Effect of ventilation on growth of *Prunus avium* seedlings grown in treeshelters

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Abstract

Treeshelters are widely used to protect tree seedlings against animal browsing or rubbing. They reduce the tree transpiration as a result of the low ventilation rate of the shelter. Photosynthesis is impeded by low levels of available CO₂ due to poor gas exchange with the outside. We assess the impact of ventilating a treeshelter on the microclimate, on the transpiration and on the photosynthesis of protected *Prunus avium* seedlings grown either in containers with different water regimes or in the field. Ventilation was achieved either by numerous holes scattered along the shelter, or by a unique inlet of air at the bottom of the shelter, inducing a draught effect. Ventilation significantly reduced air temperature and increased CO₂ availability. After one growing season, an increase in tree biomass resulted from the ventilation, ranging from +50% (container-grown trees without irrigation) to +55% (field-grown trees) and +85% (container-grown irrigated trees). These results confirm that most of the previous studies on treeshelters erroneously interpreted high CO₂ concentrations in treeshelters. The draught effect with a single air inlet at the bottom of the shelter was as effective as numerous holes. Both tree transpiration and photosynthesis were stimulated by the ventilation. Irrigated trees took more advantage of the ventilation than non-irrigated trees. All treeshelters favoured above-ground biomass irrespective of ventilation. The size of the air inlet inducing an effective draught effect is discussed. Practical recommendations regarding the design and use of improved treeshelters are finally examined. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: *Prunus avium*; Treeshelter; Greenhouse climate; Transpiration rate; Assimilation rate; Ventilation

1. Introduction

Treeshelters have been used intensively for more than one decade in Europe to protect broad-leaved tree seedlings from foliage browsing and stem rubbing by wild or domestic animals (Evans and Potter, 1985). In the early 1980s, it was reported that treeshelters enhanced both height and stem diameter growth of sheltered trees (Tuley, 1983). However, more recent and detailed observations indicated that the stem diameter growth was often reduced in treeshelters (Rendle, 1988; Dupraz et al., 1989; Dupraz and Cavet, 1991; Bergez, 1993; Burger et al., 1996; Kjelgren and Rupp, 1997; Mayhead and Boothman, 1997). Furthermore, in the only longstanding trial ever published (Dupraz, 1997), it was shown that albeit *Juglans* trees emerged from the top of the shelter during the first growing season, the negative impact of treeshelters on tree diameter growth was still significant 10 years after plantation, while the height advantage had vanished.
The microclimate surrounding the tree within a treeshelter is strongly modified (Rendle, 1985; Bergez, 1993; Kjelgren, 1994). Photosynthetically active radiation is reduced by almost 60%, daytime temperature may exceed ambient temperature by up to 10°C and the air is often saturated with water vapour. CO₂ concentration patterns are also considerably modified in the treeshelter (Dupraz and Bergez, 1999). As a result of this microclimate, the energy budget of sheltered leaves is altered. Impacts on the transpiration (Bergez and Dupraz, 1997) and on the assimilation (Dupraz and Bergez, 1999) processes of sheltered trees have been described for standard unventilated treeshelters. Assimilation rate of sheltered trees was impeded due to inadequate ventilation rate and too high temperatures (Dupraz and Bergez, 1999). Much higher ventilation rates were needed in order to fulfil CO₂ requirement for assimilation. Different possibilities may be tested to increase the CO₂ level within the treeshelter, including adding some carbonic fertiliser in the air as it is commonly done in horticultural greenhouses or using a CO₂ permeable material to construct the wall of the shelter. A simpler possibility is to take advantage of the atmospheric CO₂ by making openings in the shelter wall to enhance air movements. This may be achieved by a number of holes scattered along the shelter or by a single inlet at the bottom of the shelter. In this case, the buoyancy forces resulting from the temperature difference between the inside and the outside of the shelter will create a draught effect, the outside air being sucked through the bottom inlet and evacuated through the top opening of the shelter.

Higher ventilation rates will probably decrease air temperature as both sensible and latent heat fluxes will be enhanced. This higher transpiration rate may force the seedling to cope with some water deficit. Therefore, the effectiveness of a ventilated treeshelter should be assessed for trees with different soil water availability regimes. It was shown that stomatal conductance in standard unventilated treeshelters is very high, day and night (Dupraz et al., 1993; Kjelgren, 1994; Bergez and Dupraz, 1997). Stomatal conductance patterns inside ventilated treeshelters have not yet been documented.

The aim of this paper is to assess the effectiveness of ventilation achieved either with numerous holes or with a single inlet inducing a draught (stack) effect on the tree growth and on tree transpiration and assimilation rates. The tree seedlings used are wild cherry trees (Prunus avium L.).

2. Materials and methods

The first experiment (experiment A) involved 36 one-year-old, 0.5 m tall, cloned wild cherry trees (Inra clone 108) planted in 115 l containers. The seedlings were planted on 23 March 1989 in Montpellier, south of France (43°44'N, 3°40'E, 35 m elevation). Three protection treatments (Fig. 1) were compared: no treeshelter (NT), a standard unventilated treeshelter (ST), and a ventilated treeshelter (VT). Half the trees were weekly irrigated by daily drip irrigation to balance the evapotranspiration, half the trees were not irrigated, but were provided with some water when wilting occurred. The number of replications per treatment was therefore 6.

