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Diurnal and Seasonal Patterns of Photosynthesis and Respiration by Stems of *Populus tremuloides* Michx.[1]

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KNOWLTON C. FOOTE[2] AND MICHAIL SCHAEDLE[3]
Department of Botany and Forest Pathology, State University of New York, College of Environmental Science and Forestry, Syracuse, New York 13210

ABSTRACT

The photosynthetic and respiratory rates of 5- to 7-year-old aspen stems (*Populus tremuloides* Michx.) were monitored in the field for 1 year to determine the seasonal patterns. The stem was not capable of net photosynthesis, but the respiratory CO_2 loss from the stem was reduced by 0 to 100% depending on the time of year and the level of illumination as a result of bark photosynthesis. The monthly dark respiratory rate ranged from 0.24 mg $CO_2/dm^2 \cdot hr$ in January to a maximum 7.4 mg $CO_2/dm^2 \cdot hr$ in June. Individual measurements ranged from 0.02 mg $CO_2/dm^2 \cdot hr$ in February to 12.3 mg $CO_2/dm^2 \cdot hr$ in June. Gross photosynthesis followed a pattern similar to the dark respiratory rate. The mean monthly rate was highest in June (1.65 mg $CO_2/dm^2 \cdot hr$) and lowest in December (0.02 mg $CO_2/dm^2 \cdot hr$). Individual measurements ranged from 0.0 mg $CO_2/dm^2 \cdot hr$ in winter to 5.5 mg $CO_2/dm^2 \cdot hr$ in July.

Winter studies showed that stem respiration continued down to −11 C, the coldest temperature during this study. Upon warming to −3 C, the dark respiratory rate showed a sudden sharp increase (7- to 12-fold) which required many hours to return to normal levels. No measurable photosynthesis occurred below −3 C. Between −3 and 0 C, the maximal photosynthetic rate was reduced to less than 50% of the respiratory rate, but increased to 89% between 5 to 10 C.

On a yearly basis, bark photosynthesis in *P. tremuloides* reduced the stem respiratory CO_2 loss by 28.7% on a daytime basis and an estimated 16 to 18% on a 24-hour basis.

Bark photosynthesis has been demonstrated in twigs and stems in a variety of species (12, 15, 17, 20). With few exceptions (18, 22), mesophytic, ligneous stems were not capable of net photosynthesis, but bark photosynthesis did reduce the respiratory CO_2 loss from the stem.

No information is available on the day-to-day field performance of bark photosynthesis. This investigation determined diurnal and seasonal patterns of respiration and photosynthesis of young aspen stems under year-round field conditions that exist in central New York.

MATERIALS AND METHODS

Field Material. All experimentation used 6- to 8-year-old aspen trees (*Populus tremuloides* Michx.) from a single clone (PH). Trees were transplanted from the field to wooden boxes on the Syracuse campus. The silvicultural treatment of these trees has been previously described (7). For clonal comparisons, trees representing three other clones were also planted in boxes at the same site and treated similarly to clone PH.

Stems received shade from nearby trees which blocked 10 to 14% of incoming radiation during leafless months and up to 35% during months when the trees were in leaf. When the aspens were in full leaf, up to 70% of incoming radiation was blocked from the stem by the trees' own canopy. During periods of direct insolation, stems received up to 6,000 ft-c normal to the stem surface on the sun side and 500 to 1500 ft-c on the shade side.

Phenological events were as follows: cessation of bark slippage, last week of August 1972; leaf fall, last week of November 1972; initiation of bark slippage and bud break, April 18 to 25, 1973.

Greenhouse Material. To evaluate the effect of freezing temperatures on the seasonal pattern of bark photosynthesis, four 6- to 8-year-old trees (clone PH) were grown in a greenhouse. Trees received normal sunlight, but the temperature was adjusted so that night temperature in the greenhouse was maintained between 10 to 15 C while the day temperature ranged between 15 to 35 C. Leaf fall and leafing out occurred within 5 to 10 days of the trees out-of-doors.

