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Gas Exchange Characteristics of Mango (Mangifera indica) in Puerto Rico: Field Measurements with a Portable Photosynthesis System.

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CENTER FOR ENERGY AND ENVIRONMENT RESEARCH
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Abstract. The photosynthetic rate, stomatal conductance, and transpiration of mango (*Mangifera indica*) were measured under ambient conditions among several size classes of trees and saplings at four sites near San Juan, Puerto Rico. Rapid and highly replicated measurements were allowed by the use of a portable transient photosynthesis system (LI-6000, LI-COR Inc., Lincoln, NB 68504 USA) which was operated by one person. Determinations of average photosynthetic rate of single leaves, based on 10 measurements, could be made and recorded in less than 90 s, including selection of sample leaves and leaf area determination. Photosynthetic rates of fully expanded leaves ranged 10-fold from 0.4 to 0.04 mg CO_2 m^{-2} s^{-1} under full sun to fully shaded conditions. Stomatal conductances were observed from 1.98 to 0.4 cm/s and transpiration from less than 60 to over 160 mg H_2O m^{-2} s^{-1}.

Introduction

The mango (*Mangifera indica*) is widely planted in tropical and subtropical areas of the globe (Chaudhri 1976), Puerto Rico being no exception. Here the tree is found from sea level, immediately adjacent to the shore, to over 500 m altitude, although fruit production is said to be reduced at higher elevations. The presence of the tree in most residential areas makes it an ideal experimental plant due to easy access to individual trees of many sizes and phenological states.

This investigation was planned to examine the photosynthetic rate of several size classes of trees and leaf age classes under ambient conditions, and to inaugurate the use of a new photosynthetic system at my laboratory. The LI-COR LI-6000 portable photosynthesis system was employed in this research and field evaluation, using both the 325 cc and the 4000 cc chambers (also termed 0.25 and 4.0 liter). It is a closed transient measurement system which allowed the rapid accumulation of data from a large number of trees. Leaves were measured under ambient conditions which included air temperatures ranging from 27 to 37°C, photosynthetically active radiation (PAR) from 100 to 2200 uE m^{-2} s^{-1}, and relative humidities from less than 25 to over 65%.

Materials and Methods

Gas Exchange Determinations. Several popular approaches are currently in use for measurement of foliar gas exchange, all of which can be used with greater or lesser degrees of complication in the field. The measurement systems can be divided into two basic groups, those using $^{14}CO_2$ and those using infrared gas analysis (IRGA) techniques.

The first approach uses ^{14}carbon dioxide as a tracer for photosynthetic uptake. It has the advantages of being highly portable, with samples being made at intervals of less than 1 min (Lawrence and Oechel 1984). The apparatus is simple, consisting of a pressurized cylinder with $^{14}CO_2$ labeled air of a known specific activity (mCuries/ mmol), a low pressure regulator and valving mechanism for air delivery, and a transparent, sealed cuvette for enclosing the plant material during the labeling period (30- 60 s). There are usually no provisions for temperature control and foliar respiration cannot be measured. Although samples are easily accumulated, their analysis can be tedious and is exacting. The presence of very low levels of radioactive label requires sophisticated sample combustion and liquid scintillation facilities for detection and measurement, and the sample analysis/ data reduction phase can take days to complete.

In contrast, systems utilizing infrared gas analyzers for determination of CO_2 exchange by leaves, or other plant parts, have the initial advantage of immediate availability of data, less system lag time. The IRGA techniques are basically two; "closed" systems where absolute changes in carbon dioxide concentration are monitored as an air mass recirculates through a chamber containing plant material, and "open" where the difference in carbon dioxide concentration is measured between air streams entering and leaving a plant chamber. One complication with all these systems is the field utilization of a highly sensitive gas analyzer, its inherent inportablility, and the usual need for sophisticated support equipment.

The "open" systems generally incorporate air temperature control (Oechel and Lawrence 1979) in their cuvette design to counter the heating of the light soure and to allow manipulation of leaf temperature. This feature unfortunately makes the cuvette dependent on external cooling or heating devices and temperature controllers, all of which add bulk and complexity, whether temperature control is exerted thermoelectrially (Peltier blocks) or with waterbaths. The differential IRGA is highly accurate (fractions of a ppm CO_2), but generally sensitive to vibration, heavy (25 kg), and bulky. When step manipulations of light and/or temperature are carried out using the "open" or steady-state systems, a time (10- 60 min) must be allowed for equilibration of the plant material to the new suite of conditions, a delay which can considerably reduce the rate of data acquisition. These systems are ideally suited for use where the photosynthetic response surface of a single leaf is to be determined against a range of temperature and light levels. Replication is slow unless sophisticated computer-controlled systems are employed with multiple (3- 6) cuvettes in simultaneous use. A basic field system can be expensive (ca. $15k), once the IRGA (ca. $8k), a temperature controlled cuvette (ca. $2k), power supply ($250), temperature controller ($ 750), flow metering and control devices (ca $1k), humidity ($1k), temperature ($750), and light measurement systems ($900), and supplies (tripod, hardware, misc. wire, tubing - $1k) are assembled.

Those "closed" systems which are portable and intended for field use are typically not temperature controlled so are best suited for ambient measurements. These systems are designed for rapid, transient measurements, with as little as possible chamber effect on the leaf environment. If required, manipulative work could easily be done with a "closed" system used in conjunction with controlled environment growth chambers or by taking closely spaced diurnal measurements under natural and/or partially controlled conditions. Light levels could be controlled in the field with lamps and/or shading and the air entering the chamber can be preconditioned as to CO_2 concentration, water vapor pressure, and gas mix.

My experience with "closed" systems is limited to the LI-COR LI-6000 portable photosynthesis system, the instrument used in this research. It has the advantage of being an integrated system, including light, temperature, and humidity transducers, as well as the CO_2 analyzer needed for gas exchange measurements, all in one highly portable unit. An integral computer system with a flexible, powerful operating system provides monitoring, data reduction, recording, and output facilities, so that the user has immediate access to results in reduced form, not raw, uncalibrated output form the various sensors. I have extensive experience with the traditional "open" systems using multiple temperature controlled cuvettes, so can appreciate the compactness and versatility of the Li-Cor system. Rapid measurements (<1 min) can be made with the LI-COR LI-6000 system when leaf areas and gas exchange rate are sufficient to yield a 10-20 ppm change in the chamber CO_2 concentration over the period of measurement. Three chamber sizes, of approximately 0.25, 1.0, and 4.0 liters, are available to optimize the leaf area to chamber volume and expedite rapid measurements without excessive drawdown of the chamber CO_2 concentration. The potential for rapidity of measurement and on-line storage of data allows surveys of gas exchange among many leaves in a short time; permiting screening, evaluation of population variability, or the repeated measurement of a single leaf through time.

