Photosynthesis and water relations of almond tree cultivars grafted on two rootstocks

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Abstract

Five cultivars of *Prunus amygdalus* Batsch (Ferragnes, Ferrastar, Marcona, Garrigues, and Non Pareil) grafted on two different rootstocks (Garrigues and GF677), and two cultivars (Ferraduel and Casa Nova) grafted on GF677, were grown for three years under rainfed conditions in an orchard in northeast Portugal. Net photosynthetic rate (P_N), leaf conductance for water vapour (g_s), leaf water potential (Ψ), instantaneous water use efficiency (WUE), and internal CO_2 concentration (C_i) were measured at three periods of the growing season: spring, summer (June or July) and late summer (September) over two years. Ferraduel, Ferrastar, and Marcona presented the best performance in the periods when environmental conditions were not very hard (May or September). Casa Nova and Non Pareil were well adapted to high air evaporative demand, preventing the increase of leaf temperature (T_l). Ferrastar, although having a good performance in May and September, did well adapt to hard climatic conditions in June 1994. In the following year, although it presented the highest T_l, the values were not limiting (30.6 ± 2.1 °C), and P_N was only decreased from May to July. Marcona was highly dependent on T_l, but prevented its increasing. Garrigues showed lower P_N in most measurement periods. GF677 frequently induced the highest P_N, WUE, and Ψ. P_N was mainly dependent on T_l, radiation, C_i, month, and year. WUE depended on the same factors. Ψ depended mainly on g_s, air temperature, month, and year.

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Abbreviations: Chl - chlorophyll; C_i - internal CO_2 concentration; g_s - stomatal conductance; PAR - photosynthetically active radiation; P_N - net photosynthetic rate; T_a - air temperature; T_l - leaf temperature; WUE - water use efficiency; Ψ - leaf water potential.
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Additional key words: drought; internal CO_2 concentration; leaf water potential; *Prunus amygdalus*; seasonal course; selection; stomatal conductance; water relations; water use efficiency.

Introduction

P. amygdalus Batsch is drought resistant (Fereres *et al.* 1981) as it is able to withstand frequent periods of low soil moisture with high evaporative demand and temperature, during the growing season. Such conditions are typical of the Mediterranean basin. The need for modernisation of the production methods led to the introduction of high yielding cultivars, bred in other countries, some of them late flowering in order to avoid frost risk. However, the inadaptation to new conditions is not known.

An experimental orchard was installed in the production area comparing five almond cultivars on two rootstocks: Garrigues seedling (almond) and GF 677 (hybrid between almond and peach), and two cultivars on GF 677. According to Gall and Grasselly (1977), Ross and Catlin (1978), and Grasselly and Crossa-Raynaud (1980), this rootstock has higher drought resistance than peach and, in some cases, almond. The trees were too young for reliable yield estimation, but physiological characteristics were determined according to Matos (1990). The aim of this paper was to compare photosynthetic activity and water relations of seven almond cultivars of *P. amygdalus* all over the season, and to evaluate the influence of two rootstocks on physiological parameters.

Materials and methods

Five cultivars of *Prunus amygdalus* Batsch, two French (Ferragnes, Ferrastar), two Spanish (Marcona, Garrigues), and one from California (Non Pareil) grafted on two rootstocks: Garrigues seedling (an almond) and GF677 (a peach-almond hybrid), and French cultivar Ferraduel and Portuguese cultivar Casa Nova, grafted on GF677 were planted in 1991 in a shallow schistic soil in Northeast Portugal at 41°10'N latitude and 7°12'W longitude. Precipitation was about 600 mm per annum, and maximum air temperature (T_a) around 39 °C during summer months (Table 1).

Plant water status was characterised by xylem water potential (Ψ) measured by a pressure chamber on two detached leaves per tree (Scholander *et al.* 1985). Measurements took place from predawn to sunset, and were always made before the gas exchange determinations on adjacent leaves. P_N, g_s and C_i were measured under natural conditions using a portable CO_2/H_2O gas exchange system (*LI-6200; LI-COR*, Lincoln, USA) and calculated according to the equations of Caemmerer and Farquhar (1981). The measurements were carried out on individual, attached, sun exposed and fully expanded leaves from the middle of the canopy, in a well stirred cuvette (100 cm^3) to minimise boundary layer resistance. Diurnal courses of photosynthetically active radiation (PAR), leaf (T_l) and air (T_a) temperature, air water vapour deficit, external and internal CO_2 concentrations were followed. The periods of measurement were at the middle of May, end of June (1994) or beginning of July

(1995), and at first days of September. Each month was represented by measurements of two successive days. The days, in which measurements were carried on, were clear and sunny except the morning in May of 1994.

