PHOTOSYNTHETICA 16 (4): 514–519, 1982

Effects of Leaf Age on Photosynthesis and Water Use Efficiency of Papaya*

Z. F. LIN** and J. EHLERINGER

Department of Biology, University of Utah, Salt Lake City, Utah 84112, U.S.A.

Abstract

The photosynthetic characteristics of three cultivars of papaya (*Carica papaya* L.) were followed as leaves aged. Both maximum net photosynthetic rate (P_N) and leaf conductance (g) declined through time; intercellular CO_2 concentrations increased as leaves aged, because the rate of decrease in P_N was less than that of g. There are differences in the magnitudes of maximum P_N among the three papaya cultivars, and associated with this, a positive relationship between initial P_N and the rate of its decrease.

Leaf age is an important factor influencing photosynthetic capacity. Chloroplast structure and photosynthetic activity of the leaf change markedly during the course of leaf ontogenesis and plant development (Jordan *et al.* 1975, Čatský *et al.* 1976, Davis *et al.* 1977, Šesták 1977a, b, Samsuddin and Impens 1979). In general, metabolic activity increases from some value in the youngest developing leaf, reaches a maximum at about the point of complete leaf expansion and then decreases as the leaf ages. This trend appears to hold true for both morphological and biochemical factors affecting photosynthetic processes (Dickmann 1971, Baker and Hardwick 1973, Fraser and Bidwell 1974). Concurrent with changes in photosynthesis beyond the point of full leaf expansion there are decreases in stomatal conductance, transpiration and chlorophyll content with leaf age (Šesták 1963, Raschke and Zeevaart 1976, Davis *et al.* 1977, Constable and Rawson 1980).

We have been studying the basic photosynthetic characteristics of papaya. In this paper, we report on the effects of leaf age on net photosynthetic rate, chlorophyll content and chlorophyll *a*/*b* ratio, transpiration, and leaf conductance in three cultivars of papaya commonly grown in the People's Republic of China.

MATERIALS AND METHODS

Plants: Three papaya (*Carica papaya* L.) cultivars (2 × 0.7, 4 × 2, South China) were collected from Canton, People's Republic of China. The seeds were sown and grown in plastic pots (19 × × 25 cm). Plants were watered and fertilized every other day. Natural sunlight in the greenhouse was supplemented with 1000 W HID lamps to create midday irradiances (I) of 2.0 mmol m^{-2} s^{-1} (400–700 nm). Air temperature was approximately 30/20 °C (day/night), with a relative humidity range of 30–60%.

CO_2 exchange measurement: Net CO_2 uptake (P_N) was measured on single, attached leaves

* *Received* 29 January 1982.

** *Permanent address:* South China Institute of Botany, Academia Sinica, Guangzhou, People's Republic of China.

in an open gas exchange system similar to that described previously by Ehleringer and Björkman (1977). The assimilation chamber (total volume is 1200 cm^3) contained four high velocity fans to insure adequate air exchange and high boundary layer conductances. Two infra-red CO_2 gas analyzers (*Analytical Development Corp.*, Hoddesdon, England) were used to measure absolute and differential CO_2 concentrations. A 1000 W HID lamp was used as a radiation source. Leaf temperature was adjusted by controlling the temperature of the leaf chamber water jacket. Ambient CO_2 concentration was controlled by mixing CO_2-free air and 1% CO_2 using rotameters. Transpiration measurements were made simultaneously with the photosynthetic measurements, using two *Vaisala* relative humidity sensors (*Weathermeasure Corp.*, Sacramento, Calif., U.S.A.) to measure the incoming and outgoing water vapor pressures. Leaf conductances were calculated from the transpiration and vapor pressure deficit (leaf to outgoing air stream) measurements.

Intercellular CO_2 concentration was calculated as follows:

$$C_i = C_a - P_N/(g\,K)$$

where C_i is the intercellular CO_2 concentration, C_a is the ambient CO_2 concentration, P_N is the photosynthetic rate, g is the leaf conductance to CO_2 through stomata, and K is a constant converting the units of P_N/g to those of C_a.

The leaves used in the experiments were the fourth leaf from the apices of the plant. These leaves were measured at ages of 11, 16, 18, 20, 21, 26, 28, 29, 38 and 53 d.

