BIOLOGIA PLANTARUM 46 (4): 557-561, 2003

Leaf photosynthesis in eight almond tree cultivars

F. DE HERRALDE*, C. BIEL and R. SAVÉ

Departament de Tecnologia Hortícola, Institut de Recerca i Tecnologia Agroalimentàries (IRTA), Ctra. de Cabrils s/n, 08348 Cabrils, Barcelona, Spain

Abstract

Response of gas exchange traits to irradiance were studied in eight almond tree (*Prunus amygdalus*) cultivars: Desmayo Largueta, Falsa Barese, Garrigues, Lauranne, Marcona, Masbovera, Nonpareil and Ramillete, grafted on a hybrid rootstock almond × peach GF-677. From these responses cultivars can be classified from the best to the worst photosynthetic performance as follows: Falsa Barese, Masbovera, Marcona, Nonpareil, Ramillete, Desmayo Largueta, Lauranne and Garrigues. The highest net photosynthetic rate was 20.3 μmol m^{-2} s^{-1} in Falsa Barese. In the absence of water stress, photosynthetic rate was not limited by stomatal conductance. Consequently, non-stomatal limitations prevailed under such conditions.

Additional key words: internal CO_2 concentration, light response curves, net photosynthetic rate, *Prunus amygdalus*, stomatal conductance, stomatal limitation.

Introduction

Almond is a drought resistant species grown in all the Mediterranean climate areas of the world. Due to the economic importance of almond crops in the United States, Spain, and other countries, breeding programs and studies of methods of improving orchard management have been developed to increase the crop yield. The study of ecophysiological characteristics that determine the success of a cultivar in a particular environment is a powerful tool for both agricultural management and breeding purposes. In crops, yield is dependent on photosynthetic rate and on the allocation of assimilates to different sinks such as flowers, fruits or leaves. In fruit trees, canopy architecture makes the relationship even more complex (Pearcy and Sims 1994). However, the leaf photosynthetic characteristics are a very good initial approach to the response of plants to environmental conditions (DeJong 1986). The aim of present study was to compare the leaf photosynthetic rates in eight almond cultivars under semi-controlled growing conditions in northeastern Spain.

Materials and methods

Plants: Five 1.5-year-old almond trees (*Prunus amygdalus* Batsch) of the cultivars Desmayo Largueta (DLL), Falsa Barese (FBA), Garrigues (GAR), Lauranne (LAU), Marcona (MAR), Masbovera (MBO), Nonpareil (NPA) and Ramillete (RAM), grafted onto a hybrid rootstock almond × peach GF-677, were grown at IRTA-Cabrils, North-eastern Spain (41° 25' N, 2° 23'E). Trees were grown in 20 dm^3 pots with peat

Received 7 February 2002, *accepted* 9 May 2002.

Abbreviations: C_i - internal carbon concentration; DLL - Desmayo Largueta; FBA - Falsa Barese; GAR - Garrigues; g_s - stomatal conductance; LAU - Lauranne; MAR - Marcona; MBO - Masbovera; NPA - Nonpareil; P_N - net photosynthetic rate; P_{Nmax} maximum net photosynthetic rate; Q_{comp} - compensation irradiance; Q_{sat} - saturating irradiance; RAM - Ramillete; s_{LIM} - stomatal limitation; ϕ - apparent maximum quantum yield.

Acknowledgements: The present work was partially granted by CICYT (AGF96-0520) and by a IRTA Researchers Formation Grant. Authors gratefully acknowledge Dr. Richard Y. Evans (EHD-UCDavis) for the review of the manuscript. The authors are also grateful to Dr. Ignasi Batlle and Eng. Francisco Vargas (DAM-IRTA) for the co-operation in the research project, and Mr. José Montero and Mrs. M. Carmen Bellido for the technical assistance in field works.

*Corresponding author; fax: (+34) 93 7533954, e-mail: felicidad.deherralde@irta.es

(*Floratoff, Floragard*, Oldenburg, Germany) and perlite (*Europerl A-13, Europerlita Española,* S.A. Rubí, Spain) (2:1, v/v) as the substrate, with a tree spacing of 0.8 × 1.25 m. Trees were drip irrigated daily with a volume of water that varied weekly with the evaporative demand. From February to July plants were fertilised with *Nitrofoska azul especial®* and from July to the end of season with a nutrient solution (N:P:K 1:0.5:1.5; pH = 6.5) added to irrigation water. In January 1999, the trees were transplanted to larger pots (31 dm^3) and fertirrigation continued as before.

