THE PHOTOSYNTHETIC ACTIVITY OF PEAR LEAVES
(PYRUS COMMUNIS L.)

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Abstract

Pear leaf assimilation and transpiration were measured under both laboratory and field conditions using infrared gas analysis.

In the laboratory, leaf resistance to water vapour loss ($r_l$) was c. 1.2 sec cm$^{-1}$ at a saturating light intensity, and the mesophyll resistance to CO$_2$ uptake ($r_m$) was 4.4 sec cm$^{-1}$. These relatively low diffusive resistances were in line with the high rates of photosynthesis recorded in both the laboratory and field.

The effect of leaf water potential and the nitrogen status of the tree on leaf photosynthesis was studied in the orchard. Photosynthesis was not immediately affected until leaf water potential had fallen to below —30 atm, although a history of water shortage reduced the daily maximum rate of photosynthesis. Similarly, trees that experienced a prolonged nitrogen deficiency showed a lower rate of leaf photosynthesis in terms of both leaf area and chlorophyll concentration although the leaves recovered their green colour and photosynthetic activity following nitrogen fertilization.

I. INTRODUCTION

Despite the economic importance of pear trees, there is no detailed report in the literature on the photosynthetic activity of their leaves. The present paper attempts to document this information, and to provide background data for decisions relating to tree management. Accordingly, pear leaf photosynthesis was studied in relation to certain environmental and nutritional factors under both laboratory and orchard conditions.

II. MATERIALS AND METHODS

Well-developed pear trees, Pyrus communis (L.) cv. Williams’ Bon Chretien (syn. Bartlett), were used for all experiments. Budded trees growing in pots were used for the laboratory studies, while mature (30-yr-old) trees growing in the orchard or 1-yr-old trees in sand culture (out-of-doors) were used for the field measurements at Tatura. The trees growing in sand culture had been maintained on complete nutrient solution (Hewitt 1966), with the exception of nitrogen. Two levels of nitrate were imposed: 12 m-equiv/l which was regarded as adequate and which promoted vigorous tree growth; and 1 m-equiv/l which was suboptimal and caused reduced growth plus foliar chlorosis. These two nutritional planes provided contrasting material for experimental purposes.

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Photonsynthesis was measured under both laboratory and orchard conditions by infrared CO₂ analysis. The laboratory equipment, based upon two URAS-1 instruments manufactured by Hartmann & Braun (Germany), has been described previously (Kriedemann 1971). Briefly, this equipment enables simultaneous measurement of transpiration and photosynthesis by single attached leaves under controlled conditions. Light intensity, temperature, CO₂ concentration, and relative humidity could be controlled. Light was provided by a single mercury vapour lamp (HPLR, 400 W) mounted above a heat filter (a 2-cm depth of distilled water). Light intensity was measured on this occasion with a selenium photocell (EEL Lightmaster) corrected to the wavelength sensitivity of the human eye. Under these conditions, 1000 f.c. measured on the photocell were equivalent to 4 mW cm⁻² of photosynthetically active radiation. CO₂ and water vapour diffusive resistances were derived from photosynthesis and transpiration measurements in an oxygen-free gas stream provided by Wösthoff gas-mixing pumps. Fluxes of CO₂ and water vapour were expressed in μg cm⁻² sec⁻¹ and substituted into the equations of Holmgren, Jarvis, and Jarvis (1965) which are equivalent in form to those of Gaastra (1959) and Raschke (1958), except for the dimensions of the input data.

The total diffusive resistance to water vapour loss is referred to as Σ with component resistances rₐ and r₁, where rₐ refers to boundary layer resistance (derived from evaporation measurements on moist filter paper replicas) and r₁ is the leaf resistance. By definition Σ = rₐ + r₁. Leaf resistance embodies both stomatal and cuticular resistances to gaseous diffusion. For a given experiment using the same leaf, cuticular resistance can be regarded as constant, and rapid changes in r₁ are then attributable to stomatal behaviour.

