Leaf Age Affects Gas Exchange in Okra

W.F. Whitehead¹ and B.P. Singh²

Agricultural Research Station, Fort Valley State College, Fort Valley, GA 31030-3298

Additional index words. *Abelmoschus esculentus*, transpiration, CO₂ exchange rate, stomatal conductance, internal leaf CO₂ concentration

Abstract. Two studies were conducted to assess the effects of leaf aging on gas exchange in okra [*Abelmoschus esculentus* (L.) Moench] leaves. Gas exchange was measured at 6- to 10-day intervals starting 15 days after leaf emergence (DFE) and continuing until senescence at 50 DFE. Rates of transpiration (E), stomatal conductance (g_s) and CO₂ exchange (CER) increased as leaves matured up to ≈25 DFE, about full leaf expansion. Transpiration rate, g_s, and CER declined after 25 DFE and as leaves aged further. Internal leaf CO₂ concentration (C_i) was higher in old than young leaves. This study suggests that the most efficient okra canopy would maximize exposure of 25-day-old leaves to sunlight.

Okra is a herbaceous, annual, vegetable crop native to the South African and Asian tropics (Thakur, 1989; Thompson and Kelly, 1957). It is particularly popular in the southern United States as a home-garden vegetable and a roadside or farmer's market commodity (Singh, 1987). Research on okra production in the United States has been confined to a few management studies (Albregts and Howard, 1976; Singh, 1987). There is a significant void in information concerning the crop's physiology.

The biological and economic yield of a crop is associated closely with the rate of net CO₂ exchange per unit leaf area (CER) (Hobbs and Mahon, 1982; Zelitch, 1982). Factors, such as genotype, assimilate demand by sinks, environment, and leaf age, affect CER (Dwyer et al., 1989; Rasparuva and Rasoluv, 1989). Leaves generally reach the maximum CER at maturity and decline thereafter to senescence (Bhagsari, 1988; Dwyer et al., 1989; Osman and Milthorpe, 1971; Pettigrew and Meredith, 1994). In cotton (*Gossypium hirsutum* L.), a crop closely related to okra, gas exchange efficiency increases as the newly formed leaves expand. Once the leaves are fully expanded [20 days from emergence (DFE)], however, gas exchange activities begin to decline (Constable and Rawson, 1980; Krieg, 1981; Wulschleger and Oosterhuis, 1989, 1990). Okra, having an indeterminate growth habit, continues to produce new leaves from the main stem and on axillary branches until late in the growing season. A knowledge of the stage of growth at which leaves are most

photosynthetically efficient would be helpful in developing a canopy where sunlight is intercepted by the most efficient leaves. Therefore, the present study was conducted to determine how gas exchange in okra changes with leaf age.

Materials and Methods

Two field studies were conducted during Summer 1990 on a Dothan sandy loam (fine loamy, siliceous, thermic, Plinthic Paleudult) at the Fort Valley State College Agricultural Research Station. Experimental units were single-row plots consisting of east-west rows that were 4.6 m long and 0.92 m wide. Okra seeds ('Clemson Spineless') were planted 0.3 m apart in the row on 17 May in both fields. The design was a randomized complete block with 10 replications. The six leaf ages (beginning with 15 DFE and increasing by 6- to 10-day intervals to senescence) constituted the treatments. Recommended cultural practices

were followed (Colditz et al., 1984). Fields were irrigated as needed.

One plant within each plot was selected at random and tagged. Located near the uppermost position of the main stem, a newly emerged leaf (1 to 2 days old) was labeled on 3 July for Expt. 1 and 10 July for Expt. 2. Gas exchange measurements were initiated 15 DFE, when leaf size was large enough (≥6.25 cm²) to cover the leaf chamber. Data were collected six times at 6- to 10-day intervals, until senescence. Pods were harvested at an appropriate size.

