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Original article

Growth, gas exchange and carbon isotope discrimination in young *Prunus avium* trees growing with or without individual lateral shelters

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Summary — One-yr-old wild cherry (*Prunus avium* L) plants were grown as follows: 1) in small cylindrical shelters (diameter 50 cm, treatment S); 2) in large shelters (diameter 100 cm, treatment L); or 3) without shelter (control, treatment C) during 1 growing season. Treatment C was characterized by higher values of photosynthetic photon flux density (I_p) and of leaf-to-air water vapour pressure difference (ΔW) than treatments L and S. The plants were taller in treatments L and S than in treatment C but biomass production was higher in the latter treatment. The plants of treatment C were also characterized by higher values of CO_2 assimilation rate (A) and of leaf mass per unit area (*LMA*, ratio of leaf mass to leaf area). Relative carbon isotope composition (δ_p) of the leaves was higher in treatment C than in treatments L and S, which expresses higher time-integrated values of plant intrinsic water-use efficiency (*A/g* ratio) in the former treatment. There was a positive correlation between δ_p and *LMA*. Thus, *LMA*, a readily measurable parameter, is a relevant parameter for understanding and modelling water-use efficiency of canopies.

lateral shelter / microclimate / growth / leaf gas exchange / carbon isotope discrimination / water-use efficiency / leaf mass per unit area

Résumé — Croissance, échanges gazeux et discrimination isotopique du carbone de jeunes merisiers (*Prunus avium* L) placés ou non dans des abris latéraux individuels. *Des plants de merisier (*Prunus avium *L) âgés de 1 an ont été installés durant une saison de végétation dans 1) des petits abris cylindriques (diamètre 50 cm, traitement S); 2) des grands abris cylindriques (diamètre 100 cm, traitement L); ou 3) sans abri en plein découvert (traitement C) (fig 1). Le traitement C était caractérisé par des valeurs plus élevées de rayonnement photosynthétiquement actif (Ip) ainsi que de différence de pression partielle de vapeur d'eau entre feuille et atmosphère* (ΔW) *(fig 3). La croissance en hauteur était plus élevée pour les plants du traitement C que pour ceux des traitements L et S, alors que la production de biomasse était la plus élevée dans le traitement C* *(tableau I). Les plants du traitement C étaient également caractérisés par des valeurs plus élevées de taux d'assimilation de CO_2 (A) (fig 5) ainsi que de masse foliaire spécifique (LMA, rapport de la masse sur la surface foliaire) (fig 8). La composition isotopique relative en carbone (δ_p) des feuilles était plus élevée dans le traitement C que dans les traitements L et S (fig 8). Cela traduit des valeurs intégrées dans le temps d'efficience intrinsèque d'utilisation de l'eau (rapport A/g) plus élevées pour le traitement C (tableau I). On a noté une corrélation positive entre δ_p et LMA (fig 8). Ainsi, LMA, qui est une grandeur facilement mesurable, constitue un paramètre pertinent pour la compréhension et la modélisation de l'efficience d'utilisation de l'eau des couverts végétaux.*

abri latéral / microclimat / croissance / échanges gazeux foliaires / discrimination isotopique du carbone / efficience d'utilisation de l'eau / masse foliaire spécifique

INTRODUCTION

The neighbourhood relationships between young trees and the surrounding vegetation are the result of various below-ground (competition for water and nutrients, allelopathy) and above-ground (competition for light, modification of temperature, air humidity and windspeed) interactions (Gjerstad *et al,* 1984 ; Radosevich and Osteryoung, 1987). When neighbourhood relationships are dominated by competition processes, their global effect will be to reduce survival and growth of the young trees. However, in situations of high potential evapotranspiration, the presence of accompanying vegetation may be beneficial for the trees due to lowered evaporative demand at the tree level.

To analyze the neighbourhood relationships it is necessary to disentangle the effects of aerial and soil factors (Nambiar, 1990). The use of artificial lateral shelters built around growing young trees may be a relevant way of studying the effects of aerial microclimate modifications on the growth and function of plants (Collet and Frochot, 1992). The general effect of lateral shading will be to reduce photosynthetic CO_2 assimilation due to lowered leaf incident photosynthetic photon flux density. However, this reduction may be accompanied by a decrease in stomatal conductance and in transpirational water losses which can be beneficial for the plant water status and water-use efficiency (Aussenac and Ducrey, 1978).

