Effects of sulphur dioxide on leaf photosynthesis: the role of temperature and humidity


The effect of temperature and humidity on SO₂-induced photosynthetic depression was determined in gas exchange experiments with leaves of *Vicia faba*. Stomatal behaviour was sensitive to humidity resulting in higher uptake rates of SO₂ and stronger reductions of photosynthesis at low VPD (vapour pressure deficit). After a fumigation period of 2 h, when the photosynthetic rate had stabilized, photosynthesis of leaves exposed to SO₂ at 20°C was reduced much more than at 18°C at the same rate of SO₂ uptake. Data analysis with a mechanistic model revealed that this effect was due to the slower rate of S(IV) oxidation at lower temperatures, resulting in higher accumulation of S(IV) and thus stronger reduction of photosynthesis. These results were confirmed by experimental analyses of the S(IV) concentration in leaves following fumigation, which showed that more S(IV) accumulated in leaves exposed at a lower temperature. This may explain the high sensitivity of plants exposed to SO₂ under winter conditions, when both VPD and temperature are low.

Key words — Model, photosynthesis, SO₂, stomata, sulphur dioxide, sulphur metabolism.

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Introduction

SO₂ effects on plant growth depend upon the environmental conditions at which the plants are grown (see reviews Unsworth and Ormrod 1982, Hälgren 1984, Winner et al. 1985). It has been demonstrated that depressing SO₂ effects on plant growth were most severe during winter periods, when temperature and irradiance are low and humidity is high (Cowling and Lockyer 1978, Davies 1980, Whitmore and Mansfield 1983, Baker et al. 1986, 1987). The reported growth reductions are at least partly due to direct effects on photosynthesis and/or respiration, because no strong reductions in leaf area were detected (Whitmore and Mansfield 1983, Baker et al. 1986, 1987).

The environmental conditions in winter (low temperature, low irradiation, high humidity) may directly influence the uptake, metabolism and effects of SO₂ metabolites on photosynthesis. McLaughlin and Taylor (1981) demonstrated that pollutant uptake is significantly higher when air humidity is high, which can be understood from the well-known observation that stomatal behaviour depends upon air humidity (Losch and Tenhunen 1981, Morison 1987). When SO₂ dissolves in the aqueous phase of the leaf, the sulphite and bisulphite formed are quickly oxidized to sulphate (Miller and Xerikos 1979, Alscher et al. 1987). The rate of S(IV) oxidation in aqueous solutions is very sensitive to temperature (Martin 1984). When sulphite oxidation is slowed at low temperatures in cellular solutions, more toxic S(IV) compounds will accumulate. Because photosynthetic depression is related to the S(IV) concentration (Miller and Xerikos 1979, Alscher et al. 1987, Kröpf 1989a), stronger reductions of photosynthesis...
can be expected at lower temperatures. However, the role of temperature in SO2 uptake, SO2 metabolism in the leaf and its implications for SO2 effects on photosynthesis has not yet been analysed.

In this study influence of both humidity and temperature on the effect of SO2 on leaf photosynthesis was determined by gas exchange measurements, taking into account the strong relation between temperature and VPD. The physiological backgrounds behind the effect of these environmental factors on SO2 induced photosynthetic depression were analysed using a model for foliar SO2 metabolism in the leaf and effects of SO2 metabolites on photosynthesis (Kropff 1987, 1989a,b). This theoretical analysis was evaluated with experimental data on the S(IV) content of leaves, exposed to SO2 at two temperatures.

Abbreviations – PAR, photosynthetically active radiation; PPFD, photosynthetic photon flux density (µmol m⁻² s⁻¹); Rubisco, ribulose-1,5 bisphosphate carboxylase-oxygenase; S(IV), [SO₂]aq + [HSO₃⁻] + [SO₃²⁻]; TCM, tetra chlorine mercurate.

Material and methods

Plant material

Broad bean plants (Vicia faba L. cv. Minica) were grown in a greenhouse at 16°C and 60–80% RH. Artificial supplementary illumination (Philips fluorescence 33RS) provided a photoperiod of 16 h. Measurements were taken on the youngest fully unfolded leaves and started when the plants had about 10 leaves.