Gas exchange and photosynthetic measurement: Gas exchange was measured with an infrared gas analyser system *ADC-2* (*Analytical Development Co. Ltd.*, Hoddesdon, Herts, England). During two growing seasons (from May to September in 1998 and 1999) leaf gas exchange rates were measured to obtain irradiance saturation curves for each cultivar. More than 50 measurements per cultivar were done on south-facing, sun exposed, fully expanded leaves. On clear days, gas exchange rates were measured between 04:00 and 13:00 (solar time); temperatures were between 15.0 and 28.6 °C and relative humidity between 43 and 90 %, producing an air evaporative demand between 0.2 and 1.7 kPa; atmospherical CO_2 concentration varied between 350 and 400 $cm^3 \cdot m^{-3}$

Upper-bound analysis (Long and Hällgren 1993) was applied to each set of measurements. Each upper-bound curve consists in three phases: a linear relationship for the respiration phase ($P_N < 0$), a linear relationship in the initial stage of the assimilation, and a hyperbolic function in the saturating phase. These three upper-bound functions allowed us to relate radiation and maximum photosynthetic rates, without taking into account other environmental factors. From these functions compensation irradiance (Q_{comp}), saturation irradiance (Q_{sat}), apparent maximum quantum yield (ϕ), and maximum photosynthetic rate (P_{Nmax}) were determined for each cultivar. The results were also used to determine the relationship between P_N and g_s.

As an approach to the calculation of stomatal and metabolic limitation of photosynthesis, the equations of Farquhar and Sharkey (1982) were used, assuming there was no stomatal limitation during measurement of P_{Nmax}. Therefore, we used only values obtained at PAR higher than 1 000 μmol m^{-2} s^{-1} and temperatures between 22.5 and 27.5 °C. Stomatal limitation (s_{LIM}) was calculated from:

$s_{LIM} = 1 - (P_N / P_{Nmax})$ [%]

The relationship of s_{LIM} with internal carbon concentration (C_i) was determined because this relationship reflects the metabolic limitations.

Results and discussion

The parameters calculated from curves relating P_N to irradiance for each cultivar are shown in Table 1. Compensation irradiance (Q_{comp}) defines the minimum amount of radiation needed for a positive net photosynthetic rate (Nobel 1991). MBO and DLL had very low Q_{comp}, whereas MAR and NPA had quite high Q_{comp}, meaning that the latter cultivars need a higher irradiance to compensate for respiration rates.

Table 1. Compensation irradiance, Q_{comp} [μmol m^{-2} s^{-1}], saturation irradiance, Q_{sat} [μmol m^{-2} s^{-1}], apparent maximum quantum yield, ϕ [μmol(CO_2) μmol^{-1}(photon)] and maximum net photosynthetic rate (P_{Nmax}) [μmol(CO_2) m^{-2} s^{-1}] for almond cultivars studied.

Cultivar	Q_{comp}	Q_{sat}	ϕ	P_{Nmax}
DLL	60	1129	0.0315	15.9
FBA	78	1288	0.0355	20.3
GAR	87	1284	0.0266	14.8
LAU	88	1475	0.0237	15.6
MAR	133	1229	0.0331	16.5
MBO	56	1123	0.0375	18.5
NPA	103	1331	0.0328	18.5
RAM	70	1243	0.0271	15.4

In this study saturation irradiance (Q_{sat}) ranged from 1123 μmol m^{-2} s^{-1} in MBO to 1475 μmol m^{-2} s^{-1} in LAU. A greater difference between Q_{comp} and Q_{sat} implies a greater amount of radiation used for photosynthesis. Photosynthetic efficiency, calculated as ϕ, ranged from the 0.0237 in LAU to 0.0375 μmol(CO_2) μmol^{-1}(photon) in MBO. In our conditions, the maximum apparent photosynthetic rate (P_{Nmax}) was around 17 μmol m^{-2} s^{-1}, which is consistent with reported values for almond leaves (DeJong 1983, Matos *et al.* 1997). GAR had the lowest value [14.8 μmol(CO_2) m^{-2} s^{-1}] while FBA had the highest [20.3 μmol (CO_2) m^{-2} s^{-1})]. Almond, as a species, has higher net photosynthetic rates than those described for other fruit trees such as cherry, peach, plum, apricot (DeJong 1983), apple (Lakso 1994), citrus (Flore and Lakso 1989), hazelnut (Marsal 1996), or walnut trees (Tombesi *et al.* 1983).