This study examines the effects of artificial lateral shelters simulating the aerial effects of an accompanying vegetation – without any below-ground relationship – on young *Prunus avium* trees. Measurements of: 1) microclimatic parameters ; 2) growth ; 3) leaf gas exchange ; and 4) leaf carbon isotope composition which can lead to time-integrated plant water-use efficiency were made.

MATERIAL AND METHODS

Experimental design

Wild cherry (*Prunus avium* L) seedlings (Côte d'Or provenance, Eastern France) were grown in an experimental nursery near Limoges (Massif Central, France) from spring 1989. On February 15 1990, 48 plants (average height 30 cm) were taken from the nursery beds. In order to minimize transplanting stress, the plants were immediately placed in containers filled with organic soil and transferred to the experimental plot near Nancy (northeastern France) where they were planted. The trees were randomly distributed into 3 treatments comprised of 16 trees each:

Treatment S (small shelters). These plants were surrounded by individual cylindrical shelters with a diameter of 50 cm.

Treatment L (large shelters). These plants were surrounded by cylindrical shelters with a diameter of 100 cm.

Treatment C. Controls without shelters.

The shelters were constituted of a wire netting supporting a green plastic net with a porosity of 50% (fig 1). Initially, the shelters were 60 cm high. As the seedlings grew, the height of all the shelters was increased so that no plant was greater than its shelter. Four successive height increases were made simultaneously for all shelters (fig 2). At the end of the growing season the shelters were 2.5 m high. Bare soil conditions were maintained throughout the experiment by chemical weeding around the shelters and manual weeding within the shelters. Rainfall during the experimental period (April–September) amounted to 262 mm and no additional water was supplied to the trees.

In order to assess the microclimatic conditions inside the 2 types of shelters, photosynthetic photon flux density (I_p) was measured at 12.00 (solar time) on a sunny day with a quantum sensor (Li-Cor, Lincoln, NE, USA) at different heights above ground. These measurements were made when the shelters were 1.5 m high. At the top of the shelter Ip was similar to that outside the shelters (100%). Below 115 cm (S shelters) and 75 cm (L shelters), I_p was abruptly reduced to 30% of the ouside I_p in both types of shelters. Thus, the upper parts (≈ 30 cm for the S shelters and 40 cm for the L shelters) of the elongating stems were exposed to full sunlight around midday while the lower parts were shaded all day long.

Fig 1. Picture of the experimental plot showing the shelters (1 m high).

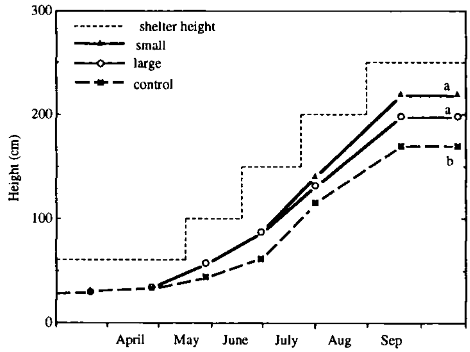

Fig 2. Growth in height in the 3 treatments and height of the shelters. For the last measurement date, data points with different letters are significantly different (Student's *t*-test, $P \leq 0.05$).

Water status and gas exchange measurements

Water status and gas exchange measurements were made periodically between July 11 and August 16. These measurements were carried out on the 6 tallest plants in each treatment in order to avoid experimental interference due to transplanting stress. Predawn leaf water potential of the seedlings was measured with a Scholander pressure chamber and was between –0.1 MPa (July 11) and –0.45 MPa (August 16), thus indicating an absence of severe drought constraints.

