Portable Through-flow Cuvette System for Measuring Whole-canopy Gas Exchange of Apple Trees in the Field

Jens N. Wünsche and John W. Palmer

HortResearch, Nelson Research Centre, P.O. Box 220, RD 3 Motueka, New Zealand

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Abstract. A monitoring and control system for sequentially measuring whole-tree-canopy gas exchange of four apple (*Malus domestica* Borkh.) trees in the field is described. A portable, highly transparent, open-top whole-canopy cuvette was developed for complete enclosure of the above-ground portion of the tree. The flux of whole-canopy CO₂ and H₂O vapor was estimated from differential CO₂ concentration and H₂O-vapor partial pressure between ambient/reference air entering the cuvette and analysis air leaving the cuvette, as measured by infrared gas analysis. The bulk air-flow rate through the chamber was measured with a Pitot static tube inserted into the air-supply duct and connected to a differential pressure transducer. Performance of the whole-canopy cuvette system was tested for its suitability for gas-exchange measurements under field conditions. The air flow through the whole-canopy cuvette was 22000 L·min⁻¹ (≈5.5 air exchanges/min) during the day, providing adequate air mixing within the cuvette, and 4000 L·min⁻¹ (≈1 air exchange/min) during the night. Daily average leaf temperatures within the cuvette were 2–3 °C higher than to those on trees outside the cuvette. Photosynthetic photon flux transmitted through the chamber walls was at least 92% of the incident ambient radiation. Moreover, the whole-canopy cuvette was evaluated without tree enclosure to determine the degree of “noise” in differential CO₂ concentration and H₂O-vapor partial pressure and was found to be acceptable with ΔCO₂ ± 0.3 μmol·mol⁻¹ and ΔH₂O ± 5 Pa. Whole-canopy carbon gas exchange and transpiration of four cropping ‘Braeburn’/M.26 apple trees followed closely incident radiation over the course of a day.

Individual leaf gas exchange has been measured in detailed field studies by using portable gas-exchange units (Monselise and Lenz, 1981; Palmer, 1992). When whole-plant productivity is of interest, however, it is difficult to extrapolate whole-tree carbon balance from a small sample of single-leaf measurements because of spatial and temporal variations of leaf and other organ (fruit, branch, etc.) gas exchange due to variable within-canopy microclimate, variation in leaf age, and various sources of stress (water, diseases, pests). Canopy light distribution appears to be a major factor for differences in CO₂ fixation and growth pattern. Understanding the whole-tree carbon balance could provide a more integrated analysis of many limitations to fruit development, e.g., the effects of shading on fruit retention, of crop load on fruit size, of temperature on respiration, and of light interception on carbon assimilation. Although some modeling approaches have been produced to correlate canopy photosynthesis with dry-matter increments of apple (Lakso, 1992; Lakso

and Johnson, 1990; Navara, 1985; Proctor et al., 1976), these simulations are based on several assumptions and simplify the reality. Therefore, field studies are needed to confirm the validity of these models and to describe accurately whole-canopy carbon balance response to environmental and orchard management factors. A first attempt to study apple-tree gas exchange in the field by using an assimilation chamber was carried out in the classical work of Heinicke and Childers (1937). An inflatable plastic air-house was constructed by Sirois and Cooper (1964) to measure carbon assimilation of mature apple trees. More recently, chamber systems for whole-canopy gas-exchange measurements were described for kiwifruit (*Actinidia deliciosa* A. Chev. C.F. Liang et R. Ferguson var. *deliciosa*) vines (Buwalda et al., 1992), apple trees (Corelli-Grappadelli and Magnanini, 1993; Wibbe et al., 1993), and grape (*Vitis vinifera* L.) vines (Katerji et al., 1994). The limitations of most of the canopy cuvettes used to date have been limited portability due to fixed supporting structures or extensive detection systems. Thus, further progress requires comprehensive techniques for measuring whole-canopy CO₂ and H₂O-vapor fluxes under field conditions by using relatively movable and easily established chamber systems.

The objectives of this study were 1) to design and build a portable, easily erected chamber system that allows rapid enclosure and data output of whole-canopy gas exchange

from small fruit trees growing under typical orchard conditions, and 2) to test the suitability of the cuvette system for measuring whole-canopy CO₂ and H₂O-vapor fluxes under field conditions.