The total diffusive resistance to CO₂ fixation is called Σr', and comprises three separate resistance terms rₐ', r₁', and rₘ', where Σr' = rₐ' + r₁' + rₘ'. Boundary layer and leaf resistances to CO₂ diffusion, rₐ' and r₁' respectively, can be derived from the equivalent resistances to water vapour exchange, and in this paper the conversion factor given by Gale and Poljakoff-Mayber (1968) was adopted. Accordingly rₐ' = 1.56 rₐ and r₁' = 1.56 r₁. The mesophyll resistance, referred to above as rₘ', is in itself a collective term and represents the total resistance encountered within the leaf by CO₂ molecules moving from the substomatal cavity to their site of fixation. In the present context rₘ' would be synonymous with the term "residual resistance" (r₁*) which has been used by other workers.

The total CO₂ diffusive resistance of the leaf (and hence rₘ') can be derived from the slope of the photosynthesis–CO₂ concentration response curve obtained in oxygen-free air under a saturating irradiance and at optimum temperature (Holmgren, Jarvis, and Jarvis 1965; Troughton and Slatyer 1969). Under these conditions, photosynthesis is virtually eliminated, so that the effective CO₂ concentration at the site of photosynthesis within the leaf approaches a minimum and, for the purpose of calculating rₘ', is generally regarded as zero. The slope of the photosynthesis–CO₂ concentration response is then a direct consequence of the overall diffusive resistance for CO₂ assimilation, i.e. Σr'.

When oxygen is present in the gas stream, the apparent CO₂ compensation point has been taken as the relevant CO₂ concentration inside the leaf (Bierhuizen and Slatyer 1964).

Portable equipment for CO₂ analysis was used in the orchard experiments. A small cuvette with built-in fan and temperature sensor was attached to the lower surface of selected leaves and net photosynthesis was calculated from the drop in CO₂ concentration of the air stream passing over the leaf. Full details of the gas circuit and measuring system have been given elsewhere (Kriedemann and Smart 1970). A pyrheliometer was used to measure total solar radiation (wavelength range 0.3–3.0 μm) and, in combination with the CO₂ analyser and leaf temperature sensor, provided data on diurnal trends in solar radiation, photosynthesis, and leaf temperature. Photosynthetically active radiation would approximate one-half (Gates 1965) of the values for total solar radiation shown in Figures 5(a) and 5(b). The experimental leaf was always maintained at right angles to the incident sunlight. Fully expanded leaves (at least 12 weeks after unfolding) were used throughout.

Leaf water potential was measured with a pressure chamber (Scholander et al. 1965). Leaf chlorophyll concentration was determined by the method described by Kirk (1968) on an 80% acetone extract from representative leaves.
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III. Results

(a) Laboratory Measurements

(i) Light Intensity

Response curves for photosynthesis and leaf resistance as a function of incident light intensity are shown in Figure 1. An intensity of 5000 f.c. can be regarded as light-saturating, because measurements on other leaves at higher intensities showed no further increase in photosynthesis. In the present case, the light compensation point was 100 f.c.

![Leaf resistance vs. Light intensity](Fig. 1)

Fig. 1.—Effect of light intensity on net photosynthesis and leaf resistance.

![Net photosynthesis vs. Leaf temperature](Fig. 2)

Fig. 2.—Net photosynthesis as a function of leaf temperature.

![Leaf resistance vs. CO₂ concentration](Fig. 3)

Fig. 3.—Effect of CO₂ concentration on photosynthesis in the presence or absence of oxygen supply.

Leaf resistance was uniformly low (Fig. 1) which indicates that stomatal aperture showed no apparent change throughout the experiment. Stomatal aperture had been kept at its maximum by starting measurements at 5000 f.c. and after a stable rate of gas exchange had been achieved the light intensity was decreased to 250 f.c. with subsequent increases up to 5000 f.c. again.

