Growth Versus Net Photosynthesis in Clones of *Ficus benjamina*

Carl-Otto Ottosen¹

Department of Horticulture, Royal Veterinary and Agricultural University, DK-1958 Fredriksberg C, Denmark

Additional index words. gas exchange, stomatal conductance, transpiration

Abstract. Clones of *Ficus benjamina* L. differed by up to 18% in leaf net photosynthetic rates (P_N) measured at various leaf positions. Differences in stomatal conductance (G_s), internal CO_2 concentration (C_i), and transpiration (T) were observed in one study. The uppermost leaves showed lower P_N and higher T rates than lower leaves. Total leaf area, total fresh or dry leaf weight, and total biomass above soil differed among clones. The difference in above-ground dry weight between the fastest- and slowest-growing clones increased during growth, reaching 37% at the end of the experiments. Photosynthetic measurements could not be correlated with growth, although, in one study, the fastest-growing clones also had the highest P_N rates.

Growth analysis by traditional means, such as measuring increases in fresh and dry weight, is time-consuming. To select fast-growing clones of ornamental species, more-rapid techniques based on measurement of growth characteristics, such as plant height and number of lateral shoots, have been evaluated (Ottosen, 1988). Measurement of gas exchange for whole plants has also been compared to measurements of plant height and of the number of lateral shoots using clones of *Ficus benjamina* (Ottosen et al., 1989a).

Only few studies have focused on the relationship between photosynthetic rate and plant productivity or growth (Zelitch, 1982). Although Elmore (1980) noted the apparent paradox in lack of correlation between measurement of single-leaf photosynthesis and growth rate, a recent review by Bunce (1986) took the opposite position. In tobacco (*Nicotiana tabacum* L. 'Connecticut Broadleaf') and black gram [*Vigna mungo* (L.) Hepper], positive relationships have been shown by Peterson and Zelitch (1982) and Babu et al. (1985). Therefore, the objective of this study was to examine the relationship between single-leaf net photosynthetic rate and growth rate of clones of *F. benjamina*.

Received for publication 5 Sept. 1989. This project was supported by the Council for Research and Experiments in Agriculture and The Danish Agricultural and Veterinary Science Council. Technical assistance of Ebbe Andersen and critical reviews by E. Ögren and J. Barrett are gratefully acknowledged. 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.

¹Former Research Assistant. Presently: Research Associate, Inst. of Glasshouse Crops, Research Centre for Horticulture, Kirstinebjergvej 10, DK-5792 Aarslev, Denmark.

Abbreviations: C_i , internal CO_2 concentration (ppm CO_2); G_s , stomatal conductance ($mol \cdot s^{-1} \cdot m^{-2}$); P_N , net photosynthetic rate ($\mu mol \ CO_2/sec$ per square meter); T , transpiration rate ($\mu mol \ H_2O/sec$ per square meter).

sulting in $\approx 80 \mu mol \cdot s^{-1} \cdot m^{-2}$ within the greenhouse (N.E. Andersson, personal communication).

Two experiments, each including five clones, were conducted. Experiment 1 was initiated 11 Nov. 1987, ≈ 8 weeks after propagation. Experiment 2 began 17 Jan. 1988, 6 weeks after propagation. To study the influence of plant age, clones in Expt. 2 were examined at an earlier stage of development. Before making measurements, eight randomly selected plants from each clone were transferred to a controlled-environment chamber maintained at 21°C with a 12-hr photoperiod provided by TL 34 fluorescent lamps (Philips, Eindhoven, The Netherlands). The lamps provided a PPF of $280 \mu mol \cdot s^{-1} \cdot m^{-2}$. After acclimatization for 3 days, gas exchange at atmospheric CO_2 level was measured using a portable infrared gas analyzer (LDC 72, Analytical Development Co., Hoddesdon, U.K.) with a Parkinson Broad Leaf Chamber (Analytical Development). Measurements were made on the first, third, and fifth fully expanded leaves. Each leaf measurement was repeated three times and the mean value calculated. Regulated fresh air supply of $500 \text{ ml} \cdot \text{min}^{-1}$ with a controlled water vapor content of $25\% \pm 3\%$ RH was supplied by a pump (Analytical Development). P_N , G_s , C_i , and T were recorded and calculated by a DL2 datalogger (Analytical Development). Ambient CO_2 concentration was 382 and 357 ppm (SD 12 ppm)

