the light intensities were measured and the actual surface of the stem.

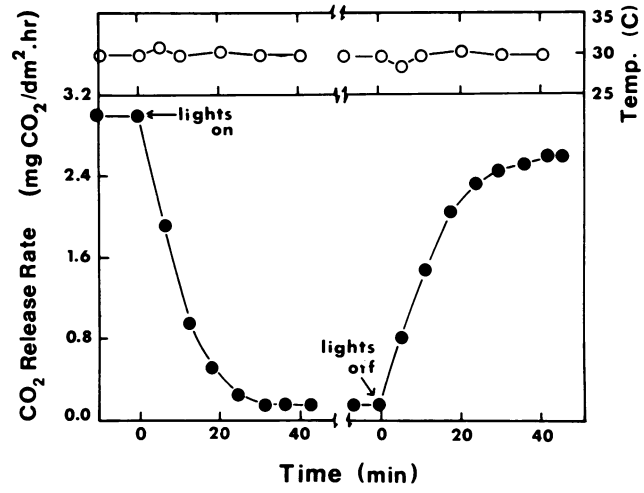

FIG. 1. Typical response change in the rate of CO_2 released from a stem going from dark to light and vice versa conditions at 30 C. Illumination around the cuvette, 1200 ft-c (4.8 mw/cm^2). Each point is the mean of three determinations. Experiment conducted August 22, 1973.

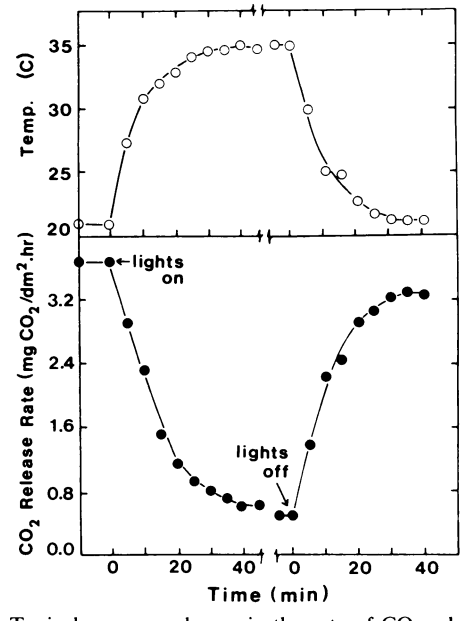

FIG. 2. Typical response change in the rate of CO_2 released from a stem going from dark to light and vice versa conditions accompanied by a temperature change. Illumination around the cuvette, 1200 ft-c (4.8 mw/cm^2). Each point is the mean of three determinations. Experiment conducted August 21, 1973.

Figure 3 shows the typical effect of light on the CO_2 release rate for summer stems. As the light intensity was increased, the rate of CO_2 loss from the stem was reduced by bark photosynthesis. However, the light compensation point was not reached so that CO_2 was released at all light intensities. When the rate of gross photosynthesis was plotted as a function of light intensity, the light response curves from this and three other stems had a linear portion between 0 to 400 ft-c (0–1.6 mw/cm^2) and a saturation plateau beginning between 1000 to 1400 ft-c (4.0–5.6 mw/cm^2), a characteristic plateau of shade plants (12, 15).

The light intensity response curves of winter stems showed remarkable similarity to the summer stem despite the fact that the winter stem had been exposed to a number of subfreezing days (Fig. 4). The cardinal light points of the winter stem light

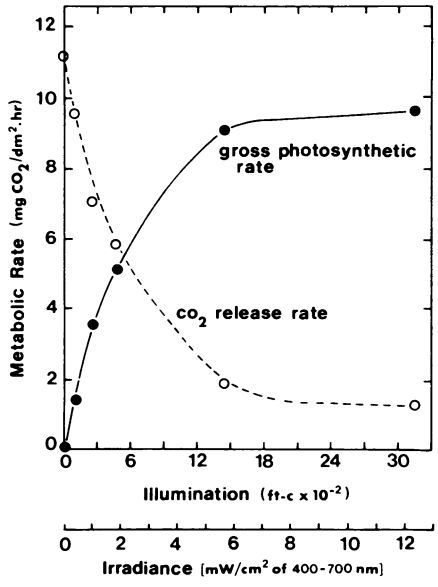

FIG. 3. CO_2 release rate and gross photosynthetic rate from a summer stem as a function of light intensity. Each point is the mean of three determinations. Temperature, 26 to 28 C; zero ft-c = dark respiratory rate; stem diameter, 3.3 cm. Experiment conducted July 16, 1973.