Table 1. Mean and maximum air temperatures, rainfall, and evapotranspiration for the years 1994 and 1995 in Mirandela.

Month	Temperature [°C] mean 1994	1995	maximum 1994	1995	Precipitation [mm] 1994	1995	Evapotranspiration [mm] 1994	1995
January	6.4	7.7	10.9	13.1	78.0	51.5	43.0	59.6
February	6.6	8.8	11.9	13.5	63.0	44.5	43.0	48.6
March	12.4	8.3	20.2	14.9	4.0	16.8	70.0	98.8
April	12.2	14.3	18.8	23.2	15.0	23.2	130.0	155.8
May	15.8	22.0	22.1	30.5	89.0	18.5	156.0	243.2
June	21.1	17.9	28.7	24.8	6.0	32.4	203.0	201.6
July	24.7	24.3	33.6	32.2	5.0	39.0	193.0	247.3
August	23.6	24.4	32.1	32.9	13.0	1.4	236.0	276.6
September	18.4	18.4	25.2	25.1	18.0	35.2	138.0	157.5
October	16.1	17.9	22.1	25.6	56.0	31.9	82.0	---
November	10.9	12.5	14.8	16.9	49.9	118.8	29.2	49.7
December	8.8	9.2	12.9	13.2	30.5	69.0	5.7	50.9
Total					427.4	482.2	1328.9	1589.6

Results were statistically analysed by the *Statistix* program version *4.1*, 1985, *94 Analytical Software*, and *Systat for Windows* version *5*.

Results and discussion

Mean air temperatures of the days of the measurements were different on the three periods: 19.1±0.3, 36.0±0.3, and 29.6±0.4 °C on May, June, and September of 1994, respectively. In 1995 they changed from 24.8±0.4, 29.6±0.4, and 24.5±0.5 °C for the same periods. Mean relative humidity (RH), mean daily leaf temperature (T_l), and predawn leaf water potentials (Ψ_0) changed as shown in Table 2. The September 1994 changes were induced by heavy rain (62.6 mm on the last eight days before measurements). Torrecillas *et al.* (1988) also refer a reduction of Ψ of almond trees cv. Garrigues as season progresses.

Mean daily values of Ψ also changed as season progressed: they decreased in 1994 from -2.4 MPa in May to -3.5 MPa in September. The 1995 values were higher all over the season (Table 2). Ψ was closely dependent on environmental conditions, mainly T_a and RH, as referred by Elfving *et al.* (1972) and Klepper (1968). The changes in gas exchange parameters (Table 2) were either the result of leaf ageing or the effect of soil and/or climate factors.

Leaf protein content decreased significantly from May (7.071±0.115 g m^{-2}) to June 1994 (6.263±0.140 g m^{-2}) (p=0.05). Chlorophyll $a+b$ content was significantly higher in May than in July and September; from July to September the differences were not significant.

Table 2. Seasonal changes in 1994 and 1995 of main mean photosynthetic [P_N - net photosynthetic rate, C_i - internal CO_2 concentration] and water relation characteristics [E - transpiration rate, WUE - water use efficiency, g_s - stomatal conductance, Ψ - leaf water potential, Ψ_0 - initial leaf water potential], and other characteristics [T_a - air temperature, T_l - leaf temperature, RH - relative humidity] of cultivars of almond trees grown in NE of Portugal under rainfed conditions.