The second experiment (experiment B) involved 20 one-year-old, 0.55 m tall, wild cherry trees (Indre et Loire type). The seedlings were planted on 25 March 1991 in a well-drained sandy loam soil in Montpellier, south of France. The soil was alkaline (pH 8.4) with 1.5% organic matter. Four shelter treatments were compared, with five replications per treatment: NT, ST and VT as in experiment A, and a draught-ventilated treeshelter (DT, D standing for draught) was added (Fig. 1). No irrigation was scheduled, but a uniform watering was delivered on 19 July, as the drought was quite severe.

In both experiments, the shelters were put around the trees at planting time. Standard unventilated treeshelters (ST) are salmon-coloured, translucent, circular, twin-walled polypropylene tubes (Tubex, Aberdare, UK), 2.1 m tall and 0.1 m wide. The wall of the shelter is totally airtight. Standard treeshelters are not ventilated, which means that the entrance of fresh air is only possible through the top of the shelter, mainly by free convection. Such tall treeshelters were used to maintain the seedlings in sheltered conditions as long as possible: in fact, most of the trees did not emerge from the top of the shelter until the last days of the growing season. Therefore, the growth results are relevant to the sheltered microclimate. The modified ventilated treeshelter (VT) is an ST with 20 round holes, 14 mm diameter, scattered along the shelter. In VT, the radiation conditions are identical.
Fig. 1. Design and set-up of the treeshelters used in experiments A, B and C.

to a standard treeshelter, but temperature, humidity and CO₂ conditions are closer to unsheltered trees. The modified draught treeshelter (DT) is an ST with a single, 14 mm diameter hole drilled 0.2 m above the bottom of the shelter. All shelters were sealed 20 mm deep into the soil except the VT was raised 0.2 m above ground level. Shelters were secured with a wooden post anchored 300 mm deep into the soil.

A third experiment (experiment C) involved three of the five seedlings of *P. avium* of experiment B protected with a DT in July 1992. After having calibrated their transpiration on 13 July with the usual DT, they were protected on 15 and 16 July with DT with different inlet sizes (7, 14, 32, and 56 mm). A permutation of the treeshelters with the different inlet sizes was performed at night between 14 and 15 July and in the early morning of 16 July. The weather during these 3 days was very stable which allowed day to day comparisons of tree transpiration.

Treeshelters may be envisaged as small greenhouses, and methods for the study of the natural ventilation of greenhouses (Teitel and Tanny, 1999) may be applied with adequate assumptions. Most recent studies on natural ventilation have used tracer gas techniques and energy balance models (Wang et al., 1999). In experiment B, ventilation rate *N* was measured by a tracer gas dilution method (Kabbaj, 1988; Fernandez and Bailey, 1992; Bouard and Baille, 1993). N₂O was chosen as it is neither absorbed nor produced by any component of the system. The top of the shelter (and the bottom inlet hole if a draught treeshelter was tested) was blocked with a plastic sheet, and the gas was injected into the shelter with a syringe. The internal air was then stirred by two small fans for 5 min. The top of the shelter (and the bottom inlet hole if a draught treeshelter was tested) was finally opened and the decrease of N₂O concentration was monitored with an infrared gas analyser (Model SB300, ADC, Hoddesdon, UK) and the analogue signal was recorded by a data logger (Model CR10, Campbell). Ventilation rates were obtained by fitting the points to a decreasing exponential function

\[ C(t) = C_0 \exp\left(-\frac{1}{3600}Nt\right) \]  

where *C*(*t*) is the N₂O concentration at time *t*, *C₀* the initial N₂O concentration and *N* the ventilation rate. Air samples were sucked at 1.4 m height in a 2.1 m tall treeshelter sheltering a 1.7 m tall tree with a 0.19 m² leaf area. The measurements were performed on 8 August 1992, from sunrise until 3 p.m. solar time. Three diameter sizes of the bottom inlet hole were tested for the draught treeshelter: 21, 30 and 42 mm. Wind velocity at the height of the top of the shelter and air temperatures inside and outside the shelter at 1.2 m height were recorded every minute throughout the day, allowing us to match precisely each ventilation rate with the simultaneous climate variables. Ventilation rate and air flux *Gᵥ* are linked by
\[ G_v = N \frac{V_t}{S_t} \hspace{1cm} (2) \]

where \( V_t \) is the volume of the treeshelter and \( S_t \) the section of the treeshelter.

Ventilation processes induce an air exchange between the interior air of the shelter and its external environment due to wind and temperature effects. Bergez and Dupraz (1997) have shown that the wind effects were negligible in the case of unventilated treeshelters. This may be the result of the horizontal position of the vent at the top of the shelter, which is always parallel to the main wind direction. Buoyancy is therefore the main driving force, as a result of the draught effect (Boulard et al., 1996) induced by a temperature and humidity gradient between the exterior air at the top of the shelter and the warmer air inside the shelter. The inside air temperature is in equilibrium with the inside surfaces temperature including the tree leaves and stems, and the wall of the shelter.