Gas Analysis. Photosynthetic and respiratory rates were determined using a closed system from September to June. An open system had to be used during June, July, and August to accommodate high rates of CO_2 exchange (6). Tygon tubing, the leakage rate of which was less than 0.1 mg $CO_2/dm^2 \cdot hr$ for the open system and less than 0.02 mg $CO_2/dm^2 \cdot hr$ for the closed system (5), was used in both systems. Carbon dioxide concentration was measured with a Beckman 215A IR gas analyzer using a flow rate of 240 l/hr (6). The acrylic stem assimilation chamber consisted of two 30-cm water-cooled halves suitable for stems up to 3.5 cm in diameter (6). Bark 5 to 7 years old was always assayed. Stem area within the cuvette was calculated from the average of two diameter measurements above and two below the cuvette.

Seasonal patterns of photosynthesis and respiration were determined from weekly diurnal (daytime) assays from July 1972 through July 1973. Instrumentation was turned on 2 hr prior to taking an assay. For respiratory measurements, the cuvette was surrounded with black polyethylene plastic which was removed for photosynthetic measurements. Photosynthetic and respiratory rates were measured alternately at 35- to 40-min intervals, the time necessary to re-establish a steady state after dark/light perturbations (7), from sunrise to sunset.

Climatological Data. Climatological parameters measured were light intensity at the cuvette, temperatures on the north and south sides of the stem within, and on a stem adjacent to the cuvette (7). Stem temperatures in Figures 1 to 4 are equilibrium stem temperatures of the dark phase as determined by thermo-

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[2] Present address: Division of Science and Mathematics, Eisenhower College, Seneca Falls, N. Y. 13148.

[3] To whom reprint requests should be addressed.

couple junctions embedded in the periderm. The thermocouple reference junction was contained in a Leeds and Northrup Speedomax W recorder. The thermocouples were checked for accuracy with a Hewlett-Packard quartz thermometer and were within ± 0.1% of National Bureau of Standard curves. The over-all tolerance of the measuring and reference junctions and the recorder was ±0.3 C.

Solar radiation at the stem was measured with a Kipp and Zonen CM-5 solarimeter positioned at the base of the cuvette next to the stem. A Weston photometer, model 756, was used to measure the level of illumination on the sun and shade sides of the stem. The light target of the photometer was placed against the surface of the cuvette and rotated around the cuvette until the highest and lowest levels of illumination were observed.

RESULTS

From July 1972 through July 1973, the monthly mean ambient temperature ranged from 23 C in July to −6 C in February with the lowest winter temperature being −24 C. The temperature was at or below 0 C on 188 days. The first frost occurred October 10, and the last 0 C day was April 15.

CO_2 released under light conditions by stem respiration and possibly photorespiration in *P. tremuloides* always exceeded any CO_2 uptake so that net photosynthesis was not observed. The bark photosynthetic rate is the gross (total) photosynthetic rate calculated by subtracting the smaller CO_2 release rate under light from the larger CO_2 release rate under dark conditions expressed in units of mg $CO_2/dm^2 \cdot hr$.

Summer-Fall Diurnal Patterns. The assay of July 5 to 6 (Fig. 1A) is representative of the period from mid-May through October. Stems received partial shade primarily from their own canopies. The stem respiratory rate followed closely the temperature course during the day. However, during morning hours as the temperature increased, the respiratory rate did not reach the same level that occurred in the afternoon at the same temperature. Woodwell and Tempel (personal communication) observed similar results in pine stems at the Brookhaven National Laboratory Forest.

At sunset in 19 out of 45 diurnal assays, the respiratory rate either remained constant or increased and did not follow the decreasing temperature (Figs. 1-3). The respiratory rate increased in some assays by as much as 50% and lasted for 0.5 to 2 hr. This respiratory rise was observed mainly on bright sunny days. A similar postsunset respiratory increase has been described in Douglas fir branches by Helms (10).

Changes in the gross photosynthetic rate were correlated with the respiratory rate and the incident light intensity (Fig. 1A). Shortly after sunrise (05:32), stem photosynthesis commenced and increased sharply in early morning hours as stem light intensity increased to 1/10 full sunlight to reduce the respiratory CO_2 loss up to 65%. The gross photosynthetic rate continued to increase throughout the day paralleling the respiratory rate and temperature. Peak photosynthetic activity occurred between solar noon and midafternoon.

