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Diurnal changes of CO₂ net assimilation rate and related parameters in *Pistacia vera* L.

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SUMMARY - In *Pistacia vera* L., the average diurnal patterns of net CO₂ assimilation, stomatal conductance and transpiration rates were assessed at the leaf surface during a clear summer day, with reference to the diurnal fluctuations of leaf temperature and photosynthetic photon flux. The rate of leaf gas exchange was highest at 9:00. The subsequent decline in net carbon assimilation did not appear to be related to changes in stomatal conductance (g_s). The latter seemed to be primarily limited by vapour pressure deficit (VPD) of 3.8 kPa and leaf temperature (T_l) of 36°C. Further, stomatal conductance declined at 13:00, at a time when VPD slightly increased to 4.2 kPa and T_l reached 38°C. The partial g_s recovery, two hours later, did not seem to be related to changes in the ambient conditions. The midday transpiration rate did not show any significant decline, hence leaf temperature did not change markedly. The photosynthetic efficiency declined at leaf temperatures higher than 31°C.

Key words: Leaf gas exchange, leaf temperature, photosynthetic photon flux, pistachio, vapour pressure deficit.

RESUME - "Changements diurnes du taux d'assimilation nette de CO₂ et paramètres associés chez *Pistacia vera* L.". Chez *Pistacia vera* L., les tendances moyennes diurnes pour l'assimilation nette de CO₂, pour les taux de conductance stomatale et de transpiration, ont été évalués à la surface de la feuille pendant une claire journée d'été, avec référence aux fluctuations diurnes de la température de la feuille et du flux photosynthétique de photons. Le taux d'échange foliaire de gaz était le plus élevé à 9.00. La baisse subséquente d'assimilation nette du carbone ne semblait pas être liée aux changements de conductance stomatale (g_s). Cette dernière semblait être limitée premièrement par le déficit de pression de vapeur de 3,8 kPa et la température de la feuille (T_l) de 36°C. En outre, la conductance stomatale a baissé à 13.00, à un moment où le déficit de pression de vapeur augmentait légèrement jusqu'à 4,2 kPa et T_l atteignait 38°C. La récupération partielle de g_s , deux heures plus tard, ne semblait pas être liée à des changements des conditions du milieu. Le taux de transpiration vers la mi-journée ne montrait aucune diminution significative, car la température de la feuille ne changeait pas de façon notable. L'efficacité photosynthétique baissait avec une température de la feuille supérieure à 31°C.

Mots-clés : Echange foliaire de gaz, température de la feuille, flux photosynthétique de photons, pistache, déficit de pression de la vapeur.

Introduction

The net photosynthetic activity is subjected to seasonal changes and to diurnal changes which are mainly influenced by the stage of shoot development, the leaf ageing, the accumulation of hormones and of carbohydrates in the leaves, as well as the by the fluctuations of light intensity, leaf temperature, air temperature and humidity (Lakso, 1985; Downton *et al.*, 1987; Flore and Sams, 1986).

Within *Pistacia* genus, some investigations have been carried out to evaluate seasonal changes of net carbon assimilation and chlorophyll content and to assess rates of net carbon assimilation, stomatal conductance, transpiration and related parameters in *P. vera* L. (Vemmos, 1994; Novello and de Palma, 1995; de Palma and Novello, 1996); moreover, the diurnal pattern of changes in net CO₂ leaf uptake and leaf conductance have been compared among several species (Lin *et al.*, 1984). However, the diurnal pattern of photosynthetic changes related to fluctuations of vapour pressure deficit, leaf transpiration and leaf temperature have not been investigated.

The aim of the present work was to study the diurnal changes of net carbon assimilation, stomatal conductance and transpiration rates on leaves of *P. vera* in relation to leaf temperature, vapour pressure deficit and photosynthetic photon flux at leaf surface.

Materials and methods

The trial was carried out at a private orchard in the Apulia region (Bari province) on four seedlings, six year old, originated from cv. 'Bianca' open pollination. Five leaves were randomly selected on each seedling for diurnal leaf gas exchange measurements. The leaf chamber was oriented to obtain maximum light interception, to get light saturated readings.

By means of a portable infrared gas analyser (ADC, LCA-4, Analytical Development Company Ltd, Hoddesdon, UK), the following parameters were assessed per unit leaf area: net assimilation (P_n , $\mu\text{mol m}^{-2} \text{s}^{-1}$), stomatal conductance (g_s , $\text{mol m}^{-2} \text{s}^{-1}$), transpiration (E , $\text{mmol m}^{-2} \text{s}^{-1}$), photosynthetic photon flux (PPF, $\mu\text{mol m}^{-2} \text{s}^{-1}$), quantum yield (Φ , $P_n:\text{PPF}$ ratio), leaf temperature (T_l , $^{\circ}\text{C}$) and vapour pressure deficit (VPD, kPa).

Measurements were performed on one cloudless day in the last week of July 1995 and 1996: data were collected every two hours from 6:00 to 18:00 (standard time) with a final measurement taken at 19:00.