Taking into account all these results, the eight almond cultivars can be classified from best to worst photosynthetic performers as follows: FBA, MBO, MAR, NPA, RAM, DLL, LAU and GAR. FBA can be considered as the best photosynthetically performing cultivar because of its high ϕ and the highest P_{Nmax}, whereas GAR showed the lowest ϕ and P_{Nmax} compared to all other cultivars. These potential yields could be used during the design of almond orchards to determine appropriate tree spacing. FBA has higher light interception because it has higher leaf density and more horizontally disposed branches (De Herralde 2000) which achieves the same primary production as GAR, which has a higher Q_{comp} but lower P_{Nmax}, with less dense tree spacing. Canopy architecture in GAR is more closed (De Herralde 2000), which restricts the penetration of incident radiation.

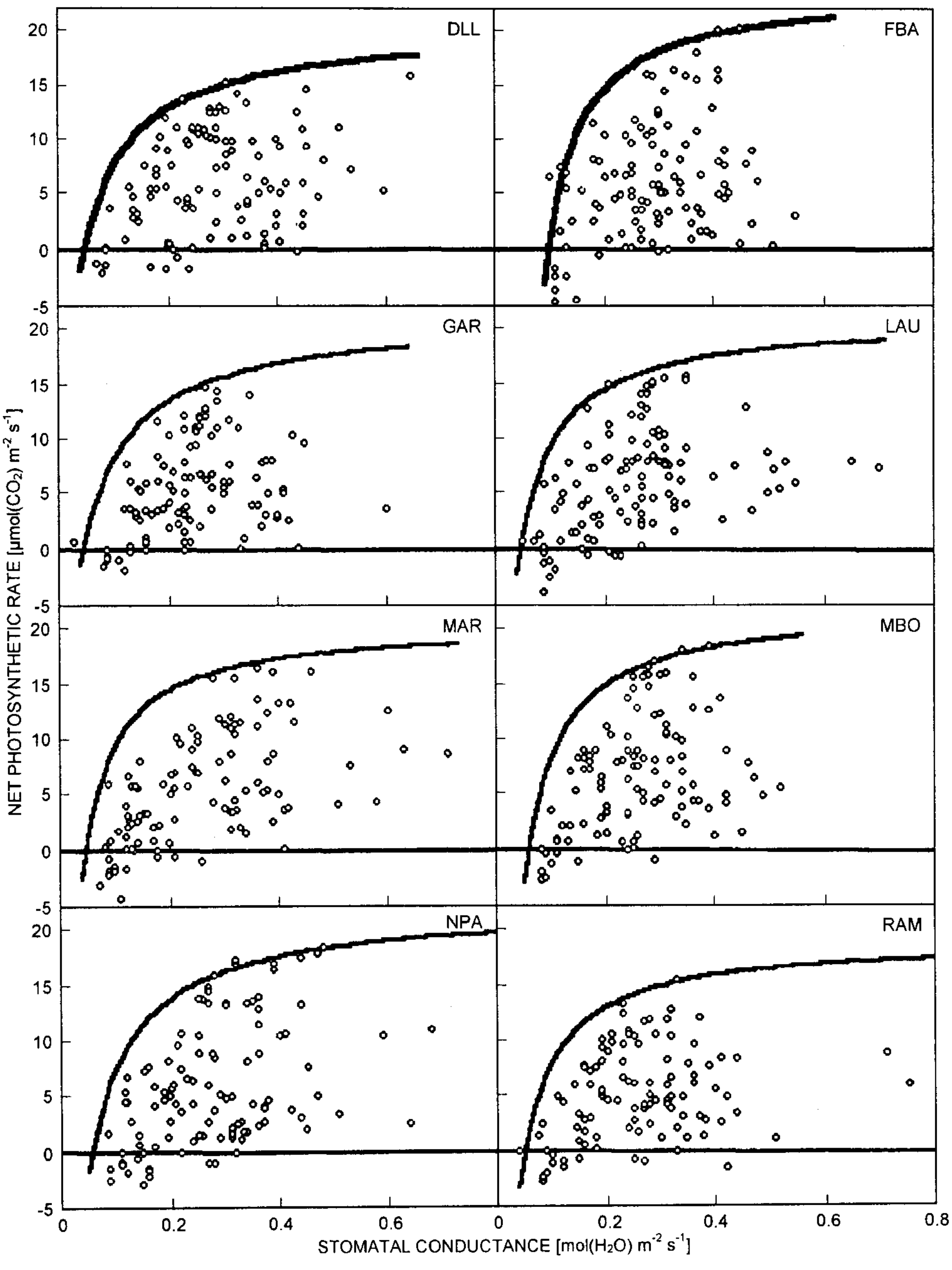

Fig. 1. Relationship between the net photosynthetic rate (P_N) and stomatal conductance (g_s) for almond cultivars studied. Black line shows upper limit adjustment.