On a cloudy summer day (Fig. 1B) when illumination did not exceed 1200 ft-c on the sun-exposed surface and 400 ft-c in the shade, photosynthetic rates were lower than in Figure 1A and the erratic pattern was due to the illumination fluctuating between 0 to 0.2 langleys/min, the range of peak sensitivity for bark photosynthesis to light intensity (7). Peak reassimilation was 30%.

Winter Diurnal Patterns. The patterns of photosynthesis and respiration during winter months (November through March) depended primarily on stem temperature. For temperatures above 0 C, respiratory and photosynthetic rates responded to light and temperature similar to summer-fall patterns, but were generally 1 to 10% of the summer rates (Fig. 2A). On February 20 (Fig. 2A), the respiratory CO_2 loss from the stem was reduced by up to 89% (13:25).

For temperatures between −5 and 0 C, stem respiratory patterns depended on the direction of temperature change during the assay. If stem temperature remained constant or decreased slightly during the day, the rate of respiration decreased 33 to 75% (Fig. 2B). Such a respiratory pattern was observed during four diurnal assays (5). If the stem temperature increased from below −4 C to above −2 C during the assay, a rapid sharp increase in respiratory rate could be observed. On February 28 (Fig. 2C), the respiratory rate increased 10-fold in 1 hr as stem temperature increased from −4.5 to −2 C. This rise was followed by a gradual decline to normal levels. Similar patterns showing respiratory jumps from 7- to 12-fold over 2 hr were observed on several other occasions (5).

Below −5 C (Fig. 2D), the respiratory rate was reduced to minimal levels, but apparently retained responsiveness to ambient temperature changes. Below −3 C, photosynthetic activity

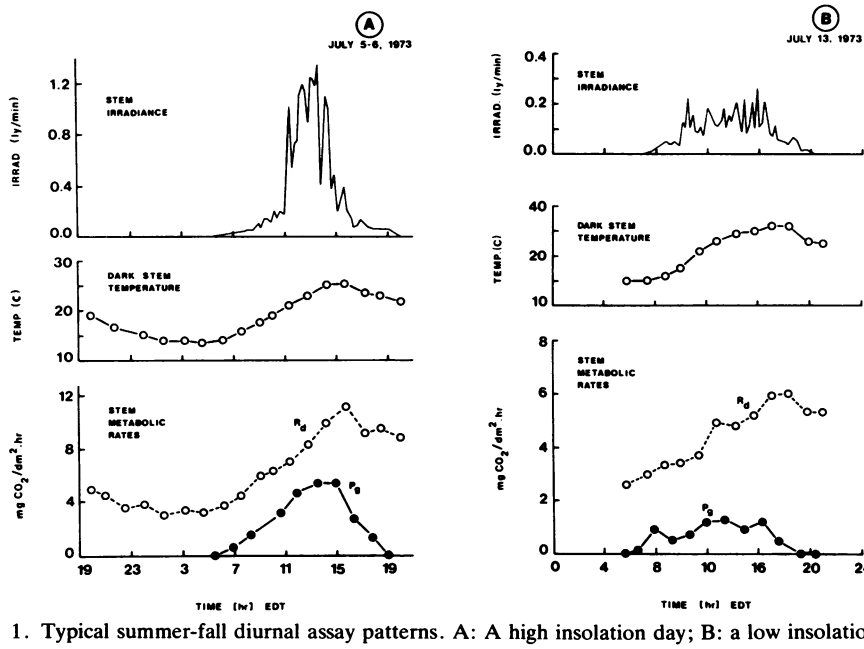

FIG. 1. Typical summer-fall diurnal assay patterns. A: A high insolation day; B: a low insolation day.