Experimental equipment

Materials which have been used for the construction of existing systems for measurement of photosynthesis absorb or react with pollutants like SO2 and O3 (van Hove et al. 1988). Quick changes in pollutant concentrations cannot be obtained and analysis of the rate of foliar pollutant uptake is impossible in these systems. Another problem is the cooling system in which water vapour often condensates, readily absorbing pollutants like SO2. To overcome these limitations a new system for gas exchange analysis during exposure to air pollutants at low concentrations was designed. This computer controlled system consisted of an air supply unit, two leaf chambers and a unit for gas analysis.

Air was dried and purified by passing the air through several filters, containing molecular sieves for removal of H₂O and CO₂ (Giertart, Hengelo), active charcoal (RL II-Norit), and a molecular sieve 5Å. Air was mixed with CO₂ from a cylinder by mass controllers. Air humidity was controlled by injection of water vapour into the air flow with computer controlled ultrasonic nebulizers (modified Heyer, USE 77) with a droplet size of 0.5–4 µm. Aerosols were removed from the air flow by a series of static mixers (Sulzer). Humidity in the chamber could be changed very rapidly (within a few minutes), without affecting the chamber temperature. The humidified air was mixed in a teflon manifold with SO2 using thermal mass flow controllers (Brooks instruments). SO2 was supplied from a cylinder containing a gas mixture of 1000 ppm SO2 in N₂. All tubing and mixing units in contact with SO2 were constructed from teflon or glass. These materials have a relatively low absorption capacity for pollutants and hardly react with the pollutants. All processing was controlled by a Hewlett Packard personal computer (HP9122) in combination with a data acquisition unit (HP 3497 A).

The leaf chamber was illuminated by a combination of high pressure vapour lights [two SON-T (sodium) and three HPI-T (iodine) lights], each 400 W (Philips), yielding a maximum PPFD of 1400 µmol m⁻² s⁻¹, equal to about 300 J m⁻² s⁻¹ PAR. Running cold water through a water bath between the light source and leaf chamber reduced the heating of the chamber. PPFD was measured by a PAR quantum sensor (Technical and Physical Research Service, Wageningen). Air humidity in the chamber was measured by Rotronic hygrometers and the difference in water vapour concentration between the inlet and the outlet of the chamber was measured with an infrared gas analyser (ADC 225 Mk3). CO₂ concentration at the inlet of the chamber was measured with an infrared gas analyser (ADC D6Y34H). The difference in CO₂ concentration between chamber inlet and outlet was measured by a second CO₂ analyser (ADC 225 Mk3). SO2 concentrations at the inlet and outlet of two chambers were analysed using a TECO 43A SO₂ monitor. Samples for the analysis of H₂O, CO₂ and SO2 were drawn from the main air lines entering and leaving the chambers by pumps.

The flow rate of the air through the system was 15.5 l min⁻¹, giving a residence time of the air in the chamber of 0.54 min. Air in the leaf chamber was mixed by recirculation through a heat-exchanger, bathed in alcohol and temperature controlled by a cooling unit (Braun Frigro mix R), which was modified to permit computer control. A teflon fan recirculated the air at a flow rate of 800 l min⁻¹, which resulted in a low boundary layer resistance (15 s m⁻¹ for H₂O). All data were collected every 5 min by the HP microcomputer. Rates of SO2 uptake, transpiration and photosynthesis were calculated from the difference in the concentration between inlet and outlet of the leaf chamber and the leaf area. Stomatal resistance and internal CO₂ concentration were calculated according to Goudriaan and van Laar (1978).