Experiments

Initial Leakdown and Noise Test- Both sizes of chambers (0.25 and 4.0 l) available to me for the LI-6000 were used in this procedure. They were individually attached to the system and flushed with air of known CO_2 concentrations, and once sealed, data logged at 1 min intervals for 10 min to determine the leakage of CO_2 into or out of the chambers. Measurements were made under ambient laboratory conditions (ca. 460 ppm), and over chamber CO_2 levels from 15 to 750 ppm. Levels higher than ambient were reached by exhaling near the open chamber, while the internal CO_2-free air supply was used to reduce concentrations below ambient within the chamber.

Boundary Layer Resistance- Leaf replicas were made from thick blotting paper and used to calculate the boundary layer resistance of the two chambers. The procedure followed that detailed in the LI-COR manual (Anon 1983). Relative humidities ranged from less than 50 to over 80% during these procedures, a common range for our island and other moist tropical or humid laboratory or field situations.

Plant Work- The first field use of the LI-6000 took place at the University of Puerto Rico's Agricultural Experimental Station in Rio Piedras. There measurements were made on attached mango leaf material growing from root suckers in both sun and shade. All suckers were approximately 1.25 m in height and 1- 2 cm in diameter. The suckers were utilized due to the ease in reaching leaves while standing on the ground. (N.B. One of the greatest difficulties in this research was not of an instrumentation or technical nature, but rather the simple process of reaching leaf material from the ground.) At the same site measurements were made on sun leaves of an individual tree 18 cm DBH (diameter breast high) and 6 m in height. Later the system was taken by car to another location in the metropolitan area of San Juan near Avenida Juncos, where measurements were made on sun leaves of a tree 25 cm DBH and 5 m tall. Additional measurements were made in the full sun, under clouds, and with fully shaded intercanopy leaves on a small tree (12 cm DBH, 2.5 m in height) and a large fruit-bearing tree (50 cm DBH, 10 m in height) next to the Baldorioty de Castro Expressway. The last measurement series was made on three age classes of leaves of a fruit-bearing tree (30 cm DBH, 6 m ht.) adjacent to 65th Infanteria.

Measurement Techniques- Chambers of two volumes (326 and 4060 cc, called the 0.25 and 4.0 liter in sales literature) were used in this evaluation. The chambers accomodate a maximum leaf area of approximately 33 cm^2 (3 X 11 cm) and 234 cm^2 (13 X 18 cm) respectively, the useful area being perhaps 30% less, in order to allow for good air circulation within the chamber. In all cases, 10 measurements were made per timed interval per leaf sample, although fewer can be selected via the LI-6000 software. The seconds between measurement within any single interval were varied between 3 and 10 seconds, giving total measurement elapsed times of 30 to 100 seconds per leaf. This interval was varied to make measurements in the shortest possible time while still acheiving a chamber CO_2 change of 10- 30 ppm. A much greater or lesser change can either affect leaf gas exchange rate or intrude on the analyzer noise level. At the end of each measurement period the LI-6000 automatically computes mean and intercept values for light, relative humidity, CO_2 concentration, photosynthesis rate, and leaf and chamber temperature. The data can be immediately reviewed by the operator at this time and redone if necessary. Data is stored in the LI-6000 internal memory for later recall.

The infrared gas analyzer (IRGA) was zeroed with the internal CO_2-free source after each 30 minutes or so of use. A standard gas, mixed to 500 ppm CO_2 in air, was used to check and adjust the IRGA gain once a day, before beginning measurements. Once power was applied to the LI-6000 in the laboratory at the start of the day, it was left on throughout field use until all measurements were completed at the day's end. Only the chamber fan and IRGA pump were turned off during any lengthy pauses between measurements to conserve power. A total of 6 rechargable batteries were available and lasted at least 60-90 minutes each. The instrument package carries an internal beeper that warns of low battery power, and batteries can be changed without turning off the device. The used batteries were recharged each night.

Data Reduction- The memory of the LI-6000 (64 kilobytes- fully expanded version) will hold more than 100 pages of data in its most detailed form. I recorded all data, although much more can be stored if abbreviated data storage formats are used. At the close of each day's work the data was dumped from the memory onto a printer attached to a personal computer (Apple II+) with a serial interface. Data could also be recorded on the computer's magnetic disk for later analysis.

The data was reviewed page by page back at the laboratory once it was in printed form. The data was also reviewed immediately after each measurement to detect faulty techniques or contamination by operator-respired CO_2. Special attention was paid to the instantaneous gas exchange rate, the range of CO_2 concentrations during the individual leaf measurement periods, and the initial CO_2 level. These key parameters help to fully evaluate the validity and applicability of any series of measurements, as errors in technique or inadvertent damage to leaves can be detected and corrections made. Additional security against logging invalid measurements can be gained by monitoring both the CO_2 concentration and the relative humidity before and during measurements. These are both parameters which can help the operator identify problems of breath contamination or poor chamber mixing.

Results and Discussion

Leak and Noise Test- When the chamber CO_2 concentration was well above (+250 ppm) or below (-400 ppm) laboratory conditions (460 ppm), leakage averaged 14 ppm and never exceeded 20 ppm per 10 min period. Such gradients would be extraordinary in normal use, as the usual CO_2 differential between the ambient air and the chamber should not be allowed to exceed 30 - 40 ppm if gas exchange rates are to remain unaffected. In any case, such a differential would only exist at the end of a measurement period. Empty chambers at ambient CO_2 were found to vary only 1 - 4 ppm in 10 min. The variability being attributable to IRGA noise and longterm output signal drift. In view of these results, a directional change in CO_2 concentration <2-3 ppm during an actual measurement of photosynthesis or respiration would be suspect and liable to operator evaluation due to its proximity to the expected system noise level.