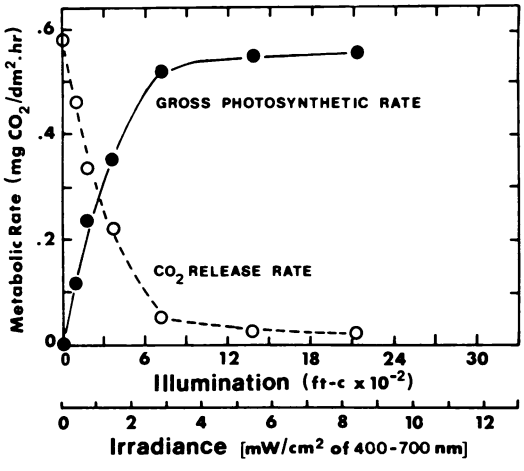

FIG. 4. CO_2 release rate and gross photosynthetic rate from a winter stem as a function of light intensity. Each point is the mean of two determinations. Temperature, 10 to 12 C; zero ft-c = dark respiratory rate; stem diameter, 3.3 cm. Experiment conducted February 22, 1973.

response curve were similar to the summer stem except that levels of illumination required for 50% and 100% saturation were moderately lower. This could be the consequence of a lower bark Chl concentration during winter which would permit saturation at lower light intensities (16).

The winter and summer light response curves showed that at saturation light intensities, the winter stem had the capacity to reassimilate 85 to 90% of the respiratory CO_2 and the summer stem 90 to 92%.

Temperature Response Studies. The respiratory and gross photosynthetic rates for winter stems (*i.e.* dormant, nongrowing) were determined as a function of temperature between 3 and 30 C on two different trees, one on January 22, and the other on March 3, 1973. Values for temperatures below 3 C were taken from diurnal measurements during this period using the same two trees. Temperature response curves for summer stems (*i.e.* nondormant, growing) between 5 and 35 C were obtained on July 20, 23, and 30, 1973. On each test day, a different tree was assayed. At each temperature, the dark and light measurements were repeated until three consecutive, consistent rates were obtained, a process requiring from 50 to 120 min. Illumination for photosynthesis was 1200 ft-c (4.8 mw/cm^2).

For summer stems, the photosynthetic and respiratory rates increased at a near constant rate for the entire temperature range with temperature coefficient (Q_{10}) varying between 1.6 and 1.8 (Fig. 5). The gross photosynthetic rate ranged from 84 to 92% of the respiratory rate over the temperature range 5 to 35 C.

For winter stems, the respiratory rate increased was curvilinear from 3 to 30 C (Fig. 5). Q_{10} values ranged from 1.5 between −12 to 10 C to 3.4 between 10 to 30 C. In general, the gross photosynthetic rate increased with temperature in a pattern similar to the respiratory rate, except for a flatter response at higher temperatures. Bark photosynthesis reassimilated 75 to 80% of the respiratory CO_2 between 3 and 17.5 C, but only 54% at 30 C. Measurable photosynthesis stopped at −3 C. It might have been possible to detect CO_2 metabolism at lower temperatures if the more sensitive $^{14}CO_2$ incorporation method was used.

Winter respiratory rates at the same temperature were half those observed during the summer. The rates of photosynthesis showed a similar pattern, but the decline was more dramatic.

CO_2 Concentration Response Studies. Carbon dioxide concentration effects on the release of CO_2 from a single illuminated stem were determined on September 20, and 25, October 4, 16, and 19, 1973. CO_2 concentration effects on dark release rates were determined October 5, 6, 9, and 11, 1973. The temperature of the stem during the assays was 22 to 24 C and the illumination was a saturation level of 1200 ft-c (4.8 mw/cm^2) around the cuvette surface. The CO_2 concentrations used were 0 μl/l, 180 μl/l, 330 μl/l, 440 μl/l, and 580 μl CO_2/l of air.

