

Photosynthetic rate and light response curve of *Bambusa vulgaris* 'Wamin'

Harry Simmons^{1,*}, Surawit Wannakrairoj¹, Alisara Menakanit¹ and Poonpipope Kusemsap²

¹ Department of Horticulture, Kasetsart University, 50 Paholyothin Road, Bangkok, Thailand 10900

² International Studies Center, Kasetsart University, 50 Paholyothin Road, Bangkok, Thailand 10900

Abstract: *Bambusa vulgaris* 'Wamin', an ornamental species, was evaluated for the change in photosynthetic rate at varying irradiance. Photosynthetic rate at 8 irradiance levels between 0 and 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was measured. A light response curve, light saturation point and light compensation point were calculated. The light response curve of *B. vulgaris* leaves showed a light saturation point at levels $>1000 \mu\text{mol m}^{-2} \text{s}^{-1}$. Maximum photosynthetic rate equaled an average of $9.31 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$. Regression analysis indicated a light compensation point of a very low $17.7 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Key words: *Bambusa vulgaris*, light compensation point, light response curve, light saturation point, photosynthesis.

INTRODUCTION

Bambusa vulgaris 'Wamin,' (= *Bambusa vulgaris* cv. *wamin* McClure) is a small bamboo frequently used as an ornamental species in areas of reduced light. Many smaller bamboos have evolved as understorey plants in forest settings with limited light resources (Saitoh *et al.*, 2002). Many of these species exhibit growth characteristics and low light compensation points (LCP) associated with shade plants when exposed to reduced light levels (Lei and Koike, 1998). As in most understorey plants, light becomes the limiting resource in understorey bamboo (Chazdon, 1988). Widmer (1998) observed a morphological difference among naturally occurring *Chusquea* species growing in full sun and those growing in shaded areas. Research performed by Saitoh *et al.* (2002) on *Sasa palmata* showed that the specific leaf area in shade grown plants was greater than that of growing in full sun, indicating a morphological plasticity which enabled individual bamboo plants to adapt to areas of low light levels.

Calculating a light response curve (LRC) is useful in determining optimum light levels and overall plant health. However, several factors can affect the LRC. Xu *et al.*

*To whom correspondence should be addressed: E-mail: HSimmons@bambooresearch.com

(1991) observed total Photosynthetic rate (P_n) decreasing as temperatures decreased and humidity decreased in *Phyllostachys pubescens*. Other researchers have observed differences in P_n at different levels in the canopy of *P. pubescens* (Yang *et al.*, 1991). These experiments measured the light compensation point (LCP) of *P. pubescens* growing in full sun to be an average of $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ for all levels of the canopy. No measurements were made for changes to LCP while light levels changed during production. They also found that leaves in the lower third of the canopy had a much lower LRC when compared to the upper third of the canopy. *P. pubescens* leaves in the lower shaded tier reached a light saturation point at a level between $200\text{-}400 \mu\text{mol m}^{-2} \text{s}^{-1}$. This value represents an overall negative P_n value. The finding is most likely due to the reduced light levels reaching the lower tier.

MATERIALS AND METHODS

In September 2005, 18 pots of culm cuttings of *B. vulgaris* 'Wamin' were purchased and repotted with a mixture 50 per cent topsoil and 50 per cent coconut coir pith. Gravel (3 to 4 cm depth) was placed in the bottom of each 11 liter, black, plastic pot to ensure proper drainage. Each plant was fertilized with 5 g 14-14-14 controlled-release fertilizer and watered thrice weekly. The culm cuttings were maintained under a uniform condition for 4 months. Healthy, 4-month-old leaves which had emerged after the plant acquisition were chosen. Leaves were measured while temperatures ranged between 25°C and 31°C to minimize leaf fluctuations due to extreme temperature differences.

The maximum net photosynthesis (P_n) of the same leaf at a daily photosynthetic photon flux density (PPFD) of 1500 micromoles per square meter per second ($\mu\text{mol m}^{-2}\text{s}^{-1}$) was then analyzed using the LI-6400 system (LI-COR, Inc). The experiments were arranged according to CRD statistical design.