The same measurements were used to study the relationship between photosynthetic rate and stomatal conductance (P_N/g_s) (Fig. 1). Upper-bound hyperbolic functions were adjusted for each cultivar. The initial stage in these functions has a very steep slope in all the cultivars. This may be due to the fact that stomatal opening at dawn is partially controlled by light (Meidner and Mansfield 1968, Hall and Rao 1994). In the majority of woody plants, g_s curves in response to light, have a very steep slope, achieving 50 % of the potential conductance at around 5 - 10 % of maximum incident radiation, with the maximum conductances occurring at 15 % of maximum sunlight, about 300 µmol m^{-2} s^{-1} (Körner 1995). The scattering of values indicates that several other factors affect P_N more than g_s does. Turner *et al.* (1984) reported that variations in stomatal conductance and transpiration rates, due to increases in environmental evaporative demand, had little effect on P_N in almond trees. In the experimental conditions for the present work evaporative demand was always between 0.2 and 1.7 kPa and plants were also well irrigated, so the influence of stomatal regulation, due to water deficits, was minimised.

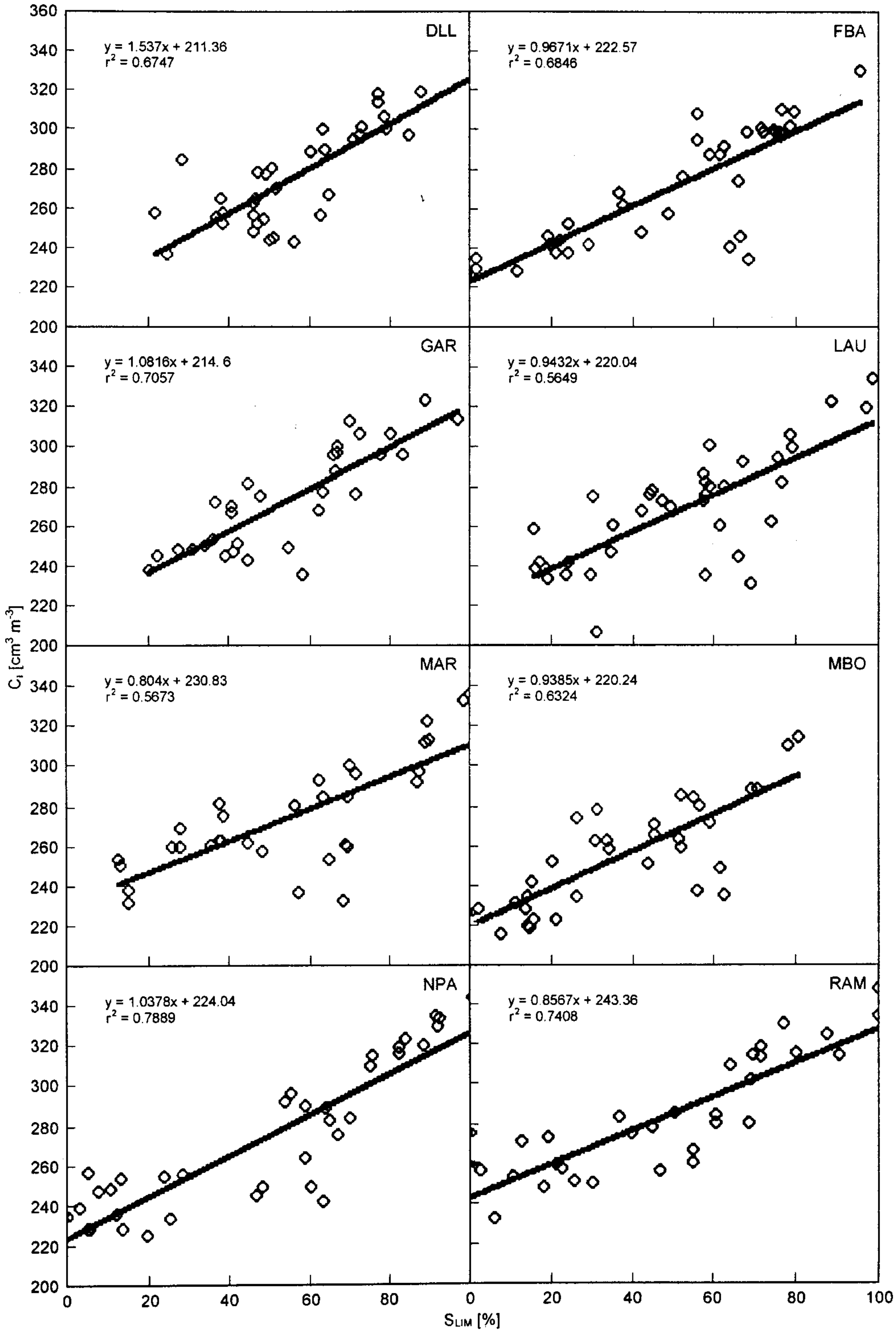

Fig. 2. Relationship between inner carbon dioxide concentration (C_i) and the percentage of stomatal limitation (s_{LIM}) calculated for each almond cultivar. Regressions were all significant at $P < 0.05$.