Boundary Layer Resistance- Leaf replicas were cut in rectangular forms of 3.25 X 5 cm for the small and 5 X 5 cm for the large chambers. The boundary layer resistances were dependent in large degree on chamber relative humidity, resistances being higher at high %RH. An average value was calculated for each chamber from resistances computed over a 45 to 80 %RH range. Boundary layer resistance averaged 1.1 s/cm for the small, and about 0.6 s/cm for the larger chamber. The differences were due in large part to better mixing of air by the two fans in the large chamber, and the lesser fraction of the total chamber area covered by wet blotting paper which can impede air circulation. When blotter paper area was halved in the smaller chamber (to 3.25 X 2.5 cm), the boundary layer resistance fell to about 0.46 s/cm because of improved air circulation pattern.

Plant Work - Agricultural Station- The first measurement on plant material was done with the small chamber on leaves of root suckers of mango. The LI-6000 software allows prompts for input of the user calculated leaf area, or for input of a leaf width which is automatically paired with lengths previously fixed in the LI-6000 memory. The latter feature was very useful in speeding up the measurements, as the length across the small chamber (3.25 cm) was fixed, and only the leaf width had to be input at the end of each measurement period. The mango leaf proved to be ideally suited for this technique as it has only a gradual taper along the length, a good approximation of average width being determined with a single measurement across the center of leaf blade held in the chamber (Fig. 1). The total area was calculated by the LI-6000 software after width input and used in calculations. Both large and small chambers were used in this manner, the smaller chamber being limited to leaf widths <5 cm due to interference with the latch mechanism and to reduce possible problems with air mixing.

A fully sunlit leaf was measured 5 times over a 9 min period to test the variation in mango photosynthetic rate and system measurement repeatability. During this period the chamber was placed on the same spot of the leaf 5 times, 10 measurements of all parameters being made 3 s apart under software control each time. The grand mean of the photosynthetic rate of the 5 measurement periods was 0.365 mg CO_2 m^{-2} s^{-1} (see Table 1 for example of one measurement period). The means of the 5 periods ranging from 0.308 to 0.3986 mg CO_2 m^{-2} s^{-1}. Photosynthetically active radiation (PAR) was saturating at all times (1500- 1700 uE m^{-2} s^{-1}). Leaf temperatures were

<0.5 °C higher than air temperature, averaging 29.7°C. The ambient relative humidity was 55%, the leaf conductance 1.3 cm/s, and the transpiration rate approximately 100 mg H_2O m^{-2} s^{-1}.

A fully shaded leaf was chosen from an adjacent sucker for a second series of repeated measurements. Four on/off cycles were made in 9 min with the chamber, returning to the same leaf area each time. The techniques were equivalent to the sun-leaf work. Steps between readings in each measurement period were changed from 3 to 10 s to try increasing the total photosynthetic reduction in chamber CO_2 concentration below that expected as noise alone (<4 ppm max.). Under low PAR (<20 uE m^{-2} s^{-1}) maximum CO_2 drawdown was only 8.3 ppm even after 100 s (10 s steps). That is only about 2X maximum noise, so a longer step may be called for when photosynthetic or repiratory rates are low as in this case where they averaged 0.04 mg CO_2 m^{-2} s^{-1}, only 1/10 of those rates in sunlit leaves. Longer on-leaf chamber residence times should not cause overheating in the shade, as the leaf was found to be at least 1°C below air temperature, even after 100 s. The repeated measurements on the same area of the leaf over the 9 minute period did reduce conductance from an average of 1.2 to 0.6 cm/s. This is probably due to the protracted exposure of the stomata to the dry air returning to the chamber in the closed-loop system during measurements. The air is dried to eliminate the interference of water vapor with IRGA CO_2 analysis. Transpiration was also reduced 20 - 40% over of sunlit leaves, some of the reduction due to the dry air effect. This effect is exacerbated by the use of the small volume chamber and repeated use of the same tiny (16 cm^2) area. Chamber effects on leaf energy balance and convection would also be greater in the small chamber. All these effects can be avoided by the simple expedient of measuring a new area of a leaf or a new leaf with each chamber placement. The system can also be configured without the dessicant, which would avoid this dry air problem in very sensitive species and/or when the chamber has to be in place for a longer (>2 min) time. Software correction for water vapor effect is provided for when the system is used without the dessicant.

The last work with the saplings derived from root suckers was aimed at evaluating the range and variation in photosynthetic rate from among several leaves on the same individual. Under full sun 8 leaves of various age classes were measured, using a 3 s step for a 30 s elapsed time on each leaf. The grand mean photosynthetic rate was 0.4 mg CO_2 m^{-2} s^{-1} for the leaves (one data set in Table 2b). Conductances were high, ranging from 1.58 to 1.98 cm/s. The leaves were about 1.5^{o}C warmer than air, and transpiration was 120- 160 mg H_2O m^{-2} s^{-1}. Passing clouds at one time dropped the PAR to less than 300 uE m^{-2} s^{-1}, which reduced photosynthesis to 0.21 mg CO_2 m^{-2} s^{-1}, and leaf temperature to below air.

On a nearby tree, three leaves were later measured with their average photosynthesis ranging between 0.4 and 0.28 mg CO_2 m^{-2} s^{-1} under PAR > 1600 uE m^{-2} s^{-1} (a single data run in Table 2c). The wide range in photosynthetic rate was probably due to different levels of insolation, water stress, and age among the leaves, since their conductances ranged from 0.92 to 0.56 cm/s. The measurement series in Table 2c shows the effect of operator respired CO_2 on measurements. The ambient CO_2 concentrations were approximately 330- 340 ppm (C2) during this period, but some contamination from exhaled CO_2 existed as a pulse in the closed circulation of the system, giving an exagerated photosynthetic rate during the first 3 readings while mixing took place in the closed system. The contamination problems are most severe with the smaller chamber since there is less dilution volume (326 vs. 4060 ml). Operator attention to monitored CO_2 concentration can avoid such problems, which can be remedied by aborting and then restarting measurements when irratic or high numbers are detected. However, all is not lost even when such a measurement is recorded in LI-6000 memory. The mean photosynthetic rate can be easily recalculated once data is printed out, as was done with this page of data, where observations 1-4 were deleted, and a new mean calculated. Data can also be edited and automatically recalculated with system software.

Reviewing the results from among the leaves of root sucker saplings, full grown trees, and distinct leaf age classes, it is remarkable that there is such a narrow range of photosynthetic values, 0.33 - 0.4 mg CO_2 m^{-2} s^{-1}, even over such a wide range of conductances. The shade leaves had rates approximately 1/10 those of sun leaves, while passing clouds could reduce sun leaf rates by 50% in seconds.

