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Seasonal changes in photosynthesis and water relations of almond tree varieties

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SUMMARY – Daily and seasonal gas exchange of fourteen rainfed almond tree varieties grafted in GF677, six years old, was monitored in the field. Pre-dawn leaf water potential (ψ_0) changed from about -0.5 MPa in May to *ca.* -1.2 MPa in October which shows a reduction in soil water availability despite some precipitation in the first days of October. As a consequence, net photosynthesis (P_n) and stomatal conductance (G_s) decreased in the same period for most varieties, although it did not in 'José Dias' and 'Duro d'Estrada'. Decreases in P_n and G_s were observed from morning to afternoon in both periods. P_n maintained reasonably high values after harvest ($\geq$10 μmol/m^2.s) in all varieties which can be ascribed to increases or maintenance of pressure potential in some varieties. Although low, the precipitation in the first days of autumn and the increases in soluble sugars and /or proline could have contributed to maintain plant water status and photosynthetic activity. Increases of WUE_i were observed in 'Duro d' Estrada', 'Duro Italiano', 'José Dias' and 'Verdeal'. Overall, the Portuguese variety 'José Dias' showed the best photosynthetic performance.

Key words: Photosynthesis, *Prunus amygdalus*, water relations.

RESUME *– "Evolution saisonnière de la photosynthèse et des rapports hydriques chez des variétés d'amandiers". L'évolution des échanges gazeux au cours du jour et des saisons de quatorze variétés de six ans de* Prunus amygdalus *Batsch greffées sur GF677, cultivées au champ, a été suivie. Les mesures commençaient avant l'aube (ψ_0). Le potentiel hydrique foliaire (ψ_0) changeait de -0.5 MPa en mai jusqu'à* ca. *-1,2 MPa en octobre ce qui montre une réduction de la disponibilité hydrique du sol, malgré quelques précipitations au début d'octobre. En conséquence on assiste à une réduction de la photosynthèse nette (P_n) et de la conductance stomatique (G_s) pour la plupart des variétés, à l'exception de 'José Dias' et 'Duro d'Estrada'. En octobre P_n présentait des valeurs considérablement hautes compte tenu de la période d'après récolte ($\geq$10 μmol/m^2 s). Ce comportement peut être attribué au maintien ou à l'augmentation du potentiel de pression. P_n et G_s, soit en mai ou en octobre, présentaient des taux élevés le matin et une réduction l'après midi. La précipitation réduite aux premiers jours d'octobre et l'augmentation de sucres solubles et/ou de proline peuvent contribuer au maintien de l'état hydrique des amandiers et, en conséquence, des activités métaboliques. Des augmentations de WUE_i de 'Duro d'Estrada', 'Duro Italiano', 'José Dias' et 'Verdeal', ont été observées. Les résultats indiquent que la variété portugaise 'José Dias' a montré le meilleur comportement photosynthétique.*

Mots-clés : *Photosynthèse,* Prunus amygdalus*, relations hydriques.*

Introduction

In Portugal most of traditional almond orchards grow under rainfed conditions in the Northeast (Trás-os-Montes) and South (Algarve), the former constituting the main important region representing about 88% of total national production. This production is assured by local or foreign varieties differing in their productivity. Several physiological mechanisms may underlie different responses shown by plants to cope with dry and hot summers. The expression of these mechanisms result from the adaptive strategies of the plants to different environments and can be used for breeding. Although almond tree full bloom occurs early in the season, usually from the end of January until the beginning of March, the fruit filling can experience periods of water shortage from which may result decreases in productivity. One physiological mechanism utilised by plants to limit water loss is stomatal control of transpiration. The sensitivity of stomata to environmental stresses, namely soil water deficit (Davies *et al.* 1986), and water vapour deficit, and temperature (Schulze, 1986; Bradford and Hsiao, 1982) and