During the growing season, tree height, basal tree diameter and tree leaf area were recorded at regular time intervals. The leaf area \( L \) of the trees was measured by counting the leaves and ranking them in size classes as explained in Bergez and Dupraz (1997), and using an allometric equation between the length of the lamina of the individual leaves \( l_i \) and the leaf area of these leaves (Bergez, 1993):

\[ L = \sum_{i=1}^{n} \exp[1.8 \ln l_i - 0.58] \hspace{1cm} (3) \]

where \( n \) is the number of leaves.

At the end of the growing season, the total tree biomass and the biomass partitioning between the shoot and the root system were recorded after digging up the trees.

In experiments B and C, transpiration rate, stomatal conductance and assimilation rate were measured at regular time intervals. Transpiration rates were measured using the stem heat balance method (Steinberg et al., 1990; Bergez and Dupraz, 1997) using commercial probes (Model SGB10, Dynamax, Houston, TX). Raw data were recorded by a data logger (Model 21X, Campbell Scientific, Shepshed, UK) via a multiplexer (Model AM416, Campbell). Special attention was given to the airtightness around the connectors of the sap flow gauges entering the treeshelters. Stomatal conductance of the leaves was measured using a porometer (Model MK3, Delta T Devices, Cambridge, UK). Assimilation rates were measured using a portable non-steady-state photosynthesis analyser (Model Li-6200, LI-COR, Lincoln, NE, USA) (Leuning and Sands, 1989; McDermitt et al., 1989). Detailed precautions were taken to get significant measurements of gas exchanges of sheltered trees as explained by Dupraz and Bergez (1999). Net photosynthesis rates of sheltered trees were measured by opening a window in the shelter wall and placing a leaf in the analyser chamber. The chamber was wrapped in a piece of shelter material, resulting in PAR conditions similar to the sheltered conditions. The measurement was performed under the ambient CO\(_2\) concentration of about 360 \( \mu l^{-1} \). The response of the net assimilation rate of sheltered leaves to the CO\(_2\) concentration had been established concurrently (Dupraz and Bergez, 1999). The CO\(_2\) concentration inside the shelter was measured prior to the window opening by sucking a very small volume of air into the analyser, allowing the measured assimilation value under 360 \( \mu l^{-1} \) CO\(_2\) concentration to be corrected to the actual sheltered value.

3. Results

3.1. Impact of ventilation on the microclimate inside the treeshelter

Measurements on climate inside the shelter were performed throughout the different growing seasons. The ventilation with numerous holes scattered along the treeshelter resulted in lower daytime temperature and air humidity inside the treeshelter compared to the conventional unventilated treeshelter. Fig. 2 presents two typical sunny days’ records. Due to the large transmission of the shelter wall in the IR band, night temperatures were 2\(^\circ\)C lower inside the treeshelters than in the open irrespective of shelter ventilation. The impact of ventilation was more efficient during the morning as the difference in air temperature was slightly smaller (4\(^\circ\)C vs. 6\(^\circ\)C in the afternoon). Maximum daily temperatures inside the unventilated treeshelters were consistently 10–12\(^\circ\)C higher than ambient temperatures in the morning. These temperature increases inside shelters are similar to results reported by Rendle (1985), Kjelgren and Rupp (1997) or Swistock et al. (1999).
Fig. 2. Daily pattern of the difference of air temperature $T$ and water vapour pressure $VP$ between the inside of treeshelters (Standard unventilated, ST or ventilated, VT) and the outside. Data recorded on (A) 4 May 1989 and (B) 11 June 1989. Boundary conditions are given in (C). The $P. avium$ tree had a 0.07 (May) and 0.11 m$^2$ (June) leaf area, and was protected by a 2.1 m tall shelter. Measurements performed at 1.20 m height.

Ventilation reduced maximum daily temperature by about 6°C. The unventilated treeshelters experienced very high water vapour pressure due to the high temperature and to the confinement of tree transpiration as already reported by Bergez (1993) or Kjelgren (1994). During the afternoon, the water vapour pressure was lower inside the ventilated treeshelter than outside.