Data were analysed for the mean standard errors using SAS software (SAS Institute, Cary-NC, USA).

Results

At the leaf surface, the photosynthetic photon flux was $290 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 6:00, increased to $1,190 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 8:00 and was $1,770$ and $1,940 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 10:00 and 12:00 respectively (Fig. 1). Values of light intensity in the afternoon were found to be similar to those in the morning hours. Leaf temperature was 25°C at 6:00, then it increased to 30°C at 8:00 and 36°C at 10:00. Small leaf temperature fluctuations were observed from midday onwards, ranging between 35°C at 12:00 and 37°C at 18:00. T_l was 28°C at 19:00. The vapour pressure deficit was found to be about 2.10 kPa at 6:00 and 19:00; a maximum value of 4.2 kPa was obtained at 14:00.

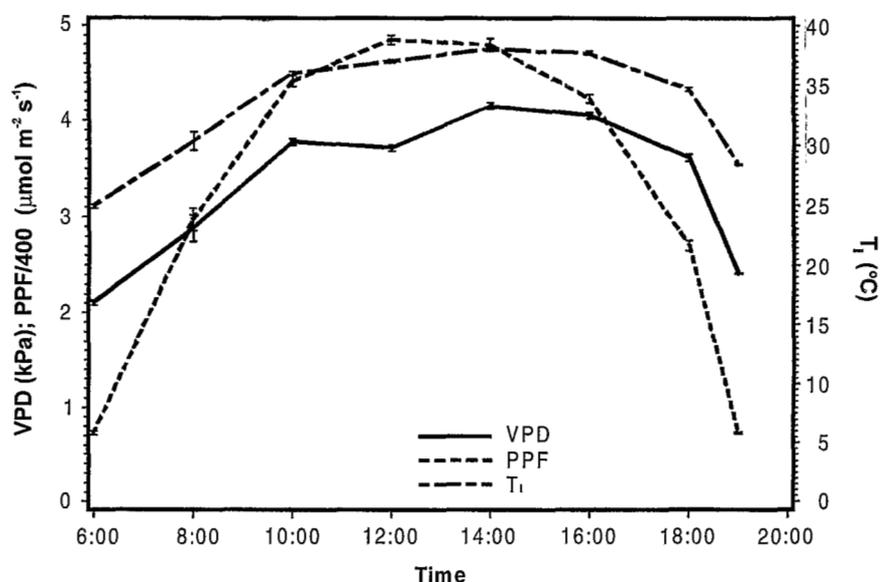


Fig. 1. Average diurnal patterns of photosynthetic photon flux at leaf surface, leaf temperature and pressure vapour deficit.

At a PPF of $290 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the leaf surface, the average leaf net CO_2 uptake was $1.07 \mu\text{mol m}^{-2} \text{s}^{-1}$ of CO_2 . The maximum net carbon uptake was $17.59 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 10:00, then it slowly decreased to $11.00 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 18:00 (Fig. 2), at a time when the PPF was still above $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$. One hour later, both PPF and P_n dropped to the same level observed at 6:00.

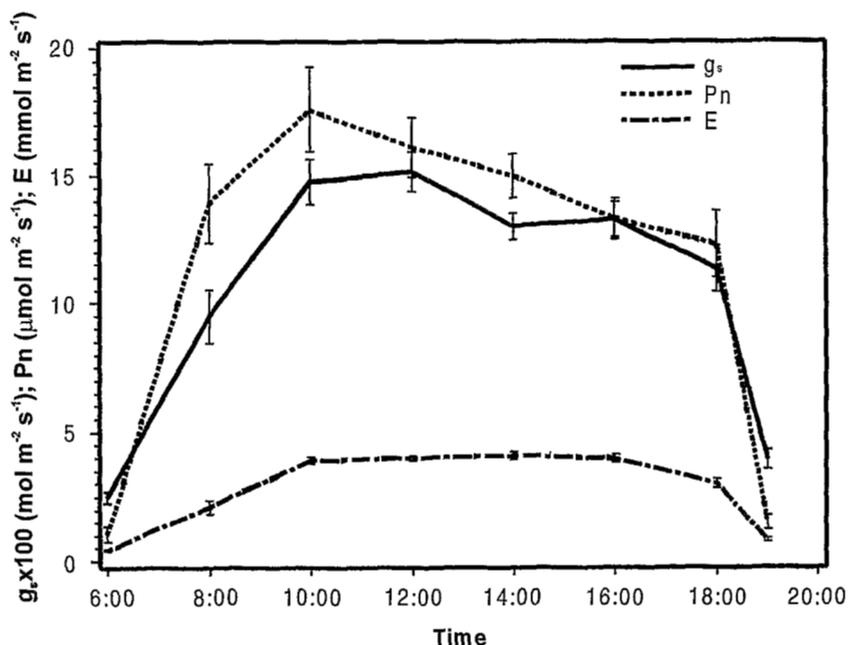


Fig. 2. Average diurnal pattern of stomatal conductance, net assimilation and transpiration rates.