RESULTS AND DISCUSSION

Light response curve

Young leaves of *B. vulgaris* were analyzed for P_n at varying degrees of irradiance and a light response curve (LRC) was created. Creating a LRC first required calculating P_n and leaf respiration. Humidity, temperature, season, leaf age, nitrogen levels and atmospheric change of CO_2 can affect P_n . Several additional factors affect the total daily photosynthesis: Diel Effect (changes in clear-day solar radiation), Depression Effect (daily plant flux in photosynthesis), Shading Effect (light limited by other leaves and structures), Cloudy Effect (changes in solar radiation due to varying cloud coverage) and Inclination Effect (leaf angle and position in canopy) (Kikuzawa *et al.*, 2004). Huang (1986) showed that bamboo leaves less than 1-year-old had a much higher P_n than leaves older than 1 year. Qiu *et al.* (1992) later confirmed that younger

leaves had up to 3 times P_n than that of older leaves. These results were attributed to both a higher nutrient and higher metabolic rate in the younger leaves.

Several measures were taken to limit these factors. All replications were grown with controlled release fertilizer and potted in the same soil mixture four months prior to the experiment. Plants were watered early morning, 1 h before the measurements were taken to prevent erroneous readings due to water stress. Measurements were taken daily from 9:00 am and 12:00 noon before temperature and irradiance peaked. The LI-6400 was calibrated daily. CO_2 and H_2O were scrubbed with soda lime and Dry Rite and measurements were matched frequently to adjust for changes.

The Blackman Model for calculating P_n uses CO_2 and H_2O retained and released in the electron transport system during leaf respiration (Marshall and Biscoe, 2001). Using this model, P_n was calculated as:

$$A = \frac{\phi PFD + (A_{SAT} - E) - \sqrt{(\phi PFD + (A_{SAT} - E))^2 - 4(A_{SAT} - E)\phi PFD}}{2\theta} - E.$$

Where: A = net photosynthesis (maximum assimilation rate) measured in $\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$; also called P_n .

A_{SAT} = saturation value of the photosynthetic curve.

E = transpiration of the leaf, $\text{mol } H_2O \text{ m}^{-2} \text{ s}^{-1}$.

PFD = Photon Flux Density, $\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$.

$(A_{SAT} - E)$ = gross maximum photosynthetic rate.

θ = convex value of the model curve, calculated based on amount of CO_2 trapped in Calvin-Benson cycle.

\hat{o} = initial slope of the curve under low incident levels.

Using readings from the LI-6400, the previous formula can be simplified into;

$$A = \frac{u_e(c_e - c_i)}{100s} - c_i E.$$

Where: A = net photosynthesis measured in $\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$.

c_e = mole fraction of CO_2 in the leaf chamber, $\mu\text{mol } CO_2 \text{ mol}^{-1} \text{ air}$.

c_i = mole fraction of CO_2 entering the leaf chamber, $\mu\text{mol } CO_2 \text{ mol}^{-1} \text{ air}$.

E = transpiration, $\text{mol } H_2O \text{ m}^{-2} \text{ s}^{-1}$.

s = leaf area, cm^2 .

u_e = mole flow rate of air entering the leaf chamber, $\mu\text{mol } \text{s}^{-1}$.

The formula can be further simplified by substituting the formula for transpiration