In order to define the importance of stomatal limitation in the almond cultivars, the method described by Farquhar and Sharkey (1982) was applied. Regression coefficients for linear relationships C_i/s_{LIM} range from 0.5649 in LAU to 0.7889 in NPA (Fig. 2). When $s_{LIM} = 0$, c_i reaches a minimum value, which represents the carbon concentration within the mesophyll when metabolism is maximised. The farther C_i is from atmospheric carbon dioxide concentration the higher the photosynthetic capacity of the cultivar. The eight studied cultivars can be classified from higher to lower potosynthetic capacity as follows: DLL, GAR, LAU, MBO, FBA, NPA, MAR and RAM.

References

De Herralde, F.: [Integral study of the ecophysiological responses to water stress: characterization of almond cultivars.] - Ph.D. Thesis. Universitat de Barcelona, Barcelona 2000. [In Spanish.]

DeJong, T.M.: CO_2 assimilation characteristics of five *Prunus* tree fruit species. - J. amer. Soc. hort. Sci. **108**: 303-307, 1983.

DeJong, T.M.: A whole plant approach to photosynthetic efficiency in tree crops. - In: Lakso, A.N., Lenz, F. (ed.): Regulation of Photosynthesis in Fruit Trees. Pp. 18-22. Cornell University, Ithaca 1986.

Farquhar, G.D., Sharkey, T.D.: Stomatal conductance and photosynthesis. - Annu. Rev. Plant Physiol. **33**: 317-346, 1982.

Flore, J.A., Lakso, A.N.: Environmental and physiological regulation of photosynthesis in fruit crops. - Hort. Rev. **11**: 111-157, 1989.

Hall, D.O., Rao, K.K.: Photosynthesis. - Cambridge University Press, New York 1994.

Körner, C.: Leaf diffusive conductances in the major vegetation types of the globe. - In: Schulze, E.-D., Caldwell, M.M. (ed.): Ecophysiology of Photosynthesis. Pp. 463-490. Springer-Verlag, Berlin 1995.

Lakso, A.N.: Apple. - In: Schaffery, B., Andersen, P.C. (ed.): Handbook of Environmental Physiology of Fruit Crops Volume I: Temperate Crops. Pp. 4-42. CRC Press, Boca Raton 1994.

Long, S.P., Hällgren, J.-E.: Measurement of CO_2 assimilation by plants in the field and the laboratory. - In: Hall, D.O., Scurlock, J.M.O., Bolhàr-Nordenkampf, H.R., Leegood, R.C., Long, S.P. (ed.): Photosynthesis and Production in a Changing Environment. A Field and Laboratory Manual. Pp. 129-167. Chapman and Hall, London 1993.

Marsal, J.: Water stress measurements in fruit trees under different regulated deficit irrigation regimes. - Ph.D. Thesis. Universidad de Lleida, Lleida 1996.

Matos, M.C., Matos, A.A., Mantas. A, Cordeiro, V., Vieira da Silva, J.B.: Photosynthesis and water relations of almond tree cultivars grafted on two rootstocks. - Photosynthetica **34**: 249-256, 1997.

Meidner, H., Mansfield, T.A.: Physiology of Stomata. - McGraw-Hill, London 1968.

Nobel, P.S.: Physicochemical and Environmental Plant Physiology. - Academic Press, San Diego 1991.

Pearcy, R.W., Sims, D.A.: Photosynthetic acclimation to changing light environments: scaling from the leaf to the whole plant. - In: Caldwell, M.M., Pearcy, R.W. (ed.) Exploitation of Environmental Heterogeneity by Plants. Ecophysiological Processes Above- and Belowground. Pp. 145-174. Academic Press, San Diego 1994.

Tombesi, A., DeJong, T.M., Ryugo, K.: Net CO_2 assimilation and characteristics of walnut leaves under field and laboratory conditions. - J. amer. Soc. hort. Sci. **108**: 558-561, 1983.

Turner, N.C., Schulze, E.-D., Gollan, T.: The responses of stomata and leaf gas exchange to vapour pressure deficits and soil water content. I. Species comparisons at high soil water contents. - Oecologia **63**: 338-342, 1984.