Avenida Juncos- A tree planted immediately adjacent to a principal downtown street was the next experimental subject. Fully sunlit leaves were chosen at random, but always from the lower canopy as accessible from the ground. The measured average photosynthesis was 0.37 mg CO_2 m^{-2} s^{-1}, while conductances averaged 0.88 cm/s. Transpiration was as high as that observed at the previous site, 158 mg H_2O m^{-2} s^{-1}. Leaf temperature was 0.5°C higher than air temperature at 36.9°C. After a few minutes under intermittent clouds the PAR fell below 300 uE m^{-2} s^{-1} and photosynthesis was reduced to 0.134 mg CO_2 m^{-2} s^{-1}, with leaf temperatures at 32°C, nearly 2° below air. This set of results, although from a completely different area and population, are very similar to those of the Experimental Station site. The Juncos site was abandoned after only a few measurements because of nearby traffic which caused background CO_2 levels to fluctuate between 340- 420 ppm, making chamber equilibration nearly impossible.

Baldorioty de Castro- Two trees of small (<3 m) and large (>10 m) size were selected at this site. The smaller tree had a very open canopy, while the large tree had fruit-bearing branches near the ground. The large volume chamber was used at this site for the first time in order to make comparisons with the smaller size chamber which had been in use up to this point in the investigation. The small chamber was used only on one tree. Under clouds and low PAR, the mean photosynthetic rate of three distinct leaves was 0.183 mg CO_2 m^{-2} s^{-1} (Table 3a), with leaf temperature of 32^o, nearly 2^o less than air. Conductance was near 0.6 cm/s and transpiration 77- 88 mg H_2O m^{-2} s^{-1}.

Once the larger chamber was fitted, a procedure that takes less than 8 minutes, leaf areas in the chamber were 4 to 5X greater than those commonly used in the smaller chamber. However, due to a lower fraction of the total system volume being occupied by the leaf in the large chamber, a longer step (5 s) had to be taken so that the CO_2 depression would be within the 15- 30 ppm range as with the smaller chamber. By this time the PAR had increased to 800- 1200 uE m^{-2} s^{-1} and observed photosynthetic rates in the small tree were 0.375 mg CO_2 m^{-2} s^{-1} (sample data in Table 3b). Remarkably, a shade leaf from this open canopied tree with an incident PAR of only 200 uE m^{-2} s^{-1} had nearly equivalent gas exchange rates, 0.3 mg CO_2 m^{-2} s^{-1}, perhaps showing light saturation at, or near this level of PAR.

The large tree was examined with the intent of determining if a ripening fruit would change the source/ sink relationships such that differences in photosynthetic rates could be detected between leaves near and far from fruit. Unfortunately these measurements are mostly incomparable because highly variable clouds caused short term shifts in PAR. A few measurements were made during periods of stable PAR, with leaves adjacent to fruit averaging 0.369 and 0.196 mg CO_2 m^{-2} s^{-1} under average PAR of 1810 and 570 uE m^{-2} s^{-1} respectively. Leaves on branches without fruit had average photosynthetic rates of 0.359 and 0.317 mg CO_2 m^{-2} s^{-1} under PAR of 464 and 160 uE m^{-2} s^{-1}. Conductances were much lower (0.4 versus 0.66 cm/s) and leaf temperature > air in the full sun leaves with adjacent fruit. As mentioned above, comparisons are difficult because of highly variable PAR, however, in the non-fruit leaves there seems to be less reduction of photosynthetic rate under lower PAR and overall higher stomatal conductances.

<u>65th Infanteria</u>- The last measurements made for this report were done on a tree with three distinct age classes of leaves, all within easy reach of the ground, and under the same exposure on the tree. The leaves were 3 types; those fully expanded, green leaves in good condition; those near senescence with marked sucking insect damage and some chlorosis; and the most recently emerged, strongly colored (nearly red) leaves which had expanded to only 25% of full size. The smaller chamber was used in all these runs, as it is more convenient to use when working alone and when leaves are narrow enough (<5 cm) to slide in easily.

The current age class of fully expanded green leaves under full sun had an average photosynthetic rate of 0.23 mg CO_2 m^{-2} s^{-1}, stomatal conductances of 0.49 cm/s, about 100 mg H_2O m^{-2} s^{-1} transpiration, and leaves at 37°C, nearly 3° over air temperature (Table 4a). The older leaves had lower and more variable photosynthetic rates, averaging 0.16 mg CO_2 m^{-2} s^{-1}. The rates depending largely on extent of insect damage and extent of chlorotic area. Conductances and leaf versus air temperatures were comparable to those of current leaves (Table 4b), such parameters being more biophysically than biochemically controlled. The newest crop of as yet unexpanded leaves were photosynthetically incompetent, respiring -0.03 mg CO_2 m^{-2} s^{-1} (Table

4c). This value is close to a break even point, although not too precise, since it close to the same magnitude as system noise. The conductance of the new leaves was lower than the other two classes, 0.196 cm/s, as was transpiration. The unexpanded leaves were very thin and not turgid. Even under these conditions unfavorable to transpirational cooling, and in the full sun, the combination of the leaf angle and area, azimuth, and non-green coloration must have contributed favorably to the leaf energy budget as leaf temperature was only 2^oC over air, less than that of the fully expanded leaves.

At the close of the measurement series another chamber noise test was run with the empty, small volume chamber in full sun. Chamber temperature increased only 1^oC in 50 s, and a total range in CO_2 concentration of 1.3 ppm was observed, which gave a calculated photosynthesis noise level of a negligible 0.007 mg CO_2 m^{-2} s^{-1}. The results of this test were roughly comparable to the worst case lab results where a 4 ppm maximum change in CO_2 concentration was found (but over 10 min).

Conclusions

Mangifera indica- The mango photosynthetic rate is relatively constant among many populations and areas within current age class leaves and under full sun and adequate water supply. In this case, water stress is arbitrarily defined as observed stomatal conductances below 0.6 cm/s. Photosynthetic rates were lower when conductances <0.5 cm/s and with leaf temperatures >35^oC under full sun, and at any PAR below 800 uE m^{-2} s. Sun leaf photosynthesis was strongly limited by low PAR, while shade leaves had higher rates under comparable, low PAR conditions.

The work with very young and very old, nearly sensescent leaves showed that photosythetic competence (rates > 0) remains in even the oldest age class of leaves, but is only gradually acquired in newly emerging leaves.