Carbon dioxide assimilation rate (*A*, µmol m^{-2} s^{-1}), transpiration rate (*E*, mmol m^{-2} s^{-1}) and leaf conductance for water vapor (*g*, mmol m^{-2} s^{-1}) were measured using a LI-6200 portable photosynthesis system (Li-Cor Inc, Lincoln, Nebraska, USA) fitted with a 4-l assimilation chamber. Leaf temperature (T_l) was monitored by means of a thermocouple in contact with the lower leaf surface. The leaf-to-air difference in water vapour partial pressure (ΔW) was calculated from T_l and air water vapour pressure. Simultaneously to the gas exchange measurements, I_p was measured with a quantum sensor (Li-Cor, Lincoln, NE, USA). Preliminary measurements were carried out in order to assess the effects of leaf ageing on gas exchange parameters. *A* and *g* were highest for leaf order between 4 and 7. All gas exchange data reported hereafter correspond to measurements made within that zone of the trees which, in the shelters, was generally at the transition between the shaded and the full sunlight exposed regions. Gas exchange measurements were performed between 11.30 and 13.30 (UT) on 2 leaves per tree. Gas exchange parameters were calculated on a leaf area basis. Leaf area was determined *in situ* just prior to the gas exchange measurements by means of a portable area meter (Licor 3000, Li-Cor, Lincoln, NE, USA).

Carbon isotopic composition

Carbon isotopic composition was determined on leaf material. Three leaves from each of the 6 trees in the different treatments were harvested on October 12. These leaves included those in which gas exchange had been measured on August 8. After determination of leaf area, the samples were oven-dried at 70°C for 48 h, weighed and finely ground. Fifteen mg of sample material was then weighed out and combusted in special quartz vessels under a pure O_2 atmosphere. The carbon was thus quantitatively converted to CO_2. Relative abundances of ^{13}C and ^{12}C were determined using a mass spectrometer (Finigan Mat). The results are expressed in terms of the conventional δ ‰ notation, according to the relation (Farquhar *et al*, 1989) :

$$\delta = R_s / R_b - 1 \qquad [1]$$

where R_s and R_b refer to $^{13}C/^{12}C$ ratio in the sample and in the Pee Dee Belemnite standard (PDB), respectively.

RESULTS

Microclimate, growth and gas exchange

Gas exchange measurements were made on 5 sunny days from July 11 to August 8 with a photosynthetic photon flux density (Ip) of ≈ 1 400 μmol m^{-2} s^{-1} in treatment C (full sunlight) (fig 3). Air temperature (control treatment) increased progressively from 22.0°C on July 11 to 34°C on August 1 and then decreased to 27°C on August 8. Leaf-to-air water vapour concentration *(ΔW)* presented similar time changes with extreme values of ≈ 14 Pa KPa^{-1} and 34 Pa KPa^{-1}. In both L and S treatments I_p was approximately half that in C, except on August 8 when I_p was identical in all treatments. The frequency distribution of I_p in the different treatments is given in figure 4.

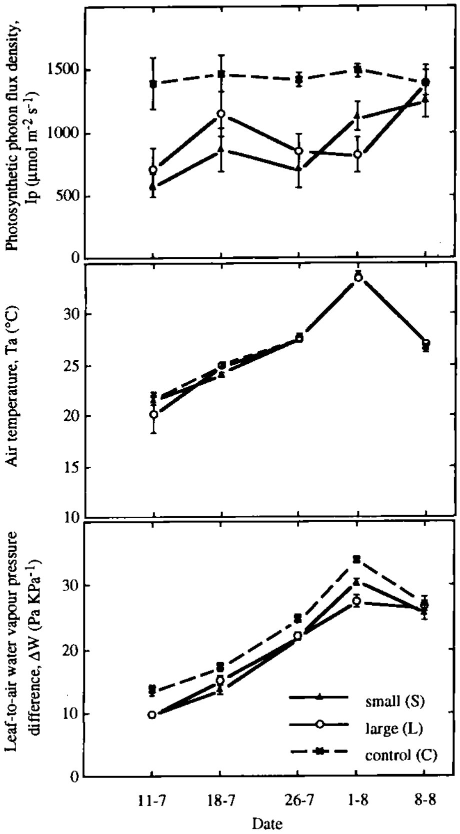

Fig 3. Photosynthetic photon flux density (I_p), leaf-to-air water vapour concentration difference (ΔW) and air temperature (T_a) in the 3 treatments at the different dates of gas exchange measurements. Measurements were made from 11:30 am to 1:30 pm. Mean values ± 1 SEM, n = 12.