The ventilation with a single inlet at the bottom of the treeshelter was efficient as illustrated by the evolution of air temperature and CO$_2$ concentration in a standard treeshelter when an inlet is opened at the bottom (Fig. 3). During the first minute after inlet opening, a strong up flow of air was evident because (i) the air temperature increases at the top of the shelter, (ii) the air temperature decreases at the bottom, and (iii) the sharp CO$_2$ concentration increases in the middle of the tree canopy. After this transient phase during which air temperatures were higher at the top of the shelter than at the bottom, a more steady-state regime was observed, with CO$_2$ values around 300 µl l$^{-1}$, about 40 µl l$^{-1}$ higher than the value in the unventilated treeshelter before inlet opening. The air temperature gradient between the bottom and the top of the shelter oscillated then, with apparent inversions of the gradient at 40 s intervals. This may be interpreted as a succession of heating phases, during which the air flow was reduced, and the air temperature at the bottom increased, and of flushing phases, during which the heated air was expelled. This hypothesis results from the fact that most decreases in CO$_2$ concentration are synchronous with reduced or inverted vertical temperature gradients. Smoke-producing devices were used to trace the air movement, and confirmed that the ascent of air took less than 5 s from the bottom entrance to the top.
At night, the soil respiration in empty treeshelters had only a very small impact on the CO₂ concentration with maximum values lower than 420 μl⁻¹. CO₂ concentration inside unventilated treeshelters increased significantly with values as high as 600–1000 μl⁻¹, resulting from the confinement of tree respiration. This was not observed in ventilated and draught treeshelters, where night values were not significantly different from outside air values (Fig. 4). During the day, CO₂ concentration in a ventilated treeshelter was only 20 μl⁻¹ lower than the outside value. After sunrise, very low values were observed in unventilated treeshelters, as already reported by Dupraz and Bergez (1999). Low values were also observed in draught treeshelters. During the afternoon, draught treeshelters exhibited the lowest CO₂ concentration. The afternoon rise in CO₂ concentration that is characteristic of unventilated treeshelters was not evidenced in draught treeshelters.

Ventilation rates measurements confirmed the efficiency of the draught effect (DT) with values ranging from 20 to 100 h⁻¹ (Fig. 5). Ventilation rates of unventilated treeshelters (ST) ranged from 3 to 30 h⁻¹ (Dupraz and Bergez, 1999) and ventilation rates of
ventilated shelters (VT) were too high to be measured by our method (the tracer gas disappeared in less than 5 s indicating ventilation rates above 500 h\(^{-1}\)). No relationship could be established between the ventilation rate of draught shelters and the wind velocity. Higher ventilation rates were observed during the afternoon when the air temperature was higher. The average ventilation rates during the measurement day were 17 h\(^{-1}\) for unventilated shelters, and 53, 38 and 45 h\(^{-1}\) for shelters with an air inlet of 21, 30 and 42 mm diameter, respectively. The ventilation rate increased when the size of the inlet hole increased (and this was consistent in all experiments), but for very large inlet sizes, no further increase was recorded. A 17 h\(^{-1}\) ventilation rate in an unventilated treeshelter corresponds to an average 0.011 m s\(^{-1}\) air velocity, which is much smaller than the air speed recorded in greenhouses under leakage ventilation (Wang et al., 1999).

3.2. Impact of ventilation on tree growth with various water availability regimes

In experiment A, ventilation stimulated the shoot growth of irrigated trees, but not of water-stressed trees, as compared to unventilated treeshelters (Fig. 6). Both irrigation and treeshelters had a strong impact on the second flush of shoot elongation, while

![Graph showing growth of apical shoot with different irrigation regimes and treeshelters.](image-url)

Fig. 6. Growth of the apical shoot of container-grown *P. avium* seedlings with different treeshelters and irrigation regimes during 1989 (experiment A). The vertical bars represent two standard errors.
the first flush was not significantly modified. In the very dry conditions experienced by the non-irrigated trees, unventilated treeshelters performed slightly better as far as apical shoot is concerned. Treeshelters extended the duration of the elongation phase. The leaf area of sheltered trees was not significantly different from the leaf area of unsheltered trees.

At the end of the growing season, the biomass of sheltered trees in unventilated shelters was significantly less than the biomass of control trees (Fig. 7). The reduction in tree biomass was very impressive for non-irrigated trees with total dry weight of protected trees as low as only 30% of the control trees. This could not be inferred from shoot elongation, which were in favour of protected trees.

Ventilated shelters increased the biomass of sheltered trees by 50% (non-irrigated trees) and 85% (irrigated trees). A significant interaction between ventilation and irrigation was evident, with irrigated trees in ventilated treeshelters matching control trees for total dry weight at the end of the growing season. Furthermore, the biomass partitioning between the shoot and the root was strongly modified by the shelter. The roots made up about 30% of the total biomass of the sheltered trees compared to about 60% for unsheltered trees irrespective of the ventilation and irrigation treatments.

In experiment B, field-grown trees experienced less-contrasted water regimes than container-grown trees. Apical shoot elongations of sheltered trees were similar, irrespective of ventilation. They were more than three times higher than those of control unsheltered trees (Table 1). Diameter growth results of control and sheltered trees indicated that ventilation was very effective in enhancing tree growth. Both scattered holes and a single inlet at the bottom of the shelter were efficient. Trees in ventilated treeshelters exceeded trees in unventilated shelters by +55% in biomass, and matched control trees for both diameter growth and biomass accretion. Control trees exhibited a 66% share of below-ground biomass, while sheltered trees had only 40%, regardless of the ventilation regime.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Elongation (m)</th>
<th>Diameter increase (mm)</th>
<th>Total biomass (g)</th>
<th>Shoot to total biomass ratio (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unsheltered</td>
<td>0.50 a</td>
<td>7.52 a</td>
<td>83.1 a</td>
<td>35.3 a</td>
</tr>
<tr>
<td>Unventilated</td>
<td>1.50 b</td>
<td>3.34 b</td>
<td>55.8 b</td>
<td>60.8 b</td>
</tr>
<tr>
<td>Ventilated</td>
<td>1.46 b</td>
<td>5.92 a</td>
<td>90.8 a</td>
<td>55.4 b</td>
</tr>
<tr>
<td>Draught</td>
<td>1.59 b</td>
<td>6.16 a</td>
<td>84.0 a</td>
<td>60.2 b</td>
</tr>
</tbody>
</table>