The typical experimental conditions were an incident I of 1.2 mmol m^{-2} s^{-1} (400—700 nm), ambient CO_2 partial pressure of 33 Pa, water vapor pressure deficit of 0.9—1.0 kPa, and a leaf temperature of 25 °C. These values represent radiation saturated conditions near the temperature optimum (Lin and Ehleringer 1982).

RESULTS

Under ambient atmospheric conditions and a leaf temperature of 25 °C, P_N was saturated at an I of approximately 0.6 mmol m^{-2} s^{-1}. Once fully expanded, the maximum P_N of leaves declined with leaf age (Fig. 1).

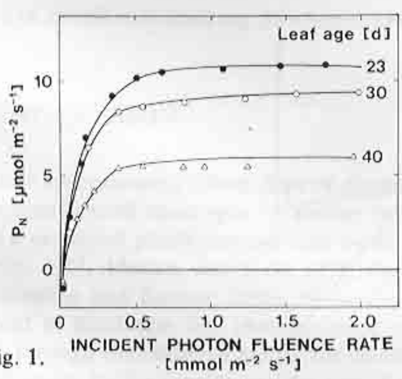

Fig. 1.

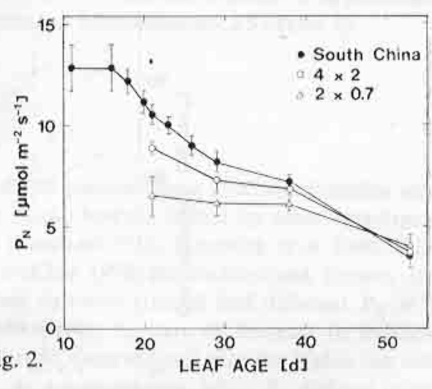

Fig. 2.

Fig. 1. The rate of net photosynthesis (P_N) in response to changes in incident photon fluence rate (400—700 nm) in leaves of papaya (cv. 4 × 2) of a different age.

Fig. 2. Net photosynthetic rate (P_N) as influenced by leaf age in three cultivars of papaya. Vertical bars represent ± one standard error. Sample size was 3—6.

Associated with these declines in maximum P_N were small decreases in the saturating irradiance and dark respiration rates. P_N of cv. South China reached a maximum at day 11 and remained at this value until day 16 (Fig. 2). Although there were significant differences in P_N of the three cultivars in the leaves younger than 30 d, P_N were essentially the same after 38 d. P_N declined at a nearly constant rate of 0.2 μmol m^{-2} s^{-1} d^{-1} in cultivars South China and 4 × 2, so that the rates on 53 d old leaves were about 30% and 40%, respectively, of the rates measured on day 21. In cv. 2 × 0.7, P_N were the lowest, but very little decline in maximum P_N was noted until day 38.

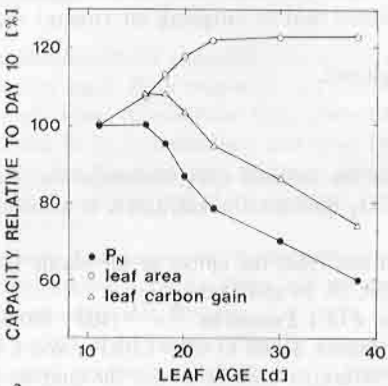

Fig. 3.

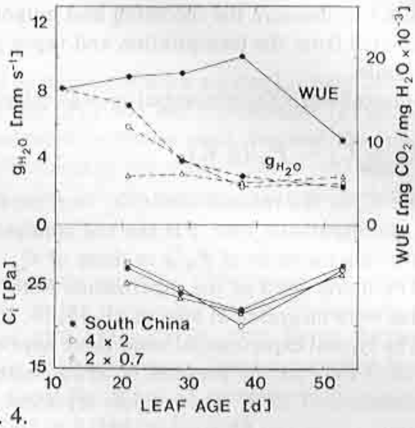

Fig. 4.

Fig. 3. The relative change of net photosynthetic rate (P_N), leaf area, and leaf carbon gain with leaf age in *Carica papaya* (cv. South China). The values given are percentages of the absolute values on a 10 d-old leaf. Samples are means of six values.

Fig. 4. The relationships of leaf conductance to water loss (g_{H_2O}), water use efficiency ($WUE = P_N/E$), and intercellular CO_2 concentration (C_i) to leaf age in three cultivars of papaya.