Materials and Methods

A portable, through-flow, field cuvette system was developed to measure canopy net carbon fixation and water-vapor exchange during the photoperiod and canopy dark respiration during the night of small trees by complete enclosure of the above-ground portion (Fig. 1). The measuring principle for whole-canopy gas exchange was based on an open-top chamber system (Field et al., 1989; Pearcy et al., 1989) and was a refinement of an earlier design (Palmer, 1990).

The whole-canopy cuvette system was tested for its suitability for estimating CO₂ and H₂O-vapor fluxes of the whole-tree canopy and to ensure that the cuvette environment was close to ambient conditions. Tests included the evaluation of the effects of cuvette air exchange rate on canopy CO₂ uptake and leaf temperature, assessment of air mixing within the cuvette, comparison of microclimatic variables inside and outside the cuvette, such as air and leaf temperature and light conditions, and diurnal patterns of ambient/differential CO₂ and H₂O concentrations.

The diurnal patterns of whole-canopy carbon exchange and transpiration of four cropping 4-year-old ‘Braeburn’/M.26 apple trees were determined 1 week before fruit harvest at ≈25 weeks after full bloom. Trees, growing at the Nelson Research Centre, Motueka, New Zealand, were planted at a spacing of 5 × 2.5 m, oriented in north-south rows, and trained as slender spindles. Final counts were between 250 to 300 fruit per tree and estimated whole-canopy leaf area ranged from 9.5 to 13.2 m².

Canopy cuvette design. A whole-canopy cuvette in the shape of a hexagonal pyramid, shown schematically in Fig. 1, was constructed from rigid, clear 2-mm-thick polycarbonate sheets. Polycarbonate combines high transparency, light weight (2.4 kg·m⁻² for 2-mm sheet thickness), strength, durability, and UV resistance. The material admits ≈95% of the visible-light spectrum, screening out ultraviolet and infrared radiation. The use of rigid, easy-to-cut, and simple-to-bond plastic sheets allowed to design a chamber such that its effect upon whole-canopy environment was minimal and that it could be readily dismantled and shifted. Moreover, to determine the response of net photosynthesis to irradiance in a future application of the cuvette system, chamber sturdiness will be required to gradually reduce the flux density of radiation incident upon the whole-canopy by using black netting. Three polycarbonate sheets were assembled to form one cuvette half by pop riveting along the 120°-bent, 2.5-cm overlapping sides. Both cuvette halves were attached at the apex, at the base, and at the side-edges to an aluminum frame of 2.5-cm-square section as a supporting structure and to hold the cuvette in place. The joining sides were sealed with clear

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silicon rubber. The volume of the cuvette was ≈ 4000 L, with dimensions of 0.5 m in diameter at the apex, 2.4 m in diameter at the base, and 2.2 m in height. Each of the two cuvette halves was clamped on a plywood floor, which was supported with short, adjustable telescopic aluminum tubing legs to elevate the whole cuvette system to ≈ 50 cm above-ground level, but below the lowermost branches. For complete enclosure of the tree canopy, the plywood floor and the cuvette halves along the aluminum-frame-supported sides could be closed tightly with toggle catches. Hence, the tree-supporting wires could pass through the cuvette. A hole of ≈ 10 cm in diameter at the center of the plywood floor allowed for the inclusion of the tree trunk, and air leaks were sealed with foam rubber. To prevent the entry of rain and air inversions into the cuvette, a molded, clear acrylic dome of 1 m in diameter was fastened, slightly overhanging, above the open top of the chamber.

Air supply system. An enclosed single-phase centrifugal fan (R4E310-AF05-05; Ziehl-ebm, Auckland, New Zealand) with a nominal maximum air-flow rate of $28000 \text{ L}\cdot\text{min}^{-1}$ was used

to draw ambient air from 2.5 m above orchard floor through a 30-cm-diameter galvanized steel air intake system. The air stream was then split and passed through two arms of 30-cm-diameter flexible aluminum ducting, with 25-mm insulation, clad in polyester sleeves (Commercial Type; Carrier Zonepak, Auckland, New Zealand). The air entering the canopy cuvette system was dispersed by a manifold on each inlet. To guarantee a reduced air-flow rate at night, as was essential for monitoring the rate of whole-canopy dark respiration, the voltage supply to the fan was regulated by a fan-speed-control relay (ZENZ 700; Ziehl-ebm) that was controlled by a control-port expansion module (SDM-CD16; Campbell Scientific, Logan, Utah).