Mango is evergreen, with periodic flushes of new growth, so at no time is the bulk of leaf tissue of either an old or young age classes as would be the case in a deciduous tree. Such a growth pattern, as in mango, reduces the carbon demand on a tree since there are no times with periods of leaflessness nor with nonphotosynthetic leaves.

LI-6000- The portable photosynthesis system used in this research proved to be an extremely valuable investigative tool. It is easily used, and data are readily acquired, although technique and care in its use are critical. The operator must know the theoretical and practical details of its operation and see that conditions are optimal for its use. The results acheived are only as good as the attention paid to their acquisition.

There is a degree of caution in this discussion, but it must be pointed out that the systems includes very sensitive analytical instruments that are adapted for use in the field. The above cautions would hold for any of the common photosynthesis measurement techniques, as all have very sensitive analyses or instrumentation that must be used correctly and with a modicum of insight if reliable, repeatable, and publishable results are to be produced.

The LI-6000 system is as robust as possible and follows in the tradition of other LI-COR instruments that I have used, with its ease of use, practical layout, and versatile operating system. It is the most highly automated and computer controlled field instrument that I have ever used, providing as it does data gathering, analysis, and storage capability in a single unit rather than in the usually expected form of a mobile laboratory or a trunk full of instruments.

An additional advantage of the LI-6000 is its utility as a portable or laboratory IRGA. Since it contains integral pumps and a real-time monitoring capability, it can be used to measure experimental processes that are based on CO_2 evolution or uptake, as long as its 1100 ppm range is not exceeded. The data can also be recorded at user selected intervals.

As an example of other LI-6000 uses, I have built a chamber for the system (Fig. 2) that allows me to measure soil respiration under ambient conditions in the field. The prototype chamber accomodates the LI-6000 instrument head sans the photosynthesis chamber. With the addition of a mixing fan (12 vdc, 1" diam., Rotron USA) which I plug into the instrument head in place of the LI-COR chamber fans, the chamber works in concert with the software intended for the photosynthesis measurements. The chamber is pushed onto the soil surface, being sealed with a 1" thick foam ring. The CO_2 flux from the forest floor is sufficient to increase the chamber concentration from 100 to 300 ppm in a 45 s measurement period. Since the volume of the soil respiration chamber and the surface area of forest floor it covers are known, the values are input to the LI-6000 software and reduced data computed and stored by the system. Typical results give a range of forest floor respiration from 4 (litter-free soils) to over 60 (dense litter areas) g carbon m^{-2} day^{-1} for the moist tropical ecosystem in which I work (Lawrence 1984). Forest floor evaporation and temperature can also be quantified as the whole instrument head is in use, only the quantum sensor being deleted for respiration measurements.

This basic respirometer configuration is also being used, in conjunction with other staff members, to measure the separate contribution of fungi and bacteria to forest floor respiration. In this work the soil is incubated after antibacterial or antifungal treatments to sort out the two organisms' respiration rate on a per gram basis, the LI-6000 being used to monitor the efflux of CO_2 from the reaction flasks.

For later manipulative photosynthetic work I plan to set up a bypass system (J. Norman, L. Middendorf pers. comm.) wherein the CO_2 and water vapor environments of the leaf in the LI-6000 chamber can be altered. This will allow the production of CO_2 curves and to test stomatal sensitivity to distinct water vapor pressure deficits. With slight modification of the bypass approach the LI-6000 system could be used with special chamber construction that would also allow temperature or light controlled work. The closed chamber could be flushed with air of known CO_2 and water vapor concentrations during light or temperature equilibration periods, and the flushing stopped only during the actual closed system measurement with the LI-6000. This flushing and temperature control technique would reduce the chamber effects of enclosing the longer periods of time as required by manipulative photosynthetic research.

Literature Cited

Anon. 1983. LI-6000 Portable Photosynthesis System. Publ. No. 8306-35. LI-COR, Inc., Lincoln, Nebraska, USA.

Chaudhri, S.A. 1976. Mangifera indica - Mango. pp. 403- 474 In R.J. Garner, S.A. Chaudhri, and staff (eds). The propagation of tropical fruit trees, Hort. Rev. #4, Commonwealth Bureaux of Horticulture and Plantation Crops, Commonwealth Agricultural Bureaux, Slough, England.

Lawrence, W.T. 1984. Forest floor respiration in a moist tropical ecosystem. Abstract, summer meetings Ecological Society of America. 7- 12 August, 1984, University of Colorado, Fort Collins, CO USA.

Lawrence, W.T. and W.C. Oechel. 1984. Photosynthesis of interior Alaska taiga trees across soil temperature gradients among several community types. (in MS).

Oechel, W.C. and W.T. Lawrence. 1979. Energy utilization and carbon metabolism in Mediterranean scrub vegetation of Chile and California: I. Methods. A transportable cuvette field photosynthesis and data acquisition system and representative results for Ceanothus greggii. Oecologia 39: 321-335.