Gas exchange rates were recorded using a portable steady-state gas-exchange system (ADC model, LAC-2) consisting of a 16-cm³ leaf chamber and an infrared gas analyzer (Analytical Development, Huddleston, U.K.). To minimize fluctuations of CO₂ found in the plant canopies, ambient air was drawn from outside of the field through a sampling tube, 0.5 cm in diameter and 6 m long, provided with a fiberglass filter at its intake. The instrument provided data on photosynthetically active radiation (PAR, μmol·m⁻²·s⁻¹), transpiration rate (E, mmol·m⁻²·s⁻¹), stomatal conductance (g_s, mmol·m⁻²·s⁻¹), CO₂ exchange rate (CER, μmol·m⁻²·s⁻¹), and internal leaf CO₂ concentration (C_i, μliters·liter⁻¹). The readings were taken between 1000 and 1300 hr with the PAR at the leaf surface exceeding 1200 μmol·m⁻²·s⁻¹. The ambient temperature ranged from 33 to 37°C in Expt. 1 and from 29 to 37°C in Expt. 2.

All data were subjected to analyses of variance (SAS Institute, Cary, N.C.). Regression analyses were conducted to assess the relationship of gas exchange rates and leaf aging.

Results and Discussion

On average, 25 days elapsed between the day of leaf emergence and full leaf blade expansion. Apparent senescence (yellowing of leaves) began ≈40 DFE, and by 50 DFE, leaves were >50% yellow.

Fig. 1. Effects of leaf age on transpiration rate (E) of okra. (—○—) Expt. 1, $y = 9.581 + 0.4528x - 0.01307x^2$, $r^2 = 0.52^{**}$; (---□---) Expt. 2, $y = 11.94 + 0.4549x - 0.01732x^2$, $r^2 = 0.89^{**}$. ** Significant at $P \leq 0.01$.

Received for publication 3 Jan. 1995. Accepted for publication 8 May 1995. Research conducted at Fort Valley Agricultural Research Station, Fort Valley, Ga. Use of trade names does not imply endorsement of the products named nor criticism of similar ones not named. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

¹Research Associate.

²Professor.

Leaf age had a significant effect on E , g_s , CER, and C_i . A quadratic equation provided the best fit for the relationship between leaf age and E (Fig. 1) in both experiments. Transpiration rate increased up to 25 to 30 DFE and declined as the leaf aged further. The maximum E rates for Expt. 1 and Expt. 2 were 13.5 and 14.7 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively. Regression of g_s on leaf age was cubic in Expt. 1 and quadratic in Expt. 2 (Fig. 2). The g_s value in both experiments peaked at ≈ 25 DFE. The relationship of CER with the age of the leaf was cubic in Expt. 1 and quadratic in Expt. 2 (Fig. 3). During the leaf expansion period, increase in CER/day amounted to 1 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The CER declined after full expansion with aging by an average daily rate of 0.22 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The relationship of C_i and leaf age was quadratic for both experiments (Fig. 4). The C_i content declined during leaf expansion. Once the leaf was fully expanded, C_i increased with age.

According to our results, water vapor and CO_2 exchange were affected similarly by leaf aging. Since the water vapor and CO_2 exchanges take place through the same leaf pores, similar behavior would be expected. Similar results have been obtained with other crops (Beardsell et al., 1973; Frank, 1981). An increase in water vapor and CO_2 exchange rate during leaf expansion may be attributable to a high level of activity in the mesophyll tissue of young leaves and wide stomatal opening (DeMichele and Sharpe, 1972). The increase in C_i of the aging leaves may have resulted from slower CO_2 fixation and smaller stomatal opening. The study suggests that an ideal okra canopy should be such that 25-day-old leaves are exposed to the maximum amount of sunlight.