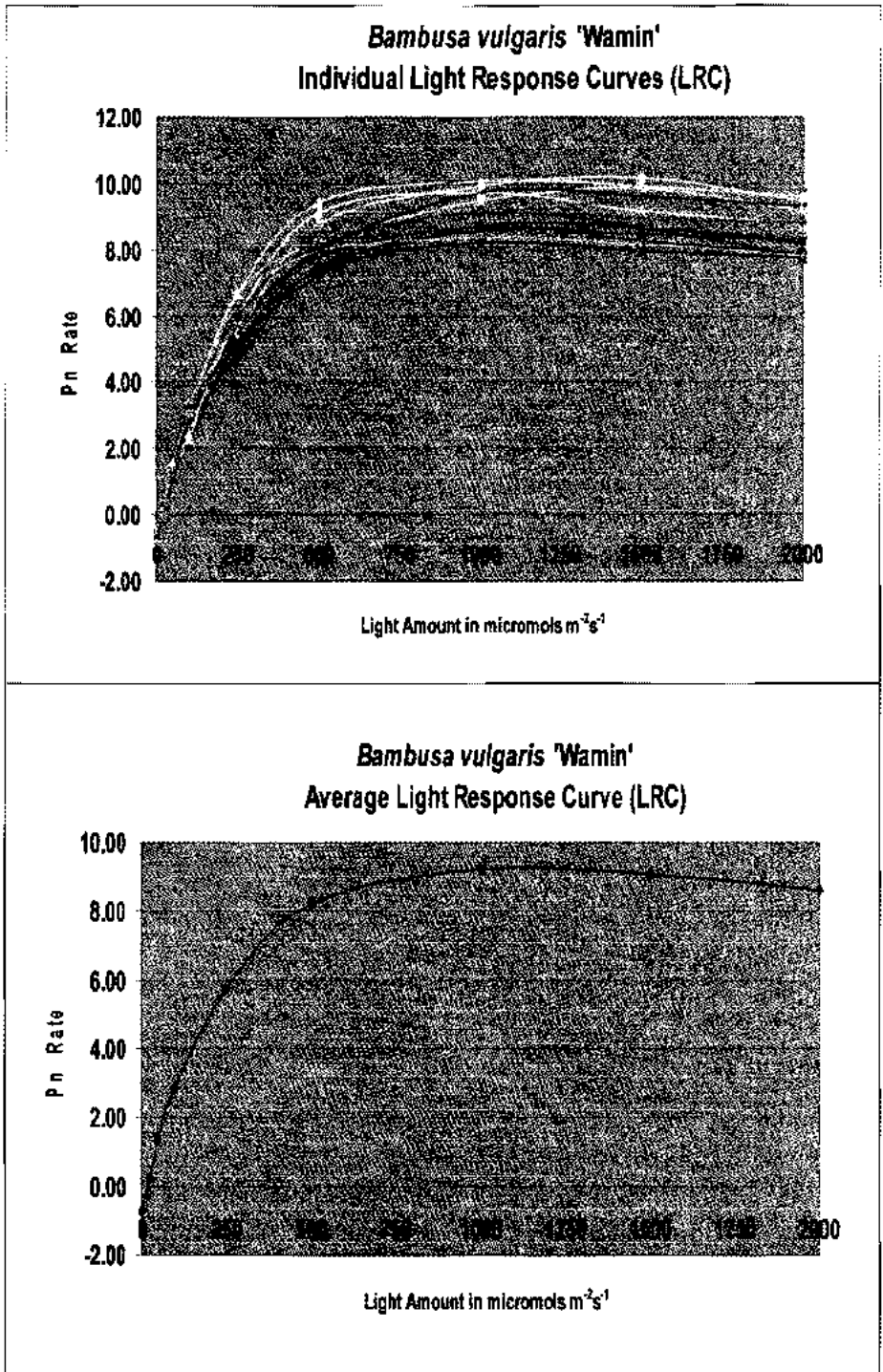


Figure 1. Individual and average light response curves of *B. vulgaris* 'Wamin'

$a = \bar{Y}$ (E in the formula). The formula for transpiration is as follows:

$$E = \frac{u_e(w_c - w_e)}{s \cdot 10^5 \left(1 - \frac{w_e}{1000}\right)}$$

Where: w_c = mole fraction of water vapor in the leaf chamber, mmol H₂O mol⁻¹ air.
 w_e = mole fraction of water vapor entering the leaf chamber, mmol H₂O mol⁻¹ air.

Using this formula, a LRC for *B. vulgaris* 'Wamin' was established. P_n values were recorded at PPFd of 0, 25, 50, 100, 250, 500, 1000, 1500 and 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ using the LI-6400. These results were analyzed and P_n at all light level values were plotted to reveal the shape of the average LRC. Average and individual results are shown in Figure 1.