The flow rate through the air intake system was estimated by continuously monitoring the air velocity pressure (difference between total and static duct pressure) at the center of the duct with a Pitot static tube (Airflow Developments, High Wycombe, United Kingdom). This device was connected to a differential pressure transducer (FC044; Furness Controls, Sussex, United Kingdom) that provided

a datalogger-recorded voltage output that was directly proportional to the applied pressure. The relationship between air velocity and *total volumetric air-flow* (f_v ; $\text{L}\cdot\text{min}^{-1}$) entering the cuvette was determined by measuring the rate of increase in cuvette CO_2 differential concentration (ΔCO_2 ; $\mu\text{mol}\cdot\text{mol}^{-1}$) while injecting a known flux of pure CO_2 (flow CO_2 ; $\text{L}\cdot\text{min}^{-1}$) into the air stream entering the canopy cuvette:

$$f_v = \text{flow } \text{CO}_2 \times 10^6 / \Delta\text{CO}_2$$

This procedure was repeated at several fan speeds; subsequently, the air-flow rates through the cuvette could be related linearly to the measured air velocity within the ducting. Hence, the calibrated pressure sensor allowed the inclusion of short-term fluctuations in air-flow rates in calculations of canopy carbon assimilation and transpiration. However, for calculation of gas-exchange parameters a conversion of volumetric flow to *mole flow of air* (f ; $\text{mol}\cdot\text{s}^{-1}$) was required accordingly to the standard equation presented by Long and Hällgren (1985).

Gas-exchange measurements. Analysis and reference air were sampled from the top and the bottom of the canopy cuvette, respec-

Fig. 1. Schematic diagram of a monitoring and control system used for measuring whole-tree-canopy gas exchange of dwarfing apple trees in the field. See text for detailed information.

tively, with a two-head diaphragm pump (DA1DE; Charles Austin Pumps Ltd., Weybridge, United Kingdom) that was mounted beneath the plywood floor. At an air-flow rate of $\approx 1.8 \text{ L} \cdot \text{min}^{-1}$, both gases were pumped continuously $\approx 40 \text{ m}$ through black, ultra-violet-resistant polypropylene tubing of 0.8 cm in diameter (Leda, Upper Hutt, New Zealand) into a three-way solenoid switching unit (model 310; Humphrey, Kalamazoo, Mich.). By maintaining the air in the gas lines at a positive pressure, leaks that inevitably occurred did not constitute a source of error. Four pairs of solenoid valves, one pair for each of the four canopy cuvettes in operation, were switched by a control-port expansion module (SDM-CD16; Campbell Scientific). Hence, the incoming gases from three canopy cuvettes were vented through a common manifold, while the gases from the fourth canopy cuvette were delivered into the infrared gas analyzer (CIRAS-1; PP-System, Hitchin, United Kingdom). The CIRAS has four gas analyzers, two each for CO_2 and H_2O . The four 8-bit digital/analog (D/A) voltage outputs from the CIRAS were monitored by a datalogger (CR10 plus AM416 multiplexer, Campbell Scientific). The stability of the infrared gas analyzer was due to a regular zeroing when CO_2 -free, dry air was passed through all cells (zero) and differential balancing by passing reference air through all cells (diff-bal) to calculate for each pair of analyzers a factor that equalized their readings. A special Eprom allowed that the D/A output was zeroed during zero and diff-bal mode as well as during a subsequent 45-s time-delay to allow a return to a steady differential reading due to the time required for flushing the gas lines. By using the CIRAS as an analyzer only, columns 3 to 6 were left empty. The drierite and molecular sieve in column 1 had to be replaced about every 80 to 100 h, whereas soda lime in column 2 exhausted very slowly. The computer, infrared gas analyzer, dataloggers, modules, and solenoid sampling unit were housed inside a small field laboratory located within the orchard block.