Ten clones selected in Danish nurseries showing a wide range in growth capacity were used (Ottosen, 1988). From each clone, 40 uniform terminal cuttings with four to five fully expanded leaves were rooted in peat in 0.36-liter pots under polyethylene and later grown on capillary mats with adequate water and nutrients (Ottosen, 1988). Day/night set points were 21/18°C, with ventilation at 3°C above set points. The photosynthetic photon flux (PPF) outside the greenhouse during the winter was at most $200 \mu mol \cdot s^{-1} \cdot m^{-2}$, re-

Table 1. Total leaf area and stem and leaf dry weights for 10 clones of *F. benjamina* at the end of experiments (day 63).²

Expt. no.	Clone no.	Plant characteristic ¹		
		Leaf area (m ²)	Stem dry wt (g)	Leaf dry wt (g)
1	38	0.108 ab	1.90 a	6.35 a
	46	0.106 ab	1.88 a	6.48 a
	50	0.115 b	1.98 b	6.58 a
	61	0.114 b	2.04 b	6.93 a
	68	0.093 a	1.51 a	5.53 a
2	14	0.054 a	0.60 a	2.94 a
	21	0.050 a	0.69 a	2.78 a
	27	0.055 a	0.80 ab	3.06 ab
	40	0.053 a	0.69 a	3.01 a
	59	0.065 b	0.89 b	3.62 b

¹Data are means of eight plants.

²Mean separation within columns for an experiment by Duncan's multiple range test, $P = 0.05$.

Table 2. Photosynthetic characteristics for clones of *F. benjamina* as means of day 0, 21, 42, and 63.²

Expt. no.	Clone no.	Characteristic ¹			
		P_N	G_s	C_i	T
1	38	2.3 ab	33.3 a	367 a	0.99 ab
	46	2.4 ab	33.6 a	370 a	1.04 b
	50	2.2 a	34.1 a	374 a	0.98 a
	61	2.4 ab	35.2 a	372 a	1.02 b
	68	2.6 b	33.3 a	375 a	1.06 b
2	14	1.8 a	38.9 b	348 a	0.81 a
	21	1.9 ab	38.6 b	355 b	0.93 b
	27	1.8 a	33.0 a	356 b	0.81 a
	40	1.8 a	38.2 ab	354 b	0.92 b
	59	2.1 b	44.9 c	353 b	1.03 c

¹Each value is the mean of eight plants, three leaves per plant.

²Mean separation within columns for an experiment by Duncan's multiple range test, $P = 0.05$.

Table 3. Photosynthetic characteristics for three leaf positions of *F. benjamina*.^z

Leaf position	Characteristic ^y		
	P _N	G _s	T
1	1.9 a	43.9 a	1.21 a
3	2.6 b	28.3 a	0.92 b
5	2.7 b	31.0 a	0.94 b

^zEach value is the mean of five clones of 32 plants each in Expt. 1.

^yMean separation within columns by Duncan's multiple range test, *P* = 0.05.

for Expts. 1 and 2, respectively.

Number, area, and fresh weight of leaves and fresh weight of stems of each plant were determined after photosynthetic measurements. Dry weights of leaves and stems were determined after drying at 80°C for 24 hr. All measurements were repeated at day 21, 42, and 63. The experimental design was randomized, with eight single plants as replicates. Data were subjected to analysis of variance procedures and regression analysis.