Variable	May		June	July	September	
	1994	1995	1994	1995	1994	1995
P_N [μmol m^{-2} s^{-1}]	9.6±0.4	15.6±0.7	6.6±0.5	10.7±0.5	5.8±0.3	9.0±0.5
P_{Nmax} [μmol m^{-2} s^{-1}]	14.8±0.5	26.4±0.8	16.0±1.0	17.3±1.4	9.7±0.5	16.6±1.5
E [mmol m^{-2} s^{-1}]	4.7±0.4	9.1±0.6	1.4±0.7	7.6±0.6	1.7±0.1	2.3±0.1
WUE [P_N/E]	2.1±0.2	1.7±0.1	4.8±0.7	1.4±0.1	3.4±0.2	3.9±0.3
g_s [mmol m^{-2} s^{-1}]	423.0±0.0	283.4±18.0	48.6±1.9	194.6±0.0	50.8±1.9	76.1±4.2
C_i [μmol mol^{-1}]	262.4±2.0	230.2±5.6	287.3±1.2	231.7±3.9	278.2±1.4	229.7±5.6
Ψ [MPa]	-2.4±0.1	-1.6±0.1	-2.7±0.1	-2.4±0.1	-3.5±0.1	-2.3±0.1
Ψ_0 [MPa]	-0.9±0.0	-1.0±0.1	-1.5±0.1	-1.2±0.0	-2.5±0.1	-1.2±0.0
T_a [°C]	19.1±0.3	24.8±0.4	36.0±0.3	29.4±0.2	29.6±0.4	24.5±0.5
T_l [°C]	19.0±0.5	25.3±0.4	38.3±0.3	29.9±0.2	30.5±0.4	25.8±0.6
RH [%]	47.2±0.8	38.0±0.5	29.4±0.6	43.6±0.9	35.2±0.3	39.1±1.4

Carbon assimilation was significantly higher in 1995 (mean 11.62±0.35 μmol m^{-2} s^{-1}) than in the previous year (7.25±0.25 μmol m^{-2} s^{-1}) (p=0.000) perhaps due to better mineral nutrition or better adaptation of the root system. Mean P_N suffered a reduction of 31.3 % from May to June 1994, 12.1 % from June to September in 1994, and 31.4 and 15.9 % in the same periods of 1995 (Table 2). Ruiz-Sánchez *et al.* (1988) found a decrease in g_s of almond trees independently of the irrigation treatment through the growing season. Also in our experiment, g_s decreased from May to June and from June to September in both 1994 and 1995. Differences in stomatal behaviour were ascribed to climate factors. Also changes on hormonal balance of the leaf (Meidner 1971) might occur. Water use efficiency (Table 2) also changed during the season: in June and September 1994 and September 1995 it was significantly higher than in May 1994 and 1995 and July 1995 (when clima was not very hard). Thus it increased when g_s decreased.

Although absolute values differred in 1994 with 1995, the relations among cultivars (Fig. 1) were similar in both years (Casa Nova was included in the experiment only after May of 1994). P_N was higher in Ferraduel, Casa Nova, and Ferrastar than in Garrigues and Ferragnes. Ferraduel had higher P_N than Non Pareil (p=0.05) (Table 3). The g_s (Fig. 2) was significantly lower in Casa Nova than in Marcona, Ferrastar, and Ferraduel; Ferragnes had significantly lower values than Marcona, Ferrastar, and Ferraduel. The g_s of Garrigues was significantly lower than that of Ferrastar. Thus Ferrastar and Ferraduel presented the highest g_s ($p = 0.05$). There were no significant differences in Ψ (Fig. 3) among cultivars as well as in C_i and T_l. Non Pareil had a significantly higher WUE than Marcona, Ferrastar, and Ferraduel.

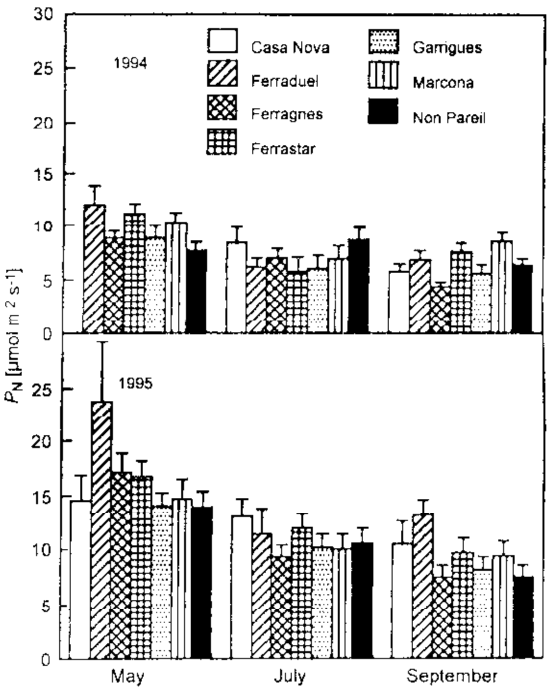

Fig. 1. Seasonal changes of mean daily net photosynthetic rate (P_N) of seven cultivars of almond tree on two consecutive years. Vertical bars indicate standard error of the mean.