For treatment C a monomodal distribution was observed with a modal interval 1 500–1 700 µmol m^{-2} s^{-1}. For the L and S treatments bimodale distribution were observed, modal intervals being 250–500 and 1 250–1 500 µmol m^{-2} s^{-1}. No significant differences were noticed between treatments for T_a, whereas ΔW was ≈ 3–4 Pa KPa^{-1} lower in the sheltered treatments as compared with treatment C. These between-treatment differences were associated with differences in leaf temperature (T_1), whereas water vapour concentration in the air was identical in all treatments (data not shown).

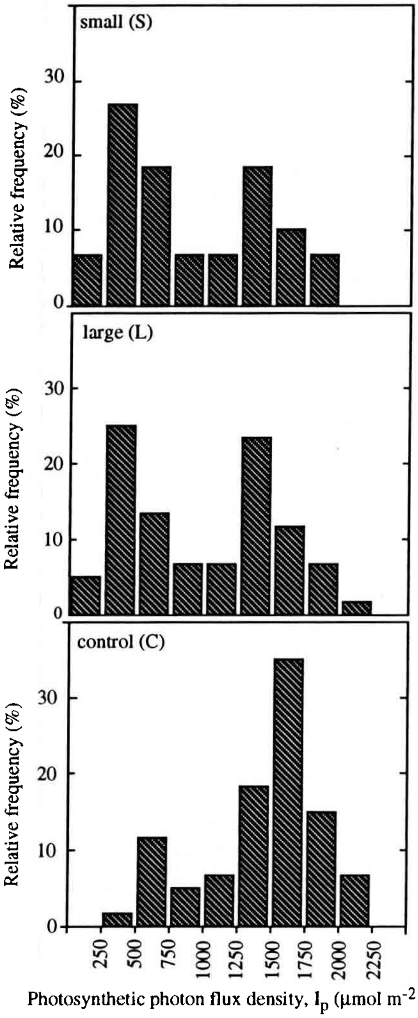

Fig 4. Frequency distribution of photosynthetic photon flux density (I_p) in the 3 treatments. Measurements were made from 11:30 am to 1:30 pm.

At the end of the growing season (beginning of October) trees of treatments L and S were taller than those of treatments C (table I), but root collar diameter and production of biomass were higher in the latter treatment. There was no significant treatment effect on root/shoot biomass ratio.

Carbon dioxide assimilation rate *(A)* in the C treatment showed a slight decrease from 18 to 13 µmol m^{-2} s^{-1} over the measurement period (fig 5). Except on August 8, *A* was ≈ 5 µmol m^{-2} s^{-1} lower in treatments L and S than in C. This difference was not only attributable to higher I_p values in treatment C, but was also linked to a higher assimilation capacity in this treatment since in saturating light conditions ($I_p > 1\,000$ µmol m^{-2} s^{-1}) *A* was ≈ 4.2 µmol m^{-2} s^{-1} higher in treatment C than in the other treatments (fig 6). Leaf conductance for water vapour diffusion *(g)* decreased progressively during the measurement period in all treatments (fig 5). With the exception of July 11, the *g* values were identical in the C and L treatments, while *g* was ≈ 80 mmol m^{-2} s^{-1} lower in S than in the former treatments. Leaf transpiration rates *(E)* were highest in all treatments on August 1 (fig 5). Between-treatment differences, similar to those for *g*, arose for *E*. Intrinsic instantaneous water-use efficiency (*A/g* ratio) increased in the 3 treatments during the measurement period (fig 7). This parameter was highest in C, lowest in L and intermediate values were noticed in S. Instantaneous water-use efficiency (*A/E* ratio) was markedly lower in L than in the 2 other treatments.

Table I. Height, root collar diameter, biomass and root/shoot biomass ratio of the trees at the end of the growing season.

Variables	*Control (C)*	*Large (L)*	*Small (S)*
Height (cm)	170 ± 7.2 ^{b}	198 ± 10.4 ^{a}	219 ± 4.8 ^{a}
Root collar diameter (mm)	18.5 ± 1.6 ^{a}	15.4 ± 0.79 ^{b}	14.9 ± 0.47 ^{b}
Total biomass (g)	182 ± 24 ^{a}	121 ± 13 ^{b}	135 ± 7 ^{b}
Toot/shoot ratio (g g^{-1})	1.01 ± 0.13 ^{a}	1.10 ± 0.10 ^{a}	1.14 ± 0.05 ^{a}

Mean values followed by different letters are significantly different (Student's *t*-test, $P \leq 0.05$).