Growth measurements. The mean number of leaves per plant in Expt. 1 increased from 34 to 50, and mean leaf area per plant increased from 0.07 to 0.11 m² during the term of the experiment (data not presented). By day 42, clones differed in leaf number, total leaf area, and dry weight (data not presented). Differences between the fastest- and slowest-growing clones in leaf area and total above-ground-dry weight were 24% and 27% at day 63, respectively (Table 1). Clone 68 was smaller than clones 50 or 61.

Leaf number per plant increased from 11 to 32 during Expt. 2 (data not presented), and total leaf area per plant increased from 1.53 to 533 cm². Mean total leaf area and dry weight per plant (stem plus leaf) of clones 21, 14, and 40 were less than for clone 59 (Table 1). Clonal growth could be separated by day 42, but only data from day 63 are shown. Differences in leaf area and total leaf dry weight per plant between the fastest- and slowest-growing clones reached 30%.

Photosynthesis. Use of ambient air resulted in some variation in CO₂ concentration not only between days, but also during the day. However, as plants were selected randomly, this did not directly affect results, except for an increase in the standard deviation. As the relative ranking of clones was the same each day, results are presented as means of days and leaf positions.

In Expt. 1, clone 68 had a higher P_N rate than clone 50 (Table 2). T rate followed roughly the same pattern as P_N. Differences between clones with the highest and lowest P_N rate were 18%. The clones could not be separated with respect to C_i or G_s.

In Expt. 2, clone 59 showed a higher P_N rate than all other clones, except 21 (Table 2). Clone 59 had higher G_s than the other clones, while clones 14, 21, and 40 had similar values.

P_N rate of the uppermost leaves was lower than of the lower leaves (Table 3, Expt. 1 only). There were no relationships between leaf P_N rate and growth rate expressed as leaf area, or leaf or top fresh and dry weight, based on regression analysis. In Expt. 1, clone 68 was the slowest growing, but had the highest P_N rate. However, clone 59 in Expt. 2 had both the fastest growth and the highest P_N rate.

Differences in final above-soil biomass between the fastest and slowest-growing clones were 27% and 30% in Expts. 1 and 2, respectively. This corresponded closely with previously recorded plant height results for these clones (Ottosen, 1988). The clonal leaf size, or chlorophyll content, (3.85 ± 0.20 μg·mg⁻¹) was uniform (Ottosen, 1989).

P_N data revealed that lower leaves had higher P_N and lower T rates (Table 3) independent of clones and plant size. This result agrees with research by Fails et al. (1982), except that they obtained a lower T rate in the uppermost leaves of *F. benjamina*.

Previously, clonal differences in whole-plant CO₂ uptake (leaf-area basis) of up to 35% were observed. However, whole-plant CO₂ uptake measured in a controlled-environment chamber showed no correlation to clonal plant height measured in the greenhouse (Ottosen et al., 1989a).

Clonal differences in CO₂ uptake (per dry weight unit) in *F. benjamina* on a whole-plant level reached 41% (Ottosen et al., 1989a). However, the results in the present experiments showed clonal differences in leaf P_N at most of 17% to 18%, which are similar to those found in clones of rubber [*Hevea brasiliensis* (H.B.K.) Muell. Arg.] (Ceulemans et al., 1984). Results from tobacco did not show genotypic variation, but a clear positive relationship between P_N rates and accumulation of dry matter was observed (Peterson and Zelitch, 1982). Lack of a positive relationship in soybean (*Glycine max* L.) was due to plant morphology (Wells et al., 1986).

Although environmental conditions were kept uniform during growth, one cannot exclude the possibility that minor environmental changes in humidity and irradiance may affect the photosynthetic apparatus of particular clones in various ways. *F. benjamina* can adapt by changing light compensation point (Collins and Blessington, 1985) and also by changing chlorophyll content of leaves in situ (C. Guy, personal communication).