Stem dark and light CO_2 release rates with the different CO_2 concentrations were recorded after the release rates had become constant, usually 30 to 60 min. This time period was required for

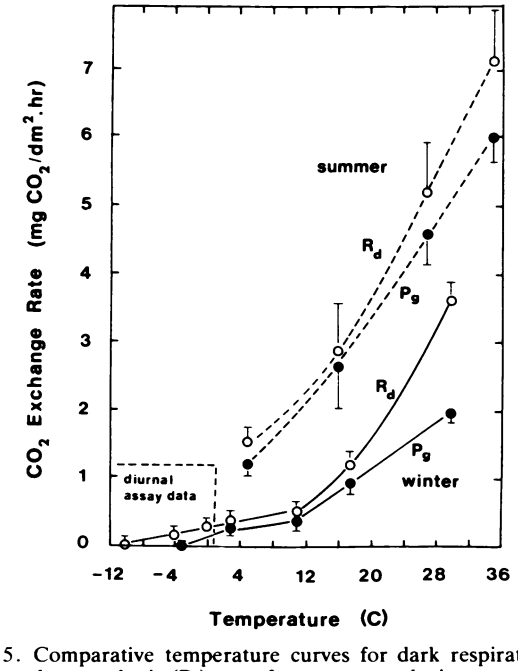

FIG. 5. Comparative temperature curves for dark respiratory (R_d) and gross photosynthetic (P_g) rates for summer and winter stems. Summer data obtained on July 20, 23, and 30, 1973; winter data obtained on January 22 and March 3, 1973 except for below 3 C data which were obtained from diurnal assays conducted between January and March, 1973. Illumination around the cuvette, 1200 ft-c (4.8 mw/cm^2). Each point is the mean of six to nine determinations from two to three trees. Vertical bars represent 1 SE of the mean.

metabolic adjustment and for a constant leakage rate to be established through the wall of the tygon tubing. The leakage rate was determined for each CO_2 concentration and corrected for in computing the results.

Carbon dioxide concentrations between 0 and 580 μl CO_2/l air had no apparent effect on the rate of photosynthesis. When CO_2 concentrations were increased above ambient levels (440 and 580 μl/l), net photosynthesis was not observed. The dark respiratory rate showed a nonsignificant declining trend amounting to 50% as the external CO_2 concentration increased from 0 to 580 μl CO_2/l air.

DISCUSSION

The aspen stem is covered on the outside by the phellem which appears to have waxy deposits on its surface. If the phellem layer was removed, the more open structure of the lower peridermal-corticular regions was observed. Shepard (18) found that the removal of the phellem in *Populus grandidentata* increased 95-fold the light-dependent $^{14}CO_2$ incorporation of the bark, suggesting that the phellem and other tissues of the periderm layer are a major resistance to gas exchange. It is doubtful that bark stomata and lenticels greatly increase gas permeability of the internal tissues to the outside air. Stomata in *P. tremuloides* were found only in 1-year-old stems at a density of 20 to 30/cm^2 and the majority rapidly occluded as a result of periderm formation beneath the lenticels during the 1st year's growth. The lenticels on 6- to 8-year-old stems are sparsely located (1 to 2/cm^2). Thus, gases are forced to move through the dense phellem, and to a lesser extent, the lenticels of mature stems (6). The low gas permeability of the stem to gases is reflected by the 20 to 30 min needed to establish a new gas diffusion steady state in the transition from light to dark and vice versa (Figs. 1 and 2).

The process of bark photosynthesis is light-saturated between 800 to 1400 ft-c (Figs. 3 and 4). It has been estimated that 10 to 20% of the incident light passes through the phellem (18, 20) so that saturation would occur between 80 to 280 ft-c. Such a light saturation point is low even for shade plants. If the analogy to shade leaves is correct, the rate of bark photosynthesis could be limited by the concentration of the chloroplastic CO_2 fixation enzymes.

During midsummer, under conditions of saturation illumination around the stem, bark photosynthesis reached 5 to 6 mg CO_2/dm^2·hr. Winter rates were lower and did not exceed 1.5 to 2 mg CO_2/dm^2·hr (Fig. 5). Similar reductions of the rates of winter bark photosynthesis were also observed using bark tissue slices in Warburg manometry under near optimal temperature and light conditions (16). Thus, the reduced winter rate CO_2 gas exchange does not reflect the seasonal changes in bark permeability or internal CO_2 concentrations, but is the result of modifications of the metabolic machinery of the stem.

The excess of respiration over photosynthesis combined with high phellem diffusion resistance increased the internal stem CO_2 concentration in stem gas during summer months to 5 to 15% (2, 7, 21). We would, therefore, not expect that the moderate changes in external CO_2 concentrations would greatly increase the rate of bark photosynthesis in this species.

Acknowledgments – We sincerely wish to thank L. P. Herrington and J. W. Geis for their technical assistance, and H. E. Wilcox for reviewing this manuscript.

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