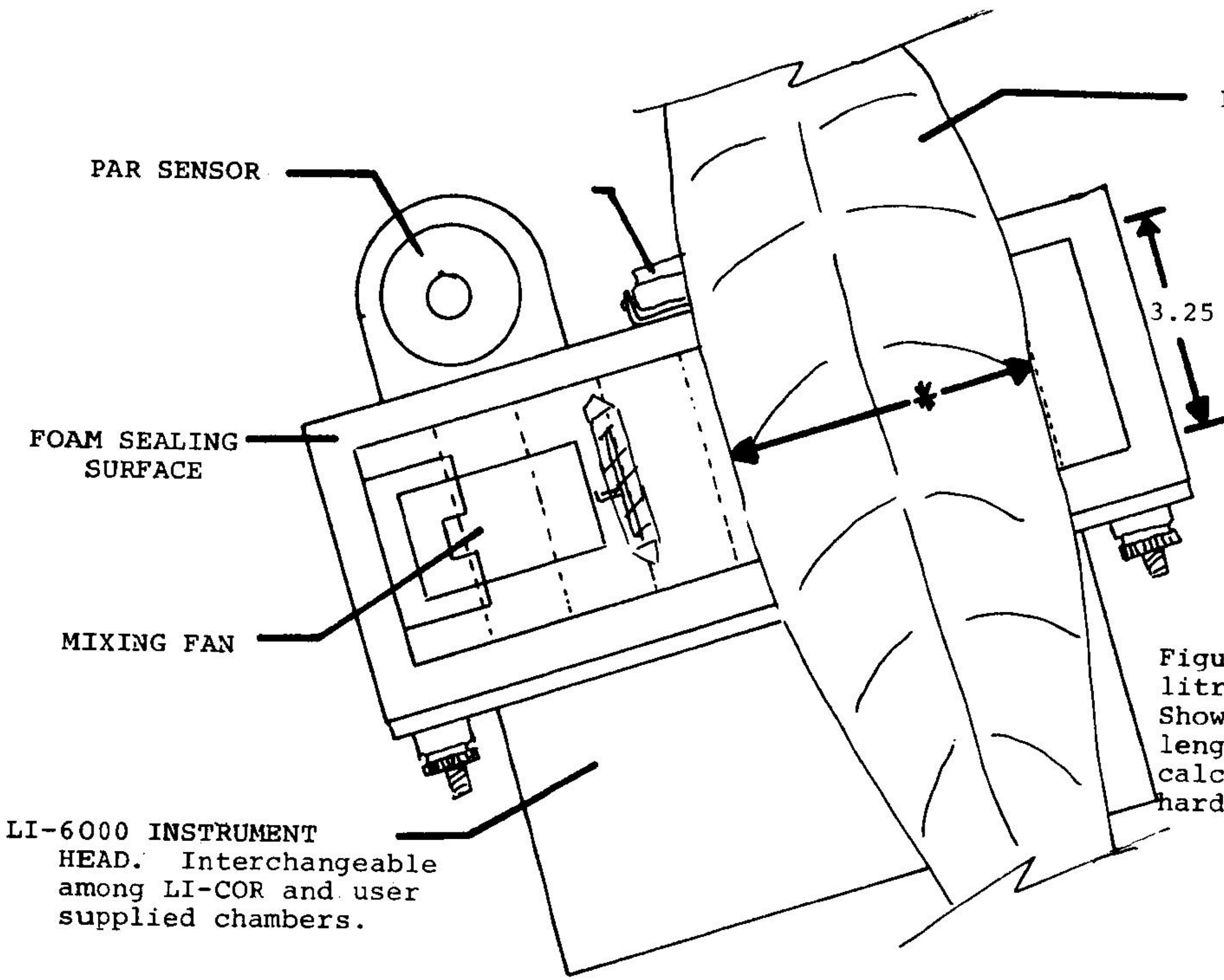

Figure 1. Schematic of 0.25 litre chamber (not to scale). Shows placement of leaf for length X width automatic area calculations. Chamber lid and hardware not shown.

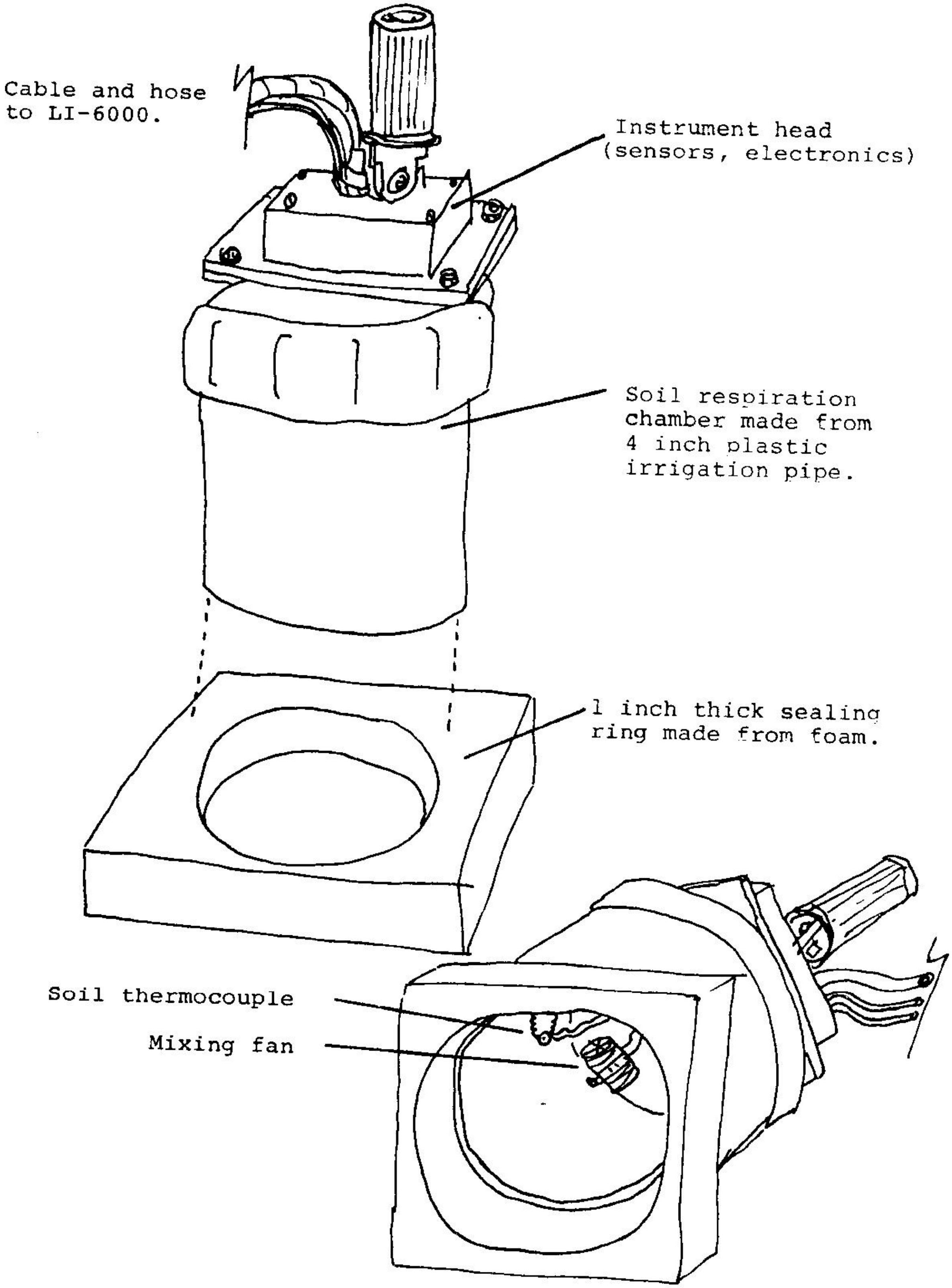

Figure 2. Exploded view (top) and end view (bottom) of the prototype soil respiration chamber. Used in substitution for the standard LI-COR photosynthesis chambers.