Concerning rootstock effect (Table 4), plants on GF 677 had significantly higher P_N (10.00±0.31 μmol m^{-2} s^{-1}) than on Garrigues (8.70±0.33 μmol m^{-2} s^{-1}). In Redspur apple, Ferree and Barden (1971) found higher P_N on plants grafted on seedling rootstocks than on MM 106. Also Marro and Cereghini (1976) referred to higher P_N in Richared Delicious apple trees on M9 than on seedling rootstock. On the contrary, Barden and Ferree (1979) did not find the effect of rootstock on apple tree P_N and other physiological characteristics of one year old Delicious trees. We did not find effect of rootstock on g_s and WUE. Bongi *et al.* (1994) found differences in WUE of peach grafted on different interspecific hybrid rootstocks. The Ψ was significantly higher in plants on GF 677 (-2.51±0.04 MPa) than in Garrigues (-2.67± 0.06 MPa). The C_i was significantly higher in Garrigues (262.53±4.36 μmol mol^{-1}) than in GF 677 (249.69±2.12 μmol mol^{-1}). Decreases in C_i without decreases of g_s may be a result of higher activity of photosynthetic machinery (cf. the increase of P_N in GF 677). Effect of rootstocks on scion performance has been pointed out by several authors, in what concerns tolerance to soil conditions or vigour of the scion; rarely the accumulation of ions in plant tissues and its association with tree performance is discussed (El-Motaium *et al.* 1994). The effect of rootstock GF 677 on increasing carbon assimilation of almond trees could be the result of a better access between roots and shoot, since Ψ was also higher than in Garrigues. Cristoferi *et al.* (1963) found that rootstock affected shoot water conductivity of the apple trees.

Table 3. Main photosynthetic and water relation characteristics in 1994 and 1995. For abbreviations and dimensions see Table 2. P_N: Ferrastar>Ferragnes (p=0.039); 1995>1994 (p=0.000). C_i: 1995<1994 (p=0.000). g_s: CasaNova>Ferraduel (p=0.001), Ferrastar (p=0.000), Ferragnes (p=0.008), Garrigues (p=0.006), Marcona (p=0.000); Ferrastar<Non Pareil (p=0.002); 1995<1994 (p=0.000); year×cv. (p=0.000). WUE: Non Pareil>Marcona (p=0.030); 1995<1994 (p=0.000); year ×cv. (p=0.000). Ψ: 1995>1994 (p = 0.000).

Cultivar	P_N 1994	P_N 1995	g_s 1994	g_s 1995	Ψ 1994	Ψ 1995	WUE 1994	WUE 1995	C_i 1994	C_i 1995
Ferragnes	5.61	11.10	67.04	140.53	-3.03	-2.19	3.80	3.05	280.05	227.48
Garrigues	5.59	10.81	67.68	153.26	-3.12	-2.12	3.76	2.82	280.52	231.16
Non Pareil	7.12	10.81	51.15	160.23	-3.07	-2.01	5.48	3.78	282.17	136.50
Ferraster	7.70	12.73	100.00	159.62	-3.12	-2.06	2.15	2.04	276.57	221.93
Marcona	7.68	11.25	93.58	159.62	-3.11	-2.17	2.37	2.07	310.53	235.67
Ferraduel	7.28	14.20	102.42	155.51	-3.23	-2.15	1.58	2.05	285.26	234.48
Casa Nova	6.32	12.81	36.98	162.07	-2.82	-2.03	4.37	3.21	282.37	228.38