*Values with the same letter are not statistically different at p=0.01.
Table 2
Transpiration of *P. avium* seedlings in unventilated and draught treeshelter as related to leaf area and canopy density (experiment B; 6–13 July 1991)\(^a\)

<table>
<thead>
<tr>
<th>Treeshelter</th>
<th>No. of replications</th>
<th>Transpiration (g per day)</th>
<th>Leaf area (cm(^2))</th>
<th>Transpiration flux density (mg H(_2)O m(^{-2}) per day)</th>
<th>Canopy leaf density (m(^2) m(^{-3}))</th>
<th>Leaf area index (m(^2) m(^{-2}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standard (unventilated)</td>
<td>3</td>
<td>113 a</td>
<td>1963 a</td>
<td>0.70 a</td>
<td>0.023 a</td>
<td>25.0 a</td>
</tr>
<tr>
<td>Draught</td>
<td>4</td>
<td>323 b</td>
<td>2315 a</td>
<td>1.38 b</td>
<td>0.028 a</td>
<td>29.5 a</td>
</tr>
</tbody>
</table>

\(^a\) Values with the same letter are not statistically different at \(p<0.01\).

3.3. Impact of ventilation on the gas exchange processes of the trees

The transpiration rate of trees was enhanced by draught ventilation, as compared to unventilated treeshelters (Table 2). The efficiency of the draught effect was probably influenced by the canopy leaf area and by the leaf density. Sheltered trees exhibited very unusual high leaf area index ranging from 20 to 30, and high leaf densities, resulting in a high resistance to air flow through the shelter. Ventilation through numerous holes increased transpiration much more than ventilation by a draught effect (Fig. 8).

Trees protected by ventilated treeshelters showed a conductance pattern very similar to control trees (Fig. 9). Trees in unventilated treeshelters exhibited high conductance day and night, and trees in draught-ventilated shelters followed an intermediate pattern. A rise in conductance was noticeable when the sun was at low elevations (around 9 a.m. and 6 p.m.). This may be related to the radiation transmission of the shelter, as the solid angle of sun radiation intercepted by the shelter is higher when the sun is low.

In experiment C, the transpiration rate was stimulated by increasing the size of the air inlet (Fig. 10). However, it appeared that this increase is not linearly related to the area of the air inlet. A fourfold increase of the inlet area from 38 to 153 mm\(^2\) increased the tree transpiration by 28%. A new further eightfold increase (2463 mm\(^2\) area) only increased the transpiration by 4%. In Fig. 10, the tree had a small leaf area (0.15 m\(^2\)), and the transpiration was not augmented when the diameter of the air inlet exceeded 14 mm. Measurements on trees with different leaf areas (Table 3) indicated that larger trees may benefit from larger sizes of the air inlet.

![Fig. 8. Transpiration flux densities of *P. avium* seedlings with different shelters recorded on 27 July 1991.](image-url)
Fig. 9. Conductance of *P. avium* leaves grown in different treeshelters as measured on 18 July 1991.

Fig. 10. Compared transpiration flux densities of a 0.15 m² leaf area of *P. avium* seedling in a draught treeshelter with three different sizes of bottom air inlet, measured during three consecutive days with similar climate conditions (14–16 July 1991).

Table 3
Influence of the size of the air inlet on the transpiration rate of sheltered *P. avium* seedlings (experiment C)

<table>
<thead>
<tr>
<th>Leaf area (cm²)</th>
<th>13 July 1991</th>
<th>15 July 1991</th>
<th>16 July 1991</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Inlet diameter (mm)</td>
<td>Transpiration flux density (mg H₂O m⁻² per day)</td>
<td>Inlet diameter (mm)</td>
</tr>
<tr>
<td>Tree 1 1511</td>
<td>14</td>
<td>1.72</td>
<td>56</td>
</tr>
<tr>
<td>Tree 2 2314</td>
<td>14</td>
<td>1.58</td>
<td>32</td>
</tr>
<tr>
<td>Tree 3 2851</td>
<td>14</td>
<td>1.80</td>
<td>14</td>
</tr>
<tr>
<td>Tree 4 1447</td>
<td>14</td>
<td>0.80</td>
<td>7</td>
</tr>
</tbody>
</table>
Potential assimilation rates (PARs) of sheltered trees (i.e. with 360 μmol·m⁻²·s⁻¹ CO₂ concentration and typical shelter radiation condition) were lower than that of unsheltered trees (Fig. 11). This decrease was mainly due to the lower radiation reaching the leaves irrespective of the shelter ventilation. Only 30–38% of PAR was transmitted by the shelter with higher relative transmission rates in the early morning and late afternoon when the solar rays are orthogonal to the shelter wall. Unventilated and draught-ventilated sheltered trees showed a similar pattern of potential assimilation during the day. These potential rates are however not representative of the actual assimilation rates inside the shelters, where the CO₂ concentration is usually very different from the standard 360 μmol·l⁻¹ value (Fig. 4).