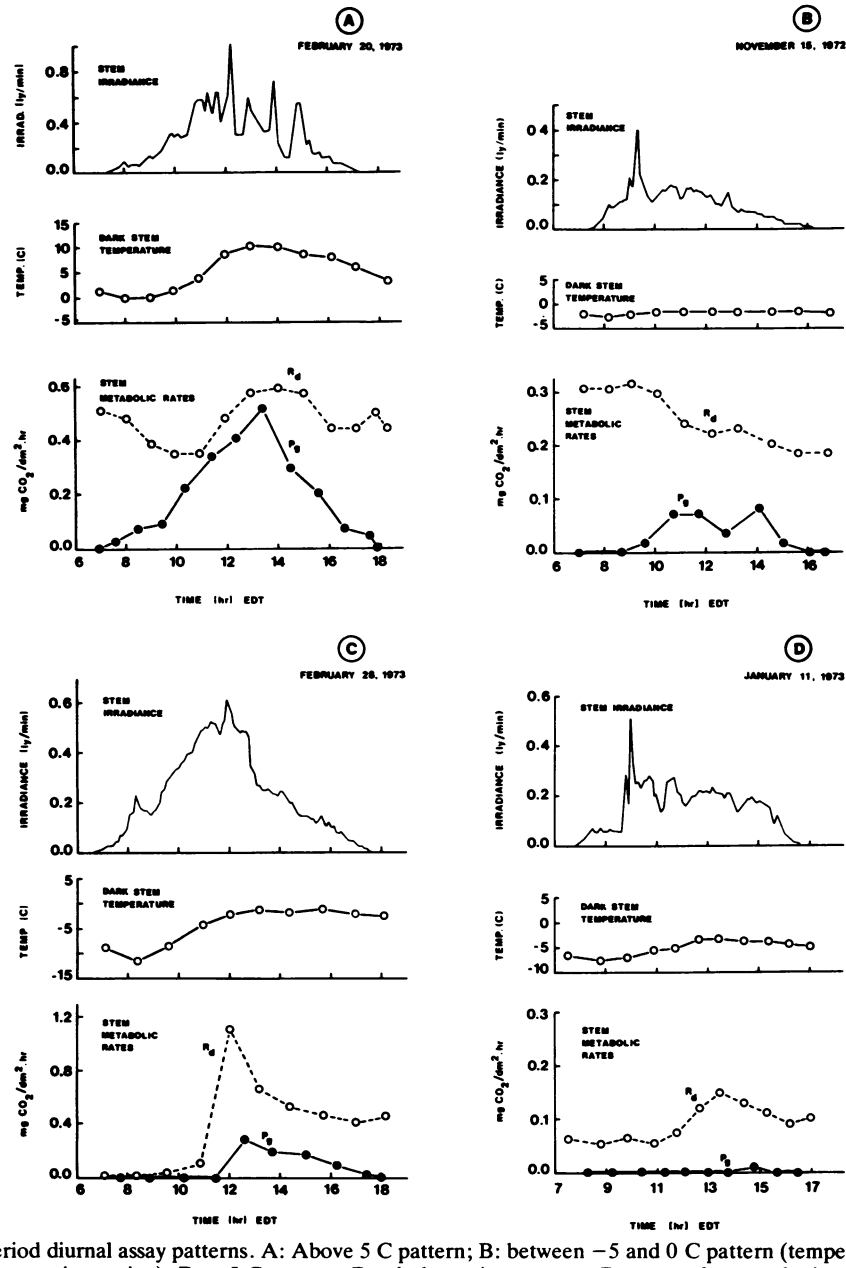

FIG. 2. Typical winter period diurnal assay patterns. A: Above 5 C pattern; B: between −5 and 0 C pattern (temperature constant); C: between −5 and 0 C pattern (temperature increasing); D: −5 C pattern. R_d: dark respiratory rate; P_g: gross photosynthetic rate.

was not detectable (Fig. 2, B–D) and between −3 and 0 C, the rate was reduced to less than 50% of the dark respiratory rate (Fig. 2, B and C).

Spring Diurnal Patterns. From April to early May, just prior to leaf emergence, the respiratory rate increased, primarily reflecting the increased ambient temperature (Fig. 3). However, the ability of bark photosynthesis to reduce the respiratory CO_2 loss increased sharply over the preceding winter months to the highest level of the year. On April 25, for instance, virtually no CO_2 loss occurred during the day.

Seasonal Patterns of Field Material. A summary of the 45 individual diurnal assays from July 1972 through July 1973, representing 558 hr of assays, is presented in Figure 4. A monthly value in this curve for photosynthesis or respiration represents the mean of all rate determinations made in diurnal assays for that month or approximately 33 gross photosynthetic and 46 dark respiratory determinations.