its relationship with leaf water potential (Turner, 1974) depend on the genotype and has been subject of many researches. Besides that, many physiological, morphological and biochemical processes in plants have been considered to be influenced by cell turgor (Turner and Jones, 1980). Assimilation and transpiration have much in common (Bradford and Hsiao, 1982) and photosynthetic process is usually correlated with stomatal conductance. Photosynthetic apparatus can be more or less damaged by environmental stresses depending on the stress intensity and duration and on the genotype. In this work our purpose was to verify if physiological and biochemical indicators can be used to predict which almond varieties best endure periods of little or no rain and still be productive. To achieve this goal diurnal measurements of net photosynthetic rate, stomatal conductance, leaf water potential and climatic factors were carried out in May and October which corresponded to periods of great activity (fruit filling) and post harvest, respectively.

Materials and methods

Plant material

Fourteen varieties of *Prunus amygdalus* Batsch were studied, from which five were Portuguese ('José Dias', JD; 'Duro d'Estrada', DE; 'Duro Italiano', DI; 'Casanova', CN; 'Verdeal', V) and the remaining were foreign ('Moncayo', Mo; 'Tuono', T; 'Guara', Gu; 'Ferraduel', Fl; 'Ferrastar', Fr; 'Ferragnès', Fs; 'Marcona', Ma; 'Nonpareil', NP; 'Garrigues', Ga). The six years old trees, grafted on GF677 (a peach-almond hybrid) rootstock, were growing in the field (Quinta do Valongo, 250 m altitude, 41° 31'N latitude and 7°12'W longitude – DRATM, Mirandela). Irrigation was applied once at the beginning of summer and plants were fertilized according to soil analysis results. Afterwards the trees were left under rainfed conditions. Measurements were carried out in May and October.

Gas exchange measurements

Diurnal courses of gas exchanges (net photosynthetic rate, P_n; stomatal conductance, G_s) were measured using a portable CO_2/H_2O gas exchange system LI-6200 (LI-COR, Lincoln, U.S.A.) and calculated according to the equations of Caemmerer and Farquhar (1981). The measurements were carried out on individual, attached adult leaves, on the outside of the middle of the canopy, in a well stirred cuvette (1000 cm^3) to minimize boundary layer resistance as referred by Matos *et al.,* (1997, 1998).

Plant water status and water relations

Daily changes in plant water status were determined by monitoring leaf water potential (ψ_w) with a pressure chamber on three detached leaves per tree, according to Scholander *et al*. (1965). Measurements took place from predawn to sunset, and were always made before the gas exchange determinations on adjacent leaves.

The osmotic potential of the cell sap (ψ_π) was determined using a dew point hygrometer (HR-33 T, Wescor Inc., USA). Samples of 3 foliar discs (0.5 cm^2 each), were homogenised in Eppendorf tubes and immediately placed in C-25 leaf chambers of the dew point hygrometer. After 20 min for sample equilibration and cooling, readings were made. The pressure potential (ψ_p) was calculated as a difference between ψ_w and ψ_π. Relative water content (RWC) was calculated according to Catsky (1960) from samples of 10 leaf discs of 0.5 cm^2, as RWC = (FW-DW/TW-DW)x100, where FW is the fresh weight, TW is the turgid weight after overnight rehydration of the discs in a humid chamber at room temperature, and DW is the dry weight after drying at 80ºC for 24 h.

Statistic analysis

Results were statistically analysed by the *Statistix* program version *7*, 1998.

Results and discussion

From data of Table 1 it can be seen that October was drier than May. The days of measurements were unclouded and the temperature rose to *ca.* 33ºC in May and 30ºC in October and with very low relative humidity (min. *ca*. 25%). The previous months (April and September) were similar in what concerns air temperature. However accumulated rainfall from January until May was 333 mm and the correspondent evaporation was 299 mm, while the rainfall and evaporation from May to October were respectively 38.9 and 847.6 mm (Table 1).