Clonal differences in temperature for optimum P_N rate were pronounced under high irradiance (Ottosen, 1989), which could influence comparisons of photosynthesis and growth. The latter seem to be even more pronounced when plants are grown under high (> 30°C) temperatures (Ottosen, unpublished data). Clonal differences in dark respiration were small (Ottosen, 1989; Ottosen et al., 1989b), but may be one of the causes for lack of correlation between growth and pho-

tosynthesis. Volenec et al. (1984) found selection for low dark respiration favorable for increasing yield in tall fescue (*Festuca arundinacea* Schreb.).

In conclusion, short-term measurements of P_N rates of leaves could not be correlated with simple growth measurements. However, since temperature optimum for P_N varied among examined clones, such correlation may exist when clones are grown continuously in a controlled environment (Ottosen et al., 1989b).

Literature Cited

- Babu, R.C., P.S. Srinivasan, N. Natarajaratnam, and S.R.S. Rangasamy. 1985. Relationship between leaf photosynthetic rate and yield in black gram (*Vigna mungo* (L.) Hepper) genotypes. *Photosynthetica* 19:159-163.
- Bunce, J.A. 1986. Measurements and modeling of photosynthesis in field crops. *CRC Critical Rev. Plant Physiol.* 4:47-77.
- Ceulemans, R., R. Gabriels, R. Impens, P.K. Yoo, W. Leong, and A.P. Ng. 1984. Comparative study of photosynthesis in several *Hevea brasiliensis* clones and *Hevea* species under tropical field conditions. *Trop. Agr.* 61:273-275.
- Collins, P.C. and T.M. Blessington. 1985. Keeping quality of *Ficus benjamina* as affected by production light levels and post production light quality and level. *HortScience* 20:390-391.
- Elmore, C.D. 1980. The paradox of no correlation between leaf photosynthetic rate and crop yield, p. 155-167. In: J.D. Hesketh and J.W. Jones (eds.). *Predicting photosynthesis for ecosystem models*. vol. II. CRC Press, Boca Raton, Fla.
- Fails, B.S., A.J. Lewis, and J. A. Barden. 1982. Net photosynthesis and transpiration of sun- and shade-grown *Ficus benjamina* leaves. *J. Amer. Soc. Hort. Sci.* 107:758-761.
- Ottosen, C.O. 1988. Selection of fast growing clones among visually inseparable genotypes of *Ficus benjamina*. *Gartenbauwissenschaft* 53:180-182.
- Ottosen, C.-O. 1989. CO₂ exchange as an indicator for growth. Attempts to develop methods for selection of clones with high growth. PhD Diss., Royal Veterinary and Agricultural Univ., Copenhagen, Denmark.
- Ottosen, C.-O., A. Andersen, and O.V. Christensen. 1989a. Clonal variation of net photosynthetic rate of *Ficus benjamina* L. in relation to height growth. *Gartenbauwissenschaft* 54:208-211.
- Ottosen, C.-O., E. Rosenqvist, and E. Ögren. 1989b. Clonal variation in oxygen evolution in *Ficus benjamina*. *Photosynthetica* 23:537-542.
- Peterson, R.B. and I. Zelitch. 1982. Relationship between net CO₂ assimilation and dry weight accumulation in field grown tobacco. *Plant Physiol.* 70:677-685.
- Volenec, J.J., C.J. Nelson, and D.A. Sleper. 1984. Influence of temperature on leaf dark respiration of diverse tall fescue genotypes. *Crop. Sci.* 24:907-912.
- Wells, R., D.A. Ashley, H.R. Boerma, and B.J. Reger. 1986. Physiological comparisons of two soybean cultivars differing in canopy photosynthesis. II. Variation in specific leaf weight, nitrogen, and protein components. *Photosynthetic Res.* 9:295-304.
- Zelitch, I. 1982. The close relationship between net photosynthesis and crop yield. *Bioscience* 32:796-802.