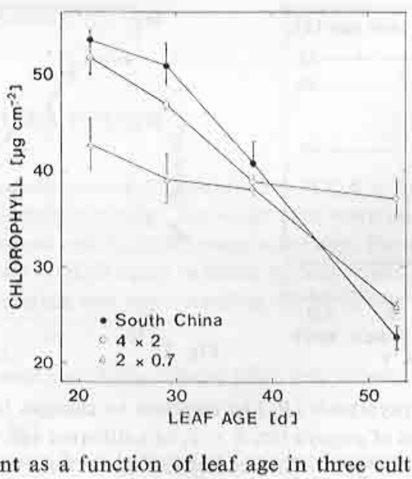

Fig. 5. Chlorophyll content as a function of leaf age in three cultivars of papaya. Sample size ranged from 2–10. Vertical bars represent ± one standard error.

P_N of the entire leaf changed through time as leaf expansion occurred and maximum P_N changed (Fig. 3). The interesting feature from these data is that the potential total photosynthetic contribution of the leaf to the plant began to decline before leaf expansion was complete. This resulted because P_N began to decline while the leaf was still expanding, and rate of decrease in P_N was greater than the rate of increase in leaf area.

Table 1

The mean chlorophyll *a*/*b* ratios of leaves of three cultivars of papaya as a function of leaf age. Sample size was six discs.

Leaf age [d]	South China	4 × 2	2 × 0.7
21	3.46	3.25	3.50
29	3.27	3.29	3.22
38	3.27	3.46	3.20
53	2.24	2.68	2.53

The leaf conductance to water loss (g_{H_2O}) declined through time in cultivars South China and 4 × 2, but remained almost constant in cv. 2 × 0.7 (Fig. 4). As with P_N, there were no significant differences in g_{H_2O} among the cultivars after day 38, although slight differences did occur in leaves younger than 38 d. g_{H_2O} declined faster than did P_N so that the intercellular CO_2 concentrations (C_i) decreased with time before day 38 (Fig. 4). The C_i increased from day 38 to 53, because g_{H_2O} did not decrease further, but P_N continued to decline in older leaves. Thus, water use efficiency (as measured by photosynthesis/transpiration ratios) was enhanced until leaves reached 38 d of age and then decreased as leaves aged further (Fig. 4).

Associated with the decrease in maximum P_N of aging papaya leaves were simultaneous decreases in total leaf chlorophyll content (Fig. 5). The decline in P_N was slightly faster than the decrease in total chlorophyll content. Chlorophyll *a*/*b* ratios remained constant at approximately 3.3 in all cultivars until day 53 when the ratios declined to approximately 2.5 (Table 1).

DISCUSSION

After approximately fifteen days of development, P_N in papaya began a constant decline which continued until senescence. A similar pattern has been observed before by other investigators in a variety of plants ranging from herbs to trees (Freeland 1952, Hardwick *et al.* 1968, Kisaki *et al.* 1973, Maslam and Hunt 1977, Davis and McCree 1978, Samsuddin and Impens 1979, Constable and Rawson 1980). In papaya, the three cultivars studied had different P_N at the point of maximum leaf photosynthetic capacity. However, the rate of decrease in maximum P_N through time differed among the cultivars. The trend observed was that the higher the initial maximum P_N the greater was the rate of decrease. As a consequence, while P_N differed initially among cultivars, they were equal by day 38. By day 53, the cultivar which initially had the lowest P_N now had a mean P_N greater than the cultivar with initially the highest P_N.

Associated with the decrease in maximum P_N were decreases in the chlorophyll content and leaf conductance (g). The chlorophyll *a*/*b* ratio remained constant until leaf senescence began at day 53. Again as with P_N among the three cultivars, there were parallel changes in the chlorophyll content and g. The cv. South China initially had the highest P_N, chlorophyll content, and g, but also had the greatest rate of decrease in all three parameters.

The intercellular CO_2 concentration decreased slightly with leaf age in all three cultivars of papaya. This was because g was declining faster than was the P_N. As a consequence, water use efficiency increased with leaf age until leaf senescence occurred. This trend is different from that found in cotton by Constable and Rawson (1980), or in bean by Davis and McCree (1978) in which intercellular CO_2 concentration and water use efficiency remained constant through time. Unfortunately there are not enough studies to date to allow us to generalize about changes in water use efficiency with leaf age.