Table 1. Mean, maximal and minimum month air temperature, total precipitation, number of the days with precipitation and total evaporation in Mirandela during 1996

Mirandela	Mean air temperature (ºC)			Precipitation (mm)		Evaporation (mm)
1996	Month	Max.	Min.	Total	No. days	Total
January	9.1	13.1	5.2	231	23	52
February	7.4	12.4	2.3	20	9	67
March	10	16	4.1	38	11	80
April	14.2	20.4	8.1	44	9	100
May	14.6	20.6	8.6	75	7	112
June	22.8	31.3	14.4	0	0	213
July	24.7	33.3	16.1	0.9	2	278.6
August	22.8	30.5	15.2	0	0	214
September	18.7	25.8	11.6	38	7	142
October	15.2	21.9	8.4	51	6	83
November	10.3	15.8	4.8	41	6	64
December	8.4	12.7	4	142	17	31

From these conditions may result drought effects in the plants. Despite the previous rainfall in September, mean predawn leaf water potential (ψ_0), that expresses soil water availability, was *ca*. -1.2 MPa in October, a very low value when comparing with that of May (-0.5 $\pm$ 0.02 MPa) what means lower soil water availability. To these values corresponded changes in mean diurnal values of ψ_w from -1.54 $\pm$ 0.07 in May to –2.56 $\pm$ 0.06 MPa in October. Mean RWC values measured in the morning were higher in October (*ca.* 83.2 %) than in May (*ca.* 78.8%). This increase in RWC in Autumn can be ascribed to the rainfall that occurred in September and in the beginning of October.

Pressure potential (Fig. 1) also increased from May to October in varieties 'Duro d'Estrada', 'José Dias', 'Nonpareil' and 'Tuono' and was maintained in 'Casa Nova', 'Ferrastar', 'Ferraduel', 'Ferragnès', and 'Moncayo'. The increase or maintenance of turgor can be ascribed to the increase of RWC and also to the decrease of leaf osmotic potential probably due to the accumulation of compatible solutes for osmotic adjustment at cytoplasm level (Morgan, 1984).

An increase in soluble sugars ($P \leq 0.05$) was observed in 'Tuono', 'Duro d'Estrada', 'Ferraduel', 'Casa Nova' and 'José Dias' while proline rose only in 'Duro d'Estrada' and 'Nonpareil' (results not shown).

The role of these solutes has been ascribed to be the maintenance of pressure turgor and consequently to sustain photosynthesis. However the increase of proline as an adaptation to water stress has been contested by some authors (Larher *et al.*, 2002) which consider it as a product of disorders resulting from water stress. In October proline did not seem to have an important role for most of the studied varieties except for DE and NP.

As the measurements in October followed a period of rainfall, presumably an increase might have occurred in summer with a subsequent metabolisation after the rainfall in the first days of October. From May to October, P_n did not change significantly ($P \leq 0.05$) in 'José Dias' and 'Ferrastar' (Fig. 2)

and increased in 'Duro de Estrada'. For the remaining varieties P_n decreased in this period. A decrease from morning to afternoon was observed for P_n (Figs 3A and 3B) and G_s (data not shown) in both months, what is in agreement with results described for *Prunus armeniaca* (Schulze *et al.* 1980).

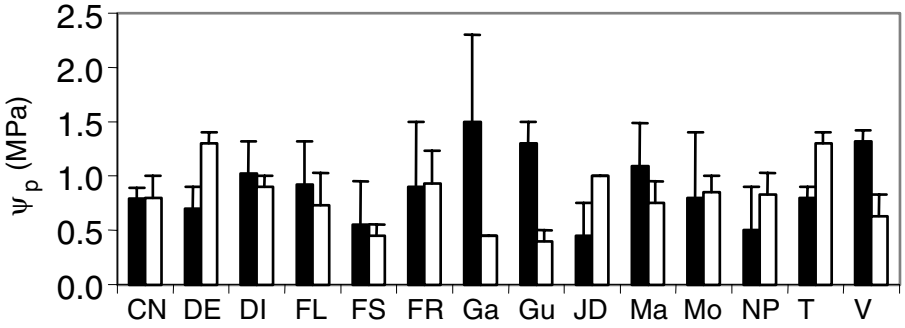

Fig. 1. Changes in pressure potential of fourteen almond tree varieties grown in field (Quinta do Valongo – DRATM, Mirandela) May ■ (fruit filling) and October □ (post harvest). Results are means of three measurements ± SE.