(ii) Temperature

At a saturating light intensity, photosynthesis showed a broad temperature optimum (Fig. 2), with a relatively small decline beyond 30°C. These temperature data are particularly relevant to the orchard situation, described later, where leaf temperature was commonly 30–35°C for a substantial part of the day. Under the laboratory conditions (saturating light and high relative humidity) prolonged exposure of the leaf to 40°C had no deleterious effect on its photosynthetic activity.
(iii) Carbon Dioxide and Oxygen

The data shown in Figure 3 demonstrate a linear relationship between photosynthesis and CO$_2$ concentration in either the presence or absence of oxygen. The removal of oxygen from the gas stream entering the cuvette caused a 30% increase in net photosynthesis at a given CO$_2$ concentration. Such an increase is generally attributed to the elimination of photorespiration (see Jackson and Volk 1970). In effect, the straight line representing the photosynthetic response is displaced so that it passes through the origin of the graph (Fig. 3). The slope of this line was virtually
unchanged in the presence of oxygen, but instead it made an intercept on the abscissa at a CO₂ concentration of 60 p.p.m. Significantly, the CO₂ compensation point, determined in a recirculating gas stream for this same leaf, was 62 p.p.m.

The calculation for mesophyll resistance was based either on photosynthetic rates in an oxygen-free gas stream, or on the rate in normal air and taking the CO₂ compensation point as the effective CO₂ concentration at the site of photosynthesis [see Bierhuizen and Slatyer (1964) for rationale]. Values for \( r'_{m} \) shown on Figure 3 were based on photosynthetic rates in an oxygen-free gas stream at the four CO₂ levels used in the experiment. The alternative \( r'_{m} \) calculation (referred to above), based on photosynthetic rates obtained immediately after the CO₂ compensation point was determined, yielded values of 4·54 and 4·32 sec cm⁻¹ in two separate measurements with this leaf.

\[(b) \text{ Measurements in the Orchard}\]

(i) *Diurnal Patterns in Photosynthesis and Leaf Water Potential*

The data in Figures 4(a) and 4(b) show the contrast in diurnal photosynthesis of leaves on a well-watered tree as compared to an adjacent droughted tree (irrigation water withheld for 6 weeks). At the start of photosynthetic activity, shortly after 0600 hr, leaf water potential in the irrigated tree was up to −10 atm. However (following the night-time, when some improvement in moisture status can be expected), the droughted tree was still at −20 atm. The trees also differed substantially in their maximum rates of leaf photosynthesis, and in the time taken to achieve this peak. In both instances, CO₂ assimilation declined later in the day, but ceased completely shortly after 1200 hr in the droughted tree.

Although leaf water potential had fallen to between −25 and −30 atm by mid-morning, this factor is not likely to have caused the decline in photosynthesis because in subsequent experiments with excised leaves of irrigated trees photosynthesis did not start to decline until leaf water potential had fallen to between −35 and −37 atm. Furthermore, the droughted tree [Fig. 4(b)] was still showing maximum photosynthesis when leaf water potential was between −25 and −30 atm. The prolonged exposure to full sunlight is a more likely explanation for this steady fall in photosynthesis (see Section IV).

(ii) *Photosynthesis and Nitrogen Nutrition*

Figures 5(a) and 5(b) demonstrate the effect of the nitrogen status of the tree on maximum photosynthetic activity and diurnal patterns in leaf assimilation. Although solar radiation (measured in a horizontal plane) reached its maximum value around noon, photosynthesis was light-saturated by 0830 hr when the total irradiance was c. 30 mW cm⁻². The photosynthetically active component would be about one-half of this energy level (Gates 1965), which in turn would approximate 4000 f.c. (see Gaastra 1959 for conversion factors). This level of light intensity had been found to saturate photosynthesis as measured in the laboratory.

At the lower level of nitrogen [Fig. 5(b)] leaf photosynthesis (per unit area) was substantially reduced. The deficiency of chlorophyll in this foliage was largely responsible, although additional factors must have been involved in lowering the
assimilation number (Table 1). In related experiments it was established that
nitrogen fertilization, after a prolonged deficiency, allowed regreening of existing

![Graph](image_url)

Fig. 5.—Diurnal changes in photosynthesis, leaf temperature, and solar radiation for a
tree growing at a high (a) and a low (b) level of nitrogen nutrition.

foliage, which then showed high photosynthetic activity. A visual regreening of the
foliage was first apparent 2 weeks after nitrogen fertilization. Subsequent measure-
ments indicated that the average chlorophyll a plus chlorophyll b concentration
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increased from 3.66 to 5.49 mg dm\(^{-2}\). Nevertheless, the tendency to show a decline in photosynthesis during the day was accentuated.