4. Discussion

The CO₂ issue in treeshelters has been overlooked or misunderstood by many authors. Following Frearson and Weiss (1987), high CO₂ concentration inside treeshelters have often been interpreted as favourable conditions to tree photosynthesis (Potter, 1988; Maile, 1990; Mayhead and Jones, 1991; Kittredge and Kelty, 1992; Burger et al., 1996). Reduced transpiration rates were therefore interpreted as improving drought avoidance through reduced soil water depletion, but the impact of reduced transpiration on reduced photosynthesis was not encompassed (Kjelgren and Rupp, 1997). Some authors even recommend the use of treeshelters for producing container-grown trees ready to be transplanted in field plantations, although their results showed a reduced root biomass of the plants (Burger et al., 1992). Reduced stem growth of sheltered trees was mainly interpreted as a result of a reduced light availability (Potter, 1988) or as a consequence of a lack of wind movement (Kjelgren and Rupp, 1997), but no experimental evidences were provided. The results by Bergez (1993) changed the scene completely. In an unventilated treeshelter, both high (above the ambient value) and low (below the ambient value) CO₂ concentrations indicated a poor photosynthesis activity. High values resulted from a negative net rate (mainly due to excessive temperature) and low values indicated a positive but low photosynthesis rate, limited by the CO₂ availability. As a consequence, ventilation of treeshelters was described as a key issue.

Our results show that the ventilation of the treeshelter improves both diameter and biomass growth of protected trees. Although the biomass is increased, a smaller proportion goes into the root than for unprotected trees. Trees growing in standard unventilated treeshelters exhibit a strong reduction in total biomass that is concealed by improved height growth. Trees growing in ventilated shelters even matched control unprotected trees for biomass accumulation in field
experiment B with an intermediate water constraint. Container-grown trees with a very strong water constraint did not take much advantage of the ventilation, but did as well as trees in unventilated shelters. Therefore, ventilation appears to be either very favourable (trees with high or medium soil water availability) or without influence (trees with a very low soil water availability) on tree biomass. Most previous studies only included unventilated shelters usually sealed at the bottom with soil. The only other results available to compare ventilated and unventilated sheltered trees are those by Mayhead and Jenkins (1992) who improved the growth of sheltered Sitka spruce by ventilating the shelter with 12 evenly spaced holes. These authors found this result surprising. They had found high daytime CO₂ concentration inside the unventilated shelters in their experiment (Maile, 1990), and were assuming that this was a favourable condition resulting from the soil respiration confinement in the unventilated treeshelters. Our results help to interpret such data: the unventilated trees were on the contrary experiencing negative net photosynthesis rates at some time of the day, probably due to high temperatures, and ventilating the shelters resulted in a favourable impact on tree growth.

Our results confirm that the well-documented enhanced height growth of tree seedlings in unventilated treeshelters is deceptive (Dupraz et al., 1993). In most cases, recently emerged trees are not able to stand alone if the shelter is removed (Burger et al., 1996; Kjelgren and Rupp, 1997; Mayhead and Boothman, 1997), and deformities of the emerged part of the tree occur (Balandier, 1997). A negative impact on diameter growth was evident in many sites and for many tree species (Dupraz et al., 1989; Dupraz, 1997). A reduced above-ground biomass of sheltered trees (Burger et al., 1996) underestimates the actual reduction in the total biomass of the tree, as the balance between above- and below-ground biomass of sheltered trees is displaced in favour of the above-ground biomass (Dupraz, 1997). Consequently, some authors discourage the use of treeshelters (Gill and Eason, 1994) or recommend short treeshelters (maximum 0.6 m tall as stated by Burger et al., 1996). But tall shelters are mandatory in the establishment of broad-leaved species in grazed silvopastoral plots, or when tall Cervidaes are abundant, as in most temperate Europe or Northern America (Swistock et al., 1999).

We therefore tried to improve the effectiveness of treeshelters on tree growth to allow the safe use of tall shelters (1.2–2.4 m tall) in broad-leaved plantations.

Unexpected low concentrations of CO₂ inside draught-ventilated treeshelters may be interpreted using a dynamic mass balance of carbon inside the shelter, taking into account the inflow of external air rich in CO₂ inside the shelter. Using a CO₂ budget, it is possible to calculate the assimilation rate of the tree when the ventilation rate of the shelter is known. Neglecting CO₂ release by the soil, as Dupraz and Bergez (1999) found it to be an order of magnitude below the tree requirements, the CO₂ balance equation can be written as

\[
d\text{CO}_2 = -A + E
\]  