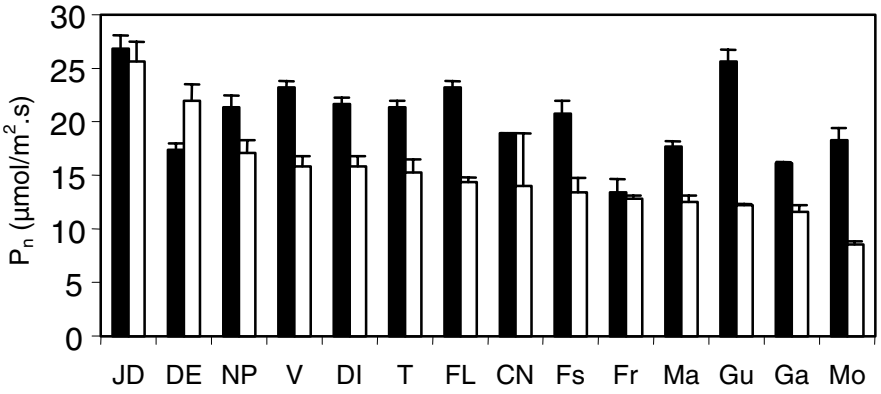

Fig. 2. Changes of net photosynthesis (P_n) of fourteen almond tree varieties grown in field under rainfed conditions (Quinta do Valongo – DRATM, Mirandela) May ■ (fruit filling) and October □ (post harvest). Results are means of three measurements ± SE.

A reduction of G_s mean values also occurred along the season in all varieties. 'José Dias' showed the lowest reduction (36.2 %), followed by 'Ferraduel', 'Tuono', 'Nonpareil' and 'Ferragnès' with reductions between 43 and 48% ($P \leq 0.05$). In the remaining varieties G_s decreasead more than 60%. In May 'José Dias', 'Duro d'Estrada' and 'Duro Italiano' showed values significantly higher than the remaining varieties, what could also be observed in October for 'José Dias' and 'Duro d'Estrada'. To higher values in G_s may not correspond higher values in P_n, since respiration and photosynthetic capacity also account for P_n. That was the case in 'Duro d'Estrada' and 'José Dias' in May. The first showed together with 'José Dias' the best G_s but while 'José Dias' also showed the best P_n, 'Duro d'Estrada' did not, although together with 'José Dias' it presented the highest values of P_n in October.

Instantaneous WUE increased from May to October for the varieties 'Duro d'Estrada', 'Duro Italiano', 'José Dias' and 'Verdeal' (Fig. 4).These increases in WUE mean that partial closure of stomata increases the resistance to water movement relatively more than the resistance to CO_2 movement and should reduce transpiration more than they reduce photosynthesis.