Monitoring environmental characteristics. Air temperature within the center of each canopy cuvette was measured with a thermistor (type 5K3A1; Betatherm Corp., Shrewsbury, Mass.) mounted inside a radiation shield. Leaf temperature was measured at the mid-leafrib of 10 randomly selected leaves on the outside of the tree canopy using copper-constantan thermocouples.

The incident photosynthetic photon flux (PPF) was measured above the tree canopy with quantum sensors (PAR-1; PP-System) positioned toward the open sky for recording direct radiation and one sensor located beneath a shade ring for monitoring diffuse radiation. Air temperature and incident radiation were recorded by a datalogger (CR10 plus AM416 multiplexer; Campbell Scientific).

Power supply. The power supply for the entire monitoring and control system was a single-phase 4.2-kW Yanmar diesel generator (YDG5001E; Yanmar Diesel Engine Co., Tokyo) supplied from a 1000-L diesel tank. The voltage requirement of the computer, cen-

Fig. 2. (A) The effect of air-exchange rate on differential CO_2 concentration (—●—) and leaf temperature (·····○·····). (B) The effects of day- and nighttime flow rates of air through the canopy cuvette on diurnal patterns of leaf and air temperature inside ($T_{\text{in air}}$ (—); $T_{\text{in leaf}}$ (---)) compared to conditions outside ($T_{\text{out air}}$ (·····); $T_{\text{out leaf}}$ (— · —)) the cuvette. $T_{\text{in leaf}}$ and $T_{\text{out leaf}}$ were measured at the mid-leafrib of 10 randomly selected leaves, respectively, using copper-constantan thermocouples. $T_{\text{in air}}$ and $T_{\text{out air}}$ were monitored with a radiation-shielded thermistor at the center of the tree canopy. (C) Diurnal pattern of incident direct and diffuse PPF inside (—) and outside (·····) the whole-canopy cuvette measured with two pyranometers positioned at the base of the cuvette and above canopy, respectively.

trifugal fans, and pumps was 220 V AC, whereas all the other measuring and controlling devices were powered by 12 V DC.

Data capture and analysis. The voltage outputs from the CIRAS, pressure transducers, light sensors, and thermistors were recorded on the analogue input channels of the datalogger (CR10 plus AM416 multiplexer; Campbell Scientific) using the standard Campbell Scientific software. The datalogger also allowed the selection of various monitoring and control decisions such as, date and time of sampling, frequency of data collection from the sensors, interval of data averaging

before being stored in final storage, interrogation time, choice of fan speed and solenoids via a control port expansion module (SDM-CD16; Campbell Scientific), indication of fan and solenoid state, as well as numerical data display on a computer screen. All settings of the monitoring and control decisions could be edited prior to the execution of the program. The frequency of data capture from all measuring devices was 1.6 s and by interrogating the datalogger with a RS232 line, 1-min averages were downloaded onto a IBM-compatible personal computer every 3 h. The four pairs of solenoid valves were switched at 15-

min intervals, i.e., 45 min passed before the same canopy cuvette was monitored again. Consequently, for each canopy cuvette, 15 records of absolute/differential CO_2 concentration and H_2O -vapor partial pressure were obtained within 1 h, respectively. Fan speed was usually set to high at dawn and to low at dusk. All data were stored in ASCII text format on the computer, and the output file was copied manually to a floppy disk without interfering with the ongoing controlling and monitoring operations.

The acquired raw data were then analyzed for whole-canopy gas exchange using a specially written SAS (SAS Inst., Cary, N.C.) software program. Reading the output file into the SAS program, the voltage outputs were first converted into conventional units by applying a specific linear calibration equations for each sensor. Moreover, the program checked the data file for values of ambient CO_2 concentration $>300 \mu\text{mol}\cdot\text{mol}^{-1}$, occurring due to the zeroed D/A output when the CIRAS was executing the zero/diff-bal mode and the 45-s time-delay step. On detecting a value below this threshold, the previous, the detected, and the following two readings of absolute and differential CO_2 concentration and H_2O -vapor partial pressure were not considered for data evaluation. Finally, the program allowed the conversion of volumetric into molar air-flow rate and the calculation of whole-canopy CO_2 and H_2O -vapor exchange using standard photosynthetic equations (Long and Hällgren, 1985). The equation for canopy assimilation considered the correction of differential CO_2 for the increase in H_2O -vapor mole fraction of the analysis air stream due to transpiration of the tree canopy.