Light compensation point

Light compensation point (LCP) was calculated once the LRC was known. The LCP equals the point at which the amount of O₂ produced equals (or exactly compensates) the amount used in the photosynthetic process. In calculating LRC, the LCP equals the least squares regression line intercept of the X axis. This process was calculated as:

$$a = \bar{Y} - b\bar{X}$$

Where: a = LCP P_n at light level measured in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

b = slope of the regression line.

\bar{Y} = average of known dependent y values.

\bar{X} = average of known independent x values.

n = number of units recorded.

And where:

$$b = \frac{n(\sum xy) - (\sum x)(\sum y)}{n(\sum x^2) - (\sum x)^2}$$

Earlier research has shown that under low irradiance, the LRC is linear (Bazzaz and Carlson, 1982). While there are some exceptions, the regression line was most accurate at interpreting the x value at the y intercept when only the lowest measurements are analyzed. The results from all replications were analyzed to find the X-axis intercept or LCP (Fig. 2). P_n was always positive when PPFd equaled 50 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. The average P_n when PPFd equaled 25 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ was 0.27 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The P_n when PPFd equaled 0.00 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ averaged a -0.71 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. When the

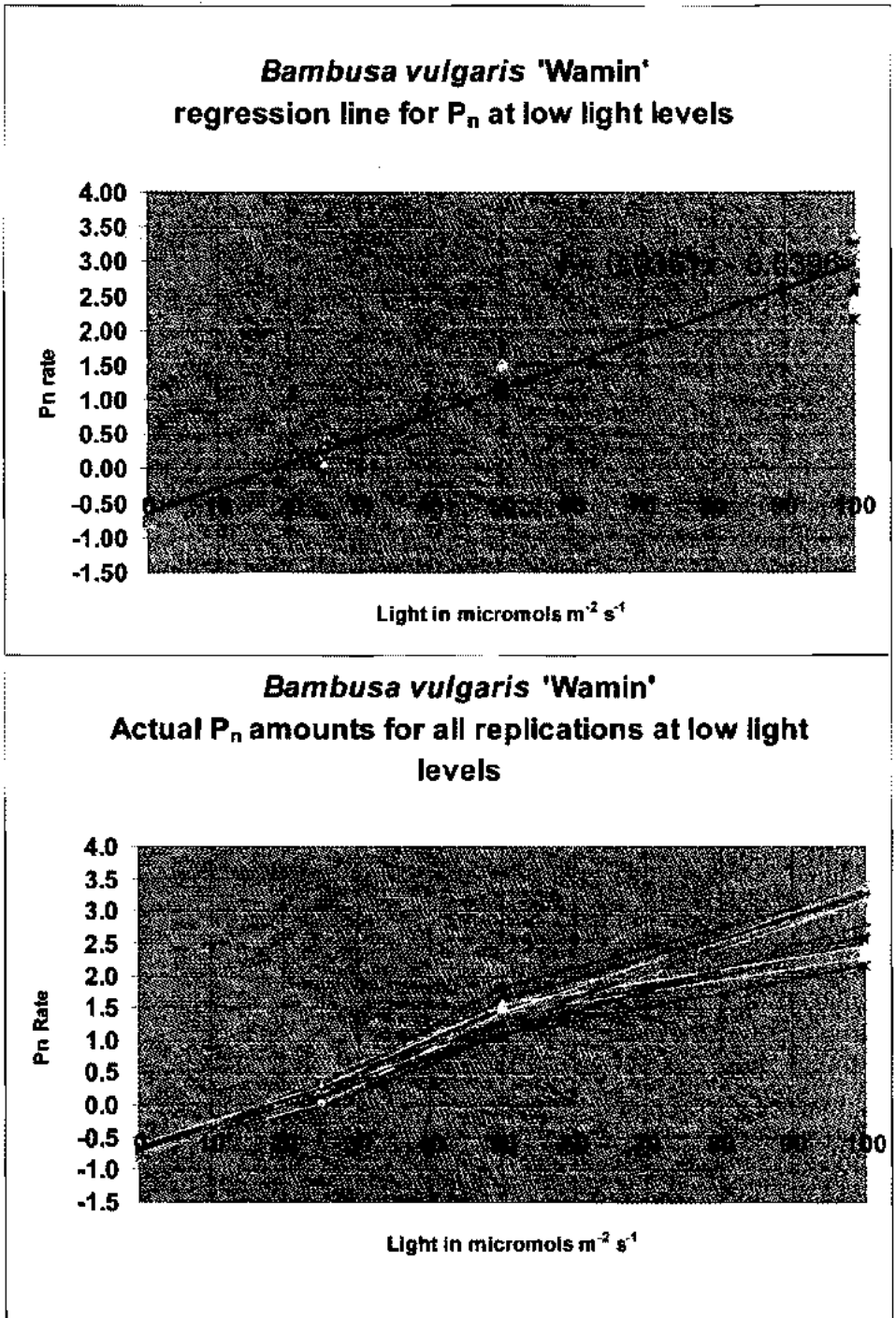


Figure 2. Actual, average and regression line readings for P_n at low light levels in *B. vulgaris* 'Wamin'

regression line was calculated, the y intercept (the point of 0 irradiance) showed $-0.64 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ with a positive slope of 0.0361 (Fig. 2). The regression line value for the LCP calculated to PPFD of $17.7 \mu\text{mol m}^{-2} \text{ s}^{-1}$ which is remarkably low and reflects the ability of *B. vulgaris* 'Wamin' to survive in very low light levels. Using a *t* value of 2.353, the standard of error was 0.38 with a 95 per cent confidence of true value placement for all points in the regression line (Table 1). According to Conover and Poole (1989) this range is well within the range of most indoor, foliage plants.

Table 1. Calculations for regression line used in determining LCP using low irradiance levels

y	X	v	y-v	(y-v) ²	Yi
-0.71	0	-0.64	-0.07	0.0049	v+/- 1.715534*
0.23	25	0.26	-0.03	0.0009	v+/- 1.444491*
1.34	50	1.17	0.17	0.0289	v+/- 1.183954*
2.88	100	2.97	-0.09	0.0081	v+/- 0.718549*

* = 95per cent confidence that Y_i includes the true P_n
 Standard Error = 0.382; y = average actual found value of P_n
 x = level of PPFD; v = estimated value of P_n ; Y_i = confidence interval