The rate of respiration declined rapidly during August and September so that the September rate was one-third of the July rate (Fig. 4). Stem respiratory activity continued a gradual decline from September to January when the seasonal minimal monthly rate was recorded. From January, the dark respiratory rate began a gradual 4-month increase to 0.68 mg $CO_2/dm^2 \cdot hr$ in April. Beginning in May, a sharp increase in the respiratory rate occurred. The May rate was three times higher than April, and the June rate 3.5 times higher than May. The rise in the respiratory rate in June occurred at the time of peak cambial activity (2). In July, the rate began to decrease. Individual measurements of respiration ranged from 0.02 mg $CO_2/dm^2 \cdot hr$ on a −11.5 C February morning to 12.3 mg $CO_2/dm^2 \cdot hr$ on a 28 C June afternoon.

The early summer rise in dark respiration was well correlated with diameter growth. Figure 5 shows the monthly diurnal dark respiratory rate during the spring and summer in relation to stem diameter increase. Radial increase in stem growth continued for 13 weeks.

The seasonal change of gross photosynthesis followed a pattern similar to the respiratory rate (Fig. 4) with the mean

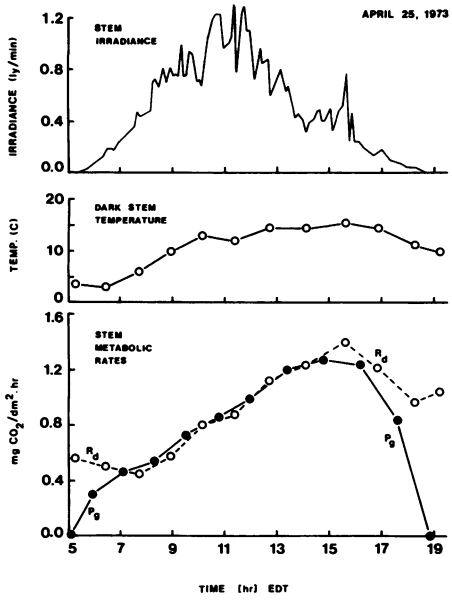

FIG. 3. Typical spring diurnal assay pattern. R_d: dark respiratory rate; P_g: gross photosynthetic rate.

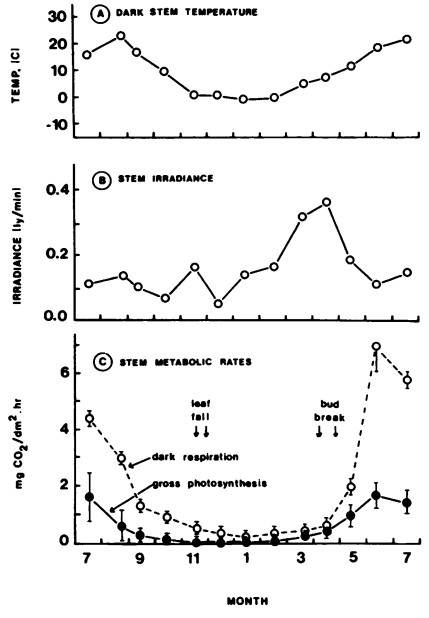

FIG. 4. Seasonal dark respiratory and gross photosynthetic rates (C) in stems in relation to temperature (A) and irradiance (B). Vertical bars in C represent ± SEM.

monthly rate highest in June and July, decreasing sharply in August, and continuing a gradual decline into midwinter. The rate increased slowly from January through April and then increased sharply in May. The monthly rate ranged from the seasonal high of 1.65 mg $CO_2/dm^2 \cdot hr$ in June to a low of 0.02 mg $CO_2/dm^2 \cdot hr$ in December. Individual measurements ranged from 0.0 mg $CO_2/dm^2 \cdot hr$ on winter days when the temperature was below −3 C to 5.54 mg $CO_2/dm^2 \cdot hr$ in July.

Seasonal Patterns of Greenhouse Material. Photosynthetic and respiratory rates of one tree in the greenhouse were determined throughout the year at 19 C and a saturation light level (7) of 1200 ft-c (4.8 mw/cm² of 400–700 nm) provided by six 300-w Sylvania lamps.