The stomatal conductance was lowest at about dawn and dusk, with values of 0.025 and $0.050 \text{ mol m}^{-2} \text{ s}^{-1}$, respectively. Its maximum value was $1.150 \text{ mol m}^{-2} \text{ s}^{-1}$ at about midday. After a slight decline at 14:00, g_s recovered thereafter and had a value of $1.000 \text{ mol m}^{-2} \text{ s}^{-1}$ at 18:00. The transpiration rate was $0.25 \text{ mmol m}^{-2} \text{ s}^{-1}$ at 6:00 and 19:00; however over the central part of the day (10:00-18:00) it maintained a value of about $3.8 \text{ mmol m}^{-2} \text{ s}^{-1}$.

Quantum yield (Φ) increased with leaf temperature until 31°C and then declined. Φ gave similar values for leaf temperature at about 26 and 38°C (Fig. 3).

Discussion

The rates of leaf gas exchange showed the highest intensity at 9:00 solar time; since the subsequent decline in net carbon assimilation did not appear to be related to changes in stomatal conductance, it might have been influenced by a feedback effect of carbohydrate accumulation in the leaves rather than by a limiting effect of stomatal opening (Herold, 1980; Azcon-Bieto, 1983; Bica and Novello, 1995).

The rate of stomatal conductance seemed to be limited by the leaf exposure to high VPD and T_l for a long time: in this trial, g_s declined when VPD and T_l slightly exceeded the threshold of 3.8 kPa and 38°C , respectively. Under these ambient conditions, resulting in high evaporative demand, a partial closure of stomata may help to avoid a critical leaf water potential (Jones, 1985; Lakso, 1985). The partial g_s recovery, occurring two hours later, does not seem to be related with changes in ambient conditions thus it might be due to an increase in leaf water potential determined by osmotic adjustment (Jones, 1983; Düring, 1984; Novello *et al.*, 1990). This could explain the relatively high transpiration rate of pistachio leaves under midday conditions. Because of the isolateral structure of pistachio leaflets and their random orientation (Lin *et al.*, 1984), and because of the low density of the

tree canopy, pistachio leaves are naturally exposed to intense solar radiation, thus the maintaining of a relatively high transpiration rate might have an important role in limiting the increment of leaf temperature that could cause damages to the photosynthetic apparatus and to the leaf tissues.

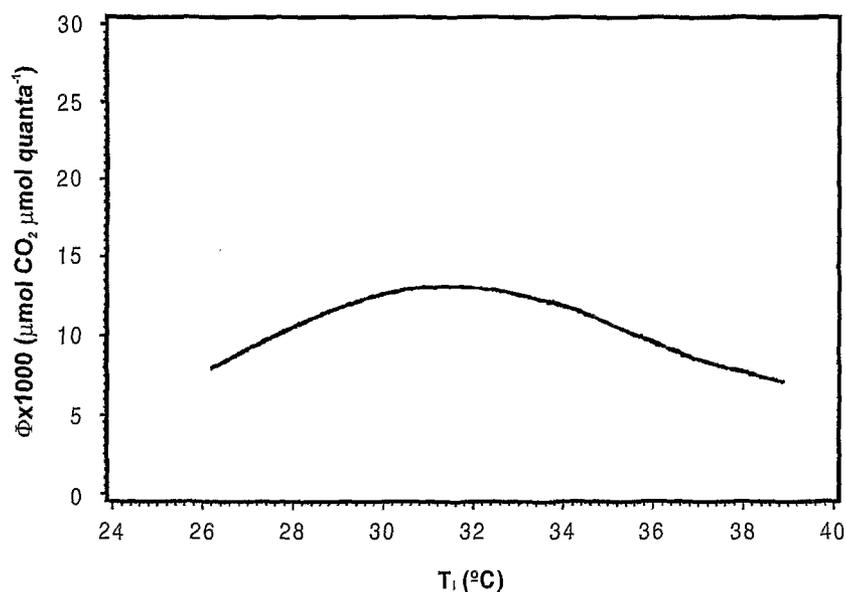


Fig. 3. Relationship between photosynthetic efficiency (Φ) and leaf temperature.

On the whole, the diurnal pattern of changes in CO₂ net assimilation and related parameters seemed to indicate that non-stomatal mechanisms of photosynthetic limitation can be relevant for *P. vera* leaves, while fluctuations of stomatal conductance could be supposed more related to changes in leaf water potential, and finally, the transpiration rate seemed to play a central role in leaf thermoregulation.

Moreover, the diurnal average leaf net CO₂ uptake pointed up a decline in quantum yield at leaf temperature higher than 31°C: in the warmest hours of the day, when either external or internal factors can limit the CO₂ uptake, a more rapid increment of the respiration than of the assimilation rate could be supposed (Jones, 1983). The influence of the leaf temperature on the photosynthetic efficiency was found higher than in a previous trial (de Palma and Novello, 1996) where leaf gas exchange was taken over summer in the central hours of the day: in that trial, the Φ vs T_l relationship was consistent with a mean seasonal response while, in the present study, the same relationship was consistent with a short term fluctuation of the quantum yield in pistachio leaves.

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