Leaf photosynthesis in eight almond tree cultivars

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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 x 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 CO₂ 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 x 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

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Abbreviations: g - internal carbon concentration; DLL - Desmayo Largueta; FBA - Falsa Barese; GAR - Garrigues; gₐ - stomatal conductance; LAU - Lauranne; MAR - Marcona; MBO - Masbovera; NPA - Nonpareil; Pₙ - net photosynthetic rate; Pₙₜₙₜ maximum net photosynthetic rate; Q₃₉₉₉ - compensation irradiance; Qₛₙₛ - saturating irradiance; RAM - Ramillete; Sₘₘₘ - stomatal limitation; φ - apparent maximum quantum yield.

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(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 \times 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 Nitrosfaska 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 dm³) 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; atmospheric CO₂ concentration varied between 350 and 400 cm⁻³ 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 (Pₐ < 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 (Qₘₐₓₜₜ), saturation irradiance (Qₘₐₓ), apparent maximum quantum yield (φ), and maximum photosynthetic rate (Pₘₐₓₜₜ) were determined for each cultivar. The results were also used to determine the relationship between Pₐ and φₕ.

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 Pₘₐₓₜₜ. 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 (sₜₜₜₜ) was calculated from:

\[ sₜₜₜₜ = 1 - \left( \frac{Pₐ}{Pₘₐₓₜₜ} \right) \% \]

The relationship of sₜₜₜₜ with internal carbon concentration (Cᵢ) was determined because this relationship reflects the metabolic limitations.

**Results and discussion**

The parameters calculated from curves relating Pₐ to irradiance for each cultivar, are shown in Table 1. Compensation irradiance (Qₘₜₜₜ) defines the minimum amount of radiation needed for a positive net photosynthetic rate (Nobel '90). MBO and DLL had very low Qₘₜₜₜ, whereas MAR and NPA had quite high Qₘₜₜₜ, meaning that the later cultivars need a higher irradiance to compensate for respiration rates.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Qₘₜₜₜ</th>
<th>Qₘₜₜ</th>
<th>φ</th>
<th>Pₘₜₜₜ</th>
</tr>
</thead>
<tbody>
<tr>
<td>DLL</td>
<td>60</td>
<td>1120</td>
<td>0.0315</td>
<td>15.9</td>
</tr>
<tr>
<td>FBA</td>
<td>78</td>
<td>1288</td>
<td>0.0355</td>
<td>20.3</td>
</tr>
<tr>
<td>GAR</td>
<td>87</td>
<td>1284</td>
<td>0.0266</td>
<td>14.8</td>
</tr>
<tr>
<td>LAU</td>
<td>88</td>
<td>1475</td>
<td>0.0237</td>
<td>15.6</td>
</tr>
<tr>
<td>MAR</td>
<td>133</td>
<td>1229</td>
<td>0.0331</td>
<td>16.5</td>
</tr>
<tr>
<td>MBO</td>
<td>56</td>
<td>1123</td>
<td>0.0375</td>
<td>18.5</td>
</tr>
<tr>
<td>NPA</td>
<td>103</td>
<td>1331</td>
<td>0.0328</td>
<td>18.5</td>
</tr>
<tr>
<td>RAM</td>
<td>70</td>
<td>1243</td>
<td>0.0271</td>
<td>15.4</td>
</tr>
</tbody>
</table>

In this study saturation irradiance (Qₘₜₜ) ranged from 1123 μmol m⁻² s⁻¹ in MBO to 1475 μmol m⁻² s⁻¹ in LAU. A greater difference between Qₘₜₜ and Qₘₜₜ 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(CO₂) μmol⁻¹(photons) in MBO. In our conditions, the maximum apparent photosynthetic rate (Pₘₜₜₜ) was around 17 μmol m⁻² s⁻¹, which is consistent with reported values for almond leaves (De Jong 1983, Matos et al. 1997). GAR had the lowest value [14.8 μmol(CO₂) m⁻² s⁻¹] while FBA had the highest [20.3 μmol(CO₂) 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 (De Jong 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 Pₘₜₜₜ, whereas GAR showed the lowest φ and Pₘₜₜₜ 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 $F_{max}$, 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.

![Graphs showing the relationship between $C_t$ and $S_{sw}$ for different almond cultivars.](image)

**Fig. 2.** Relationship between inner carbon dioxide concentration ($C_t$) and the percentage of stomatal limitation ($S_{sw}$) calculated for each almond cultivar. Regressions were all significant at $P < 0.05$. 560
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 \( C_e / \text{S}_{\text{LIM}} \) range from 0.5649 in LAU to 0.7889 in NPA (Fig. 2). When \( \text{S}_{\text{LIM}} = 0 \), \( C_e \) reaches a minimum value, which represents the carbon concentration within the mesophyll when metabolism is maximised. The farther \( C_e \) 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 photosynthetic capacity as follows: DLL, GAR, LAU, MBO, FBA, NPA, MAR and RAM.

References