where \( A \) is the net assimilation rate of the tree crown and \( E \) the mass flow rate of CO₂ due to ventilation. Eq. (4) can be integrated: for long time intervals, a CO₂ concentration steady state can be assumed, as a variation of 50 μmol CO₂ s⁻¹ of the CO₂ concentration in the 16.51 of air inside the shelter is less than 1% of the hourly \( A \) term. CO₂ values below the outside ambient value indicate a positive net assimilation rate of the tree. CO₂ values above the ambient concentration indicate a negative net assimilation rate of the tree. If CO₂ availability is not limiting (such as in the case of very high ventilation rates or very low assimilation requirements), the CO₂ concentration inside the treeshelter will be very near to the outside value. Usual ventilation rates recorded in unventilated treeshelters range from 1 to 25 h⁻¹ (Fig. 5). The \( E \) term is therefore ranging from 0.044 to 1.1 mmol CO₂ h⁻¹. For a tree seedling with a 0.2 m² leaf area, this is equivalent to a net assimilation rate ranging from 0.06 to 1.5 μmol CO₂ m⁻² s⁻¹, which is a very low net photosynthesis rate. Control P. avium seedlings with no shelter and no soil water constraint exhibit mean daytime net photosynthesis rates of 10 μmol CO₂ m⁻² s⁻¹ during a typical sunny summer day (Dupraz and Bergez, 1999).

In DT, the combination of high ventilation rates and low CO₂ values indicates high net assimilation rates (Table 4). In ST, the combination of low ventilation rates and low CO₂ values during the morning indicates low assimilation rates. When CO₂ values above the ambient outside value are recorded, such as in many previous experiments with ST, or during hot after-
Table 4
Net assimilation rates of a sheltered tree seedling with a 0.2 m$^{-2}$ leaf area as deduced from the CO$_2$ mass balance of the shelter (Eq. (4))

<table>
<thead>
<tr>
<th></th>
<th>Unventilated (ST)</th>
<th>Draught (DT)</th>
<th>Ventilated (VT)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Morning</td>
<td>Afternoon</td>
<td></td>
</tr>
<tr>
<td>Ventilation rate (h$^{-1}$)$^b$</td>
<td>10.0</td>
<td>20.0</td>
<td>80.0</td>
</tr>
<tr>
<td>Inside CO$_2$ concentration (μmol s$^{-1}$)$^b$</td>
<td>300.0</td>
<td>400.0</td>
<td>250.0</td>
</tr>
<tr>
<td>Mass flow of CO$_2$ inside the shelter (μg CO$_2$ s$^{-1}$)$^c$</td>
<td>5.4</td>
<td>-7.2</td>
<td>79.2</td>
</tr>
<tr>
<td>Assimilation rate (μmol CO$_2$ m$^{-2}$ s$^{-1}$)$^c$</td>
<td>0.61</td>
<td>-0.82</td>
<td>9.00</td>
</tr>
</tbody>
</table>

$^a$ The shelter is 2.1 m tall with a 0.1 m diameter.

$^b$ Measured data.

$^c$ Calculated data.

$^d$ Value is not accurate (see text).

noons in some of our experiments (Dupraz and Bergez, 1999), the mass balance indicates negative assimilation rates. In VT, very high ventilation rates and CO$_2$ concentrations very near to the ambient value prevent the accurate calculation of the assimilation rate by the balance equation, as a result of the high uncertainty of the multiplication of very high ventilation rates by very low CO$_2$ gradients. Instantaneous measurements of assimilation rates with a portable photosynthesis analyser under the standard CO$_2$ concentration as performed by Kjelgren et al. (1997) are therefore a wrong indicator of the actual photosynthesis status of a sheltered tree. A twinned measurement of the CO$_2$ concentration surrounding the sheltered tree and of the ventilation rate of the shelter should be preferred.

Trees in VT and DT seem to recover some extent in stomatal conductance control as compared to trees in ST. This would be very useful to avoid accidents resulting from a sudden change in tree-shelter ventilation as was observed with ST. We sometimes observed that trees protected in tight ST suddenly wilted as a result of a sudden move of the shelter (caused by animal or machinery or human activity), which created a sudden inflow of air.

The shoot/root ratio of protected trees in standard unventilated shelters is always distorted, as found by Dupraz (1997) on 10 different tree species including conifers and broad-leaved species. Dupraz indicated that about 20% of the total biomass of the tree shifts from the below-ground to the above-ground part of the tree. Such results are relevant only before the tree emerges from the shelter, which may explain why other studies of emerged trees found different results on some species (Burger et al., 1992). The data presented here confirm the shift with even higher biomass transfers (25–30%, Table 1). The ventilation of the shelters corrected the tree distortion for container-grown non-irrigated trees (Fig. 7), but did not correct the tree distortion for irrigated trees (Fig. 7) or field-grown trees (Table 1). This is disappointing and shows that the assimilate partitioning is not only influenced by the assimilation process intensity, but more probably by a variable that is not connected to the ventilation: it may be the light intensity, the light quality or the wind-induced stem and leaf movement. In greenhouse experiments, seedlings that were shaken to simulate wind effects had smaller height growth, greater diameter growth, and shorter period of extension growth compared to trees that remained motionless (Neel and Harris, 1971, 1972; Kellog and Stencek, 1976; Mitchell and Myers, 1995; Osler et al., 1996). Therefore, it should be stated that in ST, the trees should emerge as soon as possible out of the shelter to avoid both the distorted allocation of assimilates and the reduction in net photosynthesis resulting from low CO$_2$ availability. This conclusion is opposite to most previous papers such as those of Potter (1991) or Burger et al. (1996) who stated that the beneficial impact of the shelter was limited to the time when the tree seedling grows inside the shelter.