**Table 1**

<table>
<thead>
<tr>
<th>Nitrogen Supplied (m-equiv. NO(_3)/l)</th>
<th>Maximum Photosynthesis* (mg CO(_2) hr(^{-1}) dm(^{-2}))</th>
<th>Chlorophyll a + Chlorophyll b Concentration (mg dm(^{-2}))</th>
<th>Assimilation Rate No.†</th>
</tr>
</thead>
<tbody>
<tr>
<td>12</td>
<td>32.50</td>
<td>6.55</td>
<td>4.97</td>
</tr>
<tr>
<td>1</td>
<td>8.25</td>
<td>2.98</td>
<td>2.77</td>
</tr>
</tbody>
</table>

* Data taken from peak rates of photosynthesis shown in Figures 5(a) and 5(b).

† Expressed as the number of milligrams of CO\(_2\) assimilated per hour per milligram chlorophyll.

**IV. Discussion**

In common with many other deciduous perennials, the pear leaves examined in this work showed a relatively high photosynthetic activity, having at least three times the activity of evergreen perennials such as *Citrus* (Kriedemann 1968; Bielorai and Mendel 1960). Some photosynthetic data are available for a close relative of the pear, e.g. Heinicke (1966) quoted CO\(_2\) assimilation rates around 26 mg hr\(^{-1}\) dm\(^{-2}\) for apple leaves, while Looney (1968) found rates to vary between 25 and 35 mg hr\(^{-1}\) dm\(^{-2}\) for the same species.

The high photosynthetic activity of the pear leaf was associated with low diffusive resistances (both \(r_l\) and \(r'_m\)). Wuenscher and Kozlowski (1970) have recently published some relevant data on gaseous diffusive resistances in other tree species. They quote a value of \(r'_m = 5.4\) sec cm\(^{-1}\) for a species of oak, which is of the same order as our \(r'_m\) values for pear leaves. The leaves on the two other tree species examined by Wuenscher and Kozlowski (1970) showed even higher values for \(r'_m\). Woody perennials are often characterized by higher diffusive resistances which are thought to contribute to their lowered photosynthetic activity (see Jarvis and Jarvis 1964). The meagre photosynthetic activity of some evergreens is a prime example (Larcher 1969; Kriedemann 1971).

One consequence of this low leaf resistance is that the pear leaf transpires rapidly. Laboratory measurements (20 mW cm\(^{-2}\)) gave rates of up to 3000 mg water vapour hr\(^{-1}\) dm\(^{-2}\) at 25°C and at a relative humidity of 55%. Rapid transpiration would in turn induce moisture tension, although the pear leaf does seem able to endure remarkably low leaf water potential with no immediate decline in photosynthesis. We showed that a tension equivalent to between 25 and 30 atm was commonly encountered in the orchard (on irrigated trees) but that photosynthesis did not begin to decline appreciably until leaf water potential fell to at least \(-35\) atm. By contrast, a grape vine leaf virtually ceases photosynthesis once leaf water potential falls below \(-15\) atm (Kriedemann and Smart 1970).
The decline in pear leaf photosynthesis throughout the day has been attributed to the sustained high level of solar radiation because neither leaf temperature nor water potential could be regarded as unfavourable. Typical leaf xylem water potentials at the end of the day for trees growing in sand culture were between $-9.7$ and $-5.5$ atm. Despite this relatively high water potential, photosynthesis had declined steadily. Kozlowski (1949) reported a similar decline in photosynthesis during the day for three different tree species. One explanation for this decline has been provided by Böhning (1949) who referred to the bleaching of apple leaf chlorophyll, over a period of days, following continuous exposure to a light intensity of 6000 f.c. from Mazda lamps. This deteriorating effect would have been hastened in the present experiments by the higher intensity of sunlight combined with its component of ultraviolet radiation.

V. Acknowledgments

The competent participation of Mrs. E. Törökfalvy in the laboratory experiments was greatly appreciated. We are also indebted to Mr. D. W. West, Victorian Department of Agriculture, Horticultural Research Station, Scoresby, for the use of the Scholander pressure chamber; and to Mr. J. F. Angus, Department of Agriculture, University of Melbourne, for a loan of the pyrheliometer.

VI. References


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