Literature Cited

- Albregts, E.E. and C.M. Howard. 1976. Response of four okra cultivars on mulched beds to plant density. *HortScience* 11:242.
- Beardsell, M.F., K.J. Mitchell, and R.G. Thomas. 1973. Transpiration and photosynthesis in soybean. *J. Expt. Bot.* 24:587-595.
- Bhagsari, A.S. 1988. Photosynthesis and stomatal conductance of selected root crops as related to leaf age. *Crop Sci.* 28:902-906.
- Colditz, P., J.M. Barber, and D. Granberry. 1984. Okra. Univ. of Georgia, College of Agr. Coop. Ext. Serv. Circ. 627.
- Constable, G.A. and H.W. Rawson. 1980. Effect of leaf position, expansion and age on photosynthesis, transpiration and water use efficiency of cotton. *Austral. J. Plant Physiol.* 7:89-100.
- DeMichele, D.W. and P.J.H. Sharpe. 1972. A morphological and physiological model of the stomata, p. 69-85. In: C. Murphy, J.D. Hesketh, and B.R. Strain (eds.). *Workshop on tree growth dynamics and modeling*, 12 Oct. 1971, Durham, N.C.
- Dwyer, L.M., D.W. Stewart, D. Balchin, L. Houwing, C.J. Marur, and R.I. Hamilton. 1989. Photosynthetic rates of six maize cultivars during development. *Agron. J.* 81:597-602.
- Frank, A.B. 1981. Effect of leaf age and position on photosynthesis and stomatal conductance of forage grasses. *Agron. J.* 73:70-74.
- Hobbs, S.L.A. and J.D. Mahon. 1982. Variation, heritability and relationship to yield of physi-

Fig. 2. Effects of leaf age on rate of stomatal conductance (g_s) of okra. (—○—) Expt. 1, $y = 356.9 + 157.2x - 9.372x^2 + 0.1431x^3$, $r^2 = 0.50^{**}$; (---□---) Expt. 2, $y = 992.5 + 31.96x - 1.408x^2$, $r^2 = 0.66^{**}$. ** Significant at $P \leq 0.01$.

Fig. 3. Effects of leaf age on CO_2 exchange rate (CER) of okra. (—○—) Expt. 1, $y = 11.68 + 1.927x - 0.1084x^2 + 0.00151x^3$, $r^2 = 0.64^{**}$; (---□---) Expt. 2, $y = 19.72 + 0.691x - 0.02918x^2$, $r^2 = 0.80^{**}$. ** Significant at $P \leq 0.01$.

Fig. 4. Effects of leaf age on internal leaf CO_2 concentration (C_i) of okra. (—○—) Expt. 1, $y = 226.2 - 0.068x + 0.02597x^2$, $r^2 = 0.54^{*}$; (---□---) Expt. 2, $y = 226.7 - 1.158x + 0.07037x^2$, $r^2 = 0.81^{**}$. * Significant at $P \leq 0.5$ and 0.01, respectively.

- ological characters in peas. *Crop Sci.* 22:773–779.
- Krieg, D.R. 1981. Leaf development and function as related to water stress. *Proc. Beltwide Cotton Prod. Res. Conf.* 1981. p. 41–42.
- Osman, A.M. and F.L. Milthorpe. 1971. Photosynthesis of wheat leaves in relation to age, illuminance and nutrient supply. II. Results. *Photosynthetica* 5:61–70.
- Pettigrew, W.T. and W.R. Meredith, Jr. 1994. Leaf gas exchange parameters vary among cotton genotypes. *Crop Sci.* 34:700–705.
- Rasparuva, I.S. and B.R.H. Rasoluv. 1989. Influence of the unbalance source–sink relationship in the system of the whole plant on daily dynamics of carbon dioxide gas exchange components in cotton leaves (in Russian, English summary). *Feiziologiya i Biokhimiya Kui'lurnykh Rastenii* 2:107–112.
- Singh, B.P. 1987. Effect of irrigation on the growth and yield of okra. *HortScience* 22:879–880.
- Thakur, M.R. 1989. Okra, *Abelmoschus esculentus* (Linn.) Moench. *Indian J. Hort.* 33, 34:49–51.
- Thompson, C.H. and C.W. Kelly. 1957. *Veg-etable crops*. McGraw-Hill, New York.
- Wulschleger, S.D. and D.M. Oosterhuis. 1989. Water use efficiency as a function of leaf age and position within the cotton canopy. *Plant & Soil* 1:79–86.
- Wulschleger, S.D. and D.M. Oosterhuis. 1990. Photosynthesis of individual field-grown cotton leaves during ontogeny. *Photosynthesis Res.* 23:163–170.
- Zelitch, I. 1982. The close relationship between net photosynthesis and crop yield. *Bioscience* 32:796–802.