Ventilation is therefore an effective improvement as it stimulates both height and diameter growth, allowing the tree to benefit earlier from the wind action. Our results help to interpret previous results where small seedlings were not able to take advantage of the tree-shelter, while strong seedlings did (Kittredge and Kelty, 1992). Tree growth inside unventilated shelters uses mostly the carbon reserves of the seedling, as...
the net photosynthesis is reduced by the CO₂ limitation. This was confirmed by experiments where the total biomass of *Juglans* seedlings diminished during the first year of growth inside a shelter, although their height growth was impressive (Bergez, 1993; Dupraz, 1997). The average net photosynthesis of such protected trees was negative during the whole growing season, which is a very dramatic impact of unventilated treeshelters. Therefore, recommendations of using treeshelters to help naturally regenerated oaks to dominate the competing vegetation (Kittredge and Kelty, 1992) may not be relevant: the tall seedlings which emerge from the top of the shelter may not have enough sturdiness and roots to keep their height advantage. Similarly, Lantagne et al. (1990) reported that a confirmation of the effectiveness of treeshelters is the increase in the number of treeshelters used in Britain from 80 units in 1979 to over 6 million in 1986 (Potter, 1987). This may not be the correct view: mostly unventilated shelters were used at that time, and the impact on tree growth was not documented on long timescales. The height growth improvement during the first few years was very impressive and conducive to using treeshelters, and the evidence of the reduced diameter growth was not yet adequately interpreted (Dupraz, 1997). The fact that in the historical experiment by Tuley (1983), the treeshelters improved the diameter growth of the trees was used in most advertisements for treeshelters. But this was to be invalidated by most of the following experiments.

Draught ventilation appears to be effective in stimulating tree growth, and performs almost as well as ventilation with numerous holes scattered along the shelter. The effectiveness of draught ventilation may be related to the progressive moistening of the ascendant air by the transpiration of basal leaves. The leaves of the upper part of the crown therefore benefit from a humid environment, as the water transpired by lower leaves remains confined in the air flow while the leaves of the lower part benefit from the outside air rich in CO₂. The same process may be effective in ventilated treeshelters near the wall openings. A better water use efficiency of protected trees in VT and DT may therefore be hypothesised. The co-occurrence of an important improvement in biomass accretion (Fig. 7), and of a limited increase in tree transpiration (Fig. 10) in VT is in favour of this hypothesis. With DT, a single hole at the bottom of a treeshelter has other benefits: the shelter is not weakened by numerous holes, the making costs are reduced, and the tree branches may not escape through the openings, preventing herbivorous predators from damaging the tree by browsing and tearing off the branches.

Ventilation of treeshelters efficiently increases the gas exchanges of *P. avium* tree crowns. As the CO₂ availability is raised, it must be questioned if light availability may not become limiting. Previous experiments with different shelter colours or shelter opacity failed to provide evidence for an impact on tree growth (Tuley, 1985; Potter, 1987) or gas exchange (Kjelgren et al., 1997), but all these experiments used unventilated standard treeshelters. Therefore, the suggestion (Kjelgren, 1994) of using lighter-coloured material to improve tree growth is probably irrelevant or even dangerous in unventilated treeshelters as the tree may have to cope with greater increases in temperatures due to higher radiation levels in the shelter with no possibilities to lose energy. Therefore, the combination of different ventilation and light transmission rates of the shelter should be investigated, and could allow improved treeshelters design.

5. Conclusion

While the difference between unprotected trees and protected trees in treeshelters is easy to demonstrate, most studies of the impact of treeshelters on tree growth failed to provide evidence for any difference between various kinds of treeshelters on tree growth results. Previous experiments compared different kinds of treeshelters (various light transmission rates, materials, shapes or sizes) but never included the ventilation factor. We have shown that ventilation significantly improved the growth of sheltered *P. avium* trees when grown both in containers or in field conditions. The results support the hypothesis of CO₂ limitation of tree growth in shelters. The CO₂ mass balance of the shelter helped to understand why CO₂ concentration inside the shelters is a deceptive measure of the actual tree assimilation rate. A twinned measurement of the ventilation rate of the shelter and of the CO₂ concentration inside the shelter was found necessary to assess the tree photosynthesis activity.

However, the main advantage of treeshelters is to protect the tree leaves and stem from browsing or
rubbing, allowing to plant broad-leaved trees in grazed plots or Cervidae infested forests. Other key advantages include the ease of locating the tree even in the densest vegetation, the protection against herbicide application and the reduction of lateral branches which facilitates stem pruning. We therefore consider that a slight reduction in tree growth may be an acceptable counterpart to benefit from these advantages of the treeshelters. New ventilated treeshelters may reduce significantly the drawbacks of standard unventilated treeshelters, if our results of a 50% (water-stressed, container-grown trees), 55% (field-grown trees) and 85% (irrigated, container-grown trees) increases in tree biomass due to ventilation are confirmed.

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