In summary, this study has demonstrated that in papaya P_N as well as components of the photosynthetic process decrease with leaf age beyond 15 d. There are differences in the magnitudes of maximum P_N among the three papaya cultivars, and associated with this, a positive relationship between initial P_N and the rate of decrease of that capacity. Whether or not this represents a general trend among plants is unknown.

REFERENCES

Baker, N. R., Hardwick, K.: Biochemical and physiological aspects of leaf development in cocoa (*Theobroma cacao*). I. Development of chlorophyll and photosynthetic activity. — New Phytol. **72**: 1315—1324, 1973.

Čatský, J., Tichá, I., Solárová, J.: Ontogenetic changes in the internal limitations to bean-leaf photosynthesis. 1. Carbon dioxide exchange and conductances for carbon dioxide transfer. — Photosynthetica **10**: 349—402, 1976.

Constable, G. A., Rawson, H. M.: Effect of leaf position, expansion and age on photosynthesis, transpiration and water use efficiency of cotton. — Aust. J. Plant Physiol. **7**: 89—100, 1980.

Davis, S. D., McCree, K. J.: Photosynthetic rate and diffusion conductance as a function of age in leaves of bean plants. — Crop Sci. **18**: 280—282, 1978.

Davis, S. D., van Bavel, C. H. M., McCree, K. J.: Effect of leaf aging upon stomatal resistance in bean plants. — Crop Sci. **17**: 640—645, 1977.

Dickmann, D. I.: Photosynthesis and respiration by developing leaves of cottonwood (*Populus deltoides* Bartr.). — Bot. Gaz. **132**: 253—259, 1971.

Ehleringer, J., Björkman, O.: Quantum yields for CO_2 uptake in C_3 and C_4 plants: Dependence on temperature, CO_2, and O_2 concentration. — Plant Physiol. **59**: 86—90, 1977.

Fraser, D. E., Bidwell, R. G. S.: Photosynthesis and photorespiration during the ontogeny of the bean plant. — Can. J. Bot. **52**: 2561—2570, 1974.

Freeland, R. O.: Effect of age of leaves upon the rate of photosynthesis in some conifers. — Plant Physiol. **27**: 685—690, 1952.

Hardwick, K., Wood, M., Woolhouse, H. W.: Photosynthesis and respiration in relation to leaf age in *Perilla frutescens* (L.) Britt. — New Phytol. **67**: 79—86, 1968.

Jordan, W. R., Brown, W. K., Thomas, J. C.: Leaf age as a determinant in stomatal control of water loss from cotton during water stress. — Plant Physiol. **56**: 595—599, 1975.

Kisaki, T., Hirabayashi, S., Yano, N.: Effect of the age of tobacco leaves on photosynthesis and photorespiration. — Plant Cell Physiol. **14**: 505—514, 1973.

Lin, Z. F., Ehleringer, J.: Studies of photosynthesis in papaya. I. The effects of light, temperature, water vapor pressure deficit, and carbon dioxide. — Acta Phytophysiol. sin. (in press), 1982.

Maslam, S. B., Hunt, L. A.: Effect of leaf age on photosynthesis and transpiration of cassava (*Manihot esculenta*). — Can. J. Bot. **55**: 2288—2295, 1977.

Raschke, K., Zeevaart, J. A. D.: Abscisic acid content, transpiration, and stomatal conductance as related to leaf age in plants of *Xanthium strumarium* L. — Plant Physiol. **58**: 169—174, 1976.

Samsuddin, Z., Impens, I.: The development of photosynthetic rate with leaf age in *Hevea brasiliensis* Muell. Arg. clonal seedlings. — Photosynthetica **13**: 267—270, 1979.

Šesták, Z.: Changes in the chlorophyll content as related to photosynthetic activity and age of leaves. — Photochem. Photobiol. **2**: 101—110, 1963.

Šesták, Z.: Photosynthetic characteristics during ontogenesis of leaves. 1. Chlorophylls. — Photosynthetica **11**: 367—448, 1977a.

Šesták, Z.: Photosynthetic characteristics during ontogenesis of leaves. 2. Photosystems, components of electron transport chain, and photophosphorylation. — Photosynthetica **11**: 449—474, 1977b.