The photosynthetic and respiratory activities (Fig. 6) showed distinct seasonal patterns similar to the outdoor material (Fig. 4). The respiratory rate declined from November to March, showed a considerable increase in May, and by June was 15 times higher than winter rates. In early August, respiratory activity diminished to less than one-half the June rate, and by mid-September returned to winter rate levels. Photosynthetic activity closely paralleled respiration throughout the year. Bark photosynthesis reduced the respiratory CO_2 loss from the stem by the same maximal 80% in summer as in winter, illustrating no apparent seasonal endogenous reduction in reassimilation capacity by the bark in this clone.

Clonal Comparisons. Gross photosynthetic and dark respiratory rates of three other clones were determined at 30 C and 1200 ft-c between August 25 and September 8. One-way analysis of variance showed no real differences between clonal means ($P < .05$) for either type of rate (5). However, clonal differences may have existed for winter rates (20).

DISCUSSION

Winter patterns of aspen bark photosynthesis and respiration were similar to coniferous needles. Minimal temperatures for

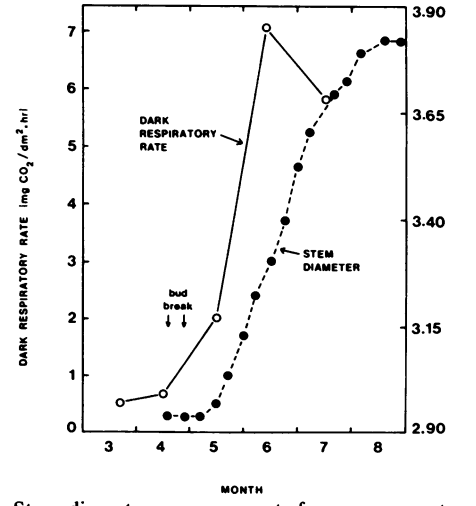

FIG. 5. Stem diameter measurements for aspen ramets used in diurnal assays with corresponding mean monthly dark respiratory rates recorded during the diurnal assays of this period. Each stem diameter measurement represents six determinations from each of eight trees.

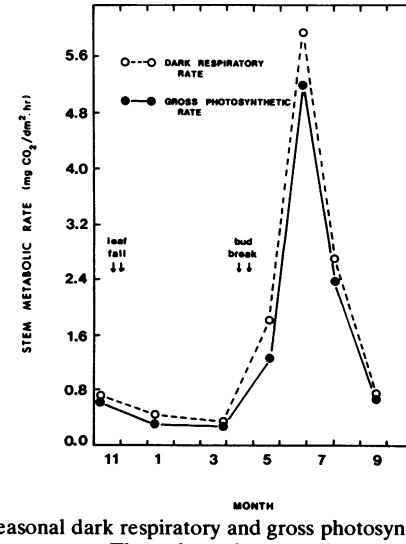

FIG. 6. Seasonal dark respiratory and gross photosynthetic rates of a greenhouse-grown tree. Throughout the year, the tree received normal sunlight, and day/night temperatures were 15 to 35 C/10 to 15 C, respectively. Rate measurements were made at 19 C and 1,200 ft-c. Each point is the mean of three determinations.

respiration in coniferous vegetation have been reported to be −19 to −12 C and −6 to −4 C for photosynthesis (13). In this study, stem respiration was observed at −11.5 C, the coldest temperature in the diurnal assays, while photosynthesis could not be detected below −3 C with the sensitivity of the system.

The response of the stem in resuming photosynthesis after exposure to freezing conditions appears to be quicker and more complete than in coniferous needles (14, 16). Depending on the species and length and severity of the cold period, conifers require several days of warm weather before resumption of normal winter photosynthetic activity. Aspen bark attained near normal rates of photosynthesis in 1 to 2 hr once the stem surface temperature warmed to −3 C after overnight exposures to temperatures as low as −20 C. In addition, exposure to subfreezing temperatures did not lower the capacity of stems to reduce respiratory CO_2 loss from the stem as comparison of field and greenhouse grown trees showed (Figs. 2A and 6).