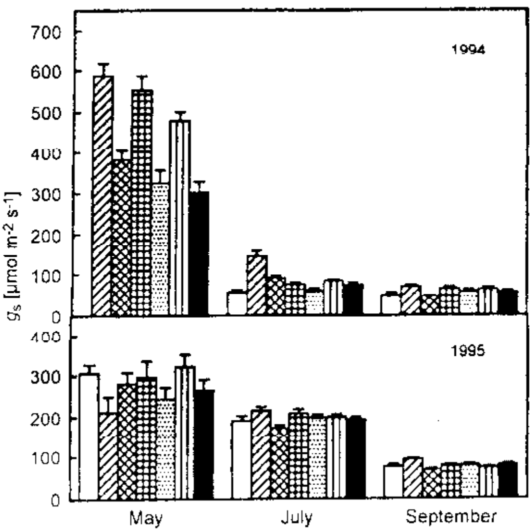

Fig. 2. Seasonal changes of mean daily leaf conductance to water vapour diffusion (g_s) of seven cultivars of almond trees on two consecutive years. Vertical bars indicate the standard error of the mean. Symbols as in Fig. 1.

Generally, P_N and WUE were mainly dependent on T_l, irradiance, C_i, month, and year. The Ψ depended mainly on g_s, T_a, month, and year. There was the usual advantage in the hybrid rootstock GF677 over almond (Garrigues), namely in P_N, C_i, and Ψ, meaning a better water status and better photosynthetic ability. The local cultivar Casa Nova had a lower g_s than most other cultivars, but was not different in P_N, C_i, WUE, and Ψ. Hence it is still a fairly good cultivar. From the foreign cultivars, Non Pareil had a higher WUE than Marcona. Of the late flowering French cultivars, Ferrastar had a higher P_N than Ferragnes, but a higher g_s than Non Pareil. The year 1995 was better than 1994, but it was difficult to ascertain if it was the result of better climatic conditions or of the growth of the root system.

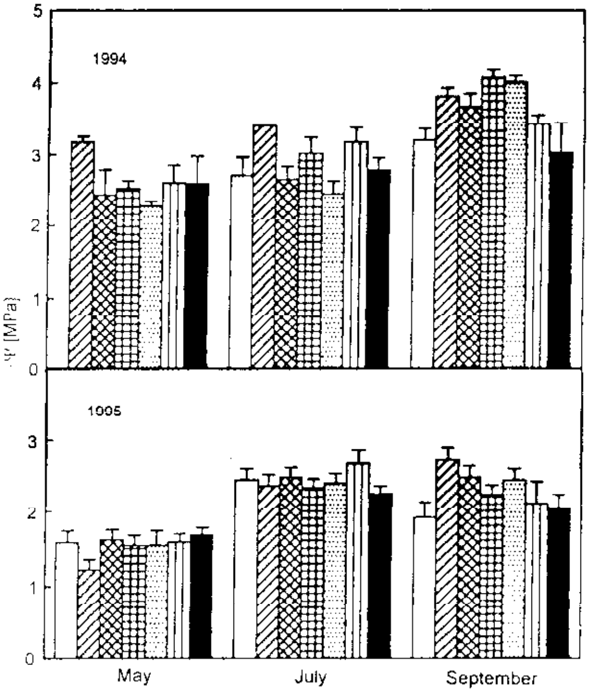

Fig. 3. Seasonal changes of mean daily leaf water potential (Ψ) of seven cultivars of almond trees on two consecutive years. Vertical bars show the standard error of the mean. Symbols as in Fig. 1.

Table 4. Main gas exchange and leaf water status characteristics of the rootstocks: net photosynthesis (P_N) [µmol m^{-2} s^{-1}], stomatal conductance (g_s) [mmol m^{-2} s^{-1}], leaf water potential (Ψ) [MPa], water use efficiency (WUE), leaf temperature (T_l) [°C], and internal CO_2 concentration (C_i) [µmol mol^{-1}], for the years 1994 and 1995. P_N: GF677>Garrigues (p=0.000); 1995>1994 (p=0.000). C_i: GF677<Garrigues (p=0.016); 1995<1994 (p=0.000); year×rootstock (p=0.036). g_s: 1995<1994 (p=0.000). WUE: 1995<1994 (p=0.000). Ψ: GF677>Garrigues (p=0.012); 1995>1994 (p=0.000); year×rootstock (p=0.003).

Rootstock	P_N		g_s		Ψ		WUE		T_l		C_i	
	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995
GF677	7.2	12.8	88.68	159.02	-2.92	-2.10	3.81	2.16	29.4	27.7	276.6	226.5
Garrigues	5.8	11.6	75.67	148.94	-3.23	-2.11	3.36	1.92	29.5	27.6	294.9	227.8

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