Light saturation point

The light saturation point (LSP) of leaves was also calculated by using the data recorded in the LRC. The LSP equals the point at which additional light gives no increase in the total photosynthetic rate. This value is found when the slope of the regression line equals 0. This was calculated with the following formula:

$$y = mx + b$$

Where: y = a function of the independent value x.
 m = slope of the regression line.
 x = independent PPFD values measured in $\mu\text{mol m}^{-2} \text{ s}^{-1}$
 b = a constant number.

The results from calculating LSP showed that 4-month-old leaves of *B. vulgaris* 'Wamin' reached maximum utilization of irradiance after $1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and remained unchanged at $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$. There was no significant difference between the P_n at $1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and $1500 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The average P_n at the LSP was 9.31. It was interesting to note that at the highest level tested, $2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$, there was a drop in P_n rates. This was most likely caused by photo inhibition from the excess irradiance at high levels.

A slightly higher LSP of $1200 \mu\text{mol m}^{-2} \text{ s}^{-1}$ was reported by Kleinhenz and Midmore

(2001) in similar tests on some temperate, monopodial bamboo species. However, the leaves of most temperate, monopodial species have a 2 year life cycle, while leaves of tropical, sympodial species have an average life cycle of 6 years or more (Shammughavel *et al*, 2003; Kleinhenz and Midmore, 2001). This difference in lifecycles might be reflected by different P_n amounts when grown under similar conditions. Kleinhenz and Midmore predicted that P_n rates in tropical, sympodial bamboos would exceed the P_n rates obtained by Koyama and Uchimura (1995) on temperate, monopodial *Phyllostachys bambusoides*. Further research is needed to see if these suspicions are true.

CONCLUSION

The photosynthetic rate of 4-month-old leaves of *B. vulgaris* showed the expected shape of a LRC. P_n increased linearly under light levels between 0 and $100 \mu\text{mol m}^{-2} \text{s}^{-1}$. The linear regression line had a LCP of a very low $17.7 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ indicating an ability to survive at low light levels. This result is consistent with the expected results for smaller bamboos adapted for survival under low light levels. The LSP occurred at $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ and remained unchanged at $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$. An average P_n of 9.31 at the LSP was recorded.