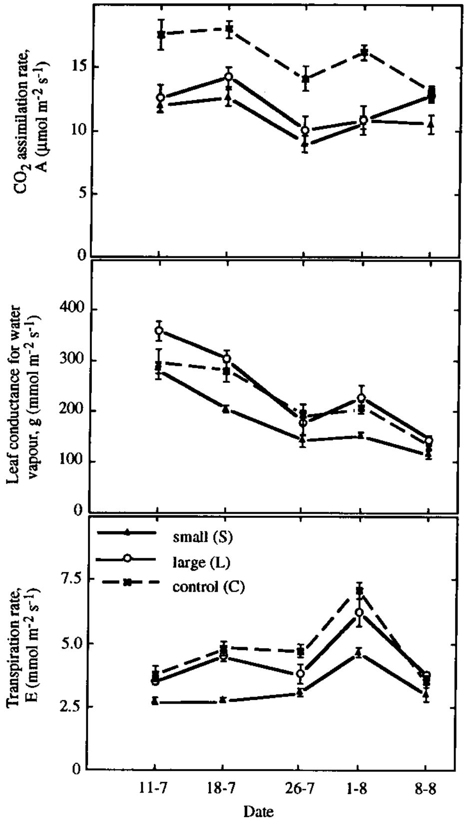

Fig 5. Carbon dioxide assimilation rate *(A)*, leaf conductance for water vapour diffusion *(g)* and transpiration rate *(E)* in the 3 treatments at the different dates of gas exchange measurements. Measurements were made from 11:30 am to 1:30 pm. Mean values ± 1 SEM. In each treatment, measurements were made on 2 leaves of 6 different trees.

Carbon isotopic composition and leaf mass per unit area

No significant difference in relative isotopic composition (δ_p) arose between treatments L and S (fig 8). Carbon isotope composition was significantly higher in the control (–26.83‰) than in treatments S (–27.75‰) and L (–27.49‰) (table II). Leaf mass per unit area *(LMA)* differed significantly between the 3 treatments with 67.89, 72.95 and 101.79 g m^{-1} in S, L and C, respec-

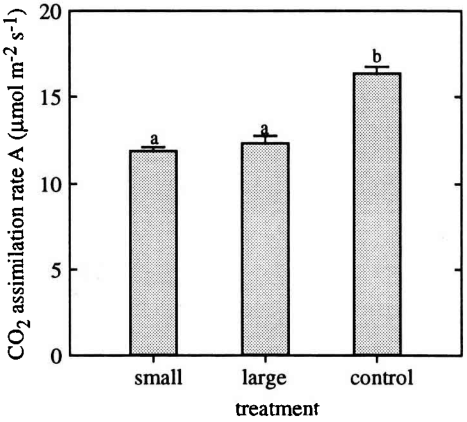

Fig 6. Light-saturated (I_p > 1 000 µmol m^{-2} s^{-1}) carbon dioxide assimilation rate *(A)* in the different treatments. Data of the different dates were pooled. Mean values ± 1 SEM.

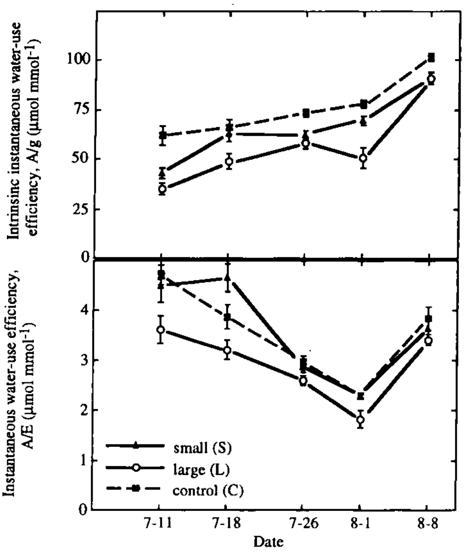

Fig 7. Intrinsic instantaneous water-use efficiency (*A/g* ratio) and instantaneous water-use efficiency (*A/E* ratio) in the 3 treatments at the different dates of gas exchange measurements. Measurements were made from 11:30 am to 1:30 pm. Mean values ± 1 SEM. In each treatment, measurements were made on 2 leaves of 6 different trees.