The various program-output parameters were summarized regularly for each whole-canopy cuvette and graphically displayed for clear presentation using SAS analysis software.

Results and Discussion

Cuvette ventilation. The ventilation rate greatly determines the thickness of the boundary layer around the leaves enclosed inside a canopy cuvette (Jarvis et al., 1971). The boundary-layer resistance, however, controls the gaseous and thermal transfer between the microenvironment and the leaf and hence the gas-exchange and energy balance of the leaves (Jarvis et al., 1971; Long and Hällgren, 1986). Therefore, the design of the cuvette system and the choice of rate of air flow through the cuvette must take the boundary-layer resistance into account, and it is desirable to approximate the prevailing environmental conditions so that major changes in the physiological response of the plant did not occur due to enclosure. Whole-canopy carbon uptake and leaf temperature were negatively and exponentially related to increased rates of air-flow through the cuvette system (Fig. 2A). Air-flow rates were selected to ensure that the CO_2 differentials were in a detectable range, yet the leaf temperature within the cuvette did not increase markedly above ambient tem-

Fig. 3. Diurnal patterns of CO_2 concentration (A) and H_2O -vapor partial pressure (B) with an empty cuvette. Reference air (—), measured at cuvette inlet, and analysis air (---), measured between cuvette's ingoing and outgoing air stream.

perature. During daytime, the flow rate of air into the cuvette was $\approx 22000 \text{ L}\cdot\text{min}^{-1}$ (5.5 air changes/min), resulting in a ΔCO_2 of $\approx 4.5 \mu\text{mol}\cdot\text{mol}^{-1}$ (Fig. 2A). The CO_2 differential probably was low because whole-canopy carbon uptake was monitored on young trees with incomplete canopy volumes in late-season. In future applications of the cuvette system, however, a ΔCO_2 of ≈ 10 to $12 \mu\text{mol}\cdot\text{mol}^{-1}$ could be recorded on mature trees, ensuring that imposed treatment differences were detectable. To obtain detectable dark respiration rates during nighttime, the air-flow rate was re-

duced to only $4000 \text{ L}\cdot\text{min}^{-1}$, representing air changes of one chamber volume/min.

Air and leaf temperature. The effects of the selected day- and nighttime flow rates of air through the canopy cuvette on diurnal patterns of leaf and air temperature inside ($T_{\text{in,leaf}}$, $T_{\text{in,air}}$) the cuvette were examined and compared at the same time to conditions outside ($T_{\text{out,leaf}}$, $T_{\text{out,air}}$) the cuvette (Fig. 2B). Measurements were taken on two adjacent trees of similar size. Leaf temperature and air temperature inside and outside the canopy cuvette were similar at night as well as in early morn-

ing and late afternoon; however, throughout the middle part of the day, the difference between leaf and air temperature was $\approx 2^\circ\text{C}$. Also, over the course of the day, $T_{\text{in,leaf}}$ never exceeded $T_{\text{out,leaf}}$ by more than 2 to 3°C . The minimized leaf-air temperature gradient, and the small gradient between $T_{\text{in,leaf}}$ and $T_{\text{out,leaf}}$ were the result of good chamber ventilation with adequate air mixing. Furthermore, the polycarbonate material, by screening out long-wave infrared radiation, contributed to preventing a greenhouse effect within the chamber.

Air mixing within the cuvette. The homogeneity of air distribution within the cuvette was tested at daytime flow rates by using smoke flares. The smoke was introduced into the air-supply system and occupied the canopy cuvette uniformly, and no smoke-free zones were noted. Active leaf movement on the cuvette-enclosed tree was considered further as an indicator of adequate dispersion of air upwards through the cuvette. Consequently, design of chamber, the manifold at the cuvette entrance, and the chosen air exchange rate avoided the creation of pockets of still air in close proximity to the walls and in the corners of the cuvette.

Light climate. Since incident radiation has a major effect on the rate of photosynthesis, the rate of transpiration, and the temperature of the leaf, it was essential that the tree canopy enclosed inside the cuvette could experience similar light conditions to those outside the canopy cuvette. Hence, the light climate within the canopy cuvette was examined under direct and diffuse incident radiation. Over the course of a day, the PPF transmitted through the cuvette-walls was at least 92% of the incident flux (Fig. 2C). That was similar to values reported on visible light transmission for 'Perspex' (Bloom et al., 1980). Care should be taken, however, to avoid scratches, smears, and abrasion that inevitably lead to a reduction in transmitted light by the plastic.