ACKNOWLEDGEMENTS

Special appreciation is expressed to the Department of Horticulture at Kasetsart University for the use of their facilities and equipment throughout the duration of this research.

REFERENCES

- Bazzaz, F.A. and Carlson, R.W. 1982. Photosynthetic acclimation to variability in the light environment of early and late successional plants. *Oecologia* 54(3): 113-116.
- Chazdon, R.L. 1988. Sunflecks and their importance to forest understorey plants. *Advances in Ecological Research* 18: 1-63.
- Conover, C.A. and Poole, R.T. 1989. Protected cultivation of ornamental plants. *Acta Horticulturae* 246: 145-153.
- Huang, Q.M. 1986. The Research about Biomass and Photosynthesis of *Phyllostachys pubescence*. Bamboo Production and Utilization. Kyoto University, Kyoto, Japan.
- Kikuzawa, K., Shirakawa, H., Suzuki, M. and Umeki, K. 2004. Mean labour time of a leaf. *Ecol. Res.* 19: 65 -71.
- Kleinhenz, V. and Midmore, D.J. 2001. Aspects of bamboo agronomy. *Advances in Agronomy* 74: 100-153.
- Koyama, H. and Uchimura, E. 1995. Seasonal change of photosynthesis rate and its relation to the growth of *Phyllostachys bambusoides*. In: R. Rao and C.B. Sastry, (Eds.). Bamboo, People and the Environment: Proceedings of the Vth International Bamboo Workshop and the IV International Bamboo Congress. Ubud, Bali, Indonesia, 9-22 June, 1995.

- International Network for Bamboo and Rattan (INBAR), Environmental Bamboo Foundation (EBF), Government of the Netherlands, International Plant Genetic Resources Institute (IPGRI) and International Development Research Centre (IDRC).
- Lei, T.T. and Koike, T. 1998. Functional leaf phenotypes for shaded and open environments of a dominant dwarf bamboo (*Sasa semanensis*) in northern Japan. *International Journal of Plant Sciences*. 159: 812-820.
- Marshall, B. and Biscoe, P.V. 2001. A model for C_3 leaves describing the dependence of net photosynthesis on irradiance *J. Exp. Bot.* 31(1): 29-39.
- Qiu, G.X., Shen, Y.K., Li, D.Y., Wang, Z.W., Huang, Q.M., Yang, D.D. and Gao, A.X. 1992. Bamboo in sub-tropical eastern China. In: S.P. Long, M.B. Jones and M.J. Roberts (Eds.). Primary Productivity of Grass Ecosystems of the Tropics and Sub-tropics, Chapman and Hall, London, U. K: 159-188.
- Saitoh, T., Seiwa, K. and Nishiwaki, A. 2002. Importance of physiological integration of dwarf bamboo to persistence in forest understorey: a field experiment. *J. Ecol.* 90: 78-85.
- Shanmughavel, P., Peddappaiah, R.S. and Liesc, W. 2003. Recent Advances in Bamboo Research. Scientific Publishers, Jodhpur, India.
- Widmer, Y. 1998. Pattern and performance of understorey bamboo (*Chusquea* spp.) under different canopy closures in old-growth oak forests in Costa Rica. *Biotropica* 30(3): 400-415.
- Xu, D.Q., Li, D.Y., Qiu G.X., Shen, Y.G., Huang, Q.M. and Yang, D.D. 1991. Stomatal limitations of photosynthesis in *Phyllostachys pubescens* leaf. In: A.N. Rao., X.P. Zhang and S.L. Zhu. (Eds.). Selected Papers on Bamboo Research in China. The Chinese Academy of Forestry, Beijing, The People's Republic of China.
- Yang, D.D., Huang, Q.M. and Gao, A.X. 1991. Changes of photosynthetic rate of bamboo leaves at different positions in the canopy. In: A.N. Rao., X.P. Zhang and S.L. Zhu. (Eds.). Selected Papers on Recent Bamboo Research in China. The Chinese Academy of Forestry, Beijing, The People's Republic of China.