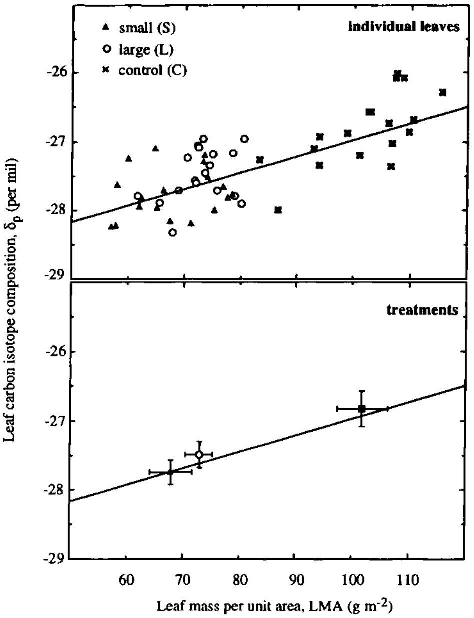

Fig 8. Leaf carbon isotopic composition ($\delta^{13}C$) in relationship with leaf mass per unit area. Data points are individual leaf values (lower part) and mean values per treatment ± 1 SEM (upper part). Regression lines are for individual leaves in both pictures; $Y = 2.612\ 10{-}2\ X - 29.47$, $r = 0.76$, $n = 54$.

Table II. Relative isotope composition (δ_p), and *A/g* ratio calculated from equation [5].

Variables	*Control (C)*	*Large (L)*	*Small (S)*
δ_p (per mil)	–26.83 ^{a}	–27.49 ^{b}	–27.75 ^{b}
Calculated *A/g* (µmol mmol^{-1})	64.3	57.6	54.9

Mean value of δ_p followed by different letters are significantly different (Student's *t*-test, $P \leq 0.05$).

tively. There was a significant positive correlation between δ_p and *LMA* both at the treatment and individual plant level (fig 8).

DISCUSSION

Climatic parameters (mainly I_p and ΔW) differed between the control treatment and the 2 shelter treatments, but no significant difference arose between the 2 latter treatments (figs 3, 4). For the leaves situated in the shaded part of the 2 types of shelters incident I_p was ≈ 30% of outside I_p. Upper leaves of the sheltered plants could be exposed to full sunlight in the middle of the day. The proportion of these leaves and the duration of full sunlight exposition depended on the ratio (tree height/shelter height) and on the diameter of the shelter. Thus, in treatments S and L, I_p presented a bimodal distribution in the first mode (shaded region of the shelters) being ≈ 30% of the second (sunlit region of the shelters) (fig 4).

The ratio of CO_2 assimilation rate *(A)* in treatments S and L to that in treatment C was ≈ 0.70, which is identical to the ratio of total plant biomass at the end of the growing season (table I). Carbon dioxide assimilation rate was higher in the control treatment, not only because of elevated I_p (figs 3, 4) but also because of higher values of light saturated assimilation capacity (fig 6). Within mature *Fagus silvatica* and *Quercus petraea* canopies, Ducrey (1981) also reported a positive relationship between light-saturated CO_2 assimilation rate and the proportion of solar radiation reaching the leaves during their ontogeny.

Leaf conductance values were lower in treatment S than in treatments L and C (fig 5) ; however, this difference cannot be clearly ascribed to differences in microclimate parameters, for example I_p and ΔW (figs 3, 4). This discrepancy between gas exchange and microclimatic variables could be linked to the fact that no time-integrated values of these 2 types of variables were assessed in this study.

Carbon isotope composition measurements of plant material can give access to time-integrated (lifetime of the measured organ) values of plant intrinsinc water-use efficiency (ratio *A/g*).