PAGE= 1
#OBS= 10
16 JAN 09:28:04
DESCRIPT .0000
REM1:SUCKER 125CM
REM2:FULL SUN
REM3:SMALL CHMB
PRESSURE = 980 MB
CHAMBER VOLUME = 326.0 CM3
LEAF AREA = 16.25 CM2
BLR = 1.100 S/CM
STM RAT = 1
FLOW = 10.50 CM3/S
RH IN = .0000 %
INIT TRAN = 101.3 MG H2O/M2/S
INIT INT CO2 = 302.2 PPM

OB	TIME	QU	RH	LT	CT	C2	CS	PH
1	0	1173.	55.60	30.13	29.63	353.4	.0000	.0000
2	3	951.4	55.36	29.88	29.64	350.7	1.261	.3076
3	6	955.4	55.06	29.70	29.65	346.7	1.277	.4614
4	9	1139.	54.67	29.75	29.67	343.7	1.238	.3383
5	12	1304.	54.33	29.95	29.71	339.4	1.228	.4921
6	15	1443.	54.11	30.21	29.79	336.7	1.261	.3075
7	18	1543.	53.84	30.43	29.84	332.4	1.142	.4919
8	21	1595.	53.74	30.59	29.92	329.7	1.196	.3073
9	24	1606.	53.70	30.73	29.98	326.5	1.166	.3687
10	27	1596.	53.67	30.85	30.03	322.2	1.145	.4916
M	3	1324.	54.38	30.19	29.78	338.2	1.213	.3963
R	27	654.5	1.928	1.15	0.40	31.15	.1353	.1847
IV	0	977.8	55.45	29.70	29.57	353.7	1.285	.3666
IE	0	70.10	.1117	0.13	0.02	.2540	.0198	.0603

Table 1. A complete page of data as output to a serial printer by the LI-6000. Results from measurements on a 1.25 m sapling from the Agricultural Experimental Station in Rio Piedras. Abbreviations are as follows:

BLR boundary layer resistance
STM RAT stomatal resistance ratio
INIT TRAN initial transpiration rate
INIT CO2 internal CO_2 concentration
OB observation number
QU photon flux density
RH chamber % relative humidity
LT leaf temperature
CT chamber temperature
C2 CO_2 concentration
CS conductance cm/s
PH photosynthetic rate
M mean of observations
R range of values
IV calculated intercept value
IE error of least sqs. fit

A

OB	TIME	QU	RH	LT	CT	C2	CS	PH
1	0	12.57	58.87	26.88	28.62	340.5	.0000	.0000
2	3	12.57	56.50	27.11	28.87	340.5	1.768	.0000
3	6	13.35	54.72	27.39	29.02	339.1	1.535	.1622
4	9	13.35	53.23	27.62	29.12	338.9	1.330	.0324
5	12	13.35	51.96	27.76	29.19	338.6	1.206	.0324
6	15	12.57	50.91	27.86	29.24	338.9	1.148	-.0324
7	18	11.78	49.91	27.96	29.27	338.9	1.037	.0000
8	21	12.57	49.08	28.02	29.32	338.3	1.047	.0648
9	24	12.57	48.30	28.09	29.35	337.5	.9752	.0972
10	27	12.57	47.64	28.12	29.38	337.0	.9641	.0648
M	3	12.74	51.99	27.70	29.15	338.8	1.223	.0468
R	27	1.571	11.22	1.24	0.76	3.491	.8041	.1947
IV	0	12.98	57.50	27.07	28.81	340.3	1.646	.0396
IE	0	.2906	.4534	0.08	0.06	.2526	.0703	.0419

B

OB	TIME	QU	RH	LT	CT	C2	CS	PH
1	0	1832.	55.62	31.93	30.58	334.6	.0000	.0000
2	3	1834.	55.36	32.24	30.86	333.0	2.056	.2298
3	6	1839.	55.36	32.48	31.05	329.7	1.996	.4594
4	9	1833.	55.45	32.61	31.15	326.2	1.853	.4974
5	12	1837.	55.67	32.66	31.25	323.3	1.962	.4208
6	15	1829.	55.84	32.73	31.33	320.6	1.927	.3824
7	18	1813.	55.97	32.75	31.39	317.7	1.885	.4205
8	21	1807.	56.14	32.74	31.45	314.7	1.963	.4205
9	24	1799.	56.26	32.78	31.51	310.9	1.976	.5350
10	27	1805.	56.36	32.87	31.55	307.7	1.922	.4585
M	3	1823.	55.78	32.60	31.23	321.9	1.949	.4249
R	27	40.06	1.000	0.94	0.97	26.85	.2025	.3051
IV	0	1842.	55.30	32.20	30.77	335.5	1.983	.3509
IE	0	4.624	.0905	0.08	0.06	.2919	.0406	.0527

C

OB	TIME	QU	RH	LT	CT	C2	CS	PH
1	0	1674.	53.72	32.29	30.78	348.8	.0000	.0000
2	3	1644.	52.52	32.22	30.95	355.5	.9075	-.8510
3	6	1661.	51.62	32.21	31.07	344.8	.9153	1.361
4	9	1635.	50.86	32.10	31.18	335.9	.9238	1.122
5	12	1623.	50.18	32.06	31.26	331.9	.9063	.5100
6	15	1631.	49.62	32.04	31.35	327.9	.9335	.5098
7	18	1637.	49.08	32.04	31.41	324.6	.8937	.4078
8	21	1508.	48.76	32.08	31.47	322.8	.9419	.2378
9	24	1659.	48.47	32.22	31.55	319.8	.9466	.3736
10	27	1693.	48.13	32.30	31.61	316.8	.8907	.3735
M	3	1631.	50.23	32.14	31.27	332.9	.9182	.4494
R	27	184.6	5.589	0.26	0.83	38.67	.0558	2.212
IV	0	1649.	52.99	32.18	30.87	351.6	.9152	.4445
IE	0	30.82	.2550	0.06	0.03	2.250	.0145	.4414

Table 2. Agricultural Experimental Station. Example data tables for single leaves. A) Measurements of shaded leaves; B) adjacent leaves in full sun; and C) a nearby tree with leaves in the sun.

