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Diurnal changes of CO$_2$ net assimilation rate and related parameters in *Pistacia vera* L.

V. Novello
Istituto di Coltivazioni Arboree, University of Bari, Via Amendola 165/a, I70126 Bari, Italy

**SUMMARY** - In *Pistacia vera* L., the average diurnal patterns of net CO$_2$ 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 ($T_\text{L}$) of 36°C. Further, stomatal conductance declined at 13:00, at a time when VPD slightly increased to 4.2 kPa and $T_\text{L}$ 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 CO$_2$ et paramètres associés chez *Pistacia vera* L.". Chez *Pistacia vera* L., les tendances moyennes diurnes pour l'assimilation nette de CO$_2$, pour les taux de conductance stomatiale 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 stomatiale ($g_s$). Cette dernière semblait être limitée premièrement par le déficit de pression de vapeur de 3,8 kPa et la température de la feuille ($T_\text{L}$) de 36°C. En outre, la conductance stomatiale a baissé à 13.00, à un moment où le déficit de pression de vapeur augmentait légèrement jusqu'à 4,2 kPa et $T_\text{L}$ 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 CO$_2$ 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 (Pn, μmol m⁻² s⁻¹), stomatal conductance (gs, mol m⁻² s⁻¹), transpiration (E, mmol m⁻² s⁻¹), photosynthetic photon flux (PPF, μmol m⁻² s⁻¹), quantum yield (Φ, Pn:PPF ratio), leaf temperature (Tl, °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 μmol m⁻² s⁻¹ at 6:00, increased to 1,190 μmol m⁻² s⁻¹ at 8:00 and was 1,770 and 1,940 μmol m⁻² 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. Tl 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.](image-url)
At a PPF of 290 μmol m\(^{-2}\) s\(^{-1}\) at the leaf surface, the average leaf net CO\(_2\) uptake was 1.07 μmol m\(^{-2}\) s\(^{-1}\) of CO\(_2\). The maximum net carbon uptake was 17.59 μmol m\(^{-2}\) s\(^{-1}\) at 10:00, then it slowly decreased to 11.00 μmol m\(^{-2}\) s\(^{-1}\) at 18:00 (Fig. 2), at a time when the PPF was still above 1,000 μmol m\(^{-2}\) s\(^{-1}\). One hour later, both PPF and Pn 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 mol m\(^{-2}\) s\(^{-1}\), respectively. Its maximum value was 1.150 mol m\(^{-2}\) s\(^{-1}\) at about midday. After a slight decline at 14:00, g\(_s\) recovered thereafter and had a value of 1.000 mol m\(^{-2}\) s\(^{-1}\) at 18:00. The transpiration rate was 0.25 mmol m\(^{-2}\) 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 mmol m\(^{-2}\) 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\(_i\) for a long time: in this trial, g\(_s\) declined when VPD and T\(_i\) 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.

![Graph showing the relationship between photosynthetic efficiency (Φ) and leaf temperature.](image)

**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 Tl 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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**References**