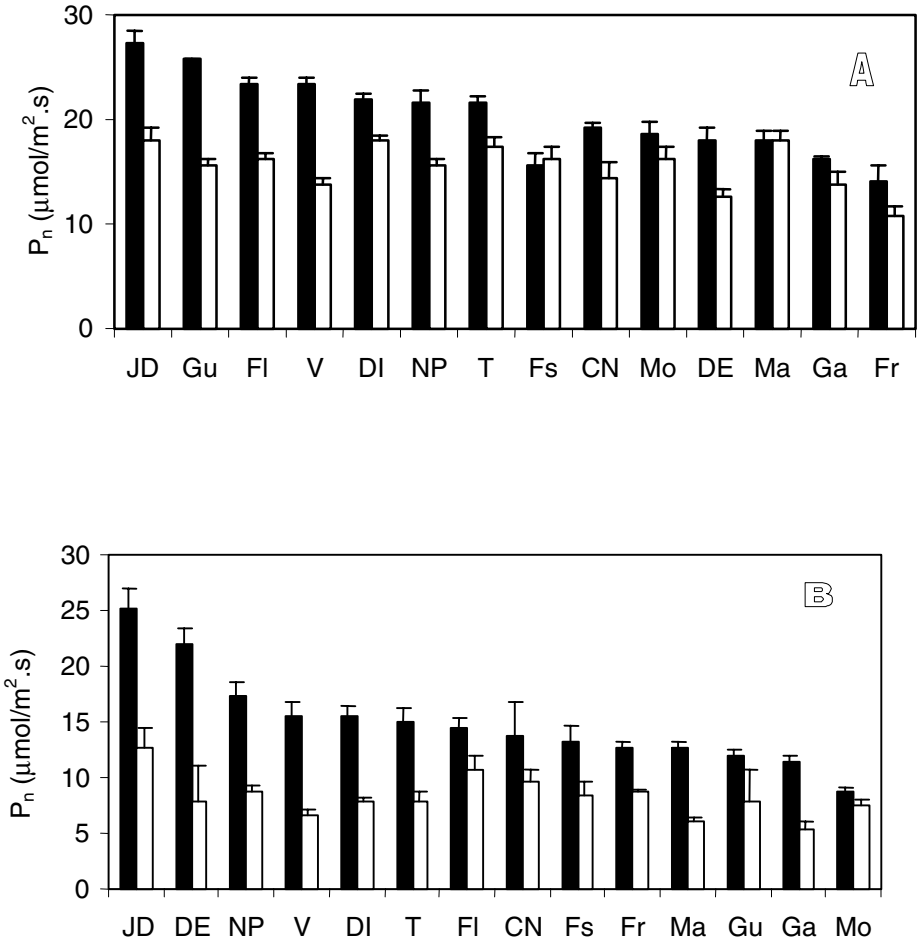

Fig. 3. Changes of net photosynthesis (P_n) from morning ■ to afternoon □, of fourteen varieties of *Prunus amygdalus* grown in field under rainfed conditions (Quinta do Valongo – DRATM, Mirandela), in May – A (fruit filling) and October – B (post harvest). Results are means of three measurements ± SE.

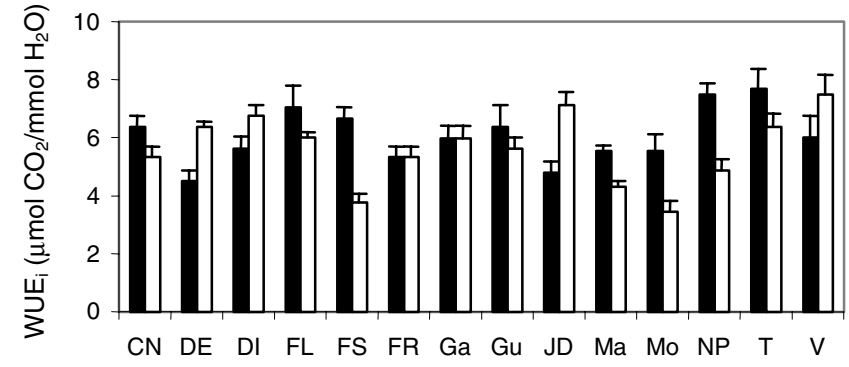

Fig. 4. Changes in instantaneous water use efficiency (WUE_i) of fourteen varieties of *Prunus amygdalus* grown in field under rainfed conditions (Quinta do Valongo – DRATM, Mirandela), in May ■ (fruit filling) and October □ (post harvest). Results are means of three measurements ± SE.

Conclusions

A seasonal decrease in P_n of all varieties was observed although it must be emphasised that relatively high photosynthetic activity could be observed in this species even after harvesting. The reduction of G_s followed the pattern of the decreases in P_n and can be responsible by them.

Decreases in leaf osmotic potential with the maintenance of RWC can be ascribed to increases in soluble sugars and/or proline, depending on the genotype and may contribute to maintain pressure potential and consequently photosynthetic activity at a reasonable level.

Considering all the studied varieties, the Portuguese 'José Dias' showed the best photosynthetic performance along the season.

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