Winter respiratory rates were observed to decline on several occasions from 33 to 75% during the day, while the stem temperature remained a near constant temperature in the −5 to 0 C range (Fig. 2B). This drop may represent an adjustment by the stem to the temperature regime of the previous night since, in all four cases in which this pattern was observed, the previous night temperature was above freezing, but declining. deLong *et al.* (13) stored apple twigs at above 0 C and then measured the respiratory rate at −6 C. The respiratory rate fell off rapidly in the first 10 hr and did not assume a constant level until after 90 hr.

Upon warming from −4 to −2 C, aspen stems showed a sudden sharp increase in the dark CO_2 release rate (Fig. 2C). Frozen coniferous branches, when warmed to similar temperatures, responded with a rapid 130 to 300% rise in the CO_2 release rate which required 6 to 24 hr to return to normal (15). The CO_2 outburst might be related to the freezing point of the stem, −4 to −2 C (19). The surface temperature of the stem responds nearly instantaneously to ambient temperature changes (4, 19). The respiratory rate outburst may be the frozen cortical layer thawing and metabolizing sugars which have been shown to accumulate from starch at temperatures below 5 C (14), while rates below −3 C would come from nonfrozen cells within the stem.

The CO_2 outburst at −3 C may represent not an acceleration of the respiratory rate, but a release of stored CO_2. Below −3 C, lenticels may occlude as a result of transpirational water freezing as it escapes through the lenticels. With lenticels frozen, the respiratory CO_2 concentration inside the stem would build up. Upon thawing, the rate of release from the stem would increase sharply as a result of the increased diffusion gradient. Observed respiratory rates below −3 C would represent diffusion through the periderm and leakage through incompletely frozen lenticels. Other possible reasons for the CO_2 outburst include CO_2 release from the cell sap due to reduced solubility with rising temperature (8), and an injury response from stem freezing (19).

The seasonal rate of gross photosynthesis showed a significant positive correlation ($r = .65$, $P = .01$) to stem respiration. This correlation may be explained by several, possibly interrelated factors: source of CO_2, stem ontogeny, and stem Chl concentration. It appears that most of the CO_2 used in bark photosynthesis comes from stem respiration rather than the atmosphere. Such an internal source of CO_2 is suggested by the considerable higher concentration of CO_2 inside the sapwood of the tree (1), the high diffusion resistance of the bark to gases (13, 21), the lack of a response of aspen bark photosynthesis to outside CO_2 concentrations as high as 580 μl CO_2/l of air (7), and the low rate of incorporation of externally supplied $^{14}CO_2$ into stem bark tissue (21). If the source of CO_2 is internal rather than external, those factors affecting the respiratory rate such as temperature and stem ontogeny would also affect the amount of CO_2 available for bark photosynthesis.

The observed correlation between photosynthesis and respiration may be further accentuated by the developmental state of the stem in relation to seasonal and environmental conditions. Young, growing, dividing stem cells have unusually high respiratory rates per volume and weight (9), and rates of photosynthesis of newly developed chloroplasts are higher than those of older organelles (11). When diameter growth of a stem is rapid in June and July, the respiratory rate is high since new cells are rapidly produced from cambial initials. New chloroplasts in the cortex, produced during girth expansion, may also have an over-all higher photosynthetic rate than cells which have overwintered.

Bark photosynthesis was most efficient in reducing the respiratory CO_2 loss in the warm, sunny, leafless months of March and April (Fig. 3). The spring increase in photosynthetic activity may reflect an increased Chl concentration (20) prior to cambial reactivation in late May so that the chlorenchyma layer becomes more efficient in trapping CO_2 as it diffuses from internal tissues to the surface.

The results of this study show that bark photosynthesis in *P. tremuloides*, while not capable of net photosynthesis, is capable of reducing substantially respiratory CO_2 loss from the stem. For the entire year, 28.7% of the respiratory CO_2 loss was reduced by bark photosynthesis on a daytime basis. On a 24-hr basis, the amount of CO_2 reassimilated is estimated to be 16 to 18% based on nocturnal respiratory studies, night temperatures of the 45 diurnal assays, and seasonally determined dark respiratory rate temperature curves (7).

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