A

OB	TIME	QU	RH	LT	CT	C2	CS	PH
1	0	271.8	40.78	30.98	33.33	331.1	.0000	.0000
2	3	286.0	39.66	31.45	33.84	329.5	.6817	.1656
3	6	282.8	39.15	31.89	34.12	328.1	.6546	.1378
4	9	283.6	38.90	32.22	34.28	325.7	.6228	.2479
5	12	306.4	38.81	32.49	34.39	323.6	.6096	.2203
6	15	323.7	38.71	32.69	34.46	322.2	.5769	.1376
7	18	338.6	38.76	32.86	34.52	319.5	.5913	.2752
8	21	337.8	38.73	32.99	34.56	318.5	.5615	.1100
9	24	338.6	38.78	33.13	34.61	317.1	.5746	.1375
10	27	339.4	38.81	33.14	34.62	315.2	.5505	.1925
M	3	311.4	39.03	32.42	34.31	323.0	.6026	.1805
R	27	67.57	2.074	2.16	1.29	15.84	.1312	.1651
IV	0	271.8	39.83	31.33	33.73	331.2	.6705	.1890
IE	0	5.538	.2778	0.13	0.12	.2464	.0104	.0405

B

OB	TIME	QU	RH	LT	CT	C2	CS	PH
1	0	790.4	54.28	30.51	29.95	326.8	.0000	.0000
2	5	801.4	54.75	30.64	30.07	324.1	.3681	.4415
3	10	914.5	55.14	30.85	30.17	323.6	.3345	.0882
4	15	975.8	55.60	31.01	30.23	320.6	.3217	.4853
5	20	1166.	56.21	31.29	30.26	316.6	.3354	.6617
6	25	1186.	56.60	31.59	30.31	314.7	.2887	.3087
7	30	1223.	57.04	31.92	30.40	312.3	.3283	.3969
8	35	1203.	57.60	32.23	30.46	311.5	.3306	.1322
9	40	1217.	58.14	32.44	30.52	307.4	.3222	.6612
10	45	1242.	58.65	32.55	30.58	305.6	.3181	.3085
M	5	1078.	56.39	31.50	30.30	316.3	.3275	.3871
R	45	451.8	4.369	2.04	0.63	21.21	.0794	.5734
IV	0	821.7	54.21	30.39	30.00	327.1	.3444	.3709
IE	0	43.43	.0379	0.05	0.02	.4798	.0128	.1452

Table 3. Data tables for a small mango tree near Baldorioty de Castro Blvd. A) Measurements with the small chamber (320 cc) under variable PAR, and B) measurements on the same tree with the large chamber (4000 cc) and higher PAR.

A

OB	TIME	QU	RH	LT	CT	C2	CS	FH
1	0	2358.	39.46	36.30	33.78	335.4	.0000	.0000
2	3	2354.	39.54	36.60	33.93	333.0	.5430	.3093
3	6	2365.	39.64	36.87	34.04	330.8	.5255	.2748
4	9	2365.	39.76	37.04	34:13	329.5	.5188	.1717
5	12	2372.	39.88	37.16	34.22	327.3	.5193	.2746
6	15	2382.	40.00	37.32	34.31	326.0	.5198	.1716
7	18	2387.	40.08	37.46	34.37	325.2	.4997	.1029
8	21	2385.	40.20	37.49	34.44	322.2	.5122	.3774
9	24	2389.	40.29	37.65	34.50	320.6	.5061	.2058
10	27	2390.	40.44	37.73	34.57	318.7	.5181	.2400
M	3	2375.	39.92	37.18	34.24	326.8	.5180	.2364
R	27	35.37	.9763	1.43	0.79	16.65	.0432	.2744
IV	0	2355.	39.44	36.49	33.85	334.9	.5323	.2548
IE	0	2.319	.0110	0.06	0.02	.2738	.0061	.0589

B

OB	TIME	QU	RH	LT	CT	C2	CS	FH
1	0	2271.	39.66	35.79	33.54	334.6	.0000	.0000
2	3	2263.	39.46	36.09	33.69	333.5	.4386	.1210
3	6	2231.	39.39	36.33	33.84	334.0	.4466	-.0605
4	9	2365.	39.32	36.57	33.94	331.6	.4246	.2721
5	12	2374.	39.32	36.76	34.05	330.8	.4318	.0906
6	15	2368.	39.32	36.97	34.15	329.2	.4250	.1813
7	18	2361.	39.39	37.10	34.24	329.2	.4292	.0000
8	21	2343.	39.42	37.19	34.32	326.2	.4198	.3322
9	24	2338.	39.49	37.26	34.40	325.2	.4271	.1207
10	27	2340.	39.56	37.39	34.48	324.4	.4278	.0905
M	3	2328.	39.41	36.76	34.07	329.9	.4300	.1275
R	27	143.0	.3417	1.60	0.94	10.20	.0267	.3927
IV	0	2279.	39.44	35.96	33.61	335.3	.4386	.0937
IE	0	25.39	.0717	0.07	0.02	.4276	.0045	.0865

C

OB	TIME	QU	RH	LT	CT	C2	CS	FH
1	0	2229.	32.26	36.73	34.32	335.9	.0000	.0000
2	5	2225.	29.46	36.84	34.72	337.3	.2171	-.1293
3	10	2163.	27.24	36.95	34.93	337.8	.1954	-.0516
4	15	1146.	25.41	36.60	34.99	337.8	.1776	.0000
5	20	1025.	23.84	36.18	34.94	336.4	.1651	.1291
6	25	1167.	22.35	36.05	34.94	337.3	.1569	-.0775
7	30	1170.	21.01	35.91	34.95	338.1	.1502	-.0775
8	35	1390.	19.74	36.20	35.05	336.7	.1453	.1291
9	40	1327.	18.69	36.24	35.12	338.1	.1417	-.1291
10	45	1095.	17.74	36.21	35.15	337.5	.1322	.0516
M	5	1475.	23.64	36.38	34.93	337.3	.1646	-.0172
R	45	1204.	14.52	1.04	0.83	2.148	.0848	.2585
IV	0	2043.	30.82	36.80	34.62	336.8	.2081	-.0579
IE	0	212.6	.4792	0.15	0.09	.4104	.0055	.0700

Table 4. Measurements from A) fully expanded, current age class leaves; B) fully expanded, but senescent leaves; and C) unexpanded, red-hued new leaves of the same individual adjacent to 65th. Infantería Blvd.