The apparent enrichment factor related to the isotopic fractionation by the photosynthesis processes may be expressed by an isotopic discrimination defined as (Farquhar *et al*, 1989):

$$\Delta = \frac{\delta_a - \delta_p}{1 + \delta_p} \qquad [2]$$

where δ_a and δ_p refer to the isotopic compositions of air CO_2 and of the photosynthetic products (*ie* the leaf material here), respectively. A typical value of δ_a is currently −0.008 (Friedli *et al*, 1986).

According to Farquhar *et al* (1989), isotopic discrimination is given by:

$$\Delta = a + (b - a)\, C_i/C_a \qquad [3]$$

where *a*, the discrimination against $^{13}CO_2$ during diffusion into the leaf, is 0.0044 ; b, the discrimination during carboxylation, is 0.027 ; C_i and C_a (mmol mol^{-1}) are intercellular and ambient CO_2 concentrations, respectively.

The diffusion of CO_2 through the stomatal pores is described by:

$$A = 1.6\, g\, (C_a - C_i) \qquad [4]$$

Combining equations [2], [3] and [4] and substituting the different coefficients by their numerical values yields:

$$A/g \quad \frac{(329 + 9931.2\, \delta_p)}{(1 + \delta_p)} \qquad [5]$$

Relative carbon isotopic composition (δ_p) was less negative (−26.83‰) in the control plants than in the plants of treatments L (−27.49‰) and S (−27.75‰) which corresponds to higher time-integrated values of *A/g* in the former treatment (table II). Lower δ_p values found in lower forest canopy leaves in comparison with upper leaves have been attributed to low relative carbon isotope composition of source CO_2 in the air (δ_a) linked to the recycling of CO_2 (depleted in ^{13}C relative to atmospheric CO_2 above the canopy) originating from soil respiration (Vogel, 1978 ; Medina and Minchin, 1980 ; Francey and Farquhar, 1982 ; Medina *et al*, 1986 ; Gebauer and Schulze, 1991). In the present study, different light regimes and associated small differences in T_1 and ΔW (fig 3) were not accompanied by differing δ_a values (constant soil respiration conditions and constant height above ground) or by changes in other microclimatic factors such as air temperature or air humidity. The difference in δ_p found between treatment C and treatments L and S can therefore be entirely ascribed to differences in isotopic discrimination by the leaves (Δ, eq [3]) which are mainly determined by the light regime. Zimmermann and Ehleringer (1990) also found a negative correlation between leaf Δ and the daily integrated values of leaf incident I_p in a Panamanian C_3 epiphytic orchid, *Casatetum viridiflavum,* growing on trees of a forest canopy.

The high δ_p (and thus low Δ) values found here in treatment C could be associated with high *A* values (figs 5, 6) and with high *LMA* values (fig 8) which probably reflect high nitrogen contents per unit leaf area (no measurements of this parameter were made in this study).

The between-treatment differences in the *A/g* ratio found here on a gas exchange basis (fig 7) were not totally consistent with the data obtained with the isotopic approach (table II). In particular, gas exchange data provided higher *A/g* values (fig 7) – linked to lower *g* values (fig 5) – in treatment S than in treatment L, whereas isotopic data also provide higher *A/g* values in treatment S than in treatment L, whereas isotopic data also provide higher *A/g* values in treatment C but identical Alg values in treatments L and S (table II). This discrepancy might be attributed to the difference in time integration scale between the 2 approaches (*ie* a better integrative value of the isotopic approach).

The close positive correlation found between δ_p and *LMA* (fig 8) at the individual leaf level shows that *LMA*, a readily measurable parameter, is not only a relevant parameter for understanding and modelling the spatial structure of CO_2 assimilation in plant canopies (Aussenac and Ducrey, 1977 ; Ducrey, 1981 ; Oren *et al*, 1986) but can also be used for understanding and modelling water-use efficiency of canopies.

In conclusion, in this study we have simulated aerial neighbourhood relationships between young *Prunus avium* trees and an accompanying vegetation in the absence of water vapour source constituted by the transpiration of the accompanying vegetation. Under these conditions the height growth of young trees was improved which may be of interest from a practical point of view. However, the trees grown without shelters were characterized by a higher biomass production, which was associated with higher A values than in the trees grown with shelters. Thus there was no positive effect of lateral shading on biomass growth. The control trees were also characterized by higher water-use efficiency than the sheltered trees.

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