Cuvette gas exchange without tree enclosure. Rapid fluctuation in ambient CO_2 and H_2O concentration of the air entering the cuvette would be apparent as random noise in the determination of CO_2 and H_2O -vapor differentials, hence decreasing the accuracy of calculation of assimilation rate and transpiration rate (Long and Hällgren, 1986). Therefore, diurnal fluxes of ambient/differential CO_2 and H_2O -vapor were measured at the cuvette inlet and between the cuvette's ingoing and outgoing air stream without tree enclosure (Fig. 3). A typical diurnal pattern was found for ambient CO_2 concentration. It was characterized by a rapid rise around dusk due to the respiratory carbon loss of trees, followed by a steady increase throughout the night before finally attaining the highest level just before dawn when a fast, sudden decline occurred due to the commencing of carbon uptake by trees (Fig. 3A). The fluctuating curve pattern at night time likely was due to still nocturnal air conditions leading to air pockets with different CO_2 concentrations, whereas the nearly steady curve pattern over most of the day time indicated sturdy air turbulence generated by

Fig. 4. Diurnal patterns of whole-canopy carbon exchange (A), and whole-canopy transpiration (B) of four cropping 'Braeburn'/M.26 apple trees. Incident PPF represented as a shaded area. Measurements were taken ≈ 25 weeks after full bloom at full canopy.

changing radiation. The differential CO_2 concentration over the course of a day never exceeded $\pm 0.3 \mu\text{mol}\cdot\text{mol}^{-1}$, an acceptable noise since it represented only $\approx 2\%$ to 3% of the carbon uptake by tree canopies (Fig. 3A). The relatively stable reference air source for the differential gas measurements was obtained by an air intake at 2.5 m above the orchard floor rather than passing the air through large buffer vessels before entering the cuvette system. Due to the steady ambient CO_2 concentration, especially during the day, the air-flows through the reference and analysis gas lines were not synchronized as could have been by positioning a balancing container into the reference line after the sampling point (Buwalda et al., 1992). The diurnal pattern for ambient H_2O -vapor partial pressure was quite variable and presumably, largely dependent on other environmental variables such as temperature and incident radiation. The measured daily variation in differential H_2O -vapor partial pressure, however, was less than ± 5 Pa, representing $\approx 3\%$ of the normally detected water loss by tree canopies (Fig. 3B).

Cuvette gas exchange with tree enclosure. The diurnal pattern of whole-canopy carbon exchange and transpiration of four cropping 'Braeburn'/M.26 apple trees at full canopy (Fig. 4) closely followed the diurnal pattern of total incident PPF, indicating that whole-canopy gas exchange was affected by light intensity. Although the diurnal pattern of CO_2 and H_2O exchange differed among the four apple trees, related to variations in whole-canopy leaf area, they had a similar whole-day mean canopy carbon uptake and transpiration when calculated on a per-leaf-area basis. Whole-canopy averaged rates of leaf net photosynthesis resulted in $\approx 4.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, which represented only 35% of the measured maximum rates on single leaves.

Conclusions

Performance testing of the cuvette system for canopy enclosure resulted in suitable attributes for gas-exchange measurements. A major advantage of the cuvette design was that

it allowed easy shifting and setup, rapid enclosure, and data output from field-grown trees. The time required for shifting the four whole-canopy cuvettes and enclosing the tree canopies was ≈ 3 h for two people. Due to the relative mobility of the chamber design, the inclusion of several replicated treatments will be possible. In future applications of the cuvette system, the subject trees usually will not be enclosed in a chamber for more than 2 to 3 d at a time, so that they can experience the same orchard and tree management practices (spray applications, summer pruning, etc.) as other trees within the orchard block.

The cuvette system can be used in detailed field studies to investigate several limitations on apple productivity by 1) examining the effects of crop load, specific pests or infections of diseases, and regulated deficit irrigation on whole-canopy carbon balance, and 2) establishing canopy carbon-exchange responses to incident solar radiation and elevated temperature.

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