Experimental procedure

The influence of SO2 at various combinations of temperature, PPFD and air humidity on photosynthesis was measured for individual leaves of V. faba. The effect of temperature (8 and 18°C) was studied at two levels of
radiation (PPFD of 450 or 900 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)) at 70% RH. The effect of air humidity (30, 50 and 70% RH) was studied at a PPFD of 900 \( \mu \text{mol m}^{-2} \text{s}^{-1} \), at 18°C. At 8°C, photosynthesis was light saturated at 450 \( \mu \text{mol m}^{-2} \text{s}^{-1} \), and at 18°C photosynthesis was saturated at 900 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). Depending on the treatment, SO\(_2\) concentrations ranged from 350 to 1500 \( \mu \text{g SO}_2 \text{ m}^{-3} \), in order to obtain reductions in photosynthesis in the range of 10–30%, necessary for reliable estimation of biochemical parameters with the model (Kropff 1989b). The average CO\(_2\) concentration of the ingoing air was 345 ppm.

Leaf thickness was determined by measuring both leaf area and volume. The leaf volume was measured by submerging the leaf in a measuring glass filled with water.

Two plants were placed in controlled climate rooms in the afternoon previous to the day the measurements were conducted, to allow adaptation to the experimental conditions (temperature and humidity). The youngest fully unfolded leaf was enclosed in a leaf chamber. The light intensity was gradually increased to the desired PPFD of 450 or 900 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). When rates of photosynthesis were stable, the enclosed leaf of one of the plants was fumigated for ca 2 h. The other plant was used as a control. Photosynthesis and transpiration were measured during the fumigation period and a subsequent recovery period of ca 2 h.

Model analysis of experimental data

A model for foliar SO\(_2\) uptake, SO\(_2\) metabolism in the leaf and effects of SO\(_2\) metabolites on photosynthesis (Kropff 1989a,b) was used to analyse the biochemical processes determining temperature effect on the depression of photosynthesis by SO\(_2\). Two model parameters determine the magnitude of SO\(_2\) effects on photosynthesis: the time coefficient for S(IV) oxidation \( (\tau_1, s) \) and a sensitivity parameter \( (k) \), which describes the reduction of photosynthesis in relation to the S(IV) concentration in the leaf (mmol S(IV) \( \text{l} \text{kg}^{-1} \)) (Kropff 1989a). These two parameters can be estimated by fitting the model to data on the time course of relative photosynthesis during a fumigation period and a subsequent recovery period (Kropff 1989b). In the calculation of the parameter values data on leaf thickness and rate of photosynthesis and stomatal resistance before the onset of fumigation are used. This procedure enables the separation of stomatal (effects on uptake rate of SO\(_2\)) and non-stomatal effects (effects on \( k \) and \( \tau_1 \)) of environmental factors on photosynthetic depression by SO\(_2\) (Kropff 1989a).

In the present study, the parameters \( k \) and \( \tau_1 \) were determined for all measured time series of photosynthesis separately. At 8°C and high PPFD, photosynthesis of the control plants showed a continuous decrease during the day. This was possibly due to photoinhibition, which is assumed to be based upon inactivation of the electron transport system in the thylakoids (Powles 1984, Öquist et al. 1987). Before model analysis, the data on photosynthesis of the fumigated plants at low temperature and low PPFD were corrected for the time trend in photosynthesis observed in the control plants.

Detection of S(IV) in leaves

To verify conclusions from model analysis of gas exchange measurements at the biochemical level, S(IV) concentrations were analysed in leaves of \textit{V. faba} after a 2 h fumigation period (1200 \( \mu \text{g SO}_2 \text{ m}^{-3} \)). The West and Gaeke (1956) procedure for the determination of SO\(_2\) was adapted to plant tissue for this purpose following Miller and Xerikos (1979). Samples of leaves (10 g fresh weight) were immediately frozen and ground in liquid nitrogen. The powder was added to 100 ml 0.2 \( M \) TCM (0.2 M HgCl and 0.4 \( M \) NaCl) and the suspension was ultrasonically vibrated for 3 min and centrifuged at 12500 \( \text{g} \). Formaldehyde (0.2 ml 0.2%) and 0.5 ml color solution (0.48 \( M \) pararosaniline in 1 \( M \) phosphoric acid) were added to 1.8 ml of the supernatant. The final pH of the solution was 1.2. After 25 min in the dark (20°C) the absorbance was measured at 575 nm. Standard additions of S(IV) to non-fumigated leaf material established the reliability of the technique and were...
used to calculate S(IV) concentrations in μg (g fresh weight)⁻¹. Glutathione, which may accumulate after SO₂ exposure (Maas 1987), did not interfere with the measurements, since it was stabilized by TCM at pH 1.2.

**Results and discussion**

A higher relative humidity or a lower temperature resulted in stronger reductions in photosynthesis during a short fumigation period and a subsequent recovery period (Fig. 1). These data illustrate the generally observed pattern of photosynthesis during short fumigation experiments (Darrall 1986). Photosynthesis quickly decreased after the onset of fumigation, followed by a stabilization within 2 h of fumigation and a recovery when fumigation was stopped. Generally, the depression of photosynthesis was more severe at higher humidity and at lower temperature (Tab. 1). Detailed information on photosynthesis, leaf thickness, SO₂ concentration and uptake rate at the end of the fumigation period for the different treatments is given in Tab. 1.

**The effect of humidity**

At 18°C a linear relation [with a slope of 4.7 (μg SO₂ m⁻² s⁻¹)⁻¹] was observed between the rate of SO₂ uptake and relative photosynthesis 2 h after the onset of fumigation. No effect of humidity (30–70% RH) on the relation between the rate of SO₂ uptake and relative photosynthesis was found at 18°C (Fig. 2, closed symbols). However, the rate of SO₂ uptake was generally higher at a higher humidity, resulting in stronger reductions in photosynthesis (Tab. 1). This was caused by the lower stomatal resistance at high humidity (Tab. 1). This difference was only clear for the 70% RH treatment vs the 30 and 50% RH treatments. Similar conclusions were drawn from preliminary experiments at the same conditions in the equipment for routine measurement of photosynthesis at the Centre for Agrobiological Research (data not shown). These results (Fig. 2) indicate that the influence of humidity on photosynthetic effects of SO₂ is a result of humidity effects on stomatal opening and thus the uptake of SO₂, but not a result of influences on the biochemical processes.

The significant role of humidity in plant responses to SO₂ was demonstrated earlier by McLaughlin and Taylor (1981). The effect of air humidity on the rate of SO₂ uptake can be easily understood from the response of stomata to humidity. Stomatal behaviour can be characterized by the ratio between internal and ambient CO₂ concentration (Cᵢ and Cₐ, respectively), which tends to be constant over a wide range of conditions in many

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**Tab. 1. Experimental details on plants of the different treatments and results of the model analysis (averages ± se of mean).**

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Temperature (°C)</th>
<th>Radiation (μmol m⁻² s⁻¹)</th>
<th>Relative humidity (%)</th>
<th>Number of replicates</th>
<th>SO₂ concentration (μg SO₂ m⁻³)</th>
<th>SO₃ thickness (mm)</th>
<th>SO₃ uptake rate at the end of fumigation (μg SO₂ · m⁻² s⁻¹)</th>
<th>Relative photosynthesis (at the end of fumigation)</th>
<th>k (mmol S(IV) l⁻¹ s⁻¹)</th>
<th>tᵢ (min)</th>
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<tr>
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<td>8</td>
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<td>18</td>
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**Fig. 2. Relative rate of photosynthesis of Vicia faba leaves after 120 min of SO₂ exposure in relation to the rate of SO₂ uptake (F in μg m⁻² s⁻¹) for plants fumigated at 18°C and 30% RH (▲), 50% RH (●) and 70% RH (■). Relative photosynthesis (18°C) (%) = 100–4.7 F; r² = 0.46, n = 18 (solid line) and plants fumigated at 8°C (●); Relative photosynthesis (8°C) (%) = 100–12.7 F; r² = 0.35, n = 15 (broken line).**

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**Tab. 2. The effect of humidity (RH in %) and vapour pressure deficit (VPD, mbar) on the ratio between internal (Cᵢ) and ambient (Cₐ) CO₂ concentration at high radiation levels. n is number of replicates.**

<table>
<thead>
<tr>
<th>n</th>
<th>Temperature (°C)</th>
<th>RH (%)</th>
<th>VPD (mbar)</th>
<th>Cᵢ / Cₐ</th>
</tr>
</thead>
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<tr>
<td>12</td>
<td>8</td>
<td>70</td>
<td>3.3</td>
<td>0.89±0.02</td>
</tr>
<tr>
<td>6</td>
<td>18</td>
<td>70</td>
<td>6.2</td>
<td>0.76±0.02</td>
</tr>
<tr>
<td>2</td>
<td>18</td>
<td>50</td>
<td>10.3</td>
<td>0.66±0.03</td>
</tr>
<tr>
<td>2</td>
<td>18</td>
<td>30</td>
<td>14.4</td>
<td>0.71±0.03</td>
</tr>
</tbody>
</table>
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sensitivity parameter \( k \), ca 1 (mmol S(IV))

mental data of Alscher et al. (1987) and Sakaki and
was very close to the value determined from experi­

Kondo (1985) by Kropff (1989a), which was 0.825

S(IV) oxidation

of stomatal responses to humidity or of interplant var­

The effect of temperature

Photosynthetic depression at the end of the fumigation
period at a given rate of \( \text{SO}_2 \) uptake was much stronger
at 8°C when compared to leaves exposed to \( \text{SO}_2 \) at 18°C
(Fig. 2). This effect can only be explained by an influence
of \( \text{SO}_2 \) on biochemical processes responsible for
photosynthetic depression by \( \text{SO}_2 \). The effect is either
due to an increased sensitivity of photosynthesis to
S(IV) metabolites or to a reduced rate of S(IV) ox­

The slope of this line can be expressed in terms
of the model by the product of the sensitivity parameter
\( k \) and the time coefficient for S(IV) oxidation \( \tau_s \) (Kropff
1989b).

The effect of temperature over all treatments on the
parameters \( k \) and \( \tau_s \) was estimated by model analysis of
the data for each plant, using measured data on leaf
thickness and rate of photosynthesis and stomatal resi­

The absence of an effect on \( \tau_s \) is interesting, because
active oxygen species should enhance the oxidation rate
of S(IV). Although the data on photosynthesis of the
plants exposed at low temperature and high radiation had
to be corrected for the time course of photosynthe­
sis in the control plants, the estimated values of the
parameters are in the same range as the values esti­
mated from plants exposed at low temperature and low
(but saturating) radiation (Tab. 1). Further causal in­
terpretation of the results from the photoinhibited
plants requires more research at the biochemical level.

Davies (1980) found a stronger effect of \( \text{SO}_2 \) on plant
growth at low radiation levels, which was suggested to
be the result of a lowered rate of S(IV) oxidation due to
a reduced assimilate supply. However, no relationship
was found between the rate of net photosynthesis at the
beginning of the fumigation period and \( \tau_s \) (Fig. 3).

Stomatal responses to \( \text{SO}_2 \)-induced changes in photosyn­
thesis were small in plants fumigated at 8°C, which
resulted in an increase in \( C/C_o \) throughout the fumiga­tion period. This effect is important when \( \text{SO}_2 \) exposure

physiological parameters of the individual
plants (Kropff 1989b). This procedure enables the estimation
of temperature effects on biochemical processes deter­
mining photosynthetic reduction by \( \text{SO}_2 \), independently
of stomatal responses to humidity or of interplant vari­
bility in stomatal opening. The time coefficient for
S(IV) oxidation \( \tau_s \) was a factor 2.5 higher at the low

This is close to the factor 2.7, which was observed (Fig.
2). More detailed information on the model param­
eters, estimated for the different treatments is given in
Tab. 1.

No effect of humidity on the biochemical parameters
was found at 18°C (Tab. 1), indicating that humidity
only affected photosynthetic depression by \( \text{SO}_2 \) through
its effect on stomatal resistance.

This analysis indicates that higher sensitivity of the
plants to \( \text{SO}_2 \) at 8°C (Fig. 2) was caused by the stronger
accumulation of S(IV) as a result of a slower rate of
S(IV) oxidation. S(IV) measurements in leaves of \( V. faba \),
exposed to 1200 \( \mu \text{g} \text{SO}_2 \text{ m}^{-3} \) for 2 h at 7 and 20°C
showed a stronger accumulation of S(IV) in the leaves
at the lower temperature (98±4 and 23±2 \( \mu \text{g} \text{ g}^{-1} \) respec­tively). S(IV) concentration is a factor 4.3 higher at 7°C
than in leaves exposed at 20°C. This is higher than the
factor 2.5 derived from the model analysis. This may be
partly explained by the greater difference in temper­
ature between the treatments. Another reason for the
difference may be that for S(IV) measurements five leaf
layers were sampled from the plants, which differed in
age in order to obtain enough material for chemical
analysis, whereas the youngest fully unfolded leaves
were used in the gas exchange measurements.

No effect of radiation level on \( \tau_s \) was observed at the
low temperature (Tab. 1). In the plants exposed at low
temperature and high radiation a continuous decrease
of photosynthesis over the day was observed. Because
this effect was not observed in the plants exposed at low
temperature and low radiation (which was light satu­
rating) this effect was assumed to be the result of pho­
toinhibition, which is thought to be the result of the
formation of active oxygen species due to inhibition of
the electron transport (Powles 1984, Oquist et al. 1987).

Fig. 3. Relation between the time coefficient for S(IV) ox­
idation \( (\tau_s \text{ min}) \) as determined by model analysis and the rate
of photosynthesis at the onset of fumigation at 8°C (A) and
18°C (B). Data were obtained at a 
PPFD of 900 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) (C) and a 
PPFD of 450 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) (D).
results in severe reductions in photosynthesis, because the rate of \( S_2O_3\) uptake is much higher when stomata do not close as a result of a decreasing photosynthesis. An illustration of this phenomenon is given in Fig. 4, where the modelled effect of 400 and 1 200 \( \mu \)g \( S_2O_3 \) m\(^{-3}\) on leaf photosynthesis is presented for a leaf in which the stomata respond to the lowered rate of photosynthesis, and for a leaf in which stomatal conductance remains unchanged. The effects of \( S_2O_3 \) are much more severe when the stomata do not close as a result of the reduced rates of photosynthesis when photosynthetic depression is high.

**Implications for plant growth**

Most studies in which the effect \( S_2O_3 \) on photosynthesis is analysed, reported very small or no effects of \( S_2O_3 \) at low concentrations (0-400 \( \mu \)g \( S_2O_3 \) m\(^{-3}\); Darrall 1989). However, the data presented in this study demonstrate that reduced photosynthesis may occur at these low concentrations in winter periods when the temperatures are low. When the results obtained in this study are extrapolated to low concentrations, a photosynthetic reduction of 5.5% is expected at 8°C at 100 \( \mu \)g \( S_2O_3 \) m\(^{-3}\) (uptake 0.5 \( \mu \)g \( S_2O_3 \) m\(^{-2}\) s\(^{-1}\); Fig. 2). However, since the values for \( \tau_s \) showed a large variation (from 23 to 93 min at 8°C), the expected range of photosynthetic reductions for the plants used in this study at 8°C exposed to 100 \( \mu \)g \( S_2O_3 \) m\(^{-3}\) is 2–10%.

The results presented in this study may explain the severe effects of \( S_2O_3 \) on plant growth in winter conditions, observed in many studies (Cowling and Lockyer 1978, Davies 1980, Baker et al. 1982, Whitmore and Mansfield 1983, Baker et al. 1986). Besides low temperatures, low radiation levels also reduce the rate of \( S(IV) \) oxidation in plant material (Rothermel and Alscher 1985), possibly explaining the extreme effect of low radiation on plant growth described by Davies (1980).

When plants with thin leaves and a low capacity for \( S(IV) \) oxidation are exposed to low \( S_2O_3 \) concentrations at low temperatures, significant reductions in photosynthesis have to be expected. The approach presented in this paper may help to quantify growth depressions in plants exposed to \( S_2O_3 \) during winter conditions, by incorporation of the submodel for \( S_2O_3 \) effects on leaf photosynthesis in crop growth models (Kropff and Goudriaan